FACTORS CONTROLLING THE DISTRIBUTION AND SPREAD OF BRACKEN (*PTERIDIUM AQUILINUM*) IN SCOTLAND

by

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Abstract

The aim of this thesis is to investigate the factors controlling the spread and distribution of bracken (Pteridium aquilinum) in Scotland.

Bracken has long been an agricultural problem and, more recently, fears have been raised about the plant's carcinogenic properties. Despite the seriousness of the problem, there has been little quantitative research into factors controlling the plant's vigour, although there are many anecdotal references on the subject. It is the aim of this thesis to; study the climatic, edaphic and biotic characteristics of the bracken zone; establish the statistical relationship between these factors and bracken vigour and to apply the findings to explain how these fators affect bracken in Scotland.

The climatic, soil, vegetation and biotic characteristics of four sites in the bracken zone (west, south-west, north-east and south-east) are reviewed first. By comparisons of inter-site factors and bracken vigour at the sites, it is possible to formulate hypotheses on the factors that control bracken vigour. Correlation and regression analyses of individual factors with frond height, density and litter depth are then carried out, followed by a Stepwise Regression Analysis. Finally the findings of the two sections are summarised and the results applied to explain bracken distribution and spread in Scotland.

The major conclusions of this thesis can be summarised as follows: Early season temperature strongly affects bracken vigour and largely accounts for the east-west difference in bracken vigour. Vigorous bracken in the west can withstand a greater degree of frosting than the less vigorous bracken in the east. Soil moisture stress, heavy frost and relatively intensive agriculture in the east

results in a higher bracken zone (and therefore suboptimal soils and temperatures) in the east than in the west.

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Chapter One

Introduction

Bracken (Pteridium aquilinum (L.)Kuhn) is one of the world's most widespread vascular plants and is Britain's most successful and aggressive upland weed. It characteristically occupies well drained slopes between enclosed lowland and unenclosed moorland where its dense canopy and litter can effectively render useless hectares of pasture. It has long been recognised to be toxic to grazing animals and recent concern has centered on the possible link between bracken infested water catchments and high rates of stomach cancer. Its resilient underground rhizomes, rapid vegetative spread, unpalatable foliage and persistence and longevity make it a very difficult plant to eradicate. Methods of bracken control have been investigated for over a century, but it is only in the last twenty years that an effective herbicide has been developed. However, the prohibitive cost of the aerial spraying necessitated by the inaccessibility of most upland bracken and the need for repeated treatments on uncultivated land often make bracken control uneconomic.

Originally an understorey species of open woodland, the plant attained greater vigour and abundance with the onset of forest clearance. Bracken is morphologically and physiologically better adapted than other ferns to cope with the increased exposure of the grasslands and moorlands that replaced the forests. Its tall stature, dense canopy and in many cases, deep litter, enable the plant to form relatively pure dense stands from which other species are largely excluded.

Over the past two centuries bracken has progressively spread over much of upland Britain up to a height of about 550 metres above sea level, a process that has been inadvertently assisted by man. Up until the 19th century, bracken was regularly cut to provide bedding, thatch and potash. Scarcities of the fern are even reported to have occured, which in one known instance precipitated a dispute over cutting rights in Dalmelly. By the beginning of 19th century, bracken cutting was on the decline, as were the other practices, cattle grazing and cultivation, that are reputed to have kept the fern in check. At the same time, the increase in sheep grazing, especially after the Highland Clearances, brought about conditions that were very favourable for bracken spread. It now became a weed and the first articles on its control appeared by the mid century. These must have had little impact for over the next fifty years bracken spread onto abandoned cultivations above the head dyke, and by the turn of the century it is thought to have gained a foothold on the lower in-bye pasture.

Braid (1934a) estimated the rate of rhizome growth in western Scotland to be 60-90 cm per annum. Recent mapping of areal change of bracken by using aerial photographs and past vegetation surveys has produced estimates of bracken cover and rates of spread. Taylor (1980, 1986) estimates a 1 to 3 percent loss of land to bracken per annum in Wales, with the total area of dense bracken cover increasing from 3 percent in 1936 to 5.8 percent in 1960. Taylor (1978) also estimates 6 percent of the land area in Scotland to be bracken covered. Hendry estimated 2.3 percent cover in 1958, but as Taylor (1980) points out, Hendry's survey excluded land owned by non-agricultural bodies and the figure may therefore be an underestimate. However, more recently, Bunce (Pers. Comm. 1987) estimated only 3.99 percent cover from the Institute of Terrestial Ecology's landuse survey. The 1 to 3 percent rates of spread obtained at various locations in Scotland by the Macaulay Land Use Research Institute would seem to support Taylor's figure for cover. Again, caution is needed in interpretation of the data, for all of the Macaulay study sites were specifically located in areas of abundant bracken.

The aim of this study is to investigate some of the factors controlling bracken distribution and spread in Scotland. Hendry's map of the distribution of bracken infested farms in Scotland (Fig.1.1) shows the plant to be very unevenly distributed throughout the country. Bracken is clearly concentrated in the west and along the southern edges of the Highlands and Southern Uplands. In contrast, bracken distribution in Wales is shown by Taylor (1968) to be evenly distributed around all sides of the Cambrian mountain mass. It is possible to accurately predict the Welsh bracken province by mapping the occurrance of the Manod Soil Series on slopes of over 5° (Thompson et.al., 1986). The wide climatic variations across Scotland do not allow a similar interpretation. Indeed, maps from the Macaulay Institute's Soil Inventory show the brown forest earths to be to be concentrated in the east of Scotland.

Some preliminary interpretation of the Hendry map is possible. Bracken is clearly showing a preference for the southern edges of the upland ranges, which suggests some kind of temperature control. The existence of the "island" of moderate infestation in an area of otherwise infrequent bracken on the southern slopes of the Cairngorm plateau is intriguing. The absence of bracken in the Central Belt and in the Eastern Seaboard can obviously be attributed to intensive agricultural and urban land use, while bracken's well known dislike of wet soils could logically explain its absence on the northern peatlands. Its preference for the west is more difficult to explain. Taylor (1980) attributes its scarcity in the north east to the ocurrence of peatland, but this does not explain the general absence of bracken around the edges of the Cairngorm plateau. The low level of infestation on the Lammermuir and Pentland Hills, south of Edinburgh, is also puzzling. It would be tempting to fall back on widely accepted "facts" regarding the climatic controls of bracken and explain the east-west difference in terms of bracken's susceptibility to frost

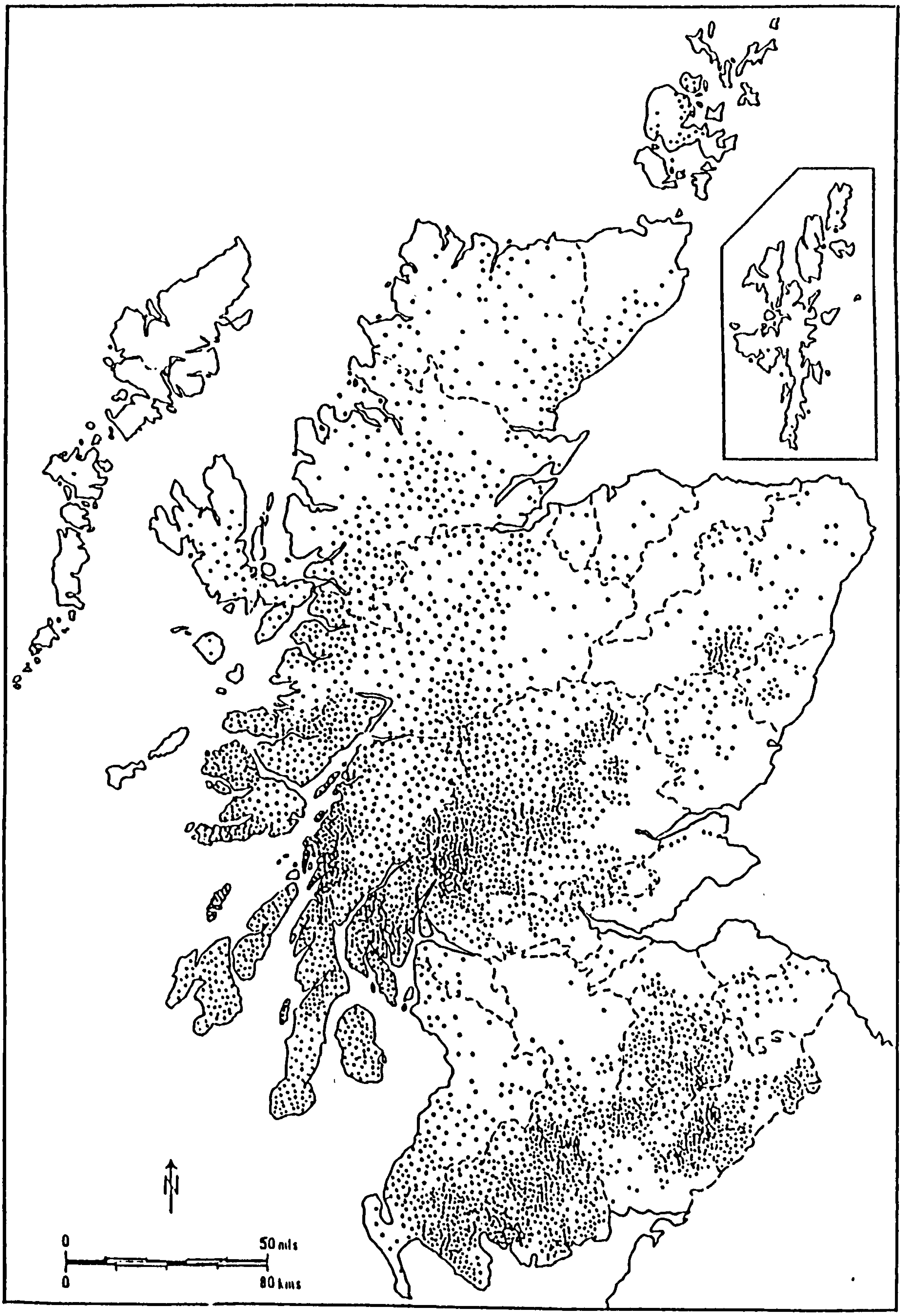


Fig. 1.1 Distribution of bracken in Scotland, 1 dot = 40 hectares bracken infested land (from: Hendry G.F., 1958).

and drought. However if the same line of thought is continued for exposure, bracken should theoretically be more abundant in the less exposed east. In comparison to other moorland plants, bracken is supposed to be intolerant to high rates of exposure.

Examination of the literature covering climatic control of bracken vigour reveals little systematically established fact beyond Watt's classic studies on the effect of frost. References are mostly descriptive or anecdotal, while the two multi-variable analyses yield very generalised or obvious results. For example, findings that altitude and aspect are important to bracken vigour can be observed in the field without recourse to complicated analyses. What is needed is information on the affect of temperature per se. To be able to explain the distribution of bracken in Scotland, one has to investigate not only the individual and interactive effects of the different factors on vigour, but also the environment of the bracken zone in different regions, to be able to apply these findings. This study therefore has two main fields of investigation; a comparative study of different hill environments within the bracken zone, from which hypotheses on the factors controlling bracken vigour in each of the different regions can be made; testing of these hypotheses by statistical analysis of the effects of environmental factors on bracken vigour. Not all the factors that are thought to affect bracken vigour could be investigated, and only the sporophtye generation is studied. It is hoped that the study will unravel some of the ecological complexities of the bracken "problem".

Chapter Two

Review of the Literature

2.1 The general background

The seriousness of the bracken problem has given rise to an extensive agriculturally orientated literature on bracken chemistry, poisoning, utilization and control and more recently to medically and biochemically orientated work prompted by fears of the carcinogenic properties of the fern. However, it is only intended to review the ecological literature; first by outlining the development and main areas of the ecological research and then by reviewing in detail the literature relevant to the study of bracken vigour. Only sporophyte vigour is investigated in this study, although gametophyte vigour is also relevant to bracken distribution and spread and both are therefore covered in this review.

Prior to 1940 the ecological literature was limited to descriptive observations in general studies on moorland (e.g. R.Smith 1900-1906; Stapledon and Davies 1936; Tansley 1939) and to often conjectural and anecdotal observations on factors affecting bracken vigour, distribution and spread (e.g. Braid 1934a,b; Farrow 1917; Gordon 1916; Jeffrys 1917; Long and Fenton 1938; Home 1926; Watson 1939; Whyte 1930). Many of the currently accepted "facts" on, for example, the affect on bracken of the Highland Clearances, exposure and soil type can be traced back to these early references. Early studies into taxonomy, life history and morphology were generally a little more systematic (e.g. Boodle 1904; Darwin 1877; Druery 1903; Moore 1851; Tansley and Lulham 1904).

During the 1940s there was a proliferation of detailed investigations into the structure and development of the prothallus and sporeling (Braid and Conway 1943; Conway 1949) and of the rhizome (Watt 1940, 1943, 1945). These workers were also the first to systematically investigte the autecology and synecology of the bracken fern. Conway (1949, 1953, 1957) and Conway and Stephens (1957) studied factors affecting spore and sporeling production and survival. Watt (1947), working in the Brecklands, proposed the spatial and temporal models of bracken succession and also investigated the ~~a~~ffect of frost and the protective e/ role of litter (1950, 1954, 1956, 1970, 1971). He also made precursory investigations into the importance of rainfall and summer temperatures (1950).

Other systematic studies up until the 1970s on factors affecting bracken vigour covered soil aeration (Poel 1949, 1951), soil depth (Watt 1964) and the nutritional requirements of the prothallus (Schwabe 1951, 1953). Autecological studies included the effect of atmospheric evaporation on frond water stress (Tinklin and Bowling 1969), decomposition rates of bracken litter (Frankland 1966, 1969) and the correlation between size and age of bracken clones (Oinonen 1967). Syncological studies included; the ground flora associations under varying degrees of bracken cover (Nicholson and Robertson 1958); competition between Calluna and bracken (Watt 1955); the contribution of bracken to nutrient cycling in oak woodland (Carlisle, Brown and White 1967) and the affect of bracken on moorland vegetation and soils (Mitchell 1973, 1977).

The 1970s saw an upsurge of mainly agriculturally orientated bracken research in New Zealand and renewed interest in bracken research in Britain. The scope of the ecological work is currently extremely diverse and includes the new fields of remote sensing and its application to bracken mapping (Birnie 1983; Birnie and Miller 1986; Curran 1986; Southgate 1986; Weaver 1986) and of biological control (Burge et.al. 1986; Lawton 1986).

Advances have been made in the fields of bracken taxonomy (Page 1976), chemotaxonomy and phytochemical ecology (Cooper-Driver 1976; Cooper-Driver et.al. 1977; Cooper-Driver 1985) and cytological and genetic polymorphism (Balick et.al. 1978; Cooper-Driver and Swain 1976; Hadfield and Dyer 1986; Page 1982a). The effects of bracken control and removal have been studied in relation to Calluna regeneration (Marrs 1987a,b), changes in sward composition (Sparke and Williams 1986) and soil water balance in moorland soils (Lockwood et.al. 1986).

Of direct relevance to the study of bracken vigour are the investigations into transpiration and evaporation from woodland and grassland bracken (Roberts 1986 and Pitman 1984 respectively), the effect of grazing on bracken (Lee et.al. 1986) and Watt's hypotheses of bracken competition and succession (Marrs 1986 and Marrs and Hicks 1986a,b). However, apart from Poel's work on soil aeration in the early fifties, there have been few systematic studies on the direct effect of climate or soil on bracken vigour since Watt's preliminary investigations. The few studies include investigation into soil type and slope under bracken in Wales (Thompson et.al. 1986), the effect of aspect and alititde (Atkinson 1986) and factors influencing distribution and abundance of bracken in New South Wales (Thomson 1986).

2.2 Review of the factors affecting sporophyte vigour

Although bracken is a natural constituent of oak and birch woodland, it attains greatest vigour in acidic grassland, demonstrating the limiting affect of shade on the plant (Page 1976, 1982; Watt 1976). Its minimum light requirement is estimated to be about 5 percent maximum diffuse illumination and 11 percent of exterior illumination for vigorous growth in woodland. Shading has also been identified as a limiting factor on spore production (Conway 1957). Pollen records show that prior to forest clearance, bracken occurred widely throughout Britain (e.g. Blackburn 1946), but probably only as a minor element of the woodland vegetation (e.g. O'Sullivan 1977). In the least disturbed parts of the world today, it is still largely confined to open woodland (Page 1979). The increasing frequency and abundance of bracken in the pollen record from the Neolithic period onwards (Turner 1965; Smith 1970) charts the progressive release of bracken from the woodland habitat as forest clearance proceeded. However, this proces would have occurred much later in the Highlands where deforestation did not begin until about the 15th century and extensive exploitation not until the 17th century (Carlisle 1977; Steven and Carlisle 1959). Tansley (1953) considers that Agrostis-Festuca grassland replaced oak-birch woodland. Here, protected from grazing by its unpalatability, bracken finds opportunity for fresh aggresivenesss and dominance.

Many of the early writers observed the destructive affect of frost on both the sporeling and adult sporophyte (e.g. Druery 1903; Gordon 1916; Long and Fenton 1938). In his study of the effect of frost on the adult plant in the Brecklands, Watt (1950, 1954) found that following a hard winter frond emergence in litter covered stands occurred before emergence in litter free stands. After a mild winter the reverse was found to be true. Frosting of underground buds was shown to delay emergence and Watt therefore hypothesised that although litter cover delayed spring soil warming, it protected the buds from winter frost. Other workers have observed that fragmentation of the litter layer by cutting machines or by burning results in earlier emergence and therefore greater incidence of spring frost kill (Atkinson 1986; Lowday 1983). Watt (1950) found that time of emergence and of frost were crucial in determining the extent of spring frost kill and that late emerging fronds could therefore escape frost completely. He also found that spring frost kill stimulated a second growth of fronds, but estimation of the proportion of replacement fronds was impossible because of the difficulty of distinguishing replacement fronds from main crop fronds.

Using data from one bracken stand over a period of eleven years, Watt (1950) obtained a significant negative correlation between spring frost and mean frond height and a significant positive correlation with frond density, but found no significant correlations with winter frost. (Data from a meteorological station four miles distant was used to estimate winter frost incidence at the site, while percentage mortality of frosted fronds was used as an indirect measure of spring frost. Soil temperature was only measured in spot readings to compare temperature under litter and grass and the occurrence of soil frost was inferred by the presence of frosted underground buds and rhizomes).

Watt (1954, 1967) later applied these findings to explain stand senescence and the advance and retreat of bracken stands. He had earlier shown (1947) the deepest rhizomes to occur in the advancing margin and the shallowest in the retreating margin or degenerate phase. He hypothesised that rhizomes in the advancing margin are therefore less prone to winter frosting than those in the retreating margin, making them more vigorous. Furthermore, the relatively shallow rhizomes in the litter covered mature phase (or crest) would become vulnerable to winter frost should the protective litter be disturbed or not sufficiently replenished. Watt (1956) uses the theory of litter disturbance to explain the occurrance of bracken rings (i.e. relatively small bracken free areas surrounded by tall bracken). He also showed that young shoots are the first to send up fronds in spring and if these fronds are frosted, the older shoots are stimulated to frond production. He therefore hypothesised that with repeated frosting, the food reserves of the older shoots rather than the younger are replenished, leading to an aging population of shoots and eventual senescence of the stand.

Bracken's preference for south facing slopes has long been noted (e.g. Gordon 1916; Smith 1900; Taylor 1980). Smith (op.cit) observed the altitudinal limit of bracken in the Pentlands to be 456 metres on south facing slopes, but only 380 metres on north facing slopes. He also recorded bracken at 547 metres on south facing slopes near Kinloch Rannoch. Atkinson (1986) found that in a stepwise regression analysis of the effects of altitude, aspect, exposure and slope on a variety of measures of frond vigour (biomass, height and density), altitude and aspect were respectively the most frequent first and second step variables. (However, the classification of exposure was very subjective and furthermore, soils were not examined). In another multi-variable study, summer maxima, winter minima and altitude, along with annual rainfall and two particular farm types were found to account for 76 percent of variance in bracken abundance in New South Wales (Thomson et.al. 1980). (Other variables analysed and found not to be significant were latitude, longitude, soil type, natural vegetation before settlement and present day vegetation association).

Watt (1950) is again the only worker to have investigated the direct effect of temperature on frond growth. Using data from the nearby meteorological station over a period of years, he found a positive correlation between rate of emergence and accumulated degrees above 0^{o} C up until mid-June. Early frond emergence on south facing slopes has been noted by other workers (e.g. Atkinson 1986), while Smith (1986) observed later emergence in marginal bracken around the edges of flushes where soil temperature is likely to be relatively cold.

The effects of exposure cannot be entirely separated from those of temperature because of the effect exposure has on temperature. For example, Taylor (1980) observes greatest bracken vigour on south facing but sheltered slopes and Thompson et.al. (1986) found bracken to be most abundant on south and east facing slopes (and therefore the most sheltered) in an analysis of the Welsh National Soil Survey records.

The other effects of exposure will be mechanical and physiological and not related to temperature. Braid (1947) observed that continuous wind blow weakens the neck of the frond (i.e. where it enters the ground), causing mechanical damage and making it open to disease. He also found that bracken lived longer in plots screened off from the prevailing wind and observed, as have other writers, the confinement of bracken to valleys and hollows in very windy regions such as Caithnness and the Shetlands. Wind damage to the fronds is also thought to decrease spore production (Conway 1957).

Bright (1928) recorded a progressive decrease in the height and diameter of the petiole (frond stem) with increasing exposure (the latter factor being only subjectively assessed). He also observed exposed bracken to have smaller lamina and fewer pinnae, which were shorter, tougher and thicker than those of bracken in sheltered localities. The amount of strengthening tissue was found to increase at the expense of storage, vascular and photosynthetic tissue. The resulting xeromorphic frond morphology therefore decreases transpiration, conserves water and provides support at the expense of photosynthesis. Other workers (Boodle 1904; Druery 1910; Woodhead 1906;) have observed similar effects of exposure on frond morphology, although soil water status was suggested by Bright (op.cit) to be important as well. Pitman and Pitman (1986) found evaporation and transpirtion rates to be about five times greater from bracken in the open than in woodland. Tinklin and Bowling (1969) found rapid stomatal closure and increasing leaf water status at high evaporation rates. Pitman and Pitman (op.cit.) recorded a similar response (reduction of stomatal conductance) to soil water deficit and hypothesised that soil water potential and vapour pressure deficits were the most likely controls of stomatal conductance. This is supported by the finding that large soil moisture deficits strongly influence transpiration in the late season (Lockwood et.al. 1986). Dieback in

September was suggested as one possible mechanism to decrease transpiration loss.

This morphological and physiological adaptation to soil moisture stress highlights bracken's greater tolerance of dry soils and exposure compared to most ferns. Compared to the assumed available soil moisture capacity of upland soils, soil moisture deficits under bracken were found to be high for upland areas (Lockwood et.al., op.cit). Smith (1986) suggests that this may indicate the plant's ability to utilise a greater depth of soil than other moorland plants, but it may merely reflect its large interception of incident rainfall. 50 percent interception is reported for the canopy (Willims et.al 1987) and Smith (op.cit) found similarly high interception for bracken litter. He hypothesised that litter accumulation will lead to increasing moisture stress and depletion of rhizome vitality, causing eventual stand degeneration. He did not however take account of reduced evaporation from the soil surface. Several writers (e.g. Gordon 1916 and Braid 1934a) mentioned bracken's preference for deep soils and Watt (1964) showed a significant correlation between indices of bracken vigour and soil depth, and suggested that this may be related to soil water supply in the dry soils of the Brecklands.

Bracken's dislike of waterlogged soils has long been appreciated (e.g. Gordon 1916; Long and Fenton 1938; Salisbury 1944) and early writers were even advocating irrigation of hill pasture as a means of bracken control (McTurk 1837; Murray 1837). Other writers (Braid 1934a; Long and Fenton 1938) considered moorland drainage schemes to have contributed to bracken spread, while Fletcher and Kirkwood (1979) point out that abandoned cultivations and lazy beds have also provided ideal conditions for spread. Poel (1951) found that poor drainage affects the rhizome much less than the frond. Braid (1934a) descibed sites on which non-frond producing rhizomes, maintained by their parent plants, penetrated poorly drained areas. Both writers also described islands of bracken on slightly raised areas and stones in poorly drained areas and commented on their potential for spread should drainage improve.

Poel (1961) later showed the oxygen diffusion rate (ODR) of soils under bracken to be relatively high and noted the absence of bracken under Juncus acutiflorus where lower ODRs prevailed. However, he also found relatively high ODRs under bracken free Nardus stricta and Molinia caerulea and considered the impenetrable nature of the close, tough grass mats to be preventing bracken invasion. Anderson (1961) found that the hollow bases of the dead fronds and the cultivating effect of the rhizomes improved local soil aeration and water supply, a mechanism also commented on by Mitchell (1977). Taylor (1980) cites that in Wales it is possible to see instances of bracken on uncharacteristically wet habitats and speculates as to the possibility of habitat expansion. However, Poel (1951) noted that although intolerant of stagnant, waterlogged conditions, bracken would tolerate excessive water provided it was adequately aerated and concluded that oxygen deficiency rather than excessive water per.se is the controlling factor.

Bracken is found mainly on acidic nutrient poor soil although Watt (1976) attributes its scarcity on more fertile soil to the greater intensity of land use. Bracken is usually associated with brown forest earths and podzolic brown earths (e.g. King and Nicholson 1964; Mitchell 1977; also Brown 1986 for the North York Moors; Nicholson and Robertson 1958 for Glensaugh; Thompson et.al. 1986 for Wales). Home (1926) reported that bracken grew on peat if sufficiently dry and Brown (1986) reports from the North York Moors that there is evidence of bracken spreading into the dessicated upper layers of fire damaged peat, tolerating much wetter conditions than it usually does. He too concluded that bracken may be spreading beyond its conventional range. Mitchell (1973, 1977) showed that bracken can alter the chemical and physical characteristics of a podsol by physical cultivation of the upper horizons resulting in mixing of the bleached A_2 and organic horizons, by more effective cycling of nutrients (especially calcium and potassium) and by mobilisation of inorganic phosphates. It was found that in the growing season levels of available potassium in bracken soils may be similar to those of adjacent soils because of the tight cycling of the element through the system. Mitchell (op.cit) showed increased amounts of the element in the soil in winter and Williams et.al. (1987) demomstrated that large amounts were leached from the fresh litter in autumn.

Long and Fenton (1938) and Salisbury (1944) concluded that 'bracken's avoidance of chalk soils demonstrated intolerance of calcareous conditions. Lime induced chlorosis in bracken is observed at relatively high calcium levels (Simpson 1938; Poel 1961), but it is not considered to be an obligate calcifuge (Watt 1976). Conway and Steven's (1957) research on sporeling establishment had shown a positive response to liming. De Silva (1934) considered bracken to have a range of pH tolerance from 4.6-6.2. Salisbury (1925) found the peak of incidence of bracken to occur at pH 5.5, which Poel (1951) cites as the value for maximum growth of roots and fronds in water culture. Hunter (1953) found no correlation of bracken performance with pH on soils with a pH range of 3.6-6.2.

There have been fewer studies into the nutritional requirements of the adult fern. Schwabe (1951, 1953) found that deficiency of phosphate and nitrogen had extremely detrimental effects on growth, with extreme nitrogen deficiency being particularly lethal. Despite the fact that high potassium levels are often found in bracken, plants were more affected by phosphorous than potassium deficiency, suggesting that luxury absorption of potassium may occur.

One of the contributory factors to the success of bracken as a persistant, invasive weed is its resistance to disease. A small number of fungi are parasitic to bracken including the three fungi (Phoma acquilina, Aschochyta pteridis and Septoria spp.) that cause pinnae blight and curltip disease. Fungal diseases of bracken in Britain have been reported mainly from Scotland where complete death over several acres has been observed (Alcock and Braid 1928). The potential of certain fungi as bio-control agents has received intermittant attention (Alcock and Braid 1928; Angus 1958; Braid 1934b, 1947; Gregor 1932). Recent investigations into the potential for biological control using the curl tip disease (Burge and Irvine 1985; Burge et.al 1986) found that while the disease severly debilitates bracken in the field, it does not become epidemic for several reasons. These include the variability of resistance in different bracken stands, the variability in virulence of pathogens and the localised climatic constraints on disease development. The disease did not appear to greatly affect the rhizome and vegetative regeneration is therefore not prevented. It is thought though that the release of the replacement fronds will result in the gradual weakening of the whole stand by depletion of the rhizome reserves. Bracken in naturally infected sites was noticably thinned and grass growth more vigorous than in healthy stands.

Native British bracken feeding insects fail to have any significant impact on the plant because most of the species are rare, relative to the biomass of the plant material available to them (Lawton 1986). Only very occasionally do native herbivorous insects become common enough to cause heavy defoliation (Lawton op.cit). Trials with the South African bracken feeding moth Pathenodes angularis are currently underway in the North York Moors.

Grazing by larger animals is thought to have some impact on bracken. While the fronds are rarely eaten, trampling of the young hooks and damage to the fronds are reputed to depress vigour. Braid (1947) cited that in New Zealand flocks of sheep were driven frequently over the same place when bracken is in the fragile hook stage (i.e. just emerging from the ground). The impact of sheep is limited, for once the canopy has developed, grazing on grass swards under bracken falls off until autumn dieback of the fronds (Hunter 1962). Cattle trampling is reputed to have more impact on bracken by actual breakage of the older fronds (Braid 1947; Fraser-Darling 1955) and it has long been contended that the replacement of black cattle with sheep after the Highland Clearances in the 18th centuary helped to hasten the spread of bracken on to valuable pasture (Braid 1934a; Home 1926; Page 1982b). It has been observed that upland sheep pastures have become particularly bracken infested over the last centuary (Coppock 1971). By the early part of this centuary some sheep pastures were thought to be halved in extent in the previous 40 years (Long and Fenton 1938), although there are as yet no data to confirm this.

The only systematic study of the effect of grazing on frond vigour showed that with moderate grazing pressure of sheep (3.2 sheep/ha), frond height was only half that of adjacent ungrazed bracken by early July (Lee et.al. 1986). Percentage mortality was much reduced, but no data on changes in frond density were given although fewer frond buds were found to maintain the same population of emerged fronds. This suggests that in a grazed or stressed situation, the plant produces more reserve buds. It was concluded that grazing pressure must to some extent maintain the floristic differences between the bracken and grass stands and the litter covered bracken stands.

Grazing also indirectly promotes bracken spread by prevention of tree establishment and removal of other natural competitors. Bracken is essentially a pioneer species probably towards seral forest (Page 1979, 1986) and tree establishment would ultimately shade and permanently reduce the vigour of the understory bracken. The apparent lack of tree regeneration in bracken has prompted some to question whether regeneration can take place in dense bracken, for it has been suggested that dense stands of clonal species inhibit succession (Finegan 1984; Niering and Godwin 1974). Watt (1976) postulated that trees do not invade dense bracken, but may invade once degeneration of the bracken stand occurs. Recent work on Watt's former study site shows quite conclusively that Pinus sylvestris can colonise dense bracken, the limiting factor appearing to be seed dispersal rather than frond density (Marrs and Hicks 1986a,b). Lakenheath Warren has not been grazed by sheep since 1956 and it would appear that removal of this factor has been influential in determining the success of tree regeneration. Bracken on the open moorland is not only usually subject to more or less continuous grazing, but also rarely has a nearby source of tree seed.

Cutting similarly depresses bracken vigour by depletion of rhizome reserves with secondary frond growth. The need for judicious timing of cutting, by removing fronds before translocation of assimilates to the rhizome begins, has long been recognised (Braid 1934a, 1947). Cutting has to be repeated over several seasons to be effective because even when the standing crop is maximal, the majority of the dry matter (60 percent) is underground (Williams and Foley 1976). Cutting once a year in late July was found to decrease frond height but increase frond density, while cutting twice a year reduced the final standing crop (Institute of Terrestial Ecology 1979). The cessation of bracken cutting is also cited as a factor in the spread of bracken (Brown 1986 - on the North York Moors; Fenton 1947). Up until the beginning of the 19th centuary, bracken was considered to be a resource and had several important uses in the rural economy as fuel, thatch, animal bedding and a source of potash for glass and soap making (Fenton 1947; Rymer 1976). Rural depopulation, the replacement of crofting with sheep farming in many areas and later mechanisation of agriculture all resulted in widescale abandonment of bracken cutting and what was once an asset became a noxious weed.

Burning is also thought to have contributed to the spread of bracken. Burning bracken as a method of control, if carried out just after frond maturity, produces the same results as cutting with an increase in frond numbers but a decrease in rhizome starch reserves and frond fresh weight (New Zealand Forest Research Institute 1978). In the wild, fires may benefit established bracken colonies (Fletcher and Kirkwood 1979) for their underground rhizomes usually remain undamaged while vegetational competitors are removed wholesale (Page 1982b). Careful muirburn should allow relatively rapid regeneration of Calluna from rootsock and although bracken may invade for the first few years, the regenerating Calluna will eventually regain dominance (Gimmingham 1972). Too intense a fire that kills off the shallow rootstocks and the seed layer in the peat will greatly delay reestablishment and bracken may come to dominate. Poor miurburning practices have been cited as contributing towards bracken spread (e.g Fenton 1947), as have accidental fires in areas subject to heavy recreational pressures (Brown 1986 - North York Moors; Brown and Wathern 1986 - North Wales). Burning is also thought to encourage sporal regeneration, as discussed in the next section.

Watt (1976) proposed four situations in which the competitive power of bracken in open habitts will vary in relation to adjacent communities. First, a static relationship will exist between bracken and surrounding Calluna and grassheath when all three are managed intensively. Second, with some let up of bracken control, spread will occur at the expense of the other two communities. Third, with no management the competitive power of each will be unrestricted and bracken dominance is checked. Fourth, where bracken comes to dominate, accumulation of litter will lead to the degeneration of the stand and eventual colonisation by scrub.

The many references on the history of bracken spread support the first two hypotheses. The other two hypothesis are more controversial to those working in the field of bracken ecology. Marrs and Hicks (1986a,b) shed some light on to the question of supression of bracken dominance in unmanaged situations. Working on Watt's old study site (which had not been grazed since the 1950s) bracken was found to have completely overrun the Calluna which Watt (1955) had previously shown to be in competitive equilibrium with adjacent bracken. However, over the whole site bracken was found to have increased only 12 percent in area since 1922 with large areas of formally dense bracken now in the sparse, grassheath phase. The hypothesis that bracken does not assume overall dominance in unmamaged vegetation would seem to be true at Lakenheath Warren, although on a site rather than a stand level.

The hypothesis of stand degeneration followed by tree invasion has been partly confirmed by Marrs (1987) and Marrs and Hicks (1986a,b). As already discussed, their work showed that tree invasion of bracken can occur. The question of stand degeneration is though hotly disputed by current bracken workers because of the apparent lack of degeneration over much of the bracken infested areas. Watt (1947) hypothesised that the bracken stand passes through a temporal and spatial successional cycle from colonising bracken on the margins of the advancing front, to building and then mature bracken in the crest, to degenerate bracken in the retreating margin, to a grass heath hinterland behind the bracken crest which may be reinvaded by vigorous bracken. As succession proceeds, the rhizomes rise up the soil profile to keep pace with litter accumulation, eventually lying just below the litter in which the fine roots are now located. Watt (1970, 1971) postulated that the shallow rhizomes in the retreating margin are less vigorous than the deep seated rhizomes in the advancing margin because of the increased competition and the greater vulnerability to winter frost. The onset of degeneration in the mature phase was hypothesised to be caused by an increasing shortage of nutrients as the fine roots grow into the accumulating litter layer. The fine roots and rhizomes then become increasingly vulnerable to frost as the amount of litter diminishes with the decreasing vigour of the stand (Watt 1950, 1970, 1976). Watt (1950) also postulates that litter disturbance by animals or man may set the process in motion.

As discussed, Marrs and Hicks (1986a,b) showed that degeneration into grassheath does occur, but on a much greater scale than Watt envisaged; over an area of 90 hectares rather than within a 30 x 30 metre grid as Watt had shown. However, this still does not answer the question of what actually triggers the mechanism of degeneration. Litter disturbance over so wide an area in the absence of grazing is highly unlikely and the theory of nutrient deficiences in the litter is still very hypothetical.

2.3 Review of the factors affecting vigour of the sporeling and prothallus

The prothallus and sporeling stages of the bracken life cycle are rarely seen out in the field in Britain. Conway (1953) noted that in twenty-five years of research Braid had only found six sites of sporeling development. However, working in western Scotland, Conway (1952) found that spore output can be potentially very high but variable, depending on the degree of shade and exposure. It would therefore seem to be only spore germination and development that is so rare.

The need for a moist environment for spore germination (as is required by all ferns) was appreciated quite early on (e.g. Benson and Blackwell 1926; Farrow 1915; Jeffrys 1917). Many writers also noted the occurrence of prothalli on disturbed areas such as burnt ground, old walls and motar heaps (e.g. Lousely 1939; Melville 1965; Ridley 1936; Thompson 1939; Whyte 1930). Conway (1949) isolated a number of limiting factors to spore germination including moisture, pH and temperature. Germination appeared to favour a medium of pH 6-7 and a temperature of 10-16 ^{o}C. She also suggested that prothallus development could be impeded by competition for nutrients with micro-organisms.

Later laboratory experiments (Conway 1953) revealed the vulnerability of the sporeling to frost. The late spore dispersal in Scotland leaves little time for succesful spore establishment before the onset of winter. A number of soil collembola and microbial species were also shown to feed on the young plant, thus partially explaining the frequent occurrence of germination on sterilised sites such as burnt ground.

Schwabe (1951) showed phosphorous to be the most critical nutrient for both germination and prothallus growth, followed by nitrogen. Potassium, sulphur and magnesium were of less importance, while calcium had no effect at all. Conway and Stephens (1957) obtained different results; nitrogen and potassium produced the most response followed by phosphorous. Calcium was also important. Schwabe tested nutritional requirement by omitting one nutrient from the growth medium at a time, but Conway and Stephens used varying but relatively high levels of different nutrients within the normal arable range.

The prothallus and sporeling would therefore seem to have very much more specific requirements than the robust sporophyte. The need for a relatively high pH is of particular interest as it suggests that the plant must change its pH requirements as it develops into the sporophyte. Burnt substrates would seem to provide a very suitable habitat for this transition. Burning is therefore cited as contributing to bracken spread by increasing areas of potential spore germination (Page 1982b).

The review of the literature has shown that while there is an extensive literature on bracken ecology, many of the references, even later ones, are based purely on observations with little quantitative investigation. To fulfill the aim of this study, there is a need for more information on the effects of temperature and exposure on bracken vigour beyond field observations and the very generalised results of the two multi-variable studies. There is a need to examine further Watt's theories on the effects of frost and on stand degeneration. Also the question of bracken spread on to soils previously thought to be unsuited to growth needs investigation. Finally, the findings must then be applied to the Scottish environment and not studied in isolation.

Chapter Three

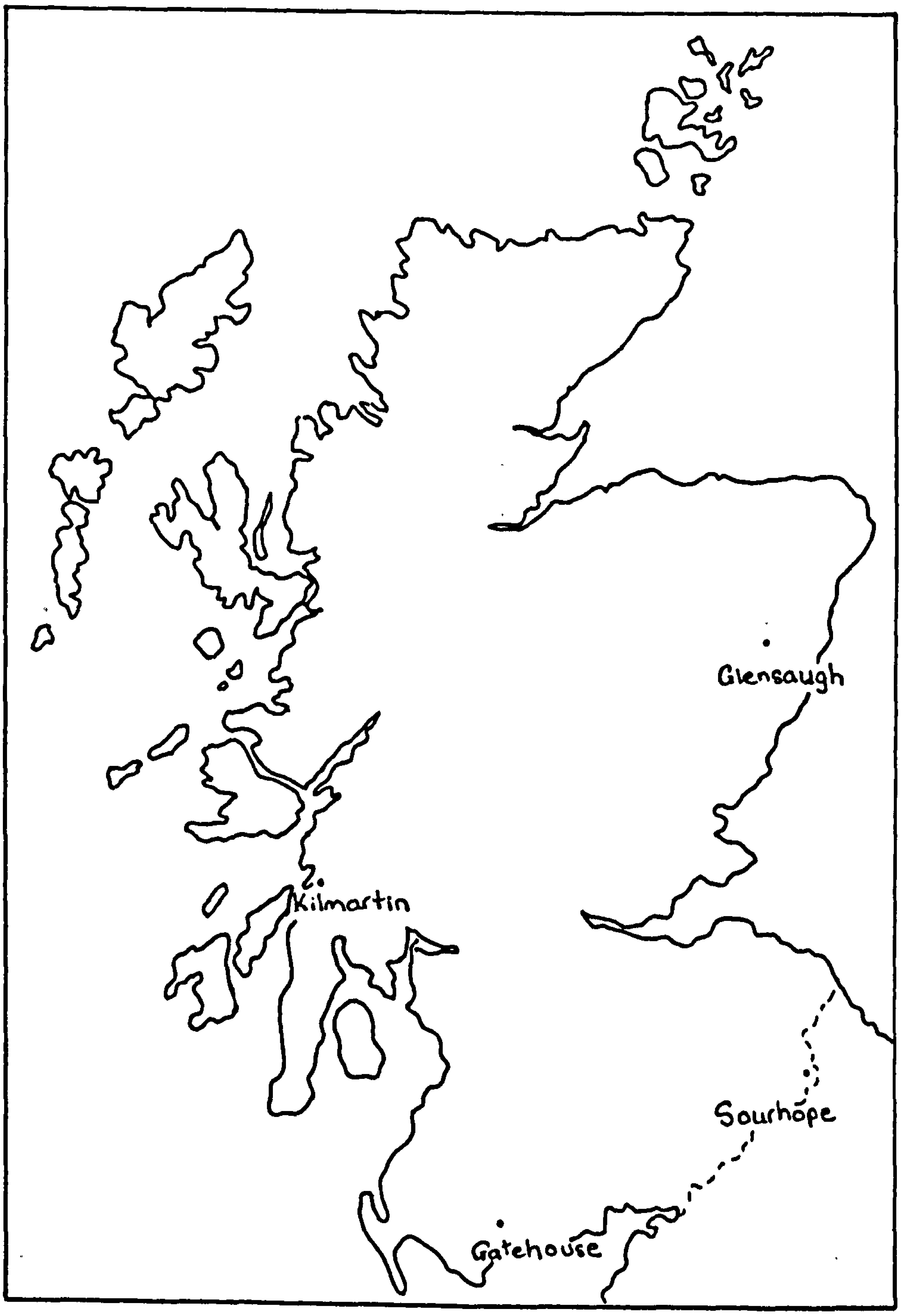
Site Selection and Description

3.1 Site selection

Four study sites were selected to represent the main hill environments of the bracken zone. These were located near Kilmartin in Mid-Argll, near Gatehouse of Fleet in Galloway, at Glensaugh Hill Farming Research Organisation (H.F.R.O.) Research Farm in Kincardineshire and at Sourhope H.F.R.O Research Farm in the Cheviot Hills (Fig. 3.1). The criteria for selection were as follows:
i.Each site had to be within a three hour drive from Glasgow since all four sites had to be visited on a three or four weekly basis during the growing season.
ii.Reasonable accessibility of the site.
iii An absence of cattle grazing unless the field equipment could be fenced off (which was only designed to be sheep proof).
iv.A range of different bracken stand types,i.e.differing height ,density, ground flora and litter cover.
v.A reasonable record of past and current landuse.

Preliminary reconnaisance surveys were carried out to establish the location of the main bracken zone in each region. (As will be discussed in Chapter Five, these proved to be higher in the east than in the west). It was decided to collaborate with the Macaulay Land Use Research Institute in selecting sites that were suitable for both the present study and their investigation into bracken spread. The two northern sites had already been partially surveyed by the Institute and these proved to be suitable

Fig. 3.1 Location of the study sites



for the purposes of this study as well. The area chosen for study at Sourhope was used by Joan Mitchell in the early 1970s for her research into bracken and soils.

It was orginally intended to select sites either with the same aspect or sites that offered a range of aspects. However, it was soon apparent that topographical controls within the areas made it impossible to implement either option. This point is further discussed in Chapter Five.

3.2 Environment of the study sites

The environmental characteristics of the sites are summarized in Table 3.1 and climatic data are given in Table 3.2. Clearly, the main climatic and geomorphic differences are between the eastern and western sites. The latter experience a more temperate and wetter climate with higher mean annual temperatures and rainfall, a longer growing season (shown by accumulated temperature above 5.6 ^{o}C) and less severe winters. The change of climatic zone with increasing altitude is very rapid within the regions of Glensaugh and Sourhope and it is therefore difficult to accurately designate classes for the two sites. All the sites may span more than one zone because of their altitudinal ranges.

The topography of the sites has been glacially eroded. At the eastern sites deep periglacial drift contributes to the smoothly contoured slopes characteristic of the Southern Uplands and the Eastern Highlands. The soils in the east are drier and more freely drained than in the west, reflecting their periglacial origin. The drier soils, lower exposure and smoother topography of the east results in higher limits of cultivation than found in the west. However, differences in the natural vegetation above the head dyke are more obvious between north and south, with the abundant Calluna at Kilmartin and Glensaugh contrasting with the acidic grassland at Gatehouse and Sourhope. The geology, soils, vegetation and landuse of

Table 3.1. Environment of study sites

	Kilmartin	Gatehouse	Glensaugh	Sourhope
Mean altitude	132m	136m	198m	319m
Exposure and frost	Exposed with fairly mild winters	Moderately exposed with moderate winters	Exposed with rather severe winters	Exposed with rather severe winters

Exposure = windspeed, miles/second. Moderately exposed 2.6-4.4 m/s, Exposed 4.4-6.2 m/s
Frost = accumulated day degrees. Fairly mild 20-50, Moderate 50-110, Rather severe 110-230
Source: Birse and Robertson (1970)

	Kilmartin	Gatehouse	Glensaugh	Sourhope
Temperature & potential water deficit	Fairly warm wet lowland and foothill	Fairly warm rather wet lowland and foothill	Cool rather wet lowland, foothill and upland	Fairly warm moist lowland and foothill

Temperature = accumulated day degrees above 5.6°C. Cool 825-1100, Fairly warm 1100-1375
Potential water deficit (mm). Rather wet 0-25, Wet 0
Source: Birse and Dry (1969)

	Kilmartin	Gatehouse	Glensaugh	Sourhope
Topography	Glacial, rugged and highly dissected	Glacial, rather dissected	Periglacial, steep slopes and plateau	Perigalcial, smooth convex slopes
Dominant vegetation (apart from) bracken	_Callunetum_, valley bogs and flushes	_Agrostis_ pasture below head dyke, acidic grassland and _Myrica_ bog above head dyke	_Callunetum_	_Nardetum_

Table 3.2 Climatic data for the study sites

	Mean annual temperature °C	Mean January temperature °C	Mean July temperature °C	Mean January minima °C	Mean July maxima °C	Mean annual precipitation mm.	Mean no. of days with snow lie
Kilmartin (132m)	8.0	3.8	13.3	1.3	16.6	1600-1800	5-10 (Dec-Mar)
Gatehouse (136m)	8.3	3.8	13.8	1.0	18.3	1600-1800	10 (Dec-Mar)
Glensaugh (198m)	6.9	2.3	13.1	-0.5	16.2	1000-1100 Farm=1041.4 (171m)	40 (Nov-Apr)
Sourhope (319m)	6.6	1.6	12.6	-1.0	17.6	1000 Farm=939.8 (274m)	34 (Nov-Apr)

Temperature data taken from: The Climatological Atlas of the British Isles (H.M.S.O. 1952) and calculated at a lapse rate of 0.64 C/100 metres.
Precipitation data taken from: Average Annual Rainfall map for northern Britain 1941-1970 (Meteorological Office 1977)
Snow lie data taken from: Climatological Memorandum No.144 (Meteorological Office 1983)

each of the sites are now described in further detail.

3.3 Kilmartin

Location

The site is situated one and a half miles inland on the Poltalloch Estate, about two miles south-west of the village of Kilmartin and ten miles north of Lochgilphead in Mid Argyl.

Geology and topography

The site lies above the smooth fluvio-glacial terraces of the Kilmartin valley, on hill land of very complex local topography consisting of small hollows, ridges and rocky outcrops. It encompasses the north and south slopes of the small hill, Barr a Chuirn, with an altitudinal range of 70 metres, from 110 to 180 metres.

The geology of the site is dominated by metamorphic epidiorite consisting of Daldradian hornblende schists, with bands of quartzite and occasional Black schists and slates. Basaltic and doleritic dykes cut east-west across the topography. Although not found on the site, Durness limestone outcrops all around the site with obvious local effects on the soils and vegetation.

Soils

The soils are of the Tarves Association formed on drift derived from intermediate rocks or mixed acidic and basic rocks. Humic gleys and peaty gleys are found in the valley floors and hollows with brown forest soils, peaty podzols and iron podsols on the slopes and steeper hollows. Due to the fragmented topography the soils of the study site form a complex mosaic which is difficult to map accurately even at a 1:10,000 scale.

Vegetation and present landuse

The site comprises moorland and what may be abandoned cultivations just above the head dyke. It is sheltered on most of the east side by a conifer plantation. The vegetation consists of a mosaic of mature and degenerating Calluna on the convex steeper spurs, Molinia-Calluna bogs and flushed relatively herb rich Juncus bogs in the valleys and Deschampsia flexuosa - Nardus stricata grassland and bracken and Agrostis stands on the lower slopes (see Fig. 3.2). Mesotrophic vegetation is found in some of the small streams and drainage ditches and on small patches of Agrostis grassland (e.g. Filipendula ulmaria, Caltha palustris, Primula vulgaris) reflecting the presence of basic metamorphic rocks and nearby limestone outcrops.

Up until spring 1986, sheep were supposed to have grazed the site at a stocking rate of one ewe per hectare, but in practice they are thought to have grazed elsewhere where Calluna is less dominant and red deer probably account for as much of the grazing (Malcolm 1985, Pers. Comm.). In spring 1986 most of the site was fenced off, ploughed and planted by the Economic Forestry Group. The Calluna was last burnt in 1973 but that adjacent to the conifer plantation (which includes much of the Calluna on the site), has not been burnt since the trees were planted over twenty years ago. Most of the Calluna on the site is therefore mature or degenerating.

3.4 Gatehouse

Location

The site is situated 5 miles north of Gatehouse of Fleet in the Galloway and Dumfries region, on the south westerly facing slopes of the valley of Little Water of Fleet, above Culroech Farm. It extends uphill from the gorge-side of Castramont Burn at 60 metres to the upper slopes of the Doon of Culreoch at 210 metres.

Geology and topography

All of the underlying rock on the site is of Silurian

Fig. 3.2 Looking south from Bar a Chuirn, Kilmartin

Fig. 3.3 The lower site at Gatehouse (below plantation)

Grits, consisting of greywacks, flags and shales of the Llandovery-Tarannan Series. Narrow bands of porphyrite, granite and Black shale occur intermittantly across the whole area, one such band of Black shale being dissected by the gorge of Castramont Burn.

The topography is generally less complex than that at Kilmartin and comprises smooth, stream dissected lower slopes below the head dyke and a more rugged topography above the head of with rocky outcops, hummocks, ridges and small streams above.

Soils

The soils, derived from lower Paleozic greywackes and shales, have been classified as brown forest soils and brown rankers of the Ettrick Association. Below the head dyke peaty and humic gleys occur locally in the hollows and small stream valleys. Above the head dyke is a mosaic of brown forest soils, rankers and peaty podsols.

Vegetation and present landuse

Two thirds of the site lies on inbye land below the head dyke (Fig. 3.3). The lowest part is located on the small area of relict woodland between the edge of the gorge of Castramont Burn and the first field wall. Apart from the lowest field, which was reseeded sixteen years ago, the in-bye pasture is predominately bracken and Agrostis tenuis grassland, with locally abundant Cirsium arvense and C.vulgare. In the higher fields there are numerous bracken free springs and flushes with Carex hostiana, Myrica gale and Sphagnum rubellum dominating the wettest parts, surrounded by closely grazed mesotrophic species rich grassland (Fig. 3.4). Above the head dyke Molinia caerulea - Myrica gale communities dominate the flatter areas while Nardus stricta - Agrostis montana - Festca ovina grass heath and Molinia - A.montana grassland, interspersed with discrete stands of bracken, dominate the slopes (Fig. 3.5). An area of old runrig in the Cleugh Burn valley is completely covered by bracken.

Fig 3.4 The upper fields at Gatehouse

Fig. 3.5 Above the head dyke at Gatehouse

Sheep are grazed all year on the site except in early spring. The stocking rate is difficult to calculate accurately due to variance in quality of the grazing on the hill, but is probably about one sheep per hectare. Cattle are grazed for part of the summer. The bracken has not been cut for at least the last thirty or forty years.

3.5 Glensaugh

Location

Glensaugh Research Farm is situated in the eastern foothills of the Grampian range below Cairn O'Mount, about twelve miles inland and four miles north of Fettercairn in Kincardineshire.

Geology and topography

The site lies on Dalradian metamorphic rocks consisting of quartz schists, quartz-mica schists and schistose grits. A deep deposit of till covers the slopes up to about 220 metres, becoming thinner on the higher ground. The site is mainly located on the southeast facing slopes of Slack Burn valley, rising steeply in a series of steps up to a smooth Calluna covered plateau-land at about 400 metres (Fig. 3.6). Several small stream valleys deeply dissect the slopes. The altitudinal range of the site is 100 metres, from 150 metres on the valley floor to 250 metres at the approximate spring line where the slope profile changes uphill from concave or straight to convex. The first 50 metres are very steep, with a slope of around 35 degrees, becoming flatter thereafter. Part of the site is situated on the even steeper west facing slope, where the slope angle is around 44 degrees.

Soils

The soils are of the Strichen Association (Glentworth, 1954), developed on till derived from quartz schist and quartz-mica schist. Two soil groups, mature and immature, are recognised. The latter is found on the

Fig. 3.6 Looking up Slack Burn valley, Glensaugh

Fig. 3.7 The upper valley, Glensaugh

steeper colluvial and scree slopes, especially on the west facing slopes, with unstable surfaces, coarse rock fragments and are excessively freely drained

Nicholson and Robertson (1958) in their survey of the farm, recognised five different soil types within the site, as follows:

Iron podsols associated with Calluna, with a freely drained profile and marked horizons.

Brown podsolics usually associated with bracken, showing weak podsolization, freely drained and coarse textured profiles.

Brown forest soils of the Fungarth series with deep undifferentiated profiles, often bearing deeply penetrating bracken and usually found in hollows.

Gley soils associated with depressions and gentle slopes.

Alluvium along the valley floor.

Vegetation and present landuse

The steep west facing slopes of Slack Burn bear almost pure even-aged mature Calluna on the skeletal soils and scree. On the opposite slopes Calluna usually occupies the rocky spurs and convex slopes, while bracken occupies the concave slopes and small hollows (Fig. 3.7), and also the grassland between flushes and Calluna stands. The ground layer of the bracken stands is either completely litter dominated or ranges from species poor *Arostis tenuis* swards to relatively herb rich *Agrostis* - *Poa pratensis* on the colluvial soils. The main valley floor bears *Juncus spp.* and bracken on damp mesotrophic grassland. The boundary between the highest bracken and the Calluna plateau beyond is very marked, occurring at the second break of slope where the slope profile becomes distinctly convex. Bracken does occur above this point, but only in discrete hollows.

Effective utilization of the hill grazings is a major problem in the region due to the large areas of Calluna. Areas of grass and arable enclosures on the farm are substantially greater than that of normal hill farms and provide much of the farm's productivity. Much of the higher hill grazing is therefore not fully utilised (H.F.R.O.). The southeast facing slopes of the site are grazed by sheep at a stocking rate of one ewe per hectare, while goats range the steep Calluna covered west facing slopes. The hill is only used by young replacement sheep, dry sheep and ewes with single lambs in the summer months. Prior to mating in the autumn, they have access to reseeded land and the site is grazed less intensively. Snow can often lie from January until April and little grazing takes place on the hill until May.

When the H.F.R.O. took over the farm in 1944, little Calluna burning had been carried out and large areas had to be burnt, resulting in large areas of even aged Calluna. An eight to twelve year rotation was then operated and largly maintained today, although the more inaccessible and isolated patches may be missed (Nelson 1986, Pers. Comm.). This would seem to be the case for the more fragmented Calluna stands on the southeast facing slopes of the site.

3.6 Sourhope

Location

Sourhope Research Farm is situated 15 miles south of Kelso at the head of the Bowmont Valley on the northern slopes of the Cheviot Hills.

Geology and topography

The farm lies on andesite lavas of moderate acidity. The topography is one of uniform rounded hills but without the extensive plateauland characteristic of the Glensaugh area. The lower concave slopes are deeply convered in drift derived from local lavas, while the upper convex slopes bear thin residual soils.

The site is centered around the west side of Dod Hill which has rounded upper convex slopes, steep sometimes scree covered middle slopes, and a concave lower slope to the valley floor (Fig. 3.8). The site extends from the far

Fig. 3.8 Dod Hill, Sourhope

side of Kaim Burn at the foot of Dod Hill at 270metres, to about half way up the hill at 380 metres, a range of 110 metres. The site also includes the adjacent north facing slope across Dod Burn to the south and the adjacent south facing slope across Rowantree Burn to the north.

Soils

The soils of Sourhope have been classified into five series, belonging to the Sourhope Association (Muir, 1956) and derived from intermediate lavas of Lower Old Red Sandstone age. These are, freely drained Brown Forest soils of low base status, freely drained peaty podsols, poorly drained non-calcareous gleys, poorly drained peaty-gleys and very poorly drained peaty gleys, plus skeletal soils. The brown forest soils characterise the lower slopes of the site while more acid peaty podsols and peaty gleys occur at higher elevations. Very stony skeletal soils occur on the steeper slopes. The bracken is associated with the skeletal and brown forest soils, while the peaty podsols are associated with Nardus and Molinia. Sourhope soils are deficient in cobalt and it is thought that an aluminium toxicity problem exists, resulting in deficiency of available phophates (Mitchell 1977).

Vegetation and present landuse

A study by King (1962) on the grasslands at Sourhope distinguished twelve different grassland types, characterized by floristic compliment and accompanying soil type. These were all variants of either Nardus - Deschampsia flexuosa - Festuca ovina grassland, or Agrostis - Festuca grasslands. At the site Nardus is very dominant on the convex spurs and middle and upper slopes. Bracken on Agrostis - Festuca or Agrostis - Poa pratensis - Holcus spp. grassland mainly occupies the lower concave slopes and the steep scree slope. The lowest part of the study site on the valley floor of Kaim Burn, comprises bracken free Molinia-Carex spp. grassland and damp mesotrophic Agrostis-Festuca grassland. Three conifer windbreaks, planted twelve years ago, separate this lowlying area from the main bracken slopes.

The area covered by Dod Hill and the nearest slopes of the two adjacent hills is divided into two grazing hefts, Rigg and Gairs, totalling 202 hectares. Stocking was originally of 130-140 South Country Cheviots but is now replaced by 550 Blackface ewes, at a stocking rate of 2.7 ewes per hectare. A suckler cow herd is grazed on Rigg and Gairs at some time each year from late spring through to the end of the year, the length of grazing varying from year to year with no set pattern (Armstrong 1986, Pers.Comm.).

Each site can therefore be seen to be representative of the main hill environments in which bracken is found, with the rugged but relatively lowlying moorland on the west coast, the bracken infested pasture of the southwest, the steep sided slopes of the *Calluna* plateau in the northeast and the rounded *Nardus* dominated hills of the southeast. The climate, vegetation and soils of the sites are further examined in relation to bracken vigour in Chapters Five and Six.

Chapter Four

Data Collection

As discussed in Chapter One, the two main areas of investigation are into the environmental characteristics of the bracken zone and the direct effect of environmental factors on bracken vigour. The same data were used for the majority of the investigations, except for the study of soil temperature and of bracken spread which were investigated separately. The method of data collection for the two main investigations is thus described first, followed by the two "subsidiary" studies.

4.1 Investigation into the environmental characteristics of the sites and their effect on bracken vigour.

4.1.1 Introduction

The study of the influence of environmental factors on plant growth can either be carried out by statistical analysis of the effect of variables on plant performance in the field, or by investigation of the effect of one or more variables in a controlled environment (Alcock et.al. 1967). The statistical approach has been critised for its inability to disentangle the infinite complexity of the environment especially since the influence of the environment may vary at different stages of development (Milthorpe 1965). On the other hand the statistical approach will better indicate which are the most important variables. It was decided to limit this study to the field since preliminary enquiries revealed that transplanted bracken rhizome material is very liable to revert to the juvenile form and would need at least two years before resuming the adult morphology. It was also felt that the highly specific data that would result from a laboratory study would not be altogether very useful as it would give no information about the effect of factors in field conditions.

4.1.2 Selection and setting up of monitoring points.

Within large areas where standard meteorological stations are used to characterize the macroclimate, local deviations occur (mesoclimate) which are largely determined by topographical features (Hogg 1965). The data from established meteorological stations gives little insight into the variations of mesoclimate. To some extent these can be inferred from established relationships between climate and physiographic variables, for example the relationship between temperature and altitude (see for instance, Gloyne 1968 and Manley 1944). Where however the density of recording stations is low, such interpolation can be misleading. Furthermore there is a dearth of weather stations in upland Britain and also of stations recording soil and earth (below 30cms depth) temperatures (Harrison 1975). It was decided therefore that rather than merely use data from the nearest meteorological stations, data on the mesoclimates of the study sites would need to be collected.

Eight points (from hereon called posts) were selected at each site to record maximum and minimum air temperature, exposure, soils, aspect, altitude and slope. Rainfall was not recorded as it was felt that it would not vary significantly over the altitudinal range of each site to warrant intra-site recording with the extra equipment that would be needed.

As discussed in Chapter Two, there have only been two instances of a multi-variable approach in the study of bracken, both of which used very generalised data.

Multi-variable studies using more specific data have been reasonably successful for investigations into grass yield by Alcock et.al.(1967), Hunter and Grant (1971) and Jones and Tinsley (1980). Alcock et.al. measured twelve climatic variables but restricted the study to one upland site and one lowland site in west Wales. Hunter and Grant measured soil temperature, soil moisture, light and exposure at a total of thirty two different points spread around three sites, two in north-east and one in south-east Scotland. Soil type was standardised by the use of growth trays and all monitoring points were located in altitudinal transects confined to south facing slopes. Jones and Tinsley measured radiation, air and soil temperatures, rainfall and exposure on two different soil parent materials using a factorial design to spread the two chosen aspects of south and north, three altitudinal bands and the two classes of land use (based on sward quality) equally between fourteen stations in the Upper Don Basin.

For this study a total of thirty-two monitoring points were set up as a compromise between the need to obtain sufficient data for the subsequent analysis, and the practicalities involved in the travelling and hill walking that was necessary to carry out regular recording.

A systematic approach was used to select the bracken stands for study, the quantification of both environmental variables and bracken vigour eliminating the need for random sampling (Greig-Smith 1983). Greig-Smith recommends that if elucidation of correlations between vegetation and environment is the primary objective, samples should as far as possible include all variants of vegetation and an equal representation of all variants. In view of the nature of bracken distribution within a site, random samples would have to be very large to achieve this end. This is neither practical in terms of the amount of equipment that would be needed, nor desirable as it would practicably exclude the use of more than one site.

It was immediately apparent during reconnaisance site visits in late winter and early spring of 1985 that on the basis of the bracken litter, there are two main bracken stand types, as described by Watt (1956). One has a grass ground layer (usually Agrostis-Festuca) and the other a deep bracken litter and very little ground flora. A less frequent intermediate type with a mosaic of litter and grass also occurrs. A systematic grid sampling system was thought to be inappropiate as it probably would not have represented the three stand types evenly over the range of variables unless many sampling points were possible. Greig-Smith (op.cit.) suggests that where there is reason to suspect that obvious environmental differences may play an important part in determining the composition of the vegetation, it is sensible to stratify in relation to these and for example, in undulating topography to ensure that equal numbers of stands are sited in valleys, on slopes and on ridges. Stratification therefore in this case aims at equal numbers of stands from different strata, not equal density of stands. Each site was therefore approximately sub-divided into different topographic and altitudinal areas and one, two or three posts, depending on the number of bracken stand types, were placed in each area. Each post was located in the middle of a reasonably homogenous stand type. Two stand types could make up one continuous stand of bracken, but for sampling purposes were considered to be two discrete units. For example, at Sourhope Post 4 is located in the "crest" and Post 5 in the "hinterland" of the same bracken stand.

At Sourhope and Glensaugh one of the eight posts at each site was located in bracken free areas as part of the investigation into bracken spread (or in both cases, lack of spread). These were not used in the statistical analysis as they do not fit into the sampling system which is based on bracken stand type. At the end of 1985, Glensaugh One and Gatehouse One were relocated to make the representation of the two stand types more equal.

Glensaugh Eight also had to be relocated because heavy sheep trampling made frond counts impossible. No data are therefore available for this post in 1985. The prefixes "Old" and "New" distinguish the posts in the two years.

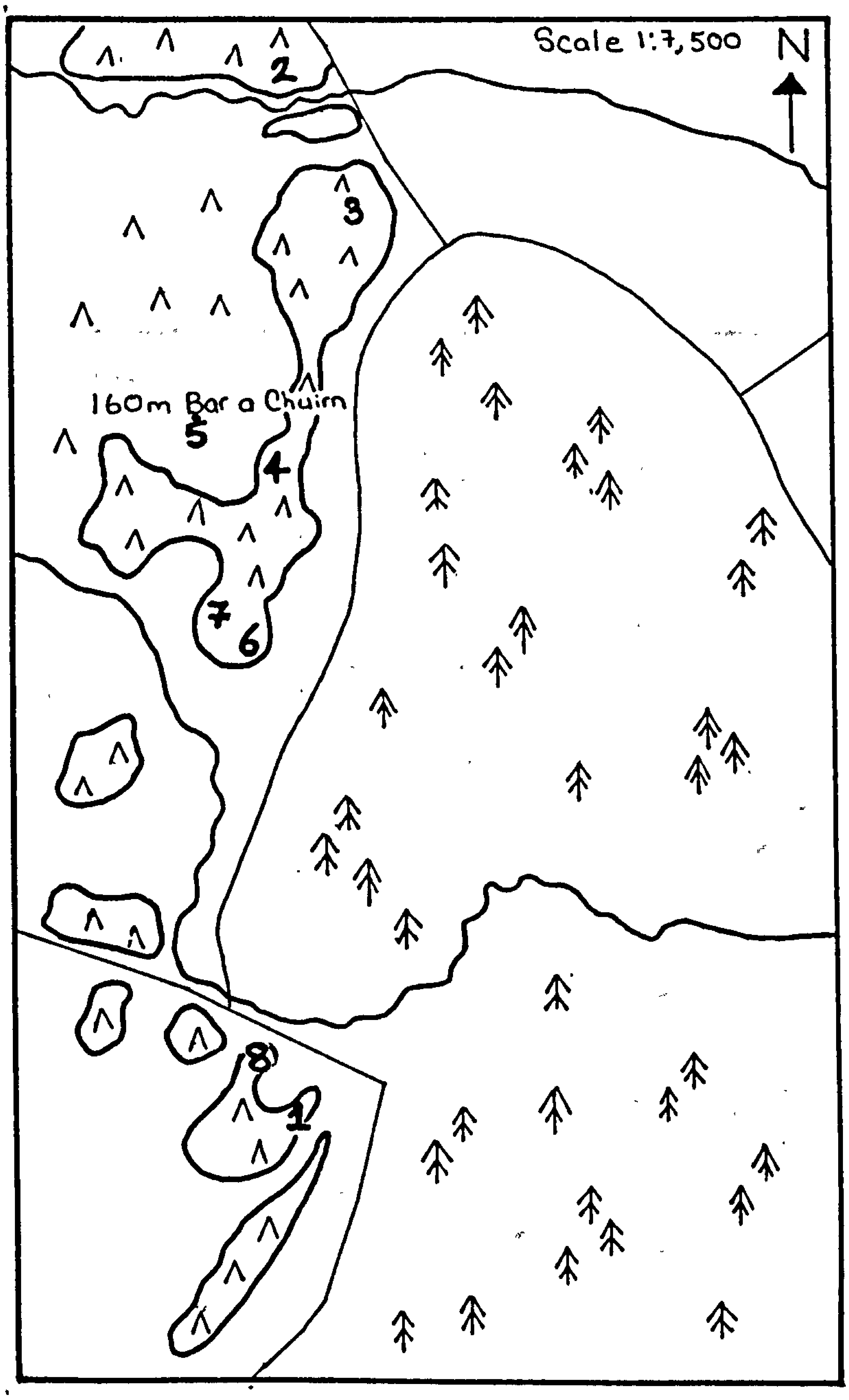
The topographic and vegetative characteristics of each sample stand are summarised in Appendix One and their locations shown in Figs. 4.1.-4.4.

4.1.3 Temperature monitoring

Past work involving temperature recording in the field has included investigations in to air and soil temperatures in different physical environments (e.g. Coutts 1955; Halstead 1974; Harrison 1975; Munro 1973), soil temperatures under different vegetation (e.g.Norman et.al. 1952; Porter 1956; Shanks 1956), and the effect of temperature on grass growth in small scale and detailed studies (e.g.Peacock 1975) and in larger scale studies which include other climatic and environmental factors (e.g. Alcock et.al. 1967; Hunter and Grant 1971; Jones and Tinsley 1980). All except Jones and Tinsley and Hunter and Grant had only a small number of sample points and were therefore able to use a range of expensive and often fragile meteorological equipment. The most popular methods of measuring temperature in these studies were the continuous recording thermomgraph and the maximum and minimum thermometers. More recently the digital recorder, which takes readings at desired intervals, has become popular.

Although continuous recorders (including thermistors, thermocouples and thermographs) provide the most complete dataset, their use is restricted by their expense and also the need for protection and regular inspection in the field. The magnitude of data that is collected may also be prohibitive if the amount of analysis and information extracted is inappropiate for the scope of the study. Ordinary thermometers can only give spot readings and unless read every day, do not yield data that is of much use. In addition, the adoption of a standard time for

Fig. 4.1 Location of monitoring posts at Kilmartin



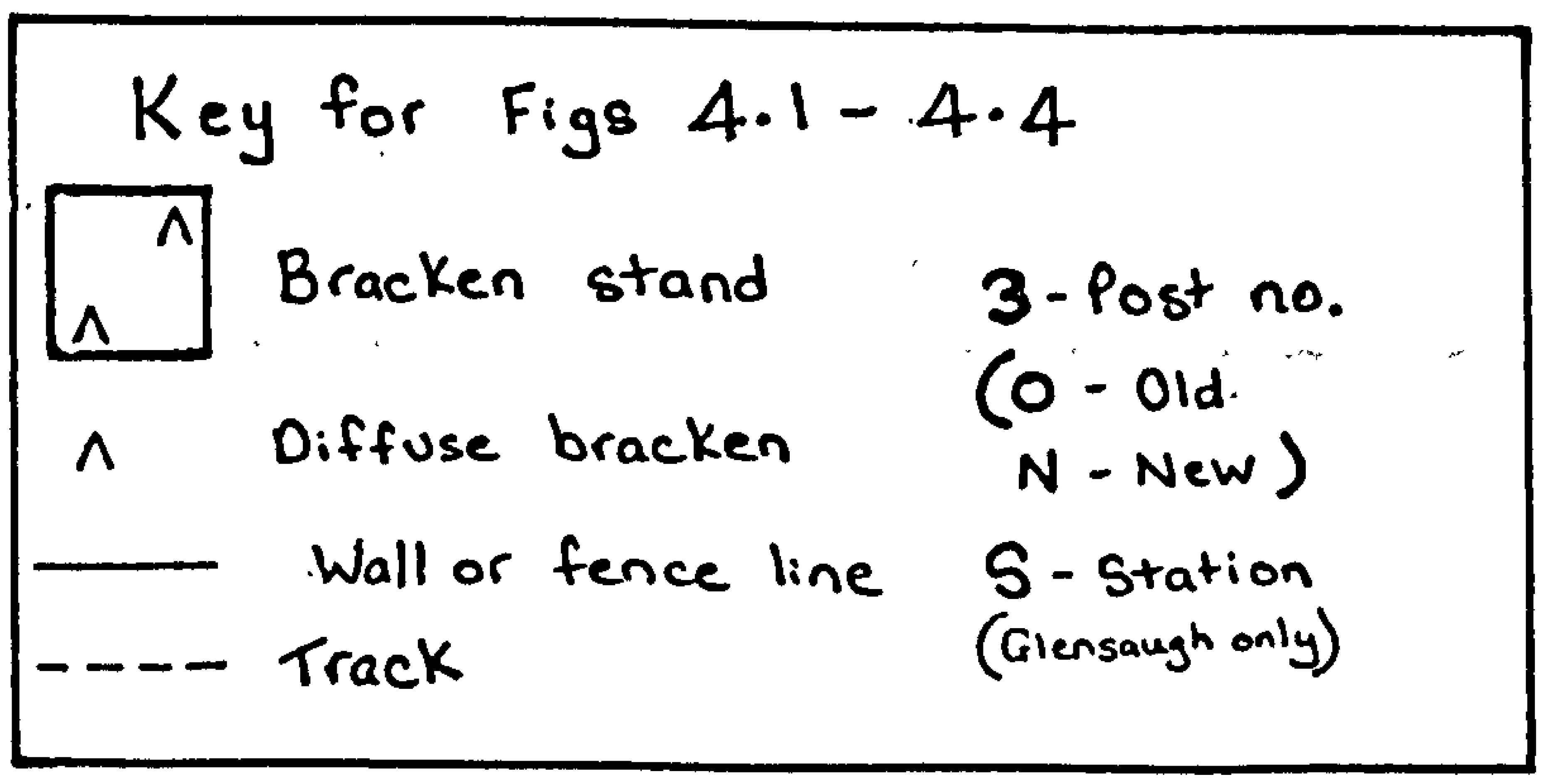


Fig. 4.2 Location of monitoring posts at Gatehouse

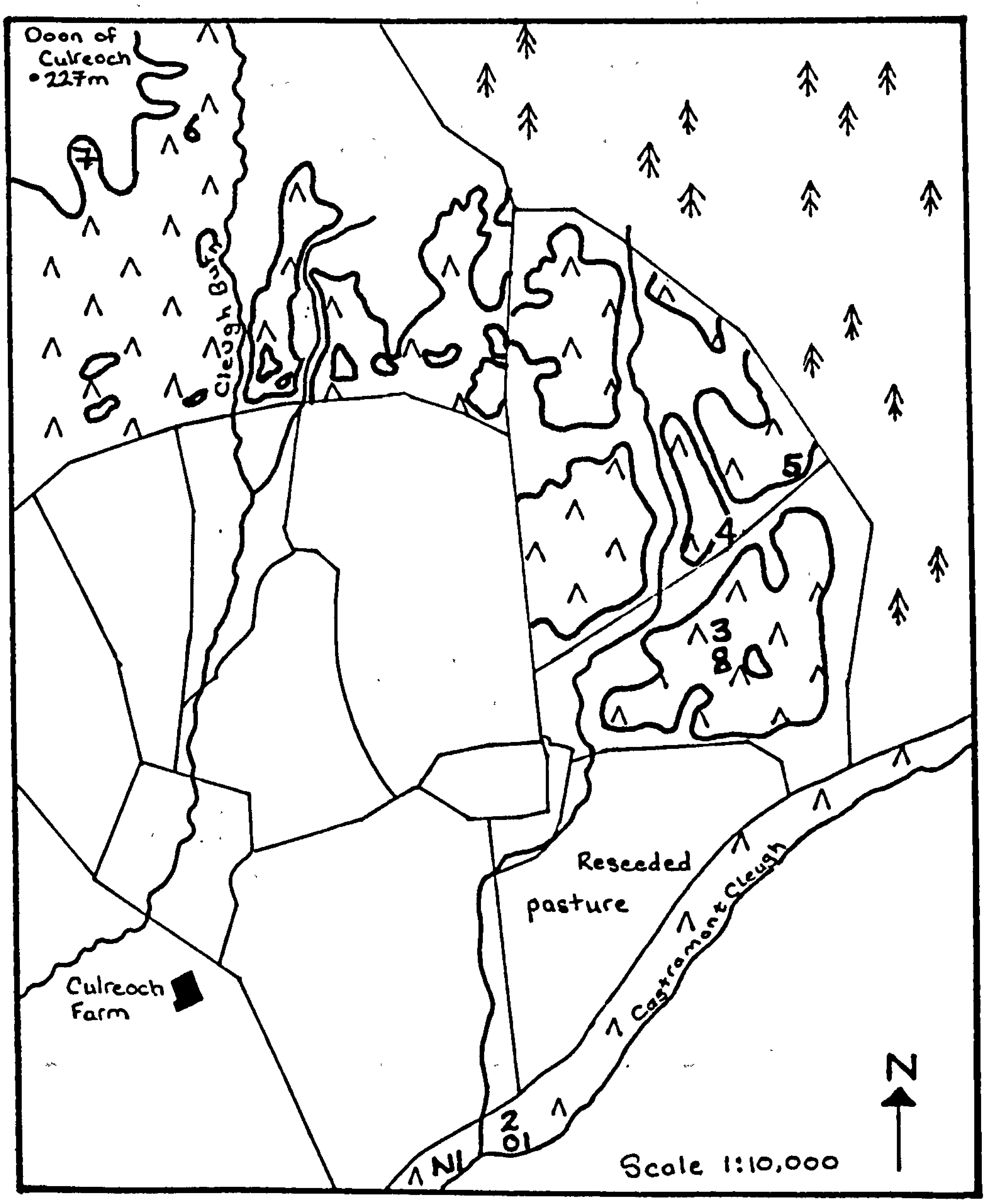


Fig. 4.3 Location of monitoring posts and stations at Glensaugh

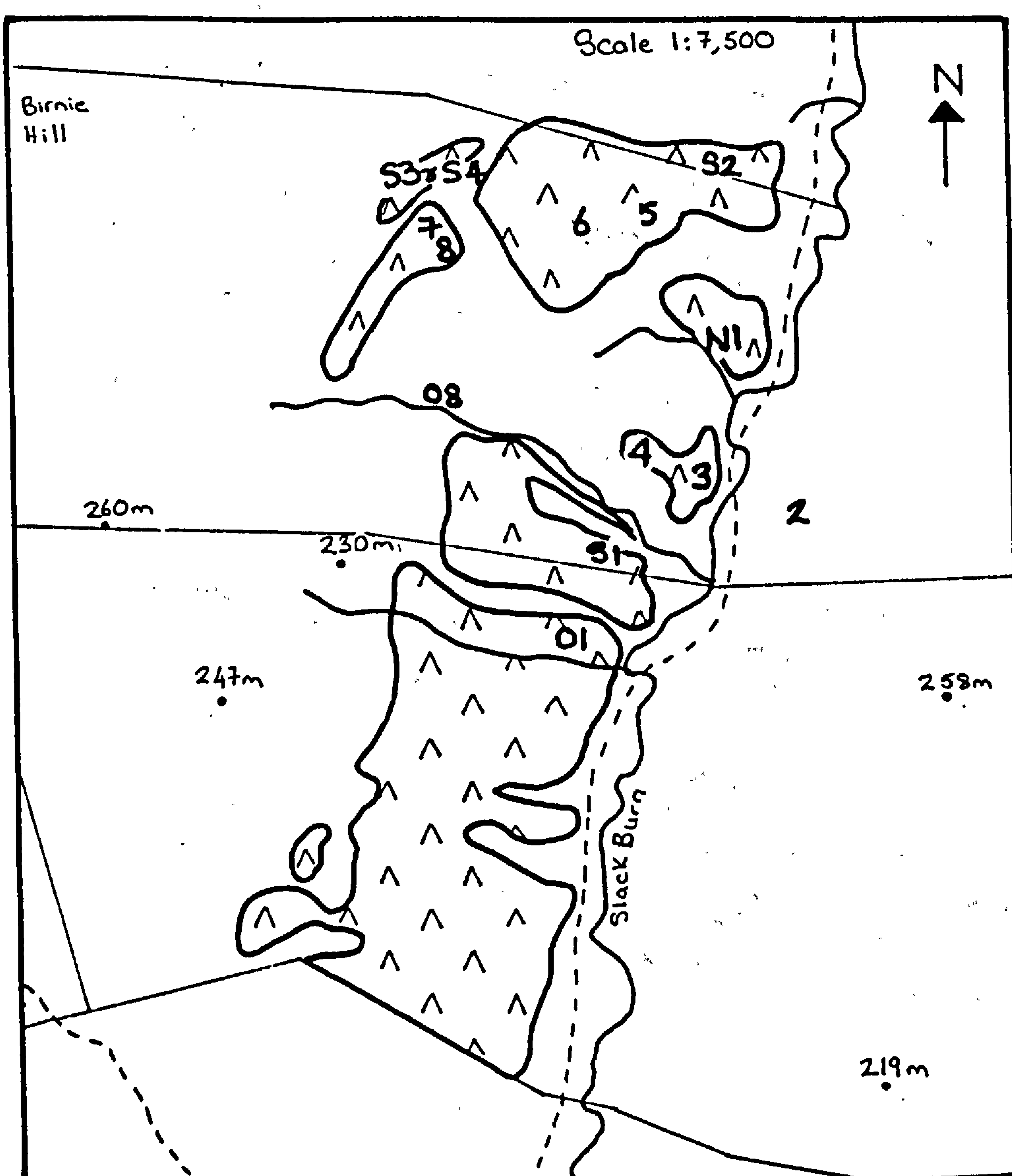
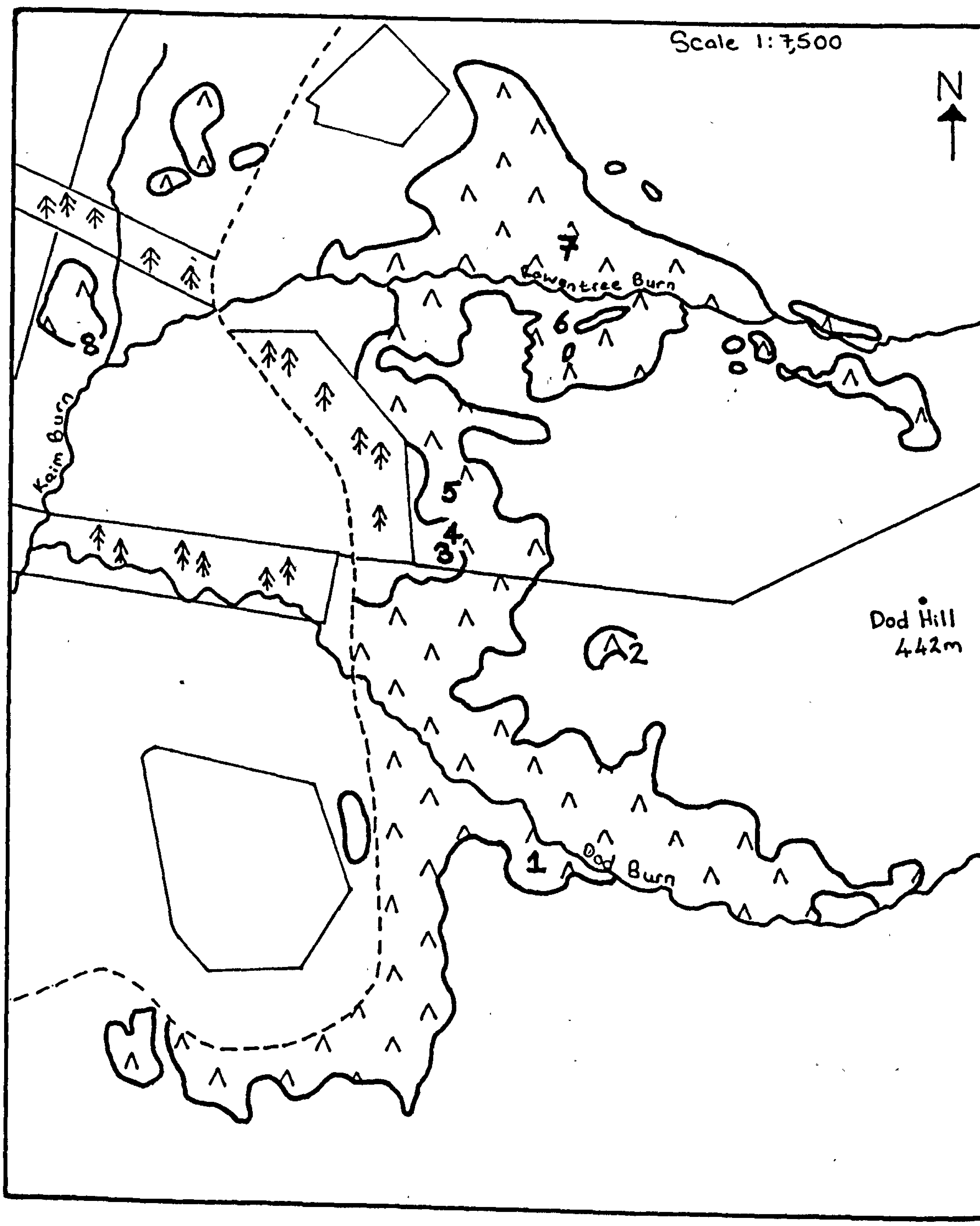


Fig. 4.4 Location of monitoring posts at Sourhope



reading soil and earth thermometers produces errors due to the dependence of soil temperature upon diurnal and annual displacement from sunrise (Harrison 1975).

Hartly and MacLauchlan (1969) and Jones (1972) describe a simple intergrating thermometer to solve the problem of temperature measurement on a large scale. This works on the principle of the irreversible chemical reaction with temperaure of sucrose in a buffer solution which pushes a small air bubble along the thermometer tube, the position of which can be read off against a scale. The total distance is divided by the reading interval in days and the mean temperaute thus obtained. This is an exponential mean rather than an arithmetic mean as fluidity is not a linear function. Jones and Court (1980) found that the exponential means obtained in this way were on average 2°C higher than the arithmetic means measured by standard instruments. The intergrating thermometer was successfully used to measure air and soil temperature in the investigation into grass yields in the Upper Don Basin (Burnham et.al. 1970 and Jones et.al. 1979), although Unwin (1980) argues that if the range of temperature being measured is large, serious errors can result. He suggests that it is a useful method for estimating the mean temperature of damp soil or water bodies, but is generally unsatisfactory for the measurement of mean air temperatures near the ground.

The integrating thermometer would seem to have been ideal for the requirements of this study, being both simple and inexpensive, but enquiries into a source of supply were not successful. Due to the pressing need to set up the field equipment by mid-April for the beginning of the growing season, it was decided to use Six's maximum and minimum thermometres instead. This design of thermometer records both maximum and minimum temperatures on the same apparatus and was successfully used by Harrison (1975) in his study of soil temperatures in west Wales. A ready supply of an inexpensive and durable plastic backed version was possible, permitting the collection of data from a large number of sample points and eliminating the need to fence off all the posts from sheep grazing. The thermometers could be read to 0.5°C (plus or minus 0.25°C), but they all had to be calibrated against an accurate glass thermometer before placing them in the field and the data adjusted accordingly as most were about 0.5°C inaccurate.

Maximum and minimum thermometers indicate a general temperature envelope. Jones et.al (1979) showed that monthly mean air temperatures calculated from daily maximum and minimum peaks proved to be almost identical with those determined by planimeter from thermograph charts. As it is inconvenient to take daily readings from remote sites, they also tested the value of monthly intervals and found a high correlation between air temperature from monthly maximum and minimum recordings and mean monthly air temperature from daily maximum and minimum recordings, both of which were used in their study. Harrison (1975), Hunter and Grant (1971) and Alcock et.al. (1967) used weekly maximum and minimum temperatures.

Two Six's thermometers were set up at each post, one on the ground (the "ground thermometer") and one secured vertically to a small post 60cms above ground level (the "air thermometer"), each protected from sheep grazing by a cylinder of wire mesh. The two layered approach was designed to be able to investigate Watt's conclusions that late spring frosts were more likely to affect the growing canopy whilst early frosts effect the emerging bracken "hooks" (Watt 1950). The height of the air thermometers was constrained by the height of the shortest bracken stands.

The posts had to be enclosed at Sourhope because of cattle grazing for some of the year and it was thus possible to use more accurate glass minimum thermometers at the ground position, taking advantage of the extra protection. These thermometres are accurate to 0.1 ^{o}C but were read to 0.5 ^{o}C to be comparable with the Six's thermometers. Maximum temperatures at ground position were not recorded at Sourhope because of the problems involved in fitting two thermometers into the wire mesh.

A major problem with the use of bulb thermometers in the field is the absorption of incoming radiation by the bulb if the thermometer is not shielded. If total incoming radiation exceeds outgoing radiation the bulb will read higher than the surrounding air temperature (Unwin 1980). The usual solution is to place the thermometers in Stevenson screens, clearly impractical for a large number of thermometers, or to fit individual radiation screens. The cylinders of wire mesh provided adequate protection for most of the thermometers. It is likely that once the canopies are fully developed the temperatures recorded are probably more a function of microclimate than mesoclimate, a point discussed in Chapter Five.

All the posts were set up in the last week of April and the first week of May in 1985. During the first growing season weekly readings taken on Mondays were made at Glensaugh, Sourhope and Kilmartin, but only every three weeks at Gatehouse where no-one local was available to take the readings. Readings were taken by local residents only at Kilmartin and Sourhope and therefore there were constraints on the frequency at which the other two sites could be visited. After the end of August all sites were read every two or three weeks until Dececmber and there after every month until the start of the second growing season. The reduction in readings over the winter resulted from the bad weather which made travel and access to the site in some cases impossible. In the second growing season all the sites except Glensaugh (which still had to be visited once a week to change the graphs) were only visited once every three weeks because of need to spend time doing other field work.

Gaps in the data resulted from breakages of thermometers by sheep trampling at all the sites. Cattle were grazed unexpectedly at Gatehouse in both growing seasons and thermometers could not be left out during these periods resulting in large breaks of data at Posts 3, 4, 5 and 8. The thermometers at Posts 1 and 8 at Kilmartin were prone to theft and the removal of Post 1 in the second growing season by forestry workers resulted in the discontinuation of recording at this post.

4.1.4 Exposure Monitoring

The relative exposure of each post and thermograph station was measured by the tatter flag method developed by the Forestry Commission (Forestry Commission 1984) and used for more than twenty years as an important aid in defining planting limits (see Savill 1974) and in wind zonation for windthrow hazard prediction (Miller 1985). Tatter flags have also been used in studies of climatic factors and plant growth (see Hunter and Grant 1971, Jones et.al. 1979 and Pears 1967). The flags are made from Madapollam cloth cut very accurately to specific dimensions and are exposed on a freely rotating mount with the top of the flag 1.5 metres above ground level (Gloyne 1975). The mount is attached to a metal pole which is in turn secured on to a fencing stake. By measuring the amount of flag lost through tattering after a set period of exposure, a mean daily tatter rate can be calculated.

In 1973 and 1976 the Forestry Commission tested 300 flags against elevation. Correlations were obtained between rate of tatter and altitude when flags from the same area were used (Reynard and Low 1984). Lines and Howell (1963) obtained high correlations between tatter flag data and anemometer readings and Rutter (1968) formulated regression equations for tatter and accumulated wind run for between site data using the square root of the tatter data.

One of the problems of using tatter flags is that they are prone to become entangled on themselves at low windspeeds and after rain. Thomas (1959) found that this effects the tatter rate at wind speeds of below 7 miles per hour, but wetting of the flag seemed to have no appreciable effect on the tatter rate. He also found that at wind speeds of over 25 miles per hour tattering was greatly increased, but considered that its accuracy can be defined within reasonably narrow limits.

The flags were provided and processed by the Forestry Commission as part of their current research programme into exposure limits in Britain. The flags were changed at synchronised two monthly intervals on or as near as possible to the first day of the change month, with a minimum exposure of 55 days and a maximum of 65 days allowed. It was not possible to set up all four sites together because of the logistics of obtaining, transporting, and carrying and setting up the supporting fencing stakes on the sites. Sourhope was set up at the beginning of May, Kilmartin and Glensaugh at the beginning of July and Gatehouse at the beginning of September 1985. Where monitoring posts were close together with a similar topography, one flag sufficed for two or three posts (i.e. Posts 3, 4, and 5 at Sourhope, Posts 3 and 8 at Gatehouse, Posts 7 and 8 and Stations 3 and 4 at Glensaugh).

Other problems encountered were torn and damaged flags which could not be processed, cattle knocking over the fencing stakes at Gatehouse and bad weather resulting in delayed flag changes at some of the sites at both the January changes of 1986 and 1987. (Unlike the temperature recording which ceased in autumn 1986, the exposure recording continued until Septembter 1987 at the request of the Forestry Commission). The delay resulted in over exposure of the flags prior to the change and under exposure of the next set of flags. However this does not affect the mean tatter rates.

The effect of the bracken on the flags is probably not as great as that on temperature recordings because at most posts the flags were above the bracken canopy, although in a large stand there is probably some decrease in wind speed as it passes over the stand due to the windbreak effect, as described by Pears (1967). The windbreak effect is no doubt greatly enhanced within the bracken stand, a phenonmena suspected to have been involved in the longevity of the bracken within the post enclosures at Sourhope, as discussed in Chapter Seven.

The topex measure of shelter / exposure, first developed by Blust and de Cooke (1960) was also recorded for each post, this being the total number of degrees to the skyline at the eight cardinal compass points (Pyatt 1977), (negative values score 0). The posts were then placed in one of five exposure classes as follows:

0-10 severly exposed
11-30 very exposed
31-60 moderately exposed
61-100 moderately sheltered
101- very sheltered

4.1.5 Soil recording

A soil pit was dug to approximately 15 cms below the top of the B horizon at each post and thermograph station, this depth being thought adequate for the purposes of the study. The soil profiles were described using a simplified version of the standard Soil Survey profile description (Soil Survey 1974), with depth of litter layers,organic matter incorporation, structure, texture, moisture content, and depth of rhizomes and fine roots being regarded as the most important characteristics. Aspect (the eight cardinal points), altitude, slope angle, slope morphology and surface drainage were noted at each point. Altitude was estimated from a 1:10,000 map and slope angle measured with a clinometer. Four classes of drainage were used as follows:

1. poor
2. impeded
3. free
4. excessive

4.1.6 Bracken recording

Two replicate 1 x 1.5 metre plots were pegged out as close as possible to each post (but outside the enclosures at Sourhope to allow for the effects of grazing) at the start of the first growing season. The plot size reflects the general variation in bracken density as initial investigations showed that the bracken tended to grow in clumps interspersed with areas of lower frond density. The chosen plot size was found to encompass this variation.

It was noticed at the end of the first growing season that the bracken inside some of the post enclosures at Sourhope was taller, denser and stayed green longer than the bracken outwith the enclosures. During the second growing season plots were pegged out inside the enclosures and the same counts and measurements made as those made on the main bracken plots. The size of the enclosures precluded the use of 1 x 1.5 metre plots and half sized, 0.75 x 1 metre plots were used instead.

At Glensaugh fronds were counted from time of emergence every week until midway through the growing season and thereafter every three weeks. At the other three sites counts were made every three or four weeks during both growing seasons. Counting ceased at the end August / beginning of September in 1985, but at the end of July in 1986 as preliminary analysis of the first season's data showed no increase and often a decrease in frond numbers after July. To facilitate counting in the second growing season, the plots were divided in half and counted separately and the fronds tagged with a strip of PVC tape tied loosely around the emerging rachis.

Average and maximum frond heights, average and maximum stages of emergence and numbers of fronds broken, frosted , diseased, or dying from other causes were recorded at every frond count. Average height was estimated by approximately measuring the average height of each half plot with a tape meaure and calculating the mean, a refinement of a similar technique used by Mitchell (1977).

Stage of emergence was recorded according to the position of the latest pinnae to unfurl (e.g. hook stage, first pinnae, second pinnae etc.).

Difficulties were encountered in classifying stage of emergence when fronds were badly diseased or frosted. In 1985 much of the bracken at the study sites and elsewhere in Scotland was afflicted by what looked to be pinnae blight, an early manifestation of the curl tip disease (see Burge and Irvine 1985) (Fig. 4.5). However, analysis of samples by the Department of Bioscience and Technology at Strathclyde University did not reveal any pathogenic organism suggesting that some other causal agent was responsible for the browning and curling up of the ends of the pinnnae (Burge Pers.Comm., 1986). It is thought that the saturated soil conditions resulting from the extraordinary wet summer in 1985 may be responsible, particularly since the bracken was more afflicted in the west.

Other problems arose as a result of cattle congregating around the posts and enclosures causing excessive trampling of some of the plots at Gatehouse and Sourhope. Some trampling is expected, being an integral part of the data but trampling caused by congregations of animals is far greater than that caused by normal grazing and some plots had to be relocated further away from the posts. Also, most of the Kilmartin site was ploughed up in the spring of 1986, but all the plots except those at Post One and plot Four b. were left intact. Temperature and bracken data at Post One (where the tatter flag was left in position) and bracken data at plot Four b. are therefore unavailable in the second growing season. As discussed, Old Glensaugh Eight had to be abandoned and no data are thus available for this post in the first growing season.

4.1.7 Ground flora recording

The ground flora of each post was recorded using the

Fig. 4.5 Diseased bracken, Gatehouse 1985

Domin Scale in July and August of 1986. Individual moss species were not recorded separately except on a few sample plots. Bracken cover, ground flora cover and bracken litter cover were estimated using percentage classes of 0-10, 10-20 etc.

4.2 Investigation into soil temperature under bracken.

Thermographs installed in Stevenson screens were set up to record air and soil temperatures at four points (Stations) at Glensaugh. Soil temperatures were recorded by distant reading thermographs with the probes inserted horizontally into prebored holes at 5 and 10cms depth (depth of F and L layers not included). These depths were chosen after exploratory pits showed the average depth of the main rhizome mass to be around 7-10 cms and the average depth of the differentiated but unemerged fronds at the beginning of the growing season to be 5cms. The air recording thermographs were situated about 30cms above ground level inside the Stevenson screens. All the stations were fenced off, with Stations Three and Four sharing the same enclosure.

The graphs were changed every week in both growing seasons and the autumn, but much less frequently during the winter because bad weather often prevented access to the site. Considerable difficulty was experienced during the first growing season in running the thermographs as some of the clocks continually stopped in mid-week. No data are available for air temperatures at Station Four in the first growing season because totally inaccurate readings were obtained. All the thermographs were taken off the hill in October 1985 and overhauled. The data from the second growing season are more complete. The thermographs were calibrated to 0.5 ^{o}C accuracy and were regularly checked against an accurate thermometer.

One 1 x 1.5 metre plot was pegged out at each Station (in which the probes were located) and bracken and ground flora recorded as for the posts. The characteristics of the bracken stands at the Stations are summarized in Appendix One.

4.3 Investigation into the nature of bracken spread within the sites

Frond density and height, percentage litter cover and ground flora (using the Domin scale) were recorded in 1.5 x 1 metre plots placed in the middle and margins of bracken stands that could be identified from aerial photographs to either have spread or remained stationary in the past forty years. Ground flora was also sampled in the adjacent bracken free vegetation. Shallow exploratory pits were often dug at the plots to establish the soil type. Extra soil pits were dug at Sourhope to form transects running from Nardetum into three separate bracken stands. The soil pits at the posts were included in the transects where possible.

The data were examined to characterise the topography and climate of the sites in Chapter Five and the soils, vegetation and bracken in Chapter Six (at the end of which hypotheses predicting the main environmental controls of bracken at the sites are formulated). Trends, anomalies and interrelationships of the data that may affect later analysis will also be discussed in these Chapters. The effects of grazing, soils and climate on bracken vigour are analysed in Chapters Seven, Eight and Nine respectively, culminating in a multi-variate analysis at the end of Chapter Nine. The findings are then discussed in Chapter Ten to determine how the various factors influence the pattern of bracken distribution and spread in Scotland.

Chapter Five

Topographic and Climatic Factors

5.1 Topographic factors

5.1.1 Altitude

Fig. 5.1 shows the altitudinal mean and range of the posts at each site (including the thermograph stations at Glensaugh) and Fig. 5.2 the mean altitude and range of all the posts. (Old Posts One at Glensaugh and Gatehouse were in the same altitudinal classes as their 1986 counterparts). All heights from here on are taken to be above mean sea level.

The overall range from 50 to 400 metres is similar to that generally quoted for bracken and the mean of 196.6 metres is within the range of the mean altitude of bracken in Scotland (243.9 $\pm$ 190.0 metres) that can be derived from the Land Use Survey of Bunce et.al. (1981). Although the mean altitude of Gatehouse is only slightly higher than of Kilmartin (136.5 and 132.25 metres respectively), the mean altitude of the bracken zone as a whole at Kilmartin is likely to be lower because posts could only be placed above the head dyke due to cattle grazing in the lower fields. Posts at Glensaugh were only located to the edge of the Calluna plateau and not in the highest bracken stands (as they were at the other sites). However, the mean site altitude (198.4 metres) is still likely to reflect the mean altitude of the main bracken zone in the locality because the bracken on the plateau is only found in small isolated patches. The highest bracken at the other sites is more or less contiguous with the lower bracken stands.

FIG. 5. 1. ALTITUDINAL RANGE AND MEAN OF MONITORING POSTS AND STATIONS

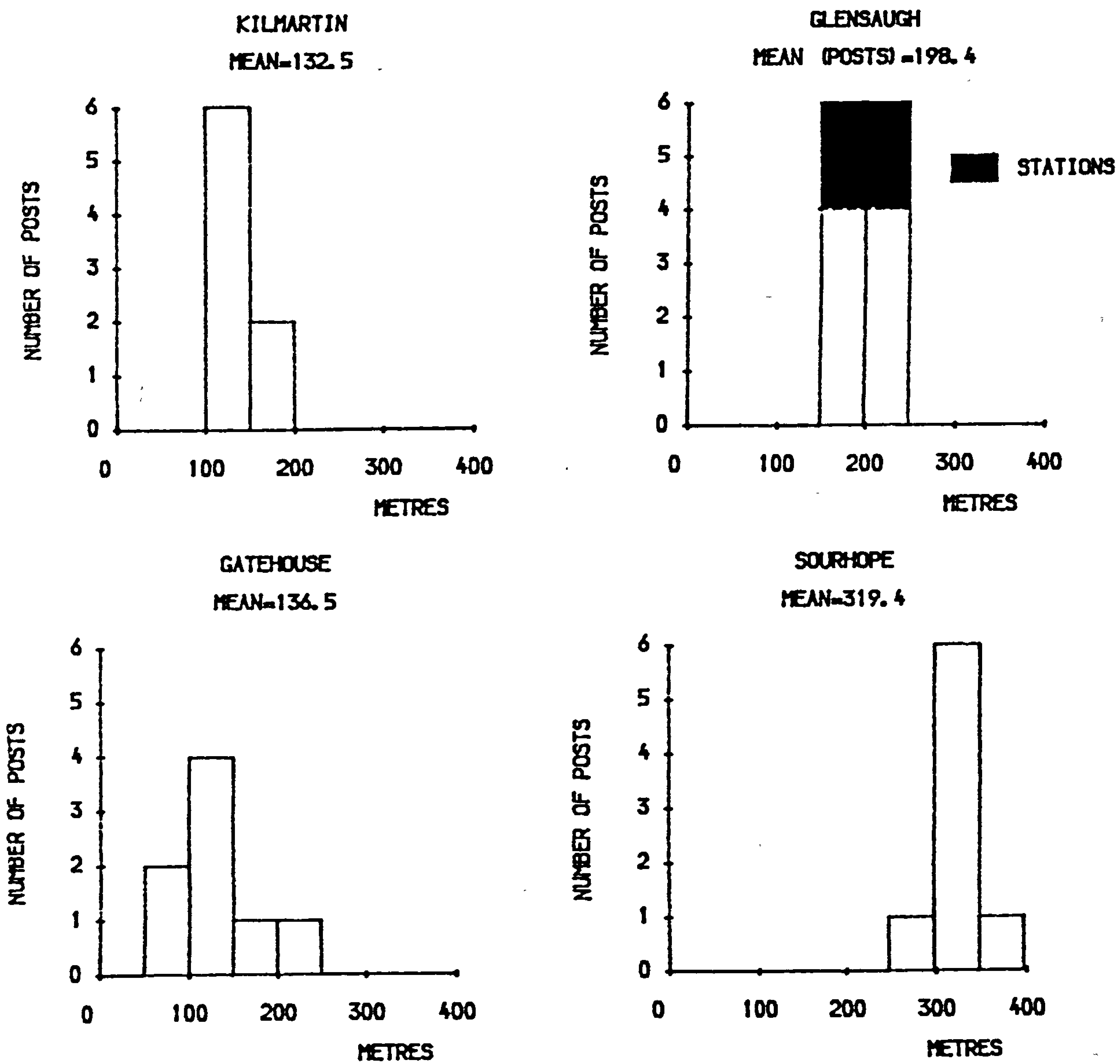
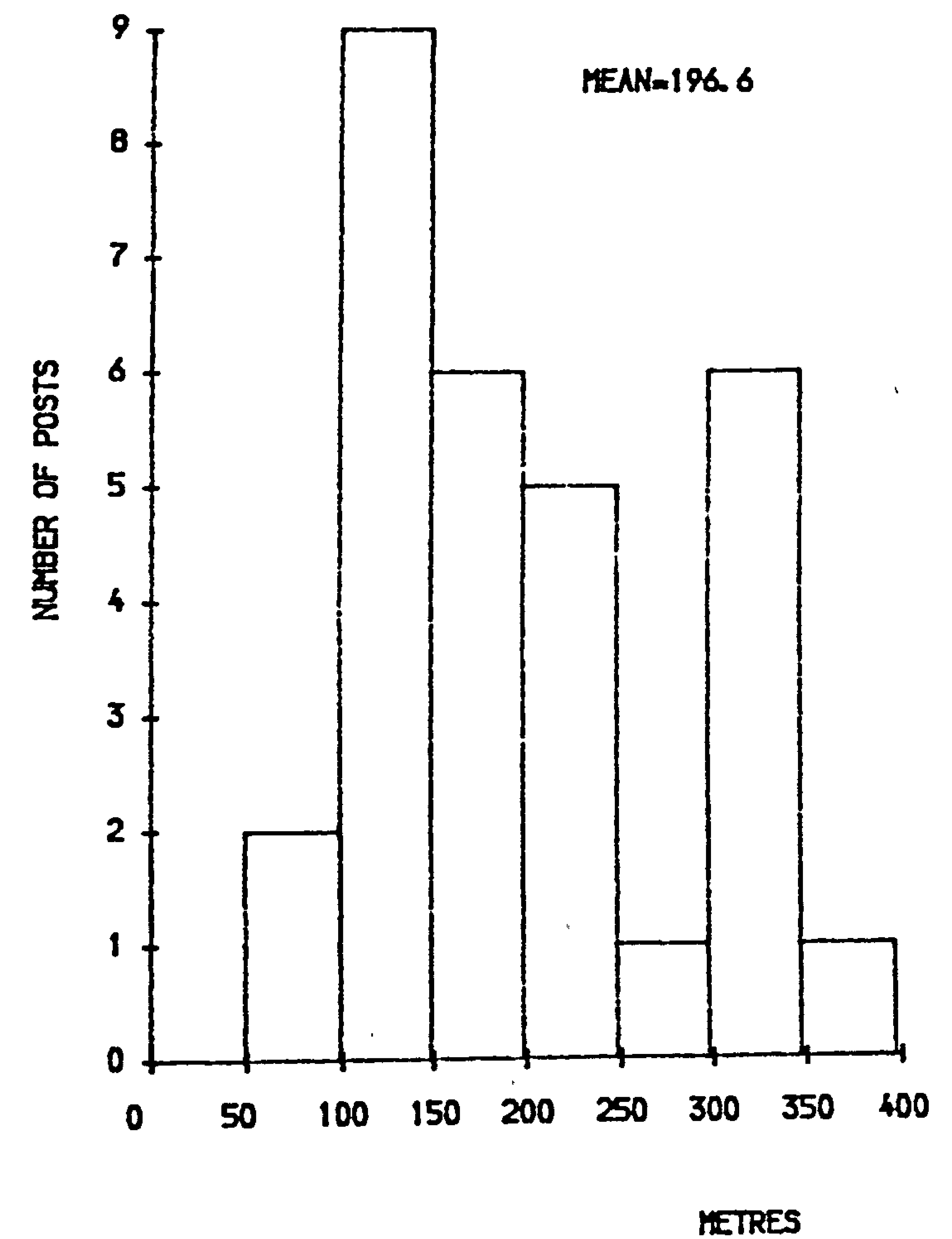


FIG. 5. 2. OVERALL ALTITUDINAL RANGE AND MEAN OF MONITORING POSTS



Because the fieldsites were selected to characterise the main bracken zones of each region, the altitudes of the sites reflect altitudinal bracken distribution in the four regions. Fig.5.1 shows the bracken zones in the east to be clearly higher than in the west. Limits of cultivation are also higher in the east. Reconnaisance surveys showed improved and semi-improved pasture to be the predominant landuse in the lower Cheviot valleys and lower slopes of the Northeast Cairngorm plateau. Equivalent altitiudes in the west are in the main bracken zone above the limits of cultivation. This suggests that the bracken zone is displaced uphill by higher limits of cultivation in the east, but this may not be the only reason for the dearth of bracken at lower altitudes, as discussed later. The absence of bracken at higher altitudes in the west indicates that the higher altitude of the bracken zone in the east may also be due to more favourable climatic conditions.

5.1.2 Aspect

Aspect of the posts and thermograph stations at each site and overall aspect in 1986 are summarised in Figs. 5.3 and 5.4 respectively. Aspect differed slightly in 1985 when Old Gatehouse One had a southeasterly aspect and Old Glensaugh One a southerly aspect. The uneven distribution of aspect presents a problem if this variable is to be used in statistical analysis. Atkinson (1986) divided the compass into ten divisions and scored each according to proximity to the south (which had the maximum score). The much lower sample number and uneven distribution precludes the use of this method. Instead, all southern aspects (i.e. south, southeast and southwest) were scored one and all others zero, resulting in two classes of comparable size.

Fig 5.4 shows that southern aspects predominate and there are no posts of northeasterly aspect. The two bracken free posts have westerly aspects. The predominance of southern aspects reflects bracken distribution on both

FIG 5.3. ASPECT DISTRIBUTION OF POSTS AND STATIONS (1986)

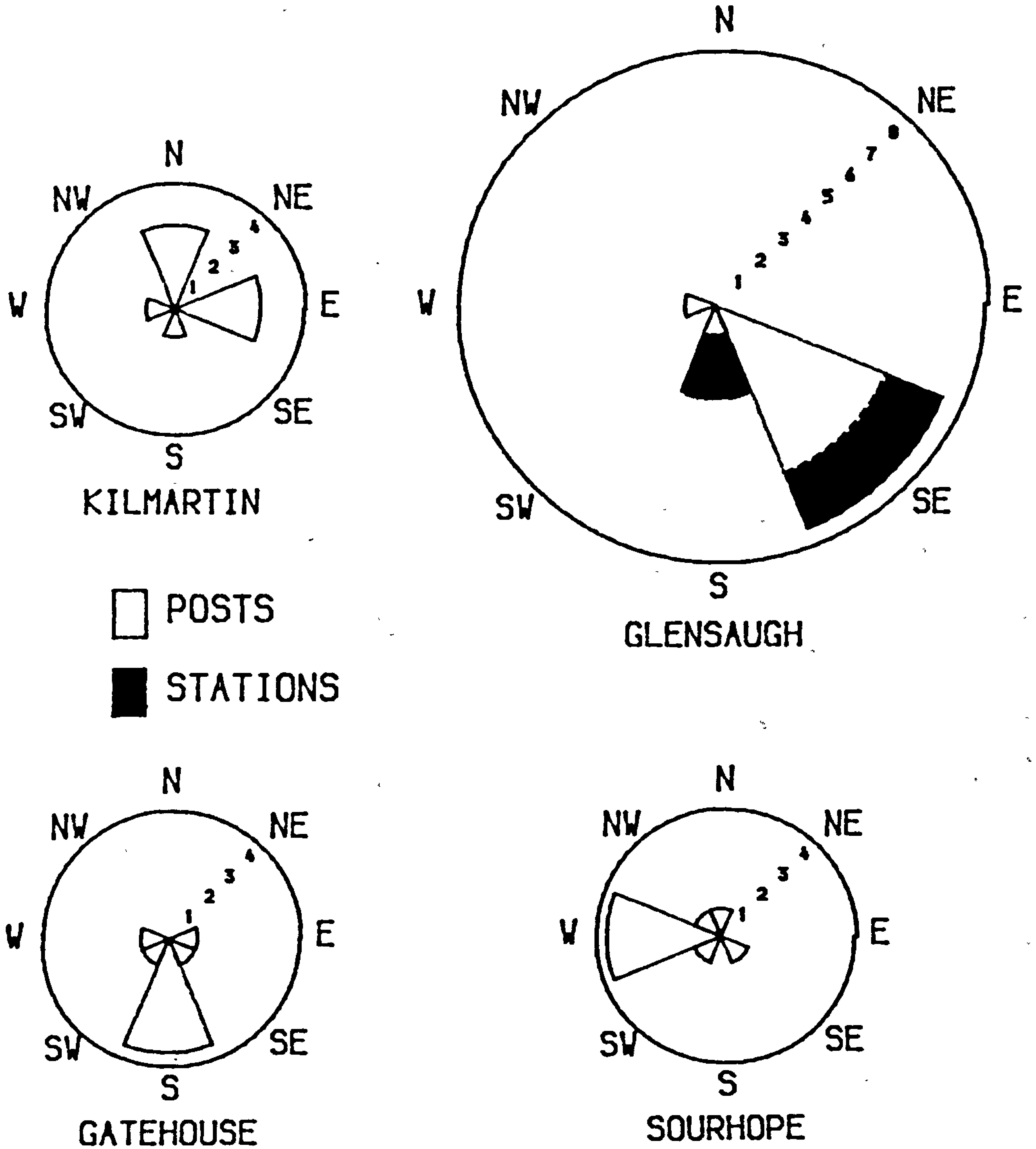
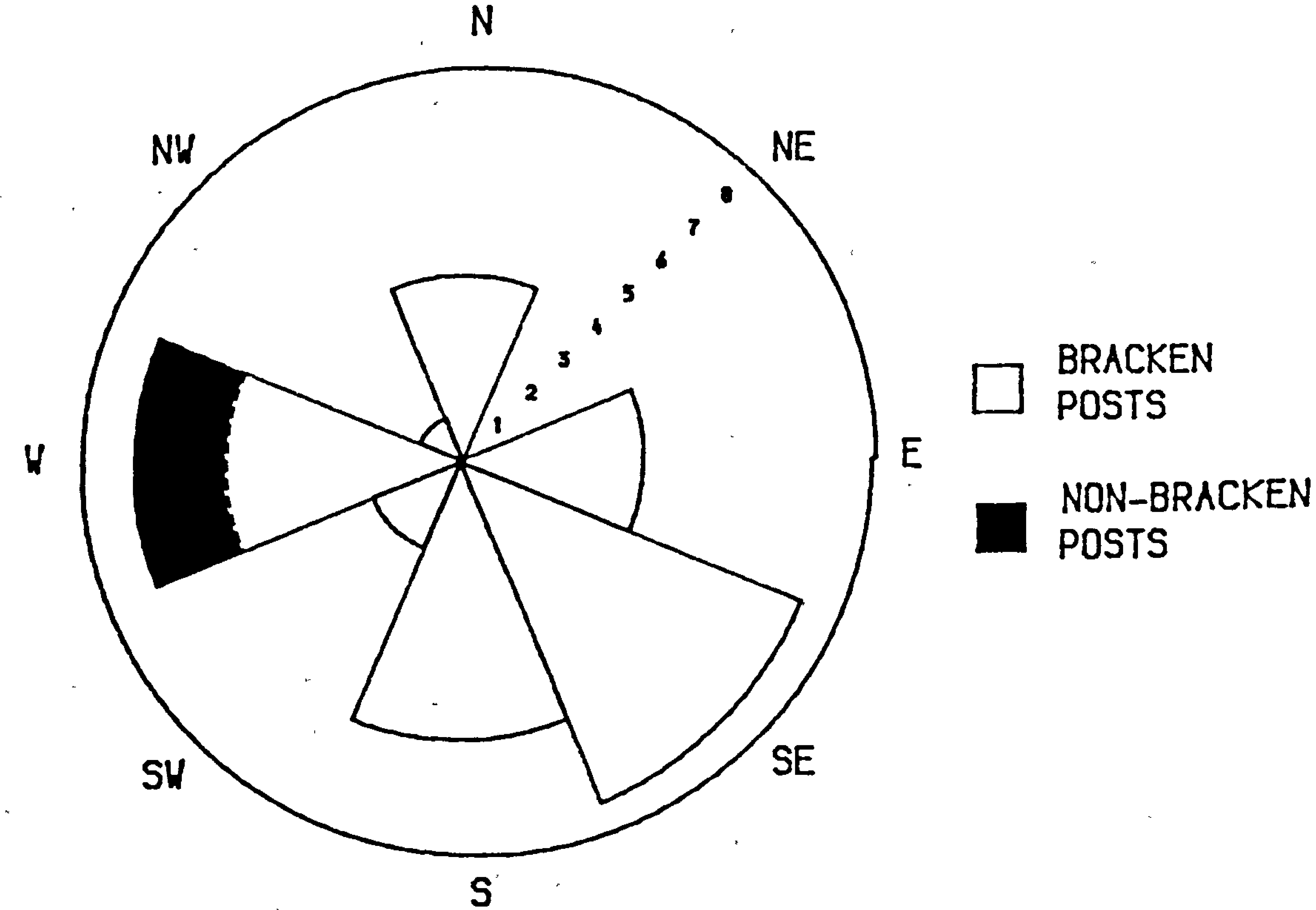


FIG. 5. 4. OVERALL ASPECT DISTRIBUTION OF POSTS



a regional and local scale. With the criteria that the sites should be located within the main bracken zones within each region, it is inevitable that the southwest and northeast study areas are dominated by slopes of a southern aspect since Hendry's bracken distribution map (see Fig.1.1) clearly shows bracken to be concentrated along the southern edges of the Southern Uplands and Highlands. The Sourhope area, being in the heart of the Cheviots, is not dominated by any one aspect. The Southern slopes of these hills, which may well have a concentration of bracken, are in England and are therefore precluded from the study. The marked preference of bracken for a southern aspect is not apparent in Argyll where the topography is dominated by west and east facing slopes.

On a local scale, reconnaisance surveys in the vicinities of Glensaugh and Gatehouse showed the southern slopes to have the most extensive bracken cover in both areas. (This is particularly obvious at Glensaugh where the northwest and west facing _Calluna_ slopes to the south of Slack Burn are a marked contrast to the opposite bracken covered southeast facing slopes). Although the topography in the vicinities of both sites does include slopes of non-southerly aspect, it is inevitable that the two sites were mainly located on slopes of southern aspect, for it is here that the stands are most extensive. Furthermore, the scale of the topography at Gatehouse and Glensaugh meant that the sites could only be practicably located on one overall hillside and therefore, despite efforts to vary aspect within each site by utilising local topography, the dominant aspect of the main slope was invariably over represented.

At Kilmartin the complex local topography allowed a greater range of aspect to be utilised. The north-south grain of the landforms masks any tendancy for concentration of bracken on southern slopes. Field observations suggest that the bracken is more extensive and vigorous on the sheltered east facing slopes where it attains higher altitudes. This effect is noticable on a very small scale on the north-south orientated ridges that characterise the site.

5.1.3 Slope

The range and mean slope of the posts and thermograph stations at each site in 1986 are shown in Fig. 5.5. and overall slope in Fig. 5.6. The site mean at Glensaugh does not include the thermograph stations and site means at Gatehouse and Glensaugh that do not include the bracken free posts are shown in brackets. In 1985, only Old Gatehouse One was in a different slope class with a slope of 35^{o}, (being located on the steep sides of the gorge). The post data did not need sorting and were directly used in the analysis.

The wide range of slope at Glensaugh reflects the two predominant features of the site, namely the valley and the steep valley slopes. With only one post located on the valley floor (where the bracken is sparse) the site has the highest slope mean of 21.3^{o}. Six posts at Glensaugh had a slope of over 14^{o} and five had a slope of over 20^{o}. Sourhope also has a relatively high mean slope (17.6^{o}) with six posts with slopes of over 14^{o}, but only one over 20^{o}. The relatively wide range of slopes at Kilmartin reflects the complex topography of the site, although the range does not include the steepest slopes of the site which tend to be <u>Calluna</u> covered, the low site mean reflecting bracken's preference for the sheltered hollows. The narrow range of slope at Gatehouse reflects the fairly constant slope of the hillside and the absence of bracken on the flatter flushed areas. Although the topography is more complex above the head dyke, the bracken avoids the steepest slopes and also the flatter bog and wet heath areas.

The similar relatively low mean slope for Kilmartin and Gatehouse not only reflects the fact that bracken avoids the steepest (and usually most exposed) slopes at these sites, but also the fact that only the lowest and therefore the flattest slopes are cultivated in the west.

FIG. 5.5. RANGE AND MEAN OF SLOPE AT POSTS AND STATIONS

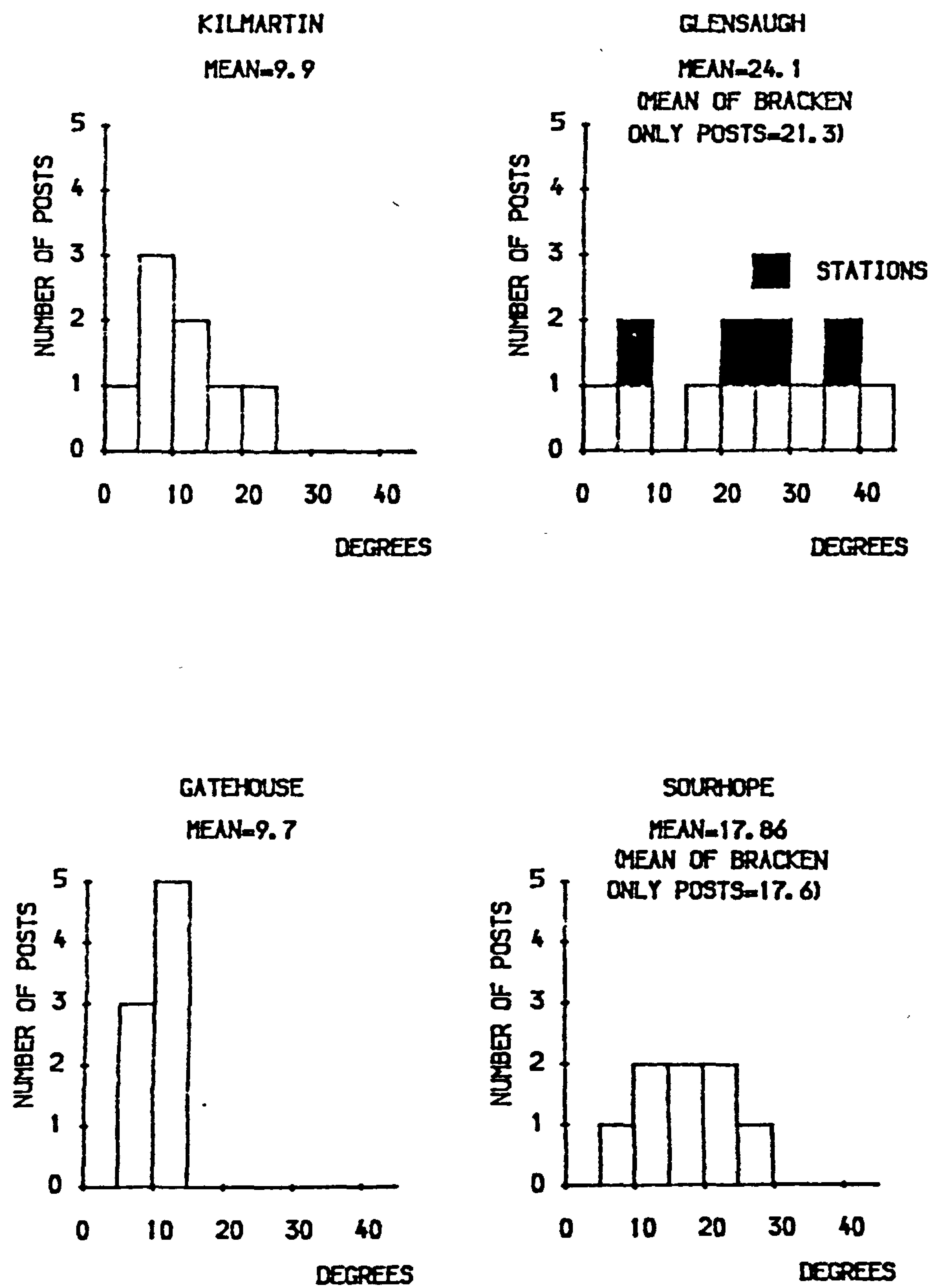
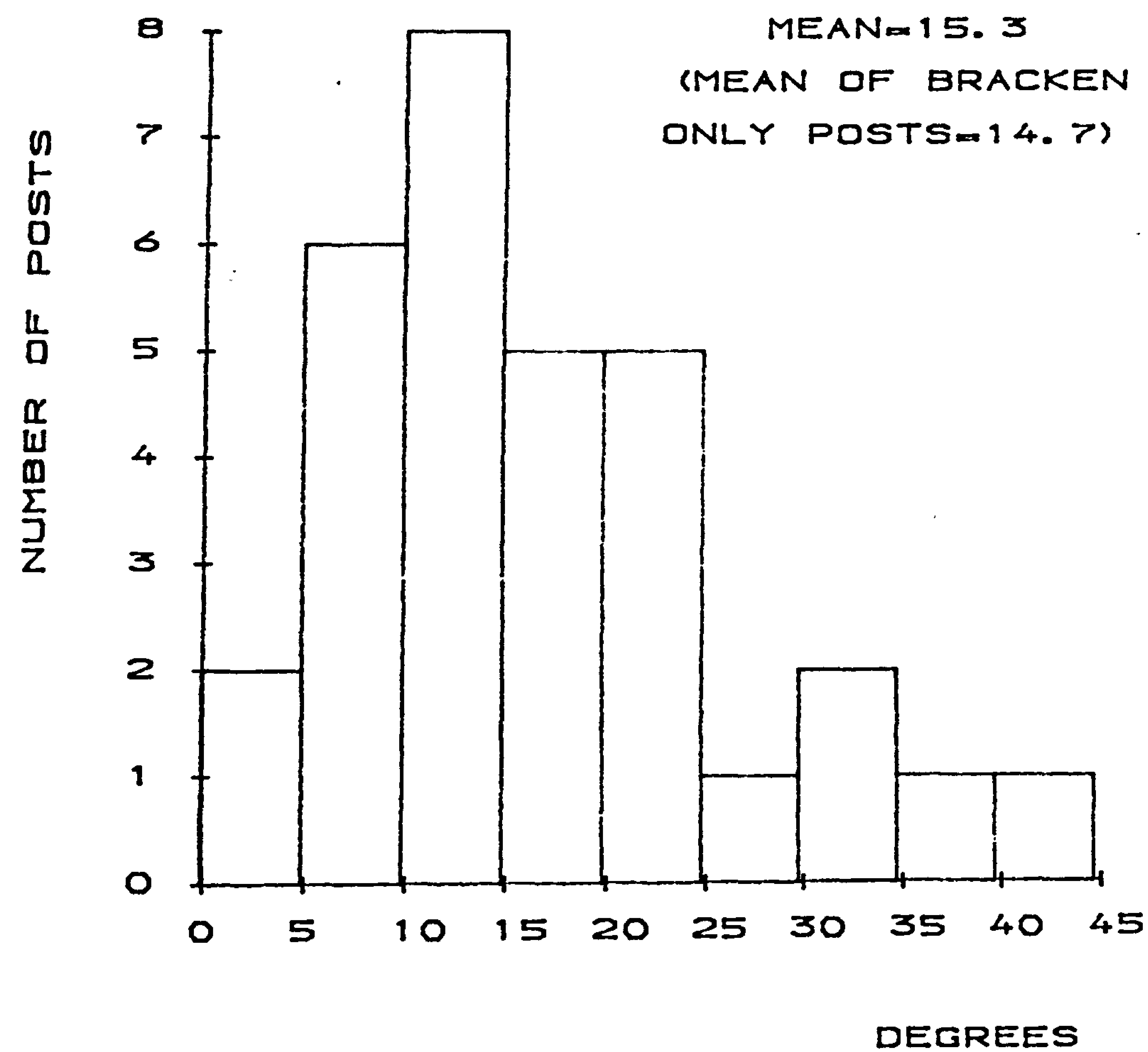


FIG. 5.6. OVERALL RANGE AND MEAN OF SLOPE AT POSTS



In contrast, the main bracken zone in the east is limited to the steepest slopes between the improved pasture on the lower slopes and the plateau above. Thus the limits of cultivation partly determine overall mean slope of the bracken zones as well as mean altitude. The overall mean slope of 14.7^{o} is lower than the mean slope obtained for bracken slopes by Thompson et.al (1986) in Wales (19^{o}) where average limits of cultivation are higher than in the west of Scotland.

5.2 Climatic factors

5.2.1

The temperature data had to be sorted before it could used in subsequent analysis in order to overcome the problem of having only a three weekly reading interval at Gatehouse in 1985. The highest maximum and lowest minimum readings in every three corresponding weeks at the other three sites were used. Readings at Kilmartin and Sourhope in 1986 were taken every three weeks and therefore only the Glensaugh data had to be sorted in this year. Missing data were extrapolated by comparison with adjacent posts and from trends observed in the data. Means of maximum and minimum temperature at each post were derived for use in the analysis for the following periods:

1. May 1985
2. May to mid June 1985
3. May to mid August 1985
4. Mid August to the beginning of November 1985
5. Beginning of November 1985 to the beginning of April 1986
6. April to the beginning of June 1986
7. April to the beginning of July 1986
8. April to the beginning of August 1986

Readings were also taken until the end of October 1986, but are not used in the subsequent analysis because autumn and winter temperatures should, logically, affect bracken vigour in the following season. Thus, Periods Four and Five in 1985 are used in the analysis of bracken vigour in 1986 and further reference to 1986 data includes these two periods. Periods One to Three do not coincide exactly with Periods Six to Eight because recording did not commence until May in 1985 and April 1986 is included in the 1986 growing season (i.e. Periods Six to Eight). Also, the dates of the periods are partly determined by the three weekly data intervals which were not the same in the two years.

The data were broken down into separate periods because it was felt that an overall annual mean would be too coarse a measure in view of the different climatic types represented by the four sites. It also allows investigation into whether temperature is only a limiting factor at certain periods of the year. Studies on the response of grass to temperature show that once a critical temperature is reached in the growing season, other factors become more limiting (e.g Alberda 1965; Grant 1968). The technique of dividing up the growing season into different periods was also used in the study by Alcock et.al (1967) in which the effect of temperature on pasture growth was studied, although these periods were not cumulative as used in the growing seasons in the present study. The use of cumulative periods means that it is not possible to obtain a mean temperature for just the middle or late season. However, one mean can be found for the whole period during which temperature is a limiting factor. Autumn and winter periods were included in the analysis because frosting of the underground parts may affect bracken vigour in the following season, as may the period of time available at the end of the growing season for translocation of material down to the rhizome before frond dieback (which may be determined by temperature).

The maximum and minimum temperatures of the sites, obtained by averaging the post data at each site, are shown in Table 5.1 and Figs. 5.7-5.10. (Maximum ground temperature at Sourhope is unavailable, as discussed in Chapter Four). The following salient points can be discerned from the data:

1. Sourhope had the warmest air minima of the four sites in both years, especially in the latter part of the growing seasons and in autumn.
2. Kilmartin had the coldest ground minima of the four sites in the first growing season and also in the air in the middle and late periods of the same season.
3. Gatehouse had the coldest ground minima of the four sites in the early growing season of 1986 and also in winter (Period Five).
4. Glensaugh had the coldest winter air minima of the four sites.
5. Glensaugh and Sourhope had the highest ground minima of the four sites in the first growing season.
6. Sourhope had the coldest air maxima of the four sites in the first growing season and the second lowest from then on.
7. Kilmartin had the warmest air maxima of the four sites in the first two periods of 1985 and the second highest in the third period, but had the lowest from then on.
8. Glensaugh had the warmest maxima of the four sites in winter and in the second growing season.

Minimum temperatures at sea level become colder from west to east across Scotland, although in winter this is modified by a latitudinal effect. If the lapse rate of $0.64^{o}C/100$ metres is applied, the ascending rank order of the minima of the sites should be Sourhope, Glensaugh, Gatehouse and Kilmartin (at sea level Glensaugh is the coldest). This is clearly not the case here, with generally low minima in the west and higher minima in the east, although Glensaugh did have the coldest air minima in winter. Furthermore, in 1985 (when weekly records were kept at all but Gatehouse) Sourhope and Glensaugh had

Table 5.1 Mean minima and maxima at sites

	Period 1	2	3	4	5	6	7	8
Mean minimum air temperatures								
Kilmartin	1.06	0.08	0.18	-0.76	-4.68	-0.60	-0.23	0.30
Gatehouse	1.19	0.56	1.86	0.18	-5.67	-1.14	-0.26	0.31
Glensaugh	0.72	0.60	1.50	-0.47	-6.70	-0.58	0.28	0.56
Sourhope	1.66	1.79	2.52	1.86	-4.68	0.73	1.30	1.76
Mean minimum ground temperatures								
Kilmartin	-2.50	-2.39	-1.67	-0.80	-8.93	-2.26	-1.93	0.91
Gatehouse	-0.66	-1.52	0.96	0.88	-9.81	-3.62	-0.26	0.31
Glensaugh	-0.09	-0.52	1.51	0.11	-6.12	-1.89	-0.89	-0.26
Sourhope	-1.81	-1.40	0.84	1.65	-6.65	-0.87	-0.16	0.73
Mean maximum air temperatures								
Kilmartin	22.22	23.00	23.92	16.79	9.11	16.07	19.41	20.31
Gatehouse	21.92	22.57	24.05	20.39	10.26	19.62	22.20	22.86
Glensaugh	20.72	20.62	22.78	21.50	10.67	20.17	22.42	23.53
Sourhope	17.12	18.94	21.05	18.47	9.38	17.60	20.11	21.11
Mean maximum ground temperatures								
Kilmartin	30.37	31.12	30.27	16.42	11.84	24.26	27.23	26.91
Gatehouse	31.41	33.48	32.22	22.64	13.95	25.08	28.19	28.85
Glensaugh	27.72	27.52	28.56	22.70	12.53	26.67	28.47	29.55
Sourhope	---- No data available ----							

1985	1986
Period 1 - May	Period 6 - April-beginning June
Period 2 - May-mid June	Period 7 - April-beginning July
Period 3 - May-mid August	Period 8 - April-begining August
Period 4 - mid August-beginning November	

FIG 5.7. MEAN MINIMUM AIR TEMPERATURES PERIODS 1-8

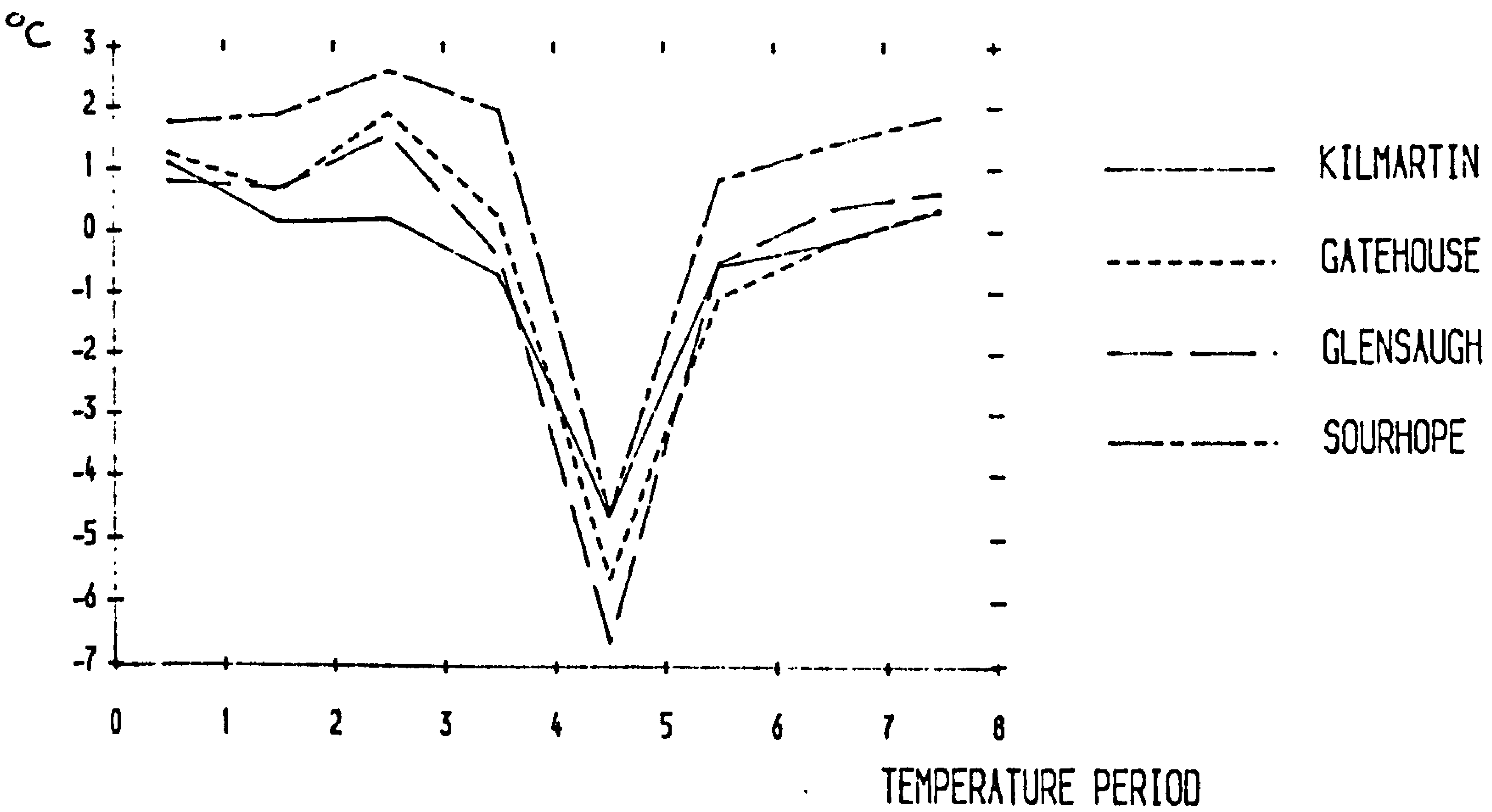


FIG 5.8. MEAN MINIMUM GROUND TEMPERATURES PERIODS 1-8

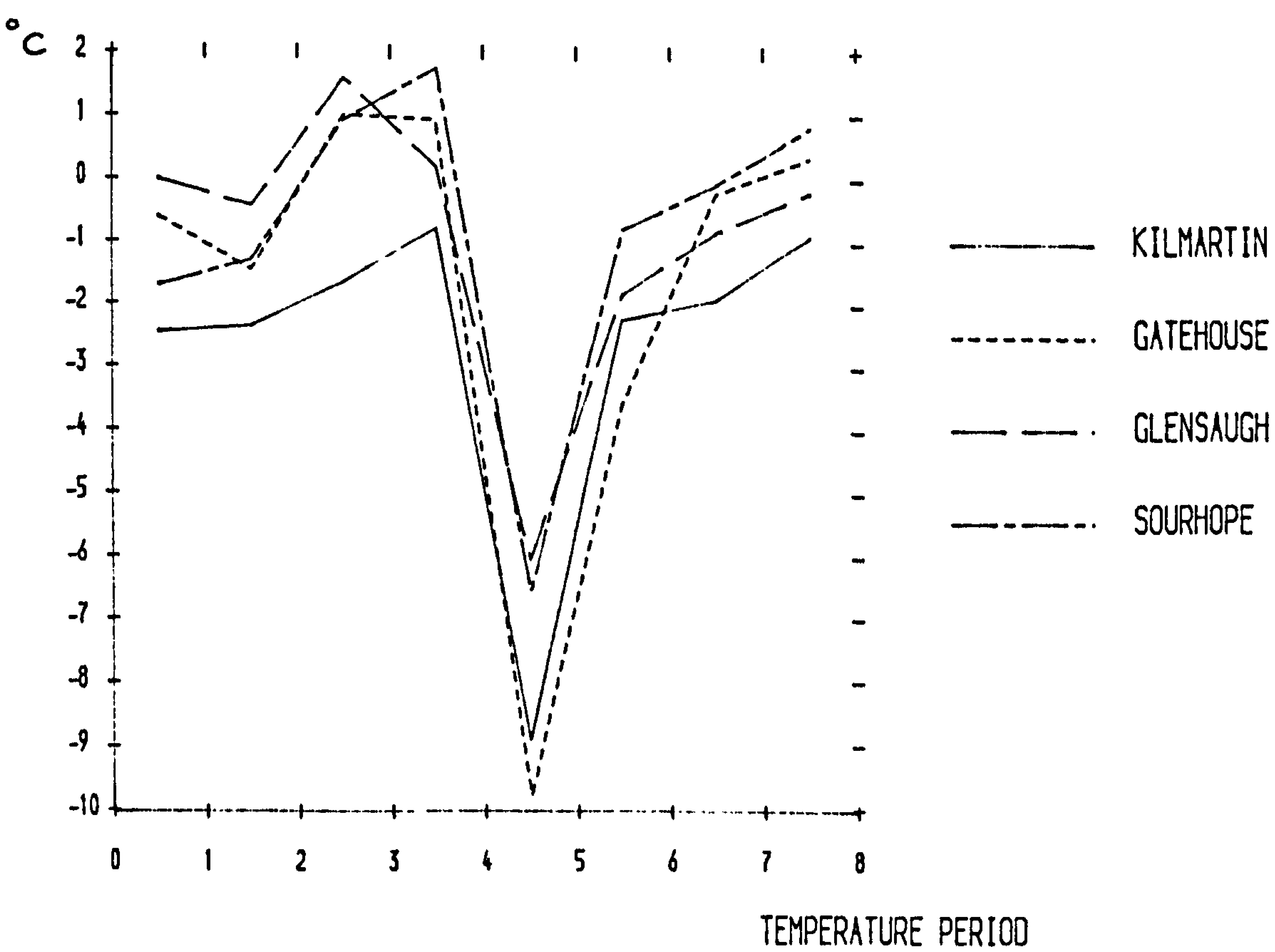


FIG 5.9. MEAN MAXIMUM AIR TEMPERATURES PERIODS 1-8

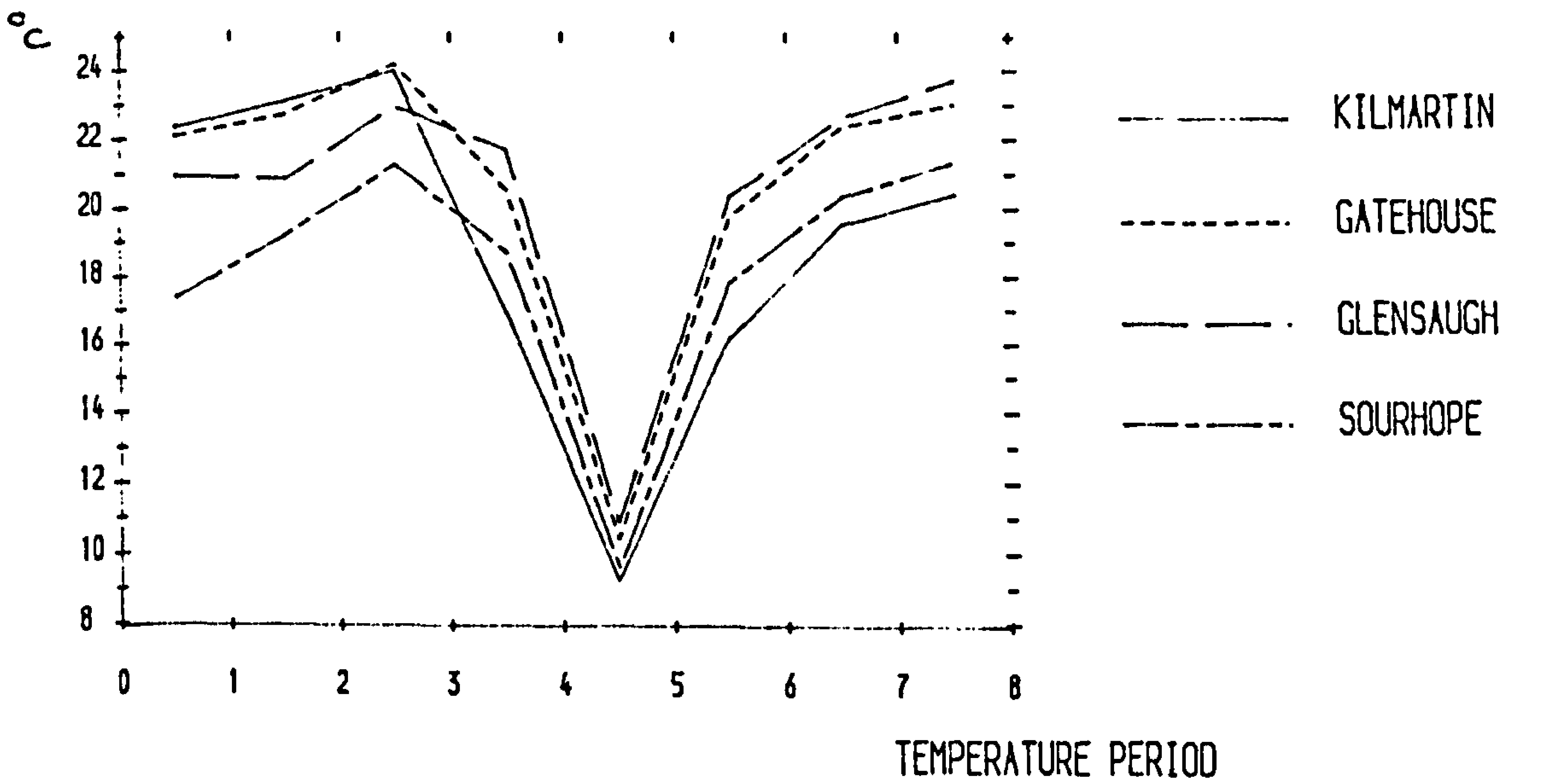
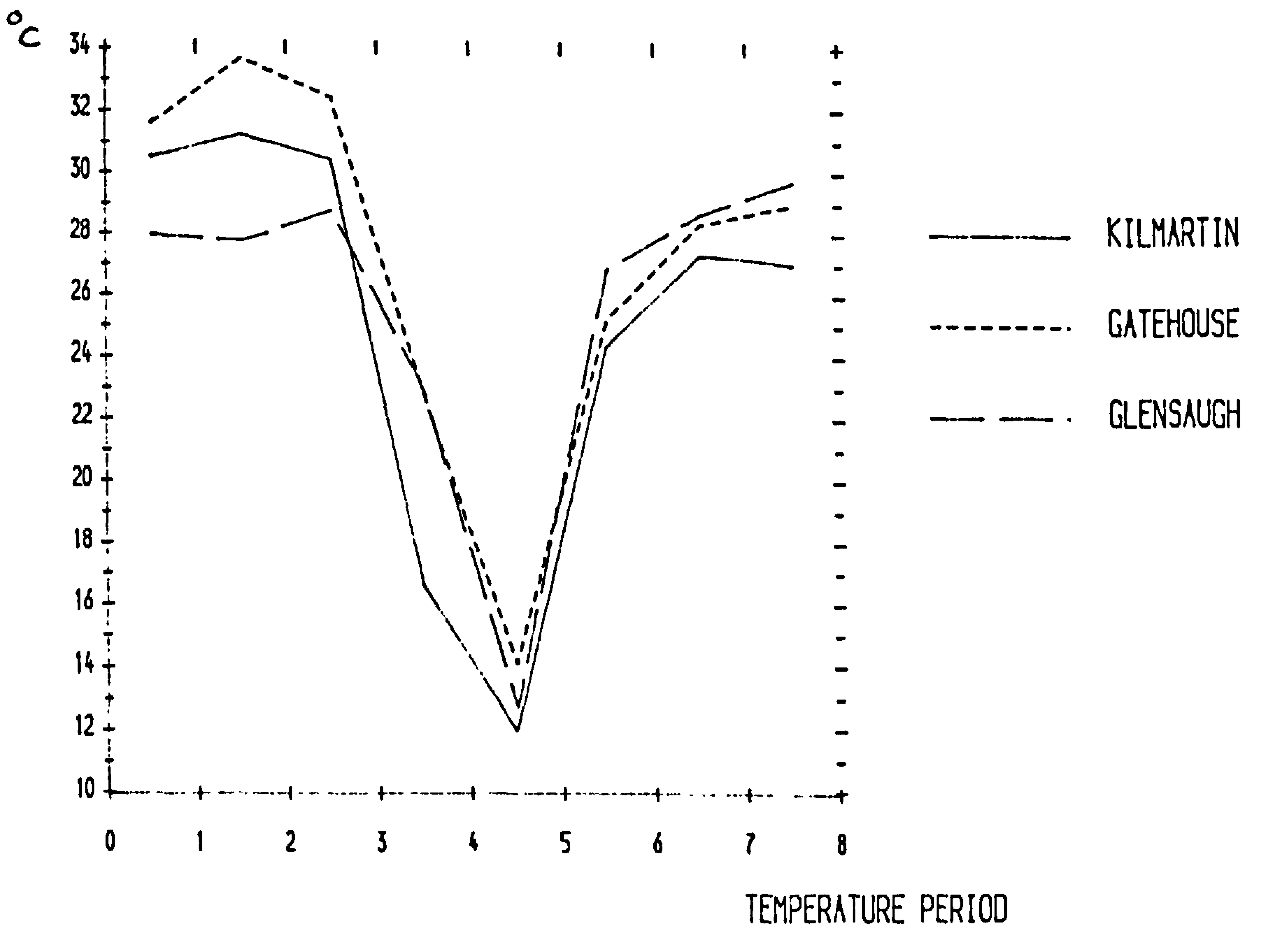


FIG 5.10. MEAN MAXIMUM GROUND TEMPERATURES PERIODS 1-8



longer frost free periods (four and three and threequarter months respectively) than Kilmartin and Gatehouse (three and a quarter months for both). Frosts were both later in the spring and earlier in the autumn at the west coast sites.

This apparent anomaly can be explained by altitudinal temperature inversion which has overridden the expected east-west frost differences. This is demonstrated by the significant positive correlations obtained between altitude and minima at the posts, shown in Table 5.2 below.

Table 5.2 Correlation between minimum temperature and altitude

Period	1	2	3	4	5	6	7	8
Air	0.26	0.51*	0.53*	0.72**	0.22	0.66**	0.67**	0.66**
Ground	0.04	0.24	0.32	0.74**	0.61**	0.62**	0.69**	0.71**
Without Sourhope	0.61*	0.55**	0.41					

*p<0.05 **p<0.01

(In many cases certain posts have a strong influence on the correlations that cannot be removed by data transformation. When this occurs, the post is removed from the correlation. If the resulting correlation is similar and has the same significance level, the original result is shown. If the correlation becomes more significant, the original result is again shown, unless otherwise stated. If the correlation becomes less significant this result is shown. Unless stated otherwise, the bracken free posts are excluded from these analyses. Thus the predictors in the analyses in this chapter are standardised with those in the analyses of bracken vigour in Chapters Eight and Nine.

Old Glensaugh Eight is not included in Periods One-Three and Kilmartin One is not included in Periods Six-Eight, as discussed in Chapter Four, and thus twenty nine predictors are used in Periods One-Three and Six-Eight and thirty in Periods Four and Five).

The use of Period-means results in blurring of the inversion effect within the sites when minima are plotted against altitude, although the effect is apparent between sites, as seen in Figs. 5.11 and 5.12 which show ground minima plotted against altitude in Period Three (May - August 1985) and Period Eight (April - July 1986) respectively. Between site inversion breaks down at Sourhope in Period Three and thus the correlation is only significant when the site is omitted from the analysis. Although the overall correlation for Period Eight is positive, a negative correlation clearly exists within Glensaugh.

The correlation of air minima in Period Five (winter) is not significant because Glensaugh, which had snow cover for three months, recorded the lowest temperatures, demonstrating that topography did not modify the regional climate. It also demonstrates that contrary to predicted temperatures (in which minima at Sourhope are colder than at Glensaugh because of the site's higher altitude), the winter is more extreme at Glensaugh. Snow lay continuously during part of January and February at Sourhope, but from the end of December to the end of February at Glensaugh. The anomally of the relatively high ground minima at Glensaugh in Period Five can be explained by the effect of snow cover on the thermometers, as discussed below.

The temperature inversion effect is not only due to the differing altitudes of the sites, but also to the complex topography at the west coast sites where frost hollows are common. This was particularly noticable after the late spring frosts in 1985 at Kilmartin where the limit of frost within the small hollows and valleys was clearly marked by the limit of frosted bracken on the

FIG. 5. 11 PLOT OF GROUND MINIMUM TEMPERATURE AGAINST ALTITUDE IN PERIOD THREE

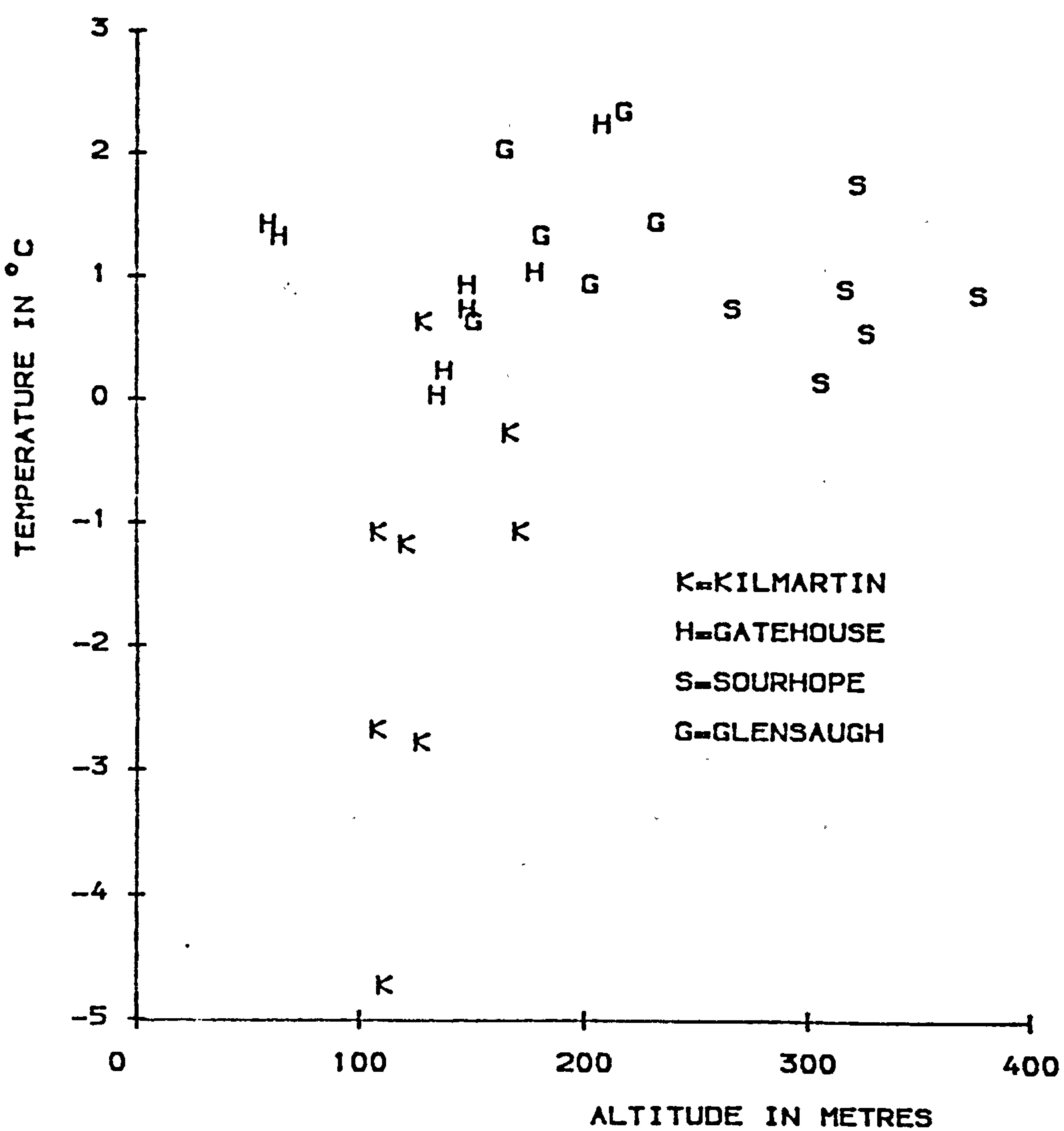
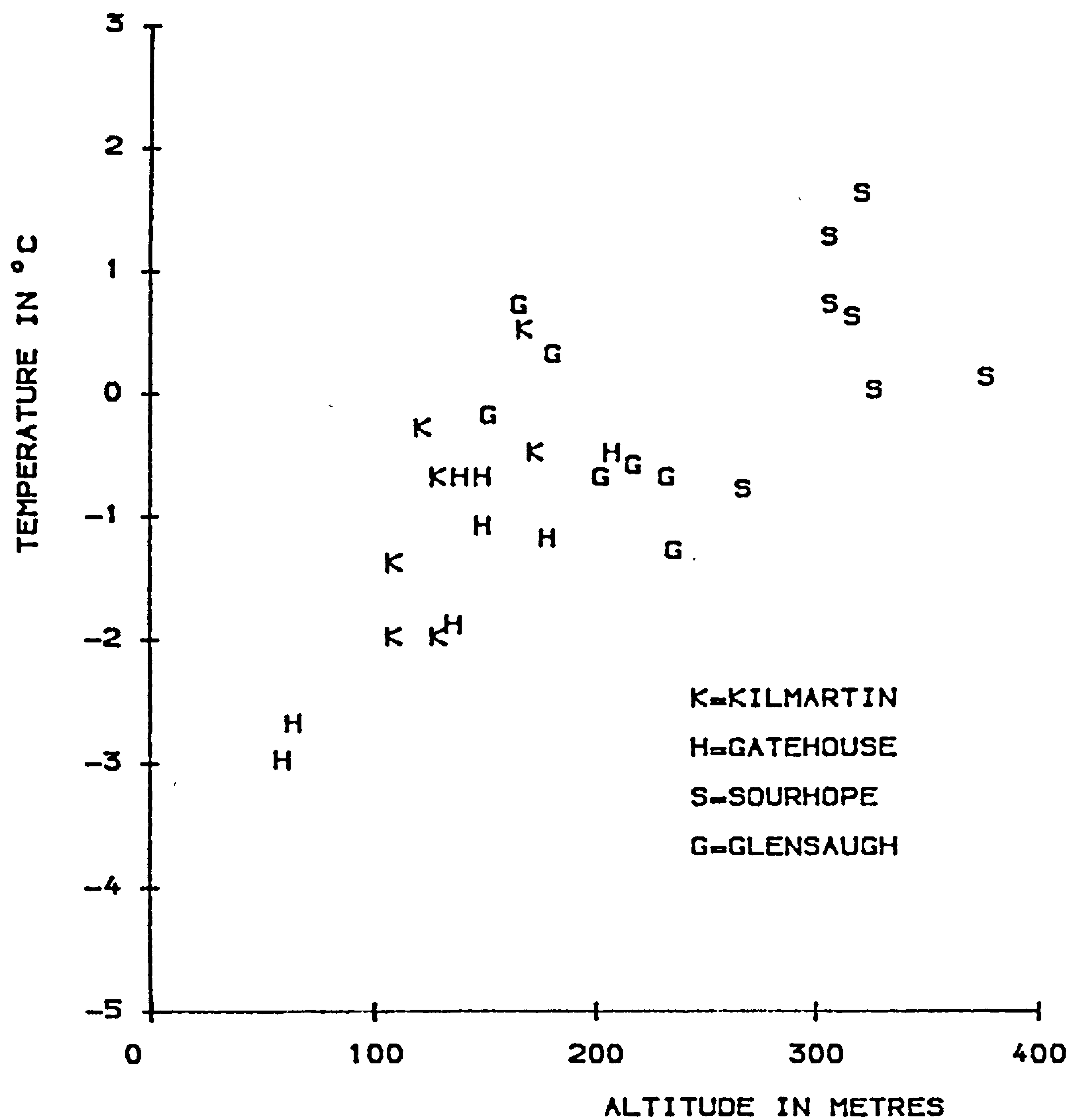


FIG. 5. 12 PLOT OF GROUND MINIMUM TEMPERATURE AGAINST ALTITUDE IN PERIOD EIGHT



surrounding slopes. During this frost air temperatures at the coldest post at Kilmartin, Post Eight, fell to -3.5 ^{o}C, while Kilmartin Five (on the summit of Bar a Chuirn) registered 5.0 ^{o}C. At Gatehouse the most frosted posts were the lowest posts, One and Two, which were located at the edge of the gorge. Differences between minima at the lowest and highest posts are more marked at the west coast sites.

The maximum temperature data also contains unexpected results. After altitudee is taken into account, the theoretical rank order of maxima at the sites in January should be (in descending order) Kilmartin, Gatehouse, Glensaugh and then Sourhope and from May to August, Gatehouse, Sourhope, Kilmartin and then Glensaugh (at sea level this would be Sourhope, Gatehouse, Glensaugh and Kilmartin). However, in the first growing season the two west coast sites have the highest maxima and Sourhope is quite significantly the coldest. In autumn and the following growing season the expected order is followed except for Glensaugh, which has the highest maxima. In winter (Period Five) this order is maintained instead of the expected return to the longitudinal influence on temperature (in which the west is warmer than the east).

To explain the anomalies of the first growing season it is necessary to look at maximum temperature trends at nearby meteorological stations at Lochgilphead, Threave, Floors Castle and Craigmoston (for Kilmartin, Gatehouse, Sourhope and Glensaugh respectively; details of their alitude and distances from the sites are given in Appendix Two). These show that the west coast sites had noticeably warmer maxima in spring of 1985 than in 1986, whereas no such difference occurred in the east. The expected spring transition from longitudinal to latitudinal influence on temperature did not occur, resulting in damping of regional differences of maxima. This is also shown by comparison of the site maxima in which the west coast sites had markedly lower maxima in 1986 than in 1985, while the eastern sites had generally slightly higher maxima in 1986. This damping of expected regional differences can probably be explained by the extremely wet season in 1985.

Because of this damping of regional differences, altitude had the greatest influence on maxima in 1985. The rank order of site maxima and altitude are the same in Periods One-Three and furthermore, the differences in maxima between Sourhope and Glensaugh and the west coast sites are approximately proportional to differences in altitude. Correlations between maxima and altitude in these three periods confirm this effect, as shown in Table 5.3 below. During the other periods, aspect has more influence on maxima

Table 5.3 Correlation of maxima with altitude and aspect at the posts

Altitude

Period	1	2	3	4	5	6	7	8
Air	-0.88**	-0.81**	-0.75**	0.00	0.18	-0.07	-0.22	-0.17
Ground	-0.42	-0.48*	-0.45*	0.41	-0.07	0.24	0.06	0.14

Aspect

Period	1	2	3	4	5	6	7	8
Air	0.26	0.05	0.16	0.71**	0.44*	0.66**	0.60	0.31
Ground	-0.29	-0.23	-0.17	0.67**	0.37	0.46*	0.30	0.39

* $p<0.05$ ** $p<0.01$

To explain why Glensaugh departs from the expected order in both seasons it is necessary to look at the site in the context of the climate of the locality. This is done by comparing mean monthly temperatures at Station One with those at Craigmoston (at 95 metres) on the landward edge of the Howe of Mearns and at the research farms's meteorological station (at 325 metres) at Redstone Hill on the lower plateau above the site. Fig. 5.13 shows that predicted temperatures for Station One in spring and summer, obtained by extrapolations from Craigmoston using a lapse rate of 0.64^{o}C / 100 metres, were lower than actual temperatures, except in May 1986. However, from the end of November to the middle of February predicted temperatures are higher than actual temperature. Although only two months data were availble for Redstone Hill, it is clear that maxima at Glensaugh are more akin to those of the agricultural plain, but the indications are that the reverse is true in winter. Fig. 5.14 shows mean weekly temperature at Station One and Redstone Hill in spring 1986, plus predicted temperatures for Station One. Predicted and actual temperatures are most comparable in early spring and at the beginning of June, again indicating low temperatures at the site over winter and that the differences between the site and the plateau temperatures start to be reduced by summer.

It would seem that Glensaugh experiences a warmer than expected local climate from early spring to autumn, but not in winter when the site is affected by the extreme conditions on the plateau above. Thus, the "rather severe winter" classification of the frost regime of the site in Chapter Three would seem to be appropriate, but "fairly warm" rather than "cool" would seem to be a better classification of the growing season temperature regime.

The cause of this warm local climate can be partly attributed to the predominance of southerly aspect at the site, to the steep slopes and narrow valley (which will create a "sun-trap") and to the shelter of the valley, as discussed in Section 5.2.2. In winter the effect of aspect is least effective and is not enough to override the extremely cold influence of the plateau. A rapid deterioration of climate towards the plateau even in spring and summer is demonstrated by the reduction in

FIG. 5. 13 COMPARISON OF ACTUAL AND PREDICTED MEAN WEEKLY AIR TEMPERATURE AT STATION 1, 1985 AND 1986

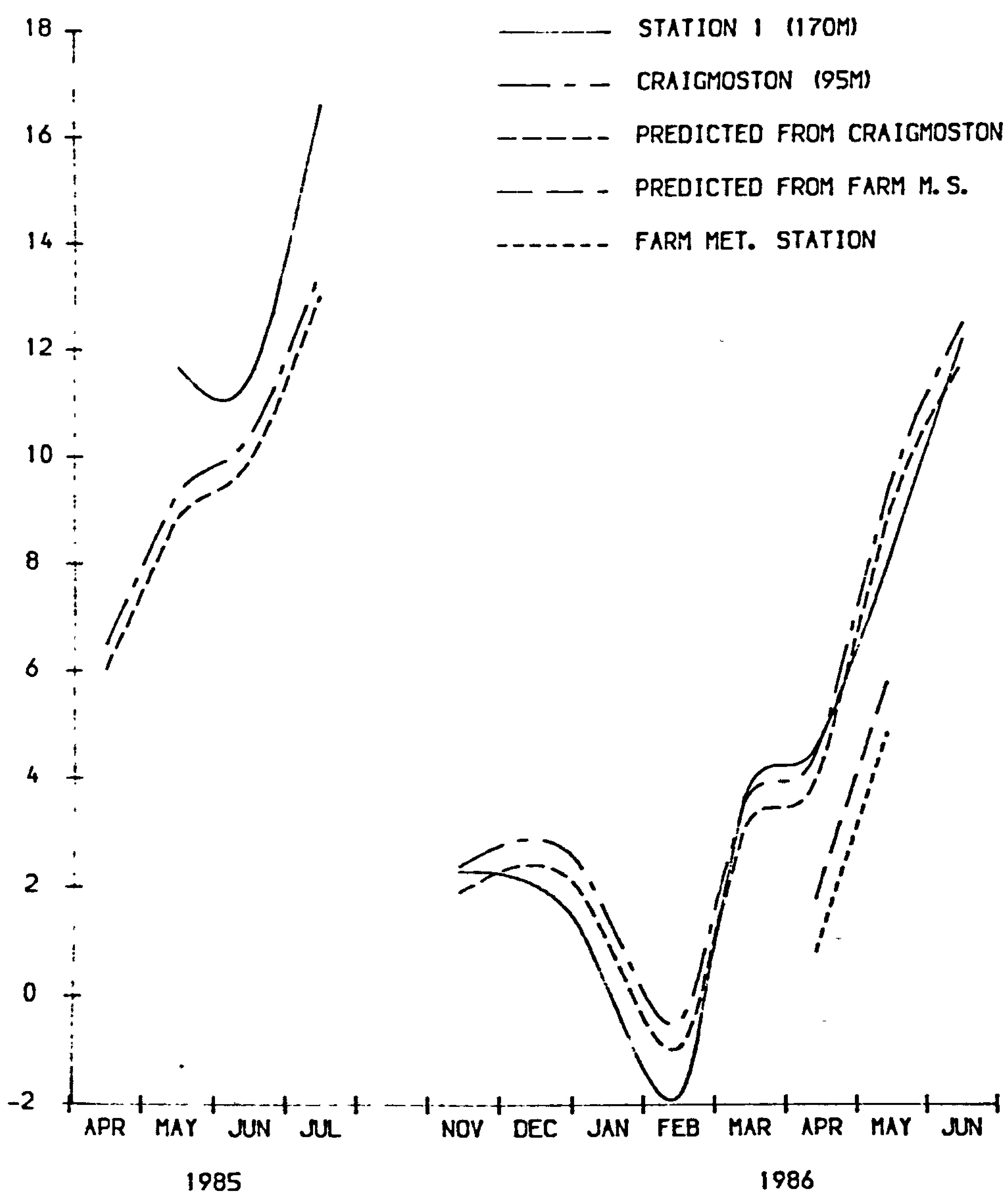
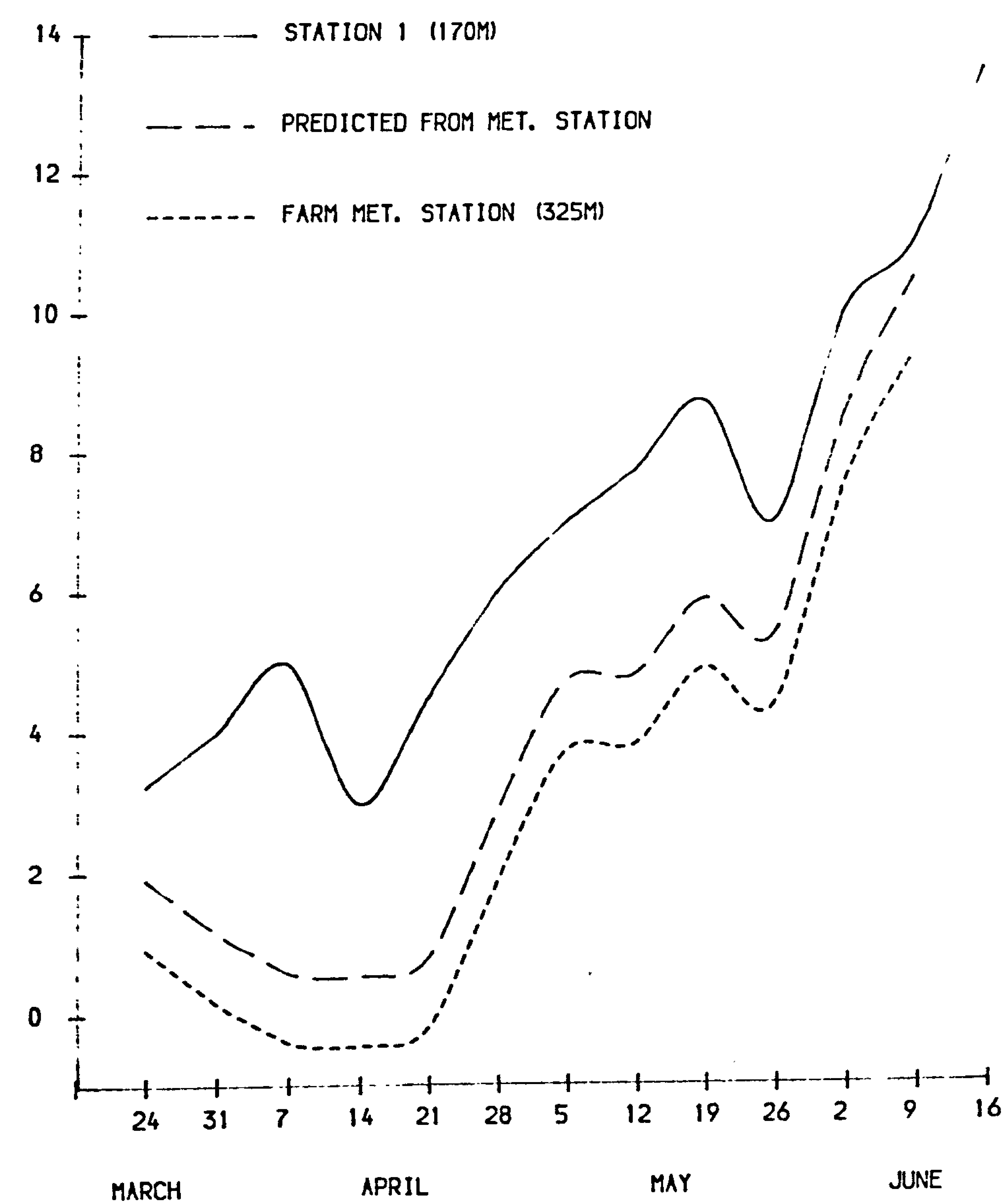


FIG. 5. 14 COMPARISON OF ACTUAL AND PREDICTED MEAN WEEKLY AIR TEMPERATURES AT STATION 1, SPRING 1986



minima with altitude at the site in Period Eight (the growing season of 1986) while a temperature inversion still occurred at Sourhope (see Fig.5.12). It is also demonstrated by the wide differences in predicted temperatures for Station One from Craigmoston and Redstone Hill.

It seems then that maxima in the growing season of 1986 followed expected trends except at Glensaugh due to its warm local climate. As seen from comparisons of mean temperature, unexpectedly high temperatures also occurred at Glensaugh in 1985, but the absence of the longitudinal shift in temperature in that year somewhat obscures this when comparing site maxima.

Explanation of the anomalously high maxima at Glensaugh and the low maxima at Kilmartin in winter is difficult. Clearly the eastern sites had colder mean temperatures than the west because of their longer snow cover. Examination of the raw data shows that maxima remained relatively high at Glensaugh until the end of November and became evident again at the beginning of March. The inclusion of November and March in the winter period has therefore transcended two distinct temperature regimes, resulting in unrealistic winter maxima. In addition, despite intermittent snow cover, relatively high maxima were recorded at Glensaugh during December, reflected in the frequent snowlie and melt during that month. After December, readings were rather infrequent and irregular until March and it would seem that they do not accurately reflect mean daily maxima at Glensaugh and a similar situation occurs at Kilmartin. Because of these inaccuracies, maxima in Period Five are not used in further analyses. This is probably of no great consequence since maxima in winter are unlikely to affect bracken vigour.

Examination of the effect of the substrate and canopy on temperatures is needed to determine whether microclimatic effects are overriding the mesoclimate. During the day the rank order of temperature in and above the ground for different substrates (in descending order) is dry bare ground, sod covered, litter covered and snow covered ground (Geiger 1950). (At night and in freezing conditions temperature in the earth under the surface cover of sod, litter or snow has the reverse order due to the insulatory effect of these layers). Maximum temperatures at the ground may therefore have been enhanced over plots with a lot of bare ground and lowered over plots dominated by bracken litter. However, Glensaugh Two (the bracken free post in mature Calluna) is the only post to have plots with much bare ground, which may explain why maxima at the post, which has a westerly aspect, were as high as those at the rest of the site which is predominantly of southerly aspect.

Snow cover affected minima and maxima in Period Five at Glensaugh, where snow lay intermittantly between the end of November to January and continuously from January until the end of February. Temperatures in the air over continuous snow cover are very much lower than in the snow, but during snow melt temperatures are higher in the adjacent air (Geiger 1950). The ground thermometers were buried in the snow for much of the period of snowlie and colder minima were therefore recorded in the air during this time. Because of the extreme cold during continuous snow cover, these air minima were also colder than ground minima in snowfree intervals. (Post Three on the valley floor recorded -21 ^{o}C in the air in February 1986). During snow melt (in particular during December and early January at Glensaugh), the air over the ground is very much warmer than in the snow and the air maxima were therefore higher than ground maxima during this time, but were not generally higher than ground maxima during snow free periods. Thus the mean air minima at Glensaugh during the winter were colder than the mean ground minima, but the mean air maxima were still colder than the mean ground maxima (see Figs. 5.15 and 5.16). The insulation of the thermometers from ground frost also explains why Glensaugh has the coldest air minima but the warmest ground minima in Period Five.

Ground maxima may have been affected by ground heating. In still daytime conditions, temperatures near the ground can be 2-3 ^{o}C warmer than at half a metre above ground, while the ground and air layer up to one centimetre above the ground can be 10-12 ^{o}C warmer than the air above (Geiger op.cit.). Examination of the raw data shows up to a 12 ^{o}C difference between ground and air maxima in Periods One, Two, Six and Seven (that is, before the canopy closed in either year) and ground maxima are clearly higher than the expected maxima for the sites. This suggests that the thermometers may have become heated inspite of their protective mesh. However, air and ground maxima reflect the same trends when the two are compared, which would be unlikeky if heating had occurred. It is more likely that the ground thermometers, which lay flat on the ground, recorded temperatures in the very warm layer of air immediately above the ground.

The microclimate of a vegetation stand can be modified as the canopy closes. In an open canopied stand, the daytime temperature gradient is the same as that over open ground. In a closed canopy maximum temperature occurs just below the canopy as radiation is intercepted before it reaches the ground and minimum temperature occurs about two thirds of the way up the stand as cold air is prevented from sinking (Geiger op.cit.). Examination of the site and post means for all the periods in the growing seasons and autumn would suggest that closure of the bracken canopy did not significantly affect the microclimate of the stand. Air maxima and minima are generally colder and warmer respectively than at the ground, although the differences between air and ground maxima are substantially reduced in Period Four, indicating that shading by the canopy reduced the ground maxima. However, when the raw data were examined a different picture of temperature modification emerges.

Figs. 5.15 and 5.16 show the number of posts per week at which the gradients of minimum and maximum temperature between air and ground were reversed at Kilmartin and Glensaugh respectively. The effect of snow cover at Glensaugh is clearly demonstrated by the reversal of the gradients in winter, particularly maxima during times of intermittant snow melt during December and early January and minima during conditions of continuous snow cover from January until early March. The effect of canopy closure on temperatures is apparent in Period Four (August - November) and at the end of Period Three (May - August) and Eight (April - August) . In 1985 the minimum temperature gradients started to be significantly reversed in mid to the end of June at both sites, but not until the beginning to mid July in 1986. Reversal of maximum temperature gradient began in mid July at Kilmartin in 1985, but not until mid August at Glensaugh and the beginning of August at both sites in 1986.

The bracken canopy therefore only significantly affected the microclimate of the stands (to the extent of reversing temperature gradients) once it was nearly or fully developed in mid to late summer and in autumn. During this time reversal of temperature gradients did not occur at every post every week and therefore in the intervening weeks "normal" gradients were recorded. Temperatures during these "normal" weeks were usually more extreme than those recorded during gradient reversal and they therefore strongly influenced the post and site means for Period Four, explaining the apparent lack of evidence for temperature gradient reversal in this period. Although the site and post means in Period Four therefore still reflect the meso rather than the microclimate, they are unlikely to be an accurate reflection of mesoclimate because different posts recorded "normal" gradients in different weeks. Period Four was therefore omitted from

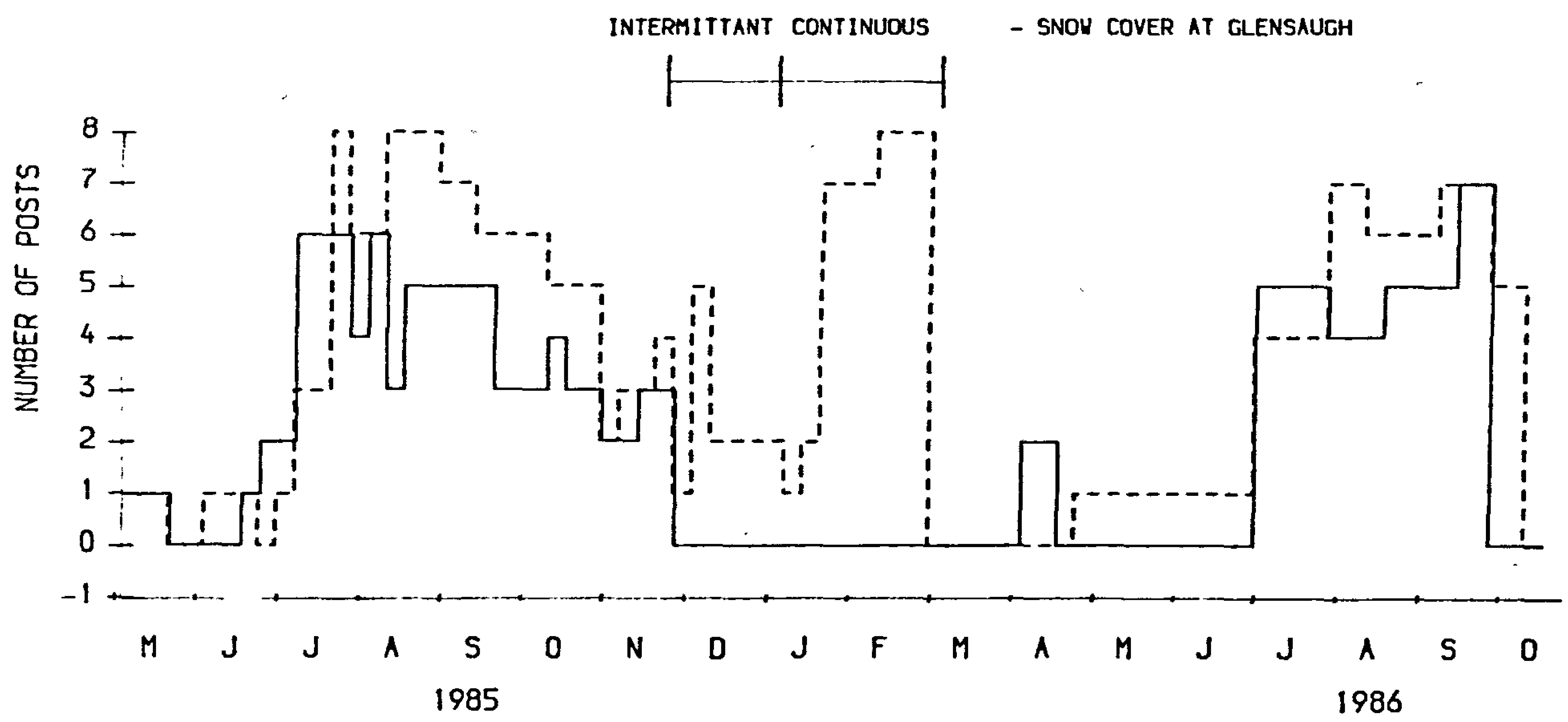


FIG. 5. 15. NUMBER OF POSTS AT WHICH MINIMUM AIR TEMPERATURE IS LOWER THAN MINIMUM GROUND TEMPERATURE, MAY 1985 TO OCTOBER 1986

- - - - - - - - GLENSAUGH

———————— KILMARTIN

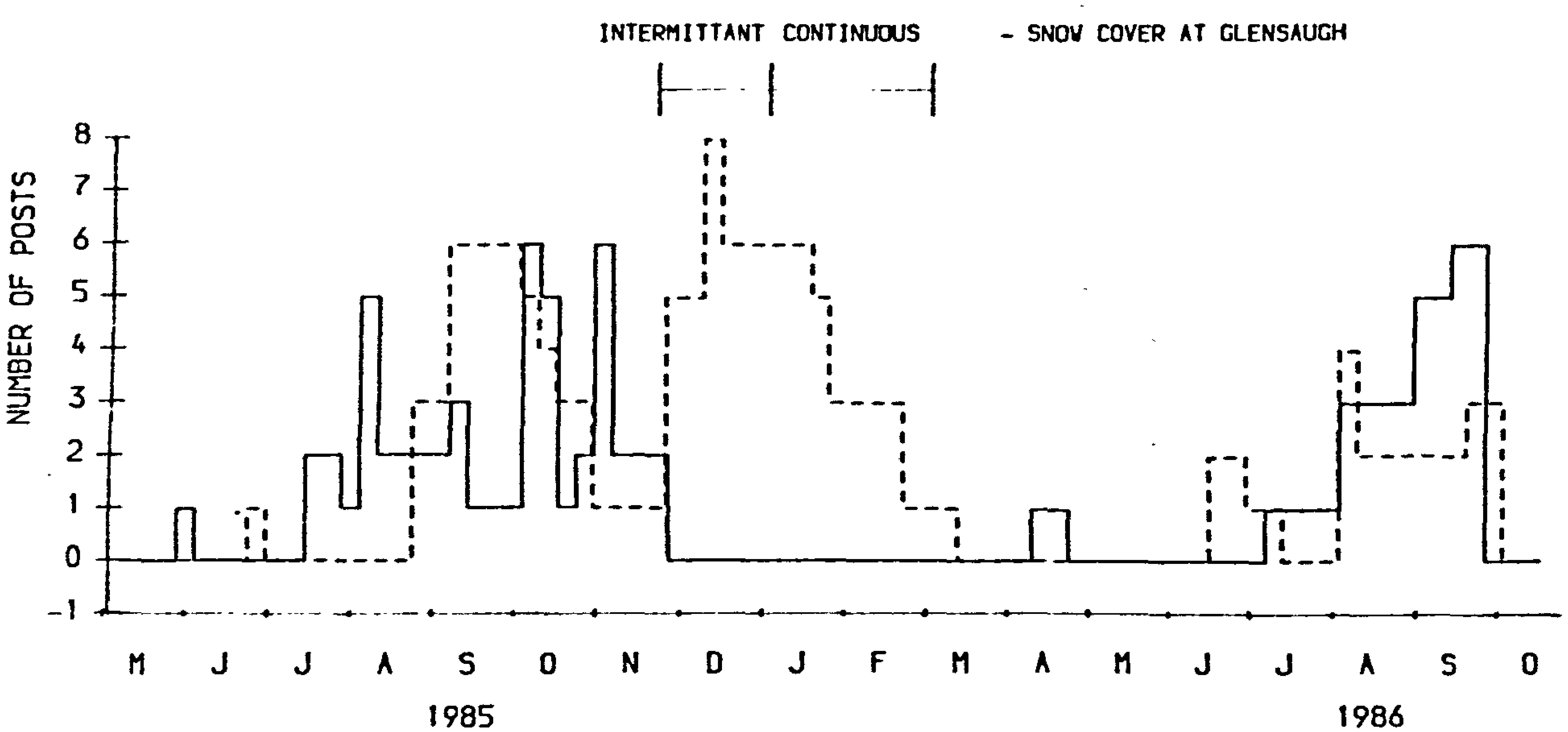


FIG. 5. 16. NUMBER OF POSTS AT WHICH MAXIMUM AIR TEMPERATURE IS HIGHER THAN MAXIMUM GROUND TEMPERATURE, MAY 1985 TO OCTOBER 1986

- - - - - - - - GLENSAUGH

———————— KILMARTIN

subsequent analysis.

A review of the temperature data has therefore revealed the following points:

1. Altitudinal temperature inversion of minimum temperature resulting in colder minima at the lower west coast sites, except in winter when Glensaugh recorded the coldest air minima of the four sites in the extremely cold air over snow cover. Thus, in winter, temperature inversion did not override the regional climate.

2. The warmest winter air minima of the four sites at Sourhope, demonstrating a less extreme winter than Glensaugh despite the site's higher altitude.

3. Ground minima in winter affected by snow cover at Glensaugh due to insulation of the thermometers from frost.

4. The damping of regional differences of maxima in spring and summer 1985 and thus the lack of longitudinal temperature differentiation due to a very wet season, enhancing the altitudinal effect on maxima.

5. A warmer than expected local climate at Glensaugh from early spring to late autumn, probably due to the predominance of southerly aspect, the steep slopes and the narrowness of the valley which create a "suntrap" effect.

6. Maximum temperatures in winter probably not adequately reflecting mean daily maxima due to the inclusion of March and November in Period Five and to the irregular rather long reading intervals.

7. Temperatures within the bracken stands affected by canopy closure in mid to late summer with reversal of minima and maxima temperature gradients between the air and ground thermometres. Such reversal is not reflected in the site and post means in Period Four because of the dominant influence of the more extreme temperatures of the "normal" gradients recorded intermittantly throughout the Period at every post.

The minimum temperature data can only show which sites registered the coldest frost, it cannot show or reflect duration or frequency of frost (which in winter is likely to strongly affect mean temperature). For example, although the mean air minima at Sourhope in Period Five (winter) was warmer than Gatehouse, this probably does not reflect differences in mean daily soil minima (which will be of most importance to the bracken in winter). Despite the higher minima at Sourhope, lower mean air temperatures will result in a longer duration of air and soil frost whether diurnally or seasonally.

At the west coast sites the heavy frosts probably only occur on radiation nights and may therefore be less frequent than in the east. This, coupled with the higher mean winter temperatures, will result in more rapid thawing at the west coast than in the east, creating greater diurnal and periodic fluctuations in mean soil temperature. By May soil frost will be rare and the effect of frost will now be on the emerging fronds. The low minima recorded at some of the west coast posts may only represent one radiation night in each data interval of three weeks, although examination of the raw weekly data in 1985 shows relatively low minima to occur at the same posts every week. Heavily frosted bracken was only observed at the west coast sites and it would therefore seem that even if the two eastern sites experienced more frequent frosts, it is the degree of frost that would seem to be more important to the bracken. This point is further discussed in Chapter Nine.

Because of the "frost pocket" effect mean temperatures determined by finding the arithmetic mean of the maxima and minima are unlikely to accurately reflect daily mean temperature. Increased shelter increases air temperature during the day more than it is reduced by night so that mean temperature is increased (Aslyng 1958). Mean temperatures were therefore not calculated. However, as maxima in 1986 followed the predicted pattern of change, there is no reason to believe that mean temperature did not follow the predicted pattern as well. The predicted mean temperature pattern for the sites contrasts with the maxima pattern in that mean temperature remains relatively high at Kilmartin throughout the growing season. The rank order of site means is therefore (in descending order) Gatehouse, Kilmartin, Sourhope and Glensaugh. (At sea level this would be Gatehouse and Sourhope, Kilmartin, Glensaugh). Because maximum and mean temperature were shown to be higher than expected at Glensaugh, the site probably comes higher in the order. Maximum temperature patterns in early spring are the same as mean temperature patterns and it is interesting to note that because the longitudinal shift in temperature did not occur in spring of 1985, the maximum temperature pattern remained the same as the mean pattern throughout the growing season. This is an important point for the later interpretation of the analysis of the effect of maxima on bracken vigour. Overall bracken vigour is more likely to reflect long term environmental trends rather than conditions in anomalous years. The results of the analysis of the effect of maxima for this particular year may therefore actually be reflecting the long term effect of mean temperature rather than of maxima.

The relatively high maxima at Kilmartin in the early spring are not reflected in the site data in 1986 because of the inclusion of March in Period Five and of April with May and June in Period Six. However, Table 5.4 below shows site maxima for individual months in early spring of 1986 in which it is clear that air maxima remain high at Kilmartin relative to the other sites until May. Ground maxima do not reflect the predicted temperature pattern as strongly as air maxima, possibly because the warmer temperatures recorded in the air layer close to the ground are a better reflection of mean temperature than of maxima.

Table 5.4 Mean monthly maxima at the sites in early spring 1986 (^{o}C)

	March		April		May	
	Air	Ground	Air	Ground	Air	Ground
Kilmartin	11.7	18.4	19.8	22.7	14.9	22.0
Gatehouse	12.7	19.9	20.4	25.6	18.25	21.87
Glensaugh	11.6	17.3	17.4	23.5	19.25	25.1
Sourhope	9.3	--	14.0	--	15.8	--

5.2.2 Exposure

Exposure is a function of windblow, humidity and temperature, while the tatter rate is purely a measure of wind blow. In this chapter the term "exposure" is used in description of tatter rates (i.e. a post with a very high tattter rate is described as very exposed), unless otherwise stated.

The data year for the tatter rates extends from September to the following August to coincide with the temperature data year and from hereon, 1985-1986 data are referred to as "1986 data" and 1986-1987 as "1987 data". No data are available for the first growing season (1985) because flags were not set up at Kilmartin, Glensaugh and Gatehouse until mid to late summer. Although not used in the analysis of bracken vigour, the 1987 data can be used to characterise exposure at the sites. Data for Gatehouse in 1987 are incomplete due to repeated loss of flags to cattle, but extrapolations for occasional data gaps were possible in 1986 when flag loss was less frequent. Tatter data are not divided into period means, one annual mean being therefore calculated for each post and site. In the analysis of bracken vigour in Chapter Seven, the 1986 means are substituted in 1985, as the strong correlation betwwen the 1986 and 1987 means ($r=0.991$, $p<0.01$) suggests that relative exposure varies little from year to year. Topex values could have been used in 1985, but the correlation with exposure is lower (e.g. 1986 $r=-0.649$, $p<0.01$). Tatter values for Old Glensaugh One and Old Gatehouse One in 1985 were extrapolated.

Table 5.5 shows mean tatter rate (cms/day) at the posts and thermograph stations in 1986 and 1987. At Glensaugh the highest flag, which is at Station Three (combined flag with Station Four) is the most exposed, being located just below the break of slope marking the transition to the plateau. Although no flags were placed on the plateau, exposure was perceived to markedly increase beyond the break of slope. Post Seven was located only 10 metres below Station Three but is nearly 50 percent less exposed, being sheltered by a small but steep break of slope a few metres uphill. The most exposed posts at Glensaugh, Five and Six, were located on the slopes between the very steep lower valley and the plateau and did not have the benefit of the local geomorphic shelter afforded to post Seven. Post Three on the valley floor does not show any influence of the strong funnel winds that often characterise long narrow valleys (see for example, Mitchell 1973). At Kilmartin the effect of local shelter is demonstrated by comparison of Posts Five and Four which are located on the summit of Bar a Chuirn and in a small gulley to the east side of the summit respectively. Exposure at Post Five (the highest post of the site) is nearly three times greater than at Post Four, although it is only five metres higher. The least exposed posts at Kilmartin (One, Six, Seven and Eight) are located on the south side of Bar a Chuirn where the complex topography and the conifer plantation afford alot of shelter. The more exposed posts, Two and Three are located on the north side of Bar a Chuirn, facing a wide valley which is very exposed to easterly winds, while the small burn valley between the two posts acts as a wind corridor for the westerlies.

The least exposed posts at Gatehouse are predictably Posts One and Two at the edge of the gorge, while the most

Table 5.5 Mean daily tatter rate (cms/day) at the posts and thermograph stations, 1986 and 1987

		Post 1	Post 2	Post 3	Post 4	Post 5	Post 6	Post 7	Post 8	Stat 1	Stat 2	Stat 3
Glensaugh	1986	2.22	2.73	2.25	2.07	3.62	3.90	2.87	2.87	2.90	2.77	3.55
	1987	1.98	2.98	2.10	1.90	3.05	2.58	2.10	2.10	3.00	2.53	3.55
Kilmartin	1986	2.35	3.95	5.62	3.98	11.50	2.88	2.65	2.83			
	1987	2.07	3.38	5.33	4.07	10.75	2.47	2.20	2.05			
Gatehouse	1986	2.13	2.08	5.12	5.32	2.63	5.45	9.30	5.12			
	1987	--	--	No data available		--	--					
Sourhope	1986	2.85	10.17	5.93	5.93	5.93	3.13	3.42	4.90			
	1987	3.13	9.35	5.38	5.38	5.83	2.58	3.28	4.18			

exposed is the highest, Post Seven on the upper slopes of the Doon of Culreoch. Post Six, also located above the head dyke, is markedly less exposed, illustrating the sheltering effect of the small, formerly cultivated valley of Cleugh Burn. At Sourhope the least exposed posts, One, Six and Seven, were located on the steep valley slopes of Dodd and Rowantree Burns, while the most exposed and highest post (Two) was located on the upper slopes of Dodd Hill.

Table 5.6 Mean daily tatter rate (cms/day) for each site, 1986 and 1987

	1986	1987
Glensaugh	2.82	2.35
Kilmartin	4.47	4.04
Gatehouse	4.64	--
Sourhope	5.28	5.00

Table 5.6 shows Glensaugh to be the least exposed site and Sourhope to be the most exposed site, while Kilmartin and Gatehouse have very similar exposure rates. The differences between Sourhope and the west coast sites is very small despite the significantly higher altitude of the former site, illustrating the different exposure regimes between the west and east of Scotland. The low exposure at Glensaugh confirms the contention made in Section 5.2.1 that the site is very sheltered due to the topography of the valley. The Birse and Robertson exposure classification of "exposed" for Glensaugh (see Chapter Four) would seem to be inappropiate. In this classification Gatehouse was supposedly the least exposed site ("moderately exposed) but clearly this is not the case, demonstrating the modifying effect of local topography at the sites. Examination of the post data in Table 5.5 shows that the highest posts at Kilmartin, Gatehouse and Sourhope are disproportionately exposed in

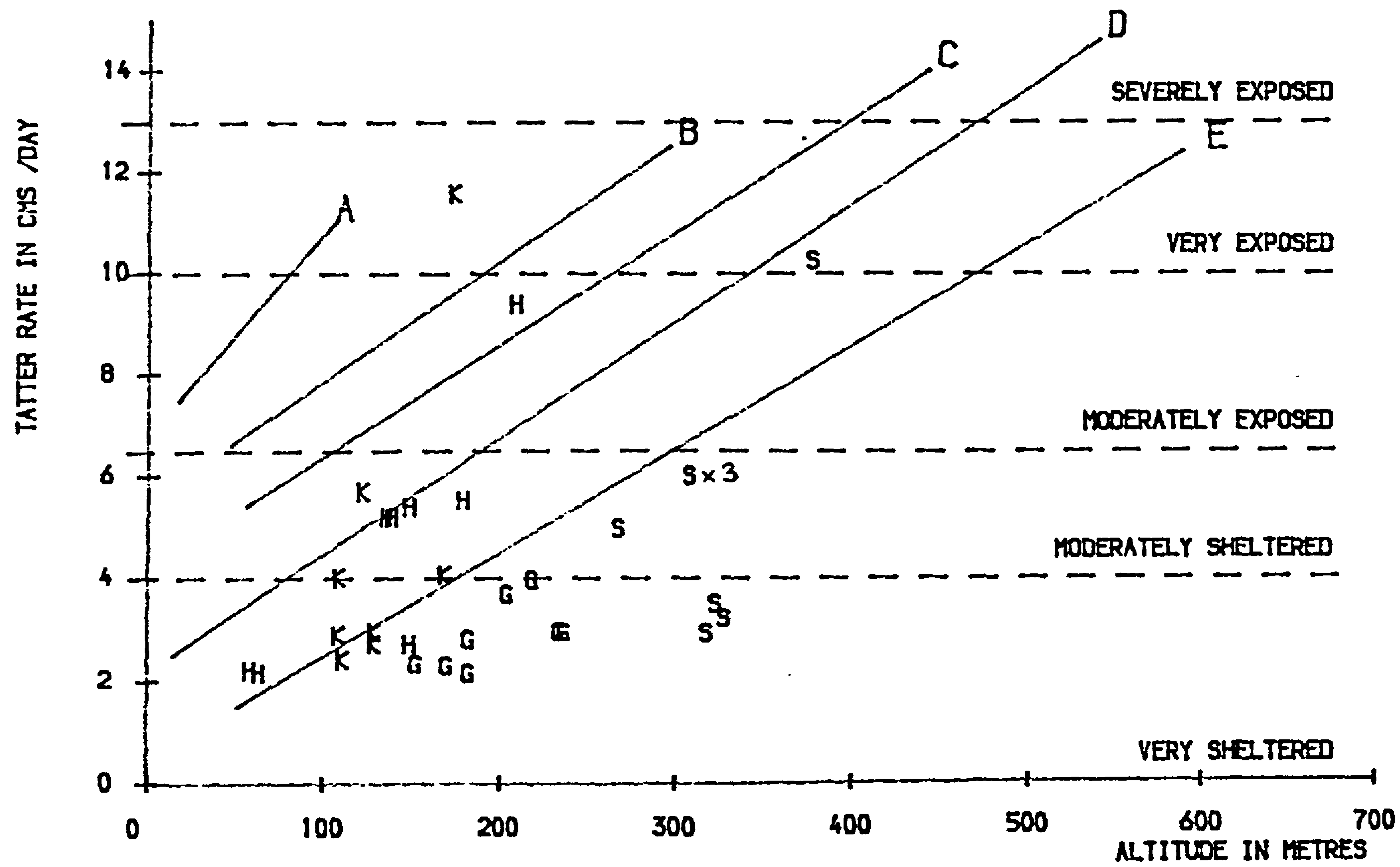
relation to altitude when compared with other posts, indicating a rapid reduction in geomorphic shelter once a certain altitude is reached. At Glensaugh, no such effect is evident, as the upper limit of bracken in the locality was not sampled (as discussed in Chapter Four) although the highest flag at Station Three is the most exposed. Omission of the highest posts at the other sites will therefore make the intersite comparisons more meaningful. Table 5.7 below shows that even with such an omission, the rank order of exposure at the sites remains the same although the differences between Glensaugh and the other three sites are reduced.

Table 5.7 Mean daily tatter rate (cms/day) for each site omitting the highest posts at Kilmartin, Gatehouse and Sourhope.

	1986	1987
Glensaugh	2.82	2.35
Kilmartin	3.47	3.08
Gatehouse	3.98	--
Sourhope	4.58	4.38

The relatively small differences between the sites, with and without the highest posts, do not reflect the range of wind zones or exposure classes that are designated for the site localities by the Forestry Commission. In the wind zones classification, based on tatter rate and altitude, Kilmartin is the most exposed site in Zone B, Gatehouse in Zone C and Glensaugh and Sourhope in Zone E. Fig.5.17 shows that only the highest posts at Kilmartin and Gatehouse approximate to the respective designated wind zones of the two sites while the rest of the posts approximate to the most sheltered Zones D and E. At Sourhope, all the posts except the highest approximate to the site's designated wind zone, Zone E, while all the posts at Glensaugh fall below the

FIG. 5. 17. EXPOSURE AT POSTS IN 1986
BASED ON FORESTRY COMMISSION WIND ZONES
AND EXPOSURE CLASSES



A TO E = WIND ZONES

'SEVERELY EXPOSED' ETC = EXPOSURE CLASSES

K = KILMARTIN G = GLENSAUGH

H = GATEHOUSE S = SOURHOPE

Zone E regression line. Thus, despite the differences in altitude and predicted wind zones, the actual exposure regimes of each site are similar, indicating a fairly standard requirement by bracken for shelter at all four sites, in contrast to the range of maxima and minima recorded. This is also shown in Fig.5.17 in which all except the highest posts at Kilmartin, Gatehouse and Sourhope are classed as either "Moderately" or "Very Sheltered" according to the Forestry Commission's exposure classes.

The importance of local topography within the sites is illustrated by the correlation of tatter with topex (e.g. 1986 $r=-0.649$, $p< 0.01$), in contrast to the weak correlation between altitude and tatter ($r=0.359$, $p<0.05$, using the square root of the tatter data). The effect of altitude within the bracken zones is therefore overridden by the effect of topography in the determination of exposure. However, altitude becomes very important at the upper limit of bracken, which as already discussed, represents the sudden reduction of geomorphic shelter with a change to a higher exposure regime.

As stated at the beginning of the section, exposure is an amalgam of wind blow, humidity and temperature. By reducing windspeed, shelter also reduces evaporation and increases day time temperature (Aslyng 1958). Exposure and maxima should therefore be correlated. Ground maxima and tatter rate are negatively correlated in 1986 but only significantly in Period Six (April and May), $r=-0.441$, $p< 0.05$ (this omits Sourhope, no ground maxima being recorded there). No correlation was found with air maxima in either year or with ground maxima in 1985. That more, or stronger correlations were not obtained reflects the masking effect of other factors upon maxima, shown for example, by the strong correlation between altitude and maxima in 1985 when regional temperature differences were damped. Because exposure is only weakly correlated with altitude within the bracken zone, the absence of correlation between exposure and maxima in 1985 is thus not unexpected. It is likely that exposure will have an increasing effect on temperature at the limit of bracken where exposure was shown to suddenly increase.

Examination of the exposure data has revealed the following:

1. Relative exposure varies little from year to year.
2. A stronger relationship between exposure and topography than between exposure and altitude.
3. Sourhope is the most exposed site, but not in proportion to its altitude, demonstrating the different exposure regimes between east and west Scotland and also the similar exposure regimes between the sites.
4. Glensaugh is the most sheltered site, supporting the hypothesis that shelter is important to the local climate of the site.
5. A sudden increase in exposure at the upper bracken limit at Kilmartin, Gatehouse and Sourhope, indicating that altitude becomes more important in determing exposure.
6. No significant correlation between maxima and exposure except in Period Six which is fairly low, even though maxima of the three sites (i.e. omitting Sourhope) in this period are fairly similar. The affect of exposure on temperature may increase at the upper bracken limit.

Chapter Six

Soils and Vegetation Characteristics of the Sites

6.1. Soils and ground flora

The soil types of the posts and thermograph stations are summarised in Table 6.1. These reflect the range of all but the wettest soils found at the sites in general. The majority are either acidic brown earths or degraded podsols. The characteristics of the latter include modification of the A horizon by organic matter and ferric iron incorporation, the partial or complete breakdown of the iron pan and modification of the illuvial B horizon. As discussed in Chapter Two, these processes can be attributed to the physical "cultivation" by the rhizomes and roots, relatively rapid cycling of nutrients and to mobilisation of phosphates (Mitchell 1977). The profile of a typical degraded podsol (at Glensaugh Five) is summarised below.

Summarised profile of the degraded iron podsol at Glensaugh Five

Thickness/ Depth(cms)	Horizon	Description
5/7	L	Partly comminuted bracken litter.
0.5	F	Dark brown, well comminuted litter occasional fine root.
5/7	H	Slightly stony , very dark brown, moist amorphous humus with quartz grains. Weakly developed large subangular blocky structure. Common pores, abundant fissures. Abundant rhizomes and bracken fine

Table 6.1 Summary of soil types at posts and stations

Kilmartin

Post 1	Degraded humus-iron or peaty podsol
2	Acidic brown earth
3	Acidic brown earth
4	Podsolic brown earth
5	Podsolic brown earth
6	Acidic brown earth with ground water gley
7	Degraded peaty podsol with ground water gley
8	Degraded peaty podsol with ground water gley

Glensaugh

New Post 1	Colluvial brown earth
Old Post 1	Degraded humus-iron podsol
Post 2	Skeletal ranker
3	Flushed brown earth and ground water gley
4	Acidic brown earth
5	Degraded humus-iron podsol
6	Podsolic brown earth
7	Degraded humus-iron podsol
8	Degraded humus-iron podsol with surface water gley
Stat 1	Degraded humus-iron podsol
Stat 2	Degraded humus-iron podsol
Stat 3	Flushed brown earth
Stat 4	Degraded humus-iron podsol

Sourhope

Post 1	Podsolic brown earth with slight gleying
2	Acidic brown earth
3	Skeletal podsolic brown earth
4	Skeletal acidic brown earth
5	Skeletal acidic brown earth
6	Podsolic brown earth with slight gleying
7	Colluvial brown earth
8	Skeletal acidic brown earth

Gatehouse

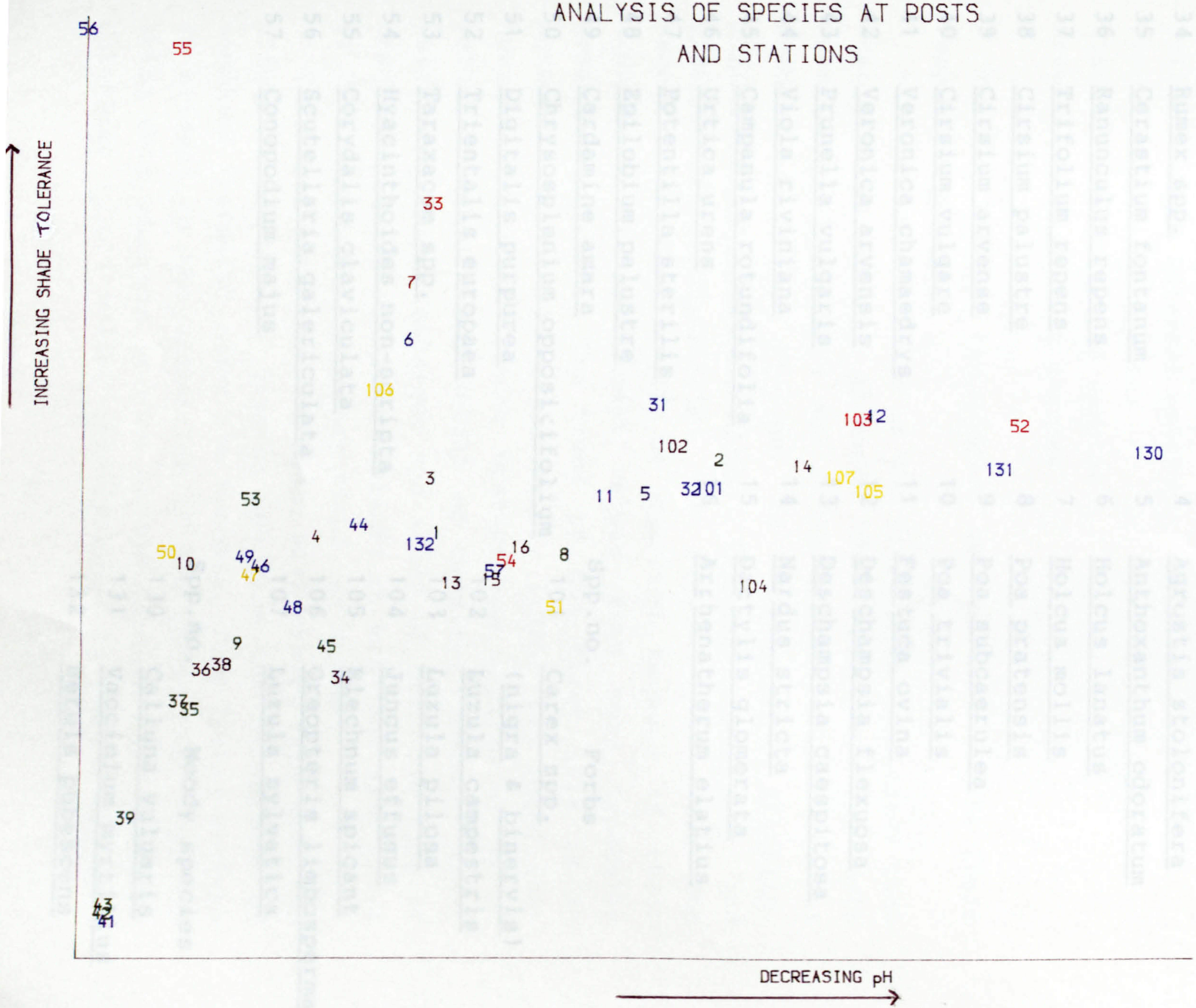
New Post 1	Podsolic brown earth with ground water gley
Old Post 1	Acidic brown earth with periodic gleying
Post 2	Acidic brown earth with periodic gleying
3	Acidic brown earth with periodic gleying
4	Flushed brown earth with periodic gleying
5	Acidic brown earth with periodic gleying
6	Acidic brown earth, formerly cultivated
7	Acidic brown earth
New Post 8	Flushed brown earth with periodic gleying

		roots. Narrow merging boundary.
0-5	A_1/A_2	Stony, slightly moist, dark grey slightly sandy loam. Moderately developed subangular blocky. Moderate humus incorporation Common rhizomes and fine roots. Sharp boundary.
5-23	B	Very stony, slighlty moist, dark brown slightly sandy loam. Weakly developed subangular blocky breaking down to granular. Low humus incorporation.
23+	C	Excessively stony, very weakly developed to structureless, mid to light brown loamy coarse sand. No humus incorporation

These degraded podsols are best described as organic from the point of view of bracken growth for in nine out of the twelve podsols examined, most of the rhizomes and fine root systems were concentrated in the amorphous mor humus. Although humus does not normally have structure in the pedogenic sense, a subangular blocky structure was observed to be formed in situ by the abundant root and rhizome channels. There is no evidence of the original plant remains in the humus (even where ploughing revealed an organic soil of up to one metre depth at Kilmartin Eight) and the horizon does not normally exceed 20cms depth. The chemical properties of these soils are discussed in Chapter Eight.

The range of soils sampled is reflected in the Detrended Correspondance Analysis of the ground flora. In the species graph (Fig. 6.1, key shown in Table 6.2) species characteristic of very acidic habitats (e.g. Calluna vulgaris, Vaccinium myrtilus and Trientalis europaea) are placed at the far right of the first axis and species characteristic of less acidic habitats (e.g. Chrysosplenium oppositifolium, Cirsium arvense and

FIG. 6.1 DETRENDED CORRESPONDANCE ANALYSIS OF SPECIES AT POSTS AND STATIONS



FOR SPECIES KEY SEE TABLES 6.2 AND 6.3

COLOUR CODE.-

RED=WOODLAND SPECIES

YELLOW=SHADE TOLERANT SPECIES

BLUE=UBIQUITOUS SPECIES

BLACK=LONG GRASSLAND SPECIES

GREEN=SHORT PASTURE SPECIES

Table 6.2 Species list for Fig. 6.1

Spp.no.	Herbs
31	Galium saxatile
32	Potentilla erecta
33	Oxalis acetosella
34	Rumex spp.
35	Cerastium fontanum
36	Ranunculus repens
37	Trifolium repens
38	Cirsium palustre
39	Cirsium arvense
40	Cirsium vulgare
41	Veronica chamaedrys
42	Veronica arvensis
43	Prunella vulgaris
44	Viola riviniana
45	Campanula rotundifolia
46	Urtica urens
47	Potentilla sterilis
48	Epilobium palustre
49	Cardamine amara
50	Chrysosplenium oppositifolium
51	Digitalis purpurea
52	Trientalis europaea
53	Taraxacum spp.
54	Hyacinthoides non-scripta
55	Corydalis claviculata
56	Scutellaria galericulata
57	Conopodium majus

Spp.no.	Grasses
1	Agrostis tenuis
2	Agrostis canina var. montana
3	Agrostis canina var. canina
4	Agrostis stolonifera
5	Anthoxanthum odoratum
6	Holcus lanatus
7	Holcus mollis
8	Poa pratensis
9	Poa subcaerulea
10	Poa trivialis
11	Festuca ovina
12	Deschampsia flexuosa
13	Deschampsia caespitosa
14	Nardus stricta
15	Dactylis glomerata
16	Arrhenatherum elatius

Spp.no.	Forbs
101	Carex spp. (nigra & binervis)
102	Luzula campestris
103	Luzula pilosa
104	Juncus effusus
105	Blechnum spicant
106	Oreopteris limbosperma
107	Luzula sylvatica

Spp.no.	Woody species
130	Calluna vulgaris
131	Vaccinium myrtillus
132	Betula pubescens

Prunella vulgaris) on the far left. The pH gradient between the two extremes is reflected in the alignment of the remaining species, while ubiquitous species are placed in the middle of the graph. The trend of the second axis corresponds to shade tolerance, with species characteristic of woodland habitats mainly located high up the axis and those of short pasture mainly low down. The species are colour coded to highlight the trend of the second axis as follows:

Red - woodland species
Yellow - shade tolerant species
Blue - ubiquitous species
Black - long grassland species
Green - short pasture species

Table 6.3 shows the species catergorised within their respective groups.

As expected the trend of the first axis is clearer than that of the second, although the eigenvalues are both reasonably high (0.674 and 0.524 respectively). Species numbers 47, 50, 51 and 54 (Potentilla sterilis, Chrysosplenium oppositifolium, Digitalis purpurea and Hyacinthoides non-scripta) are placed lower down the second axis than would be expected because of their occurrence at low domin values with more typically grassland species. The trend of the first axis is in agreement with work by Lee et.al. (1986) who found that species composition under bracken was controlled by pH rather than by frond height or density. However, their polar ordination technique and study of only one type of bracken (i.e. on acidic grassland) at only one site makes it likely that the secondary trend was missed.

The trend for shade tolerance will result from both the effect of shading by bracken and from the occurrence of woodland "refugia" under the bracken. This latter feature is evident in the ordination of the plots (Fig 6.2) in which very vigorous bracken on old pasture and runrig at Gatehouse (plots colour coded yellow) is placed low down

Table 6.3 Species according to second axis classification

Spp.no.	Woodland Species
7	Holcus mollis
33	Oxal/is acetosella
52	Trientalis europaea
54	Hyacinthoides non-scripta
55	Corydalis claviculata
103	Luzula pilosa

Spp.no.	Shade Tolerant Species
47	Potentilla sterilis
50	Chrysosplenium oppositifolium
51	Digitalis purpurea
105	Blechnum spicant
106	Oreopteris limbosperma
107	Luzula sylvatica

Spp.no.	Ubiquitous Species
1	Agrostis tenuis
5	Anthoxanthum odoratum
6	Holcus lanatus
11	Festuca ovina
12	Deschampsia flexuosa
31	Galium saxatile
32	Potentilla erecta
41	Veronica chamaedrys
44	Viola riviniana
46	Urtica urens
48	Epilobium palustre
49	Cardamine amara
56	Scutellaria galericulata
57	Conopodium majus
101	Carex spp. (nigra and binervis)
130	Calluna vulgaris
131	Vaccinium myrtillus
132	Betula pubescens

Spp.no.	Long Grassland Species
3	Agrostis canina var. canina
4	Agrostis stolonifera
10	Poa trivialis
13	Deschampsia caespitosa
14	Nardus stricta
15	Dactylis glomerata
16	Arrhenatherum elatius
34	Rumex spp.
36	Ranunculus repens
38	Cirsium palustre
102	Luzula campestris
104	Juncus effusus

Spp.no.	Short Pasture Species
2	Agrostis canina var. montana
8	Poa pratensis
9	Poa subcaerulea
35	Cerastium fontanum
37	Trifolium repens
39	Cirsium arvense
42	Veronica arvensis
43	Prunella vulgaris
45	Campanula rotundifolia
53	Taraxacum spp.

the second axis, indicating the failure of woodland species to recolonise the pasture bracken despite the shade conditions produced by the bracken canopy. That woodland species can survive in dense bracken litter is shown by the occurrence of Oxalis acetosella, Trientalis europaea, Luzula pilosa and Corydalis claviculata in dense bracken at the other sites. Tansley (1939) maintained that bracken on open moorland provided a micro-environment in which woodland species can survive and Nicholson and Robertson (1958) regarded the bracken stands on brown earths at Glensaugh to be relicts of former woodland. However the question of whether the woodland species can actually colonise bracken stands is open to debate. The evidence from the Gatehouse pastures would suggest not, but Oxalis acetosella is found growing in Agrostis-Festuca bracken hinterland on mediaeval runrig at Sourhope. The steep slopes of the nearby Rowantree Burn bear dense bracken and Oxalis acetosella and it may therefore be a question of nearness of a seed source that determines the success of colonisation.

The range of species found under vigorous bracken in this present study concurs with fndings of other workers (e.g. Jarvis 1974; Jeffrys 1917; Lee et.al. 1986; Mitchell 1977; Nicholson and Patterson 1976; Nicholson and Robertson 1958) and includes Holcus mollis, Deschampsia flexuosa, Oxalis acetosella, Galium saxatile, Trientalis europaea and Luzula pilosa.

The graph showing the ordination of the plots (Fig. 6.2) has beeen colour coded by site as follows:

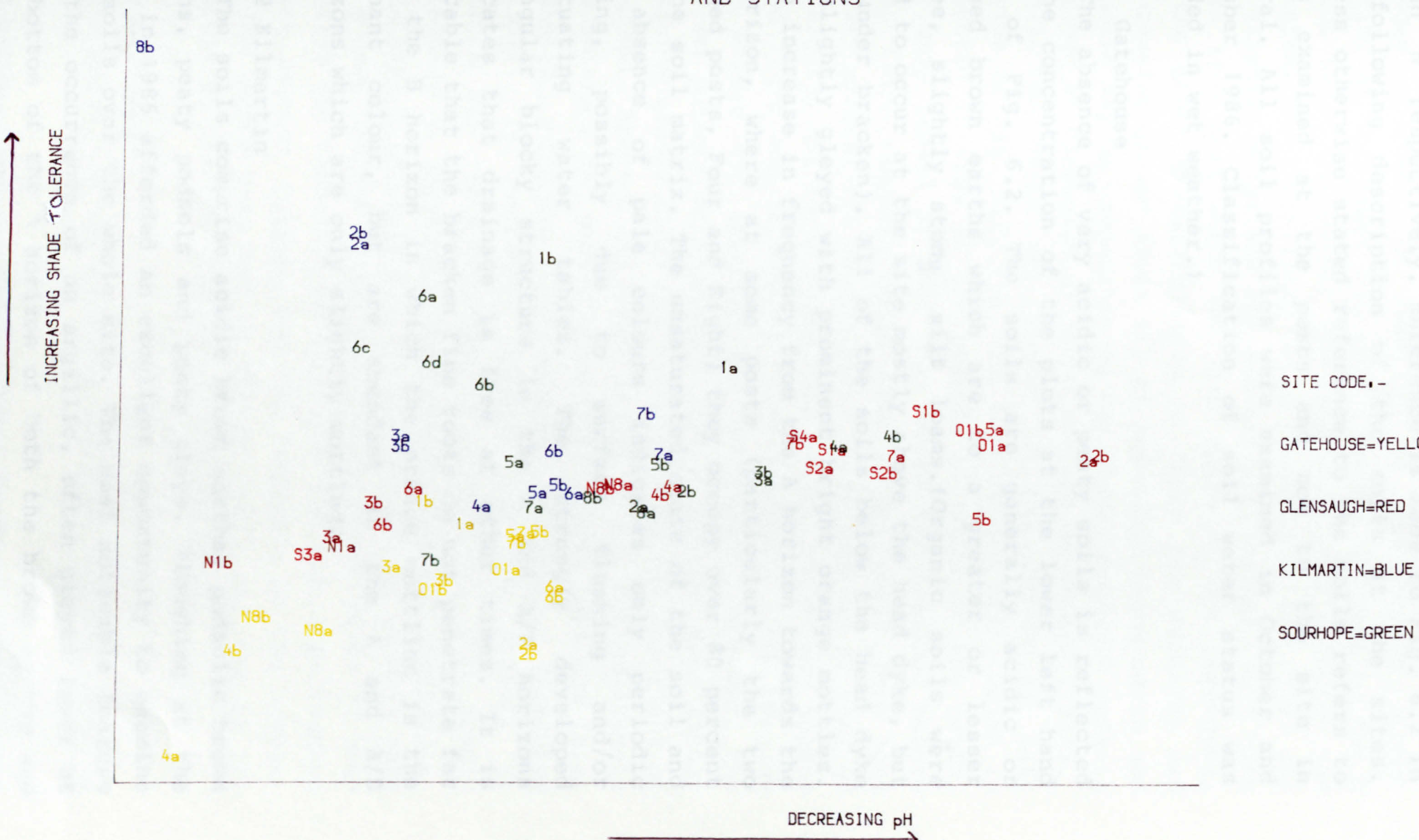
Gatehouse - yellow
Kilmartin - blue
Glensaugh - red
Sourhope - green

Both replicate plots are used in the analysis except where ploughing at Kilmartin resulted in loss of one or both plots at some of the posts. The thermograph plots are prefixed by an "S" and the "Old" and "New" posts by an "O"

FIG. 6.2 DETRENDED CORRESPONDANCE

ANALYSIS OF PLOTS AT POSTS

AND STATIONS



and an "N" respectively. Reference is made to Fig. 6.2 in the following description of the soils at the sites. (Unless otherwise stated reference to the soils refers to soils examined at the posts and not to the site in general. All soil profiles were examined in October and November 1986. Classification of soil water status was avoided in wet weather.)

6.1.1 Gatehouse

The absence of very acidic or peaty soils is reflected by the concentration of the plots at the lower left hand side of Fig. 6.2. The soils are generally acidic or flushed brown earths which are to a greater or lesser degree, slightly stony silt loams.(Organic soils were found to occur at the site mostly above the head dyke, but not under bracken). All of the soils below the head dyke are slightly gleyed with prominent bright orange mottles. These increase in frequency from the A horizon towards the B horizon, where at some posts (particularly the two flushed posts, Four and Eight) they occupy over 80 percent of the soil matrix. The unsaturated state of the soil and the absence of pale colours indicates only periodic gleying, possibly due to surface flushing and/or fluctuating water tables. The strongly developed subangular blocky structure in the A and A/B horizons indicates that drainage is free at other times. It is noticable that the bracken fine roots do not penetrate far into the B horizon in which the orange mottling is the dominant colour, but are abundant in the A and A/B horizons which are only slightly mottled.

6.1.2 Kilmartin

The soils comprise acidic brown earths, podsolic brown earths, peaty podsols and peaty gleys. Ploughing at the site in 1986 afforded an excellent opportunity to examine the soils over the whole site. The most noticable feature was the occurrence of an argillic, often gleyed layer at the bottom of the A horizon of both the brown earths and the podsols. This was less evident in brown earths under vigorous bracken. In contrast to the bright orange mottling at Gatehouse the gleyed layers (always in the B horizon under the posts) are generally pale coloured and saturated. The two hilltop soils (Posts Four and Five) are only slightly moist and are excessively drained. Both have relict iron pans which the fine roots do not penetrate. All the other characteristics of these two profiles and accompanying ground flora are of an acidic brown earth and the soils may be comparable to the highly degraded podsols described at Glensaugh by Nicholson and Robertson (1958).

All the plots are placed in the centre or left handside of Fig. 6.2, i.e. the less acidic half, which is unexpected in view of the podsols at three of the posts. (The peaty podsol at Post One, which was ploughed before ground flora sampling could take place, would have been simarily placed, its ground flora being similar to that of Post Eight). All three posts have a deep litter and sparse ground flora and it was at first suspected that the low Domin values had affected the ordination. However, the plots on podsols at Glensaugh have a similar deep litter and sparse ground flora but are placed to the far right of the graph. Species of these latter plots are relatively shade tolerant and characteristic of acidic habitats (e.g. Trientalis europaea, Deschampsia flexuosa, Vaccinium myrtillus). In contrast, species on the podsols at Kilmartin are characteristic of shaded but less acidic habitats (e.g. Corydalis claviculata, Oxalis acetosella, Scutellaria galericulata). (The occurrence of podsols only with a deep bracken litter and sparse ground flora at both Kilmartin and Glensaugh results from the fact that bracken growing amongst Calluna was not included in the sample. When the posts were set up during April and May it was difficult to discern bracken amongst Calluna).

6.1.3 Glensaugh

Glensaugh has the greatest range of bracken soils of the three sites, reflected in the spread of plots from far left to far right of Fig. 6.2 . The soils comprise flushed, acidic and slightly podsolic brown earths and degraded humus-iron pdsols. They are generally freely or excessively drained sandy loams, although two of the profiles are gleyed (including the profile on the valley floor). The mineral horizons are therefore generally drier than those of the west coast sites. One of the profiles on the steep lower slopes is coluvially flushed but is still excessively well drained. The two bracken free plots in Calluna at Post Two are placed on the far right of Fig. 6.2. The soil at this post is coarse, shallow and of weak structure.

6.1.4 Sourhope

All of the soils (including those of the bracken free post, Post Three, on Nardetum) are either acidic brown earths or posolic brown earths. All are skeletal or very stony and are the driest of the four sites. Most have a distinct humus horizon which physically resembles a mor. The soils are highly resistant to the spade partly due to their stoniness, but also to compaction in some of the profiles which display compression lines and a platey structure in situ. All the soils are excessively well drained, due to the stoniness and to textural controls rather than to structural controls. Fragipans, features associated with peri-glacial activity (Fitzpatrick 1956) are present in the B/C horizons of some of the profiles and were also observed in some of the additional pits that were dug at the site. Gleying was observed in the fragipans of two of the profiles, (the podsolic brown earths at Posts One and Six), although both are freely drained above this layer.

The absence of podsols and flushed brown earths is reflected by the lack of plots at either extreme of the first axis of Fig. 6.2. The two podsolic brown earths have relatively deep mor humus layers of up to 10cms but their sparse ground flora is not indicative of very acidic conditions (e.g. Holcus mollis, Holcus lanatus, Oxalis acetosella) and they are thus placed centrally on the graph.

The main differences between sites are therefore; a general absence of peaty soils under bracken at the two southern sites; generally drier soils at the two eastern sites, particularly Sourhope; markedly stonier and shallower soils at Sourhope. The relative dryness of the eastern soils will be due to their coarser structure, steeper slope and the lower precipitation levels.

6.2 Catergorisation of soils

Soils are catergorised for the analysis in two ways, by soil type (Table 6.4) and by soil drainage status (Table 6.5). "Soil type" covers the three classes, mesotrophic brown earth, acidic brown earth and podsol, thus representing an approximate gradient of pH. The mesotrophic brown earths all support a ground flora indicative of flushed or relatively fertile conditions (e.g. Poa pratensis, Ranunculus repens, Trifolium repens, Dactylis glomerata, Cirsium palustre, Urtica urens). The three drainage classes, impeded, well drained and excessively drained are based on the drainage status of the mineral horizons. The impeded drainage class includes all the gleyed profiles.

6.3 Bracken characteristics

6.3.1 Canopy characteristics

Nicholson and Patterson (1976) distinguish two main topographic patterns of bracken namely, continuous and discontinuous, the latter describing either a mosaic of bracken or linear stands of bracken along stream sides.

Table 6.4 Classification of soils by soil type.

podsol		acidic brown earth				mesotrophic brown earth		
KM1	OGS1	KM2	SH1	NGH1	GS4	SH7	GH4	NGS1
KM7	GS5	KM3	SH2	OGH1	GS6		GH8	GS3
KM8	GS7	KM4	SH4	GH2				
	NGS8	KM5	SH5	GH3				
		KM6	SH6	GH5				
			SH8	GH6				
				GH7				

Key - KM=Kilmartin O=Old plot
SH=Sourhope N=New plot
GH=Gatehouse
GS=Glensaugh

Table 6.5 Classification of soils by drainage.

impeded				well drained			excessively well drained			
GS3	KM6	SH1	NGH1	GS7	KM1	OGH1	OGS1	KM4	SH2	GH6
NGS8	KM7	SH6	GH8		KM2	GH2	NGS1	KM5	SH4	GH7
	KM8	SH6			KM3	GH3	GS4		SH5	
						GH4	GS5		SH7	
						GH5	GS6		SH8	

Bracken at Gatehouse is fairly continuous below the head dyke, broken by small streams and flushes and occasional rocky outcrops. Above the head dyke distribution is discontinuous creating a pattern of discrete stands interspersed with acidic damp grassland, wet heath, bog and rocky outcrops, although the old area of runrig in the small valley of Cleugh Burn bears continuous bracken. Bracken distribution at Kilmartin is the most fragmented of the four sites forming a mosaic amongst the rocky outcrops, valley bogs and marshes and generally ocupying the concave slopes between Calluna on rock outcrops and valley bog. However, below the head dyke distribution is more continuous on the formerly cultivated fields (although this area was not sampled because of the cattle grazing). On the steep lower slopes at Glensaugh, bracken forms large continuous stands alternating with areas of Calluna across the slope, the latter being occasionally broken by small bracken filled gulleys. On the gentler slopes above, bracken is again relatively continuous, although is absent from quite extensive areas of marsh. At Sourhope the more uniform land surface results in the most continuous bracken distribution of the four sites, although the bracken is mainly restricted to the lower concave slopes between the damp grassland of the valley floor and the steep convex upper slopes.

The main difference in bracken canopy characteristics between eastern and west coast sites is therefore the greater fragmentation of stands in the west caused by the more complex topography and more numerous streams and flushes. The other contrast relates to the boundaries of the bracken stands. At Sourhope the transition from bracken to adjacent Nardetum is very marked, in contrast to the more gradual transition into adjacent vegetation stands at the other three sites. This gives the bracken stands at Sourhope clear boundaries which are further emphasised by the narrow fringes or "crests" of more vigorous bracken between the Nardetum and bracken-and-grass. Sourhope also has several bracken "rings", circular stands of bracken fringed by crests with sparse, or sometimes no bracken in the centre, as described by Watt (1956). This feature is also seen at Glensaugh, albeit only once. These "crests" correspond to the building and mature phases of Watt's (1947) spatial model of succession across a bracken front. The pioneer phase is only represented by a very narrow margin at Sourhope and so sudden is the transition to the tall crest that it is hard to distinguish the building phase from the mature phase. The crests vary in width from about three or four metres to up to twenty metres. The transition from crest to bracken-and-grass (the latter corresponding to Watt's hinterland phase) is also fairly marked, ocurring generally over about one metre. Such a pattern of crests and hinterlands is not seen at the other three sites except at the stand of Gatehouse Seven which is fringed by a narrow crest adjacent to Molinetum.

6.3.2 Morphological characteristics

The Sourhope bracken is morphologically different from that at the other three sites in that it has narrower, shorter and more closely spaced pinnae and pinnules and has a greater proportion of strenghthening tissue. As discussed in Chapter Two, Bright (1928) and others recognised a similar xeromorphic frond morphology in exposed bracken, although Bright also recognised that soil moisture deficit could have the same effect.

6.3.3 Frond characteristics

The systematic sampling system rules out the use of means and confidence intervals for comparison of characteristics between sites. At Sourhope the majority of stands are of the grass hinterland type, with taller, litter covered stands generally only found in the narrow crests. At the other three sites, tall litter covered stands are more extensive, as are areas of marginal (short and very sparse) bracken which are not a common feature at Sourhope because of the marked boundaries between bracken and adjacent Nardetum. The systematic sampling system of one litter covered plot to one grass plot cannot accurately reflect these differences in abundance of the different bracken stand types. (The problems of using random sampling in a study of this nature are discussed in Chapter Four). Comparisons between the sites can be made using boxplots (which show median, upper and lower quartiles and range) bearing in mind that comparison is directly between the posts and does not represent significant differences between the populations as a whole. However, intersite differences as a whole can certainly be inferred from these comparisons.

Figs. 6.3 and 6.4 show boxplots of frond height and density at the four sites. These confirm the visual impression of shorter and denser bracken at Sourhope. The shortness of the bracken at Sourhope is apparent even though the sampling system did not reflect the lesser amount of tall, litter covered bracken at the site. Direct intrasite comparison between the two years is not possible because of the relocation of Glensaugh One and Eight and Gatehouse One and the relocation of plots around the posts at Gatehouse and Sourhope after cattle trampling.

Litter depth is summarised in Fig. 6.5. The inclusion of the litter covered and litter free posts in the same class results in very large ranges. However, there are indications that litter formation is greater at the west coast sites than in the east. Litter depths of more than 20cms were recorded at Kilmartin and Gatehouse, but of no more than 10cms at Glensaugh even though the frond heights of Gatehouse and Glensaugh are similar.

Finally, frond characteristics of the hinterlands and crests are compared. Paired t tests on nine crests and their adjacent hinterlands show that the crest bracken is significantly taller ($t=3.84$, $p<0.01$) and denser ($t=4.01$, $p<0.01$) than hinterland bracken, although in some cases only height or density are greater. Furthermore, crests are only taller and,or denser than their adjacent hinterlands but not necessarily than other hinterlands, thus the use of the paired t test.

FIG. 6. 3 BOXPLOTS OF SITE FROND HEIGHTS

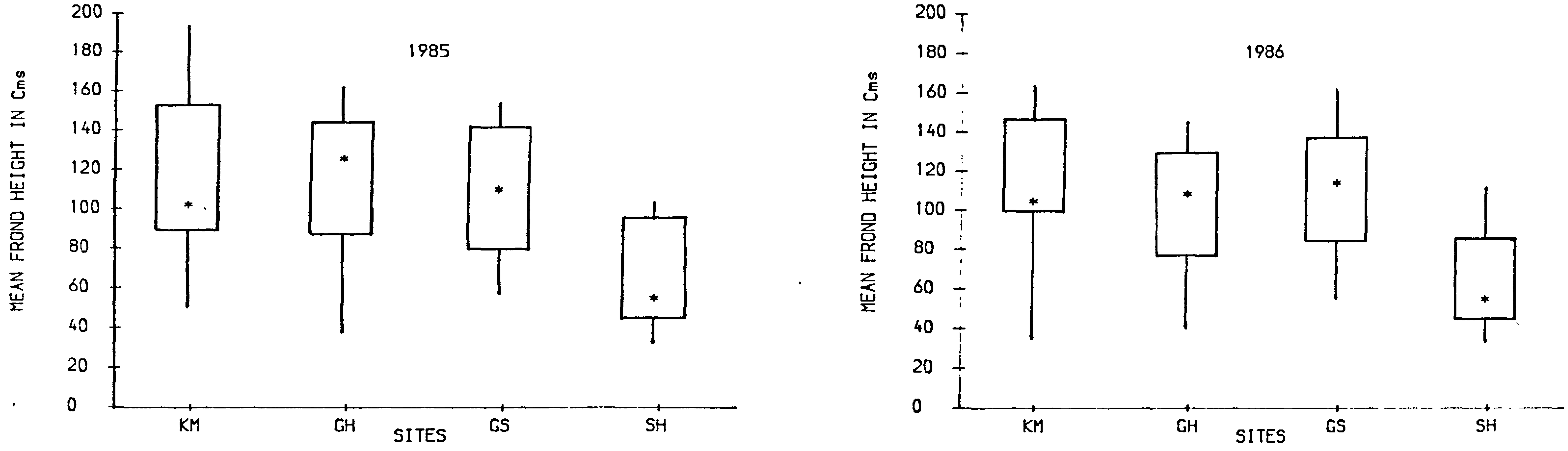


FIG. 6. 4 BOXPLOTS OF SITE FROND DENSITIES

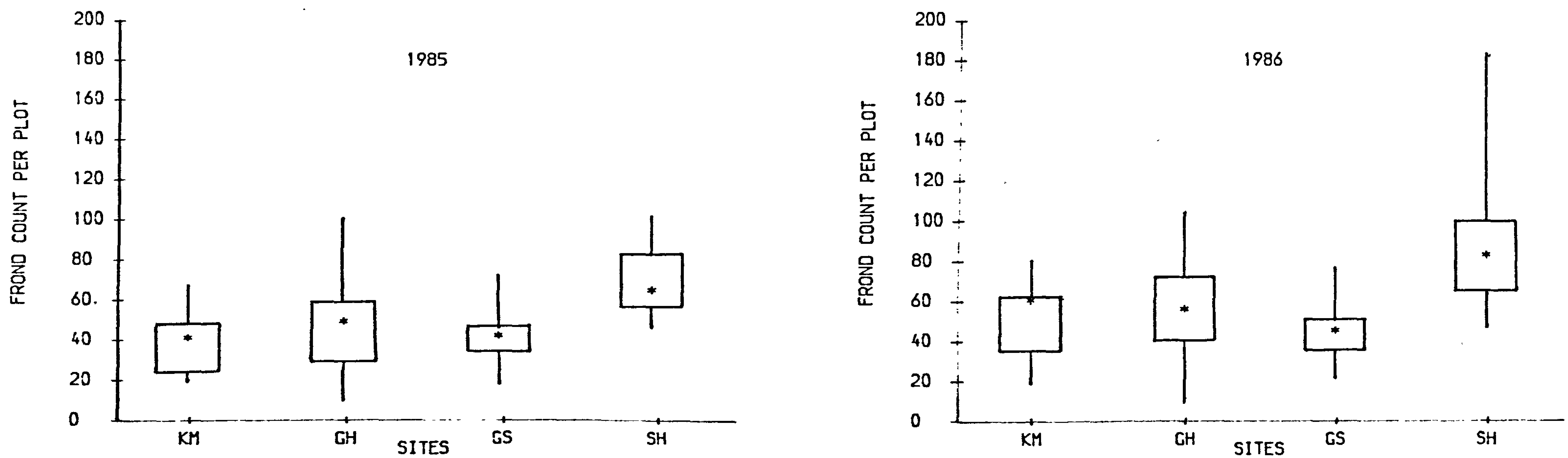
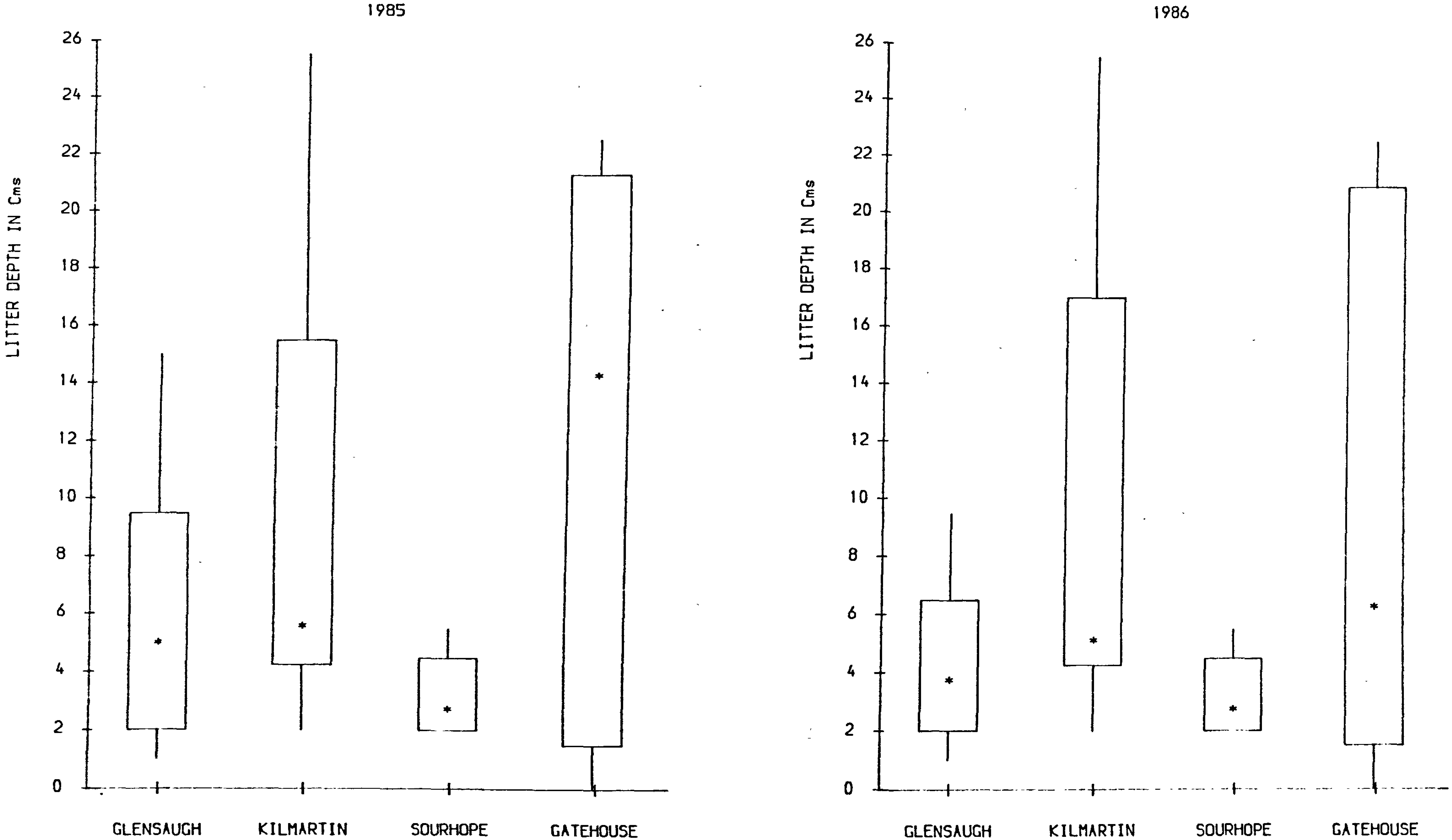


FIG. 6.5 BOXPLOTS OF LITTER DEPTH AT EACH SITE



6.3.4. Rhizome characteristics

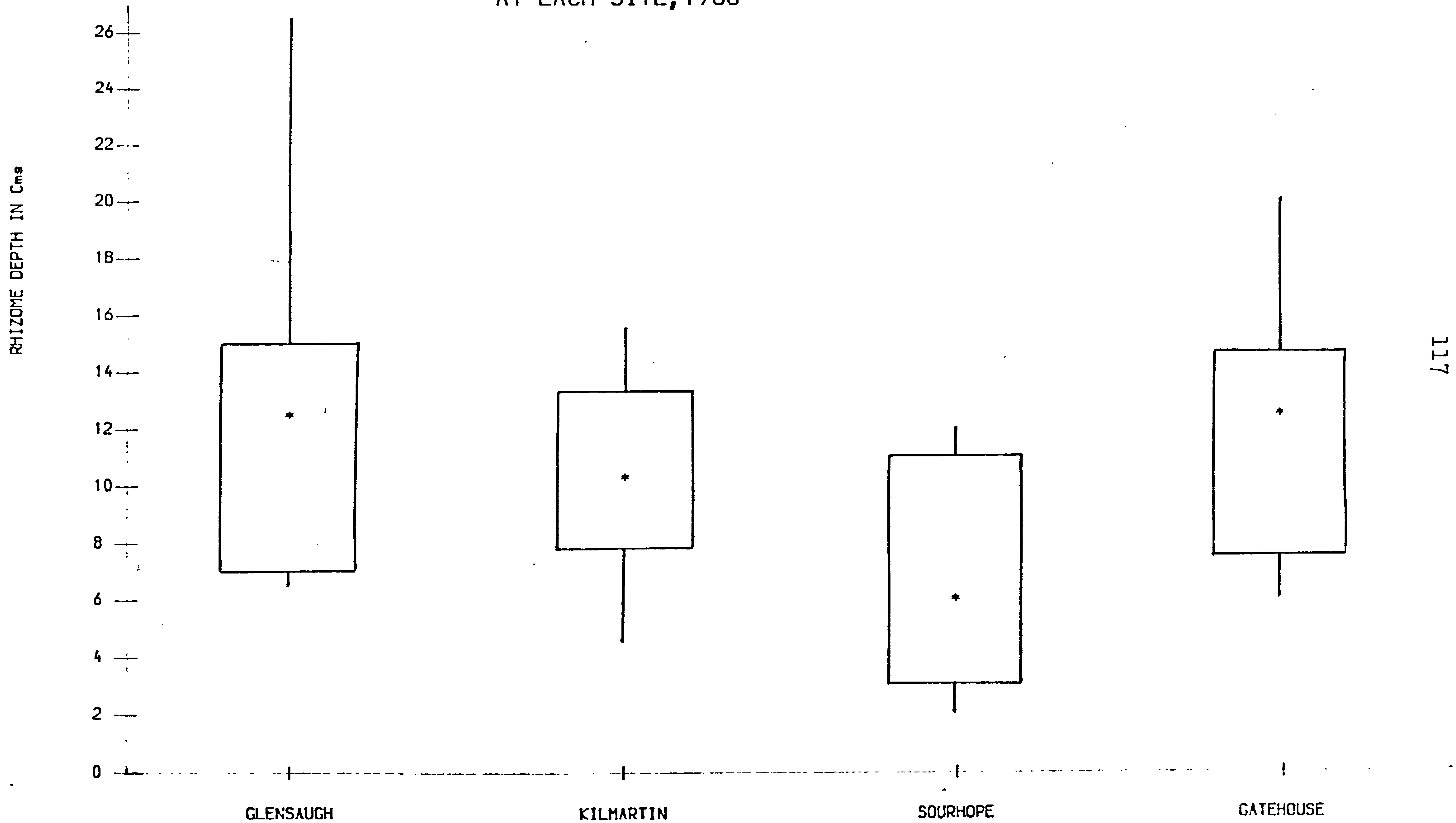
Comparison of the mean depth of the main area of rhizome concentration is shown in Fig. 6.6. Rhizome depth at Sourhope is generally shallower than at the other sites, a feature also observed in the extra soil pits that were dug at the site. Rhizomes under the crests (where the soil is most stony) were found to be particularly shallow, being concentrated in the thin mor humus layer.

6.4 The measurement of bracken vigour

As seen in Chapter Two various criteria have been used by other workers to measure bracken vigour including; frond density and height; length and weight of petiole, lamina, short and long shoot rhizome; weight of litter and complete frond. Biomass (dry weight) is the most accurate measure of vigour but frond density and height tend to be the most commonly used, being more practical to measure. It is recognised that the underground parts of the bracken plant make up the greater part of the total plant biomass (see Lee et.al. 1986; Williams and Foley 1976), but the dimensions and characteristics of the fronds will reflect underground vigour. Before advancing to the analysis of frond vigour, it is important that the criteria used to measure bracken vigour in this study, frond height and density (i.e. numbers per 1.5x1 metre plot) and litter depth are evaluated.

Mitchell (1976) used an index of vigour which combined density and height, i.e. $\frac{\text{Densityxheight}}{100}$, with density corresponding to frond number in a four square metre plot. Use of this index assumes that height and density are positively correlated and that both are equal indicators of bracken vigour. However, non significant correlations between frond density and height of the plots (using both plots at each posts) are obtained for both years (e.g.

FIG. 6.6 BOXPLOTS OF MEAN DEPTH OF RHIZOME CONCENTRATION AT EACH SITE, 1986



1986 r=-0.246, n=57). It was thought that the removal of the Sourhope plots from the correlation may make the relationship clearer since Sourhope has been shown to have shorter and denser bracken, but the resulting correlations are still non significant (e.g. 1986 r=0.120, n=43).

Litter depth is an indirect measure of biomass production, assuming that litter depth increases with biomass production and therefore vigour. Exposure and soil type may directly affect litter depth to some extent by wind removal and by affecting the rate of decomposition respectively. It is therefore a direct measure of the plant's success in dominating its environment (i.e. by reducing competition from sward species) and an indirect measure of frond vigour. Correlation of frond height and density with litter depth is shown below.

Table 6.6 Correlation of frond height and density with litter depth, 1985 and 1986

	Height(sq.rt.)	Density
1985 n=29	0.825 $p<0.01$	0.108 N.S.
1986 n=29	0.706 $p<0.01$	0.048 N.S.

(Only the plot at which litter depth was measured is used, hence the lower sample number than used for the correlations of height with density). Clearly frond height would seem a more accurate measure of bracken vigour. To elucidate this further, percentage litter cover from the total number of bracken plots sampled at the four sites is correlated against density and height. (As discussed in Chapter Four, further plots were sampled for the investigation into bracken spread). Litter cover is not as accurate a measure as litter depth, but is useful when used in large samples. Density is this time significantly correlated, (r=0.403, n=130, $p<0.01$) but certain samples have a strong influence on the correlation which cannot be removed by transformation, while omission results in other samples having the same effect which keeps reoccurring after repeated omission of "rogue" data. The correlation is therefore rather an untidy one. In contrast, the correlation with frond height is stronger ($r=0.766$, $n=130$, $p<0.001$) and is obtained by data transformation alone (square root of both variables). If density is correlated with height using the larger sample ($n=130$), a non significant result is obtained ($r=0.142$). If the Sourhope plots are removed from the analysis, a positive significant correlation is obtained ($r=0.445$, $n=93$, $p<0.001$)

Density would therefore seem to be an indicator of bracken vigour in certain circumstances, albeit rather a weak one. However, since the correlations of density with height and litter depth were not significant using the post data, the use of an index in the analysis of bracken vigour would be inappropiate. More consideration will therefore be given to the results of height in the analysis, although the effects of factors on density will still be examined.

6.5 Appraisal of environmental and bracken characteristics of the sites

The examination of bracken characteristics indicates that bracken at Sourhope is less vigorous than at the other sites, confirming the visual impression. In view of the difference in altitude between Sourhope and the other sites this result is not unexpected. Bracken vigour does not seem to vary greatly between the other three sites although there seemed a greater tendancy towards deep litter formation at the west coast sites.

Sourhope was shown to have the shallowest and most weakly structured soils and also the driest soils. Soil moisture stress exacerbated by shallow soil depth can therefore be hypothesised to affect bracken vigour at the site. This is borne out by the xeromorphic frond morphology which is unlikely to be caused by exposure, the findings of Chapter Five having shown exposure to be only marginally greater at Sourhope than at the west coast sites and nearly all the posts of the site to be in the Forestry Commission's "Very" and "Moderately Sheltered" exposure classes. Furthermore, bracken at equivalent exposures at the other sites does not have a xeromorphic frond morphology (e.g. Glensaugh Five and Gatehouse Three).

Contrary to the expected results, the degree and annual duration of frost was shown to be greatest at the west coast sites (except in winter) as a result of their lower altitude and temperature inversion, plus the microclimatic effect of their complex relief. This would suggest that frost is unlikely to be an important factor at Sourhope or indeed at any of the sites. Maximum temperature was found to be relatively low at Sourhope, again due to its higher altitude, but was found to be lower at Kilmartin in the middle and late growing season, as would be expected. This would suggest that maxima in the early season will be an important factor affecting bracken vigour at Sourhope (and therefore bracken generally). Mean temperature could not be monitored at the sites (except at the thermograph stations at Glensaugh), but predicted means show that Kilmartin and Gatehouse remain the highest of the four sites all season while remaining the lowest at Sourhope. (Mean temperature is predicted to be lowest at Glensaugh in May and June, but was shown to be higher than predicted at the site). Mean temperatures throughout the season or just in the early season may therefore be important to bracken vigour. The variation in maxima and predicted mean temperature between sites contrasts with the small variation in exposure which supports the hypothesis that temperature is more important than exposure in determining differences in bracken vigour between the sites. This does not mean to say that exposure has no effect on bracken vigour within the sites.

Despite its cold winters, mean and maxima at Glensaugh were shown to be similar to those of the west coast sites, from early spring on. It can be hypothesised that this warmer than expected local climate in spring and summer allows vigorous bracken growth in a region where vigorous bracken is not commonly observed.

The other factor that has not yet been considered is grazing pressure. The stocking rate at Sourhope is nearly three ewes per hectare in contrast to approximately one per hectare at the other sites and therefore grazing may well be affecting bracken vigour at Sourhope. The extent to which grazing affects vigour must be determined before the analysis of the other factors can proceed so as to decide whether it is necessary to take account of this factor (being unique to Sourhope it is likely to produce a "site" effect in the results). This is carried out in the next chapter.

Chapter Seven

The Effect of Grazing

7.1 Effect on bracken vigour

As described in Chapter Four, frond density and height and ground flora were recorded in 1x0.75 metre plots inside the enclosures (one plot per enclosure) at Sourhope in 1986 after differences in vigour were noticed between bracken inside and outside the enclosures in 1985 (see Fig. 7.1) To produce plots of comparable size the post plots were divided in half and each half counted separately at the final frond count. Frond height was still taken to be the average of the whole plot. Figs. 7.2 and 7.3 show comparisons of frond height and density between post and enclosure plots. It is not possible to test for significant differences between enclosure and respective plots because only one measurement is available for the enclosure bracken. The heights of both plots at each post and densities in the four half plots (scaled up to number per square metre) are compared with the respective enclosure plot. There would seem to be less variation in height than in density between enclosure and adjacent plots.

The apparent decrease in height in Enclosure Four results from the location of the plots a little distance away from the posts because of trampling around the enclosure soon after erection. Enclosure bracken is taller than adjacent plot bracken at Posts Two and Eight, less so at Posts One and Five and only possibly so at Posts Six and Seven (where enclosure bracken is only taller than one

Fig. 7.1 Bracken at Sourhope Eight, August 1985

FIG. 7.2 COMPARISON OF FROND HEIGHTS BETWEEN POSTS AND ENCLOSURES AT SOURHOPE 1986

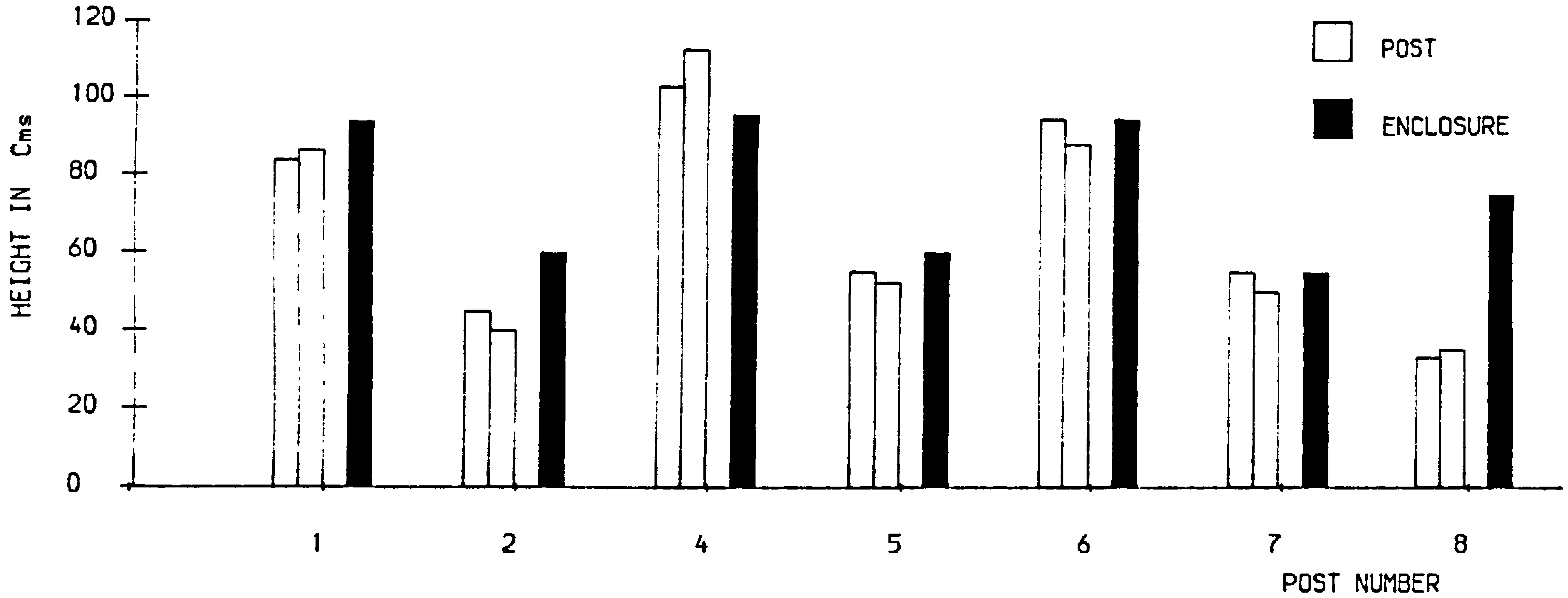
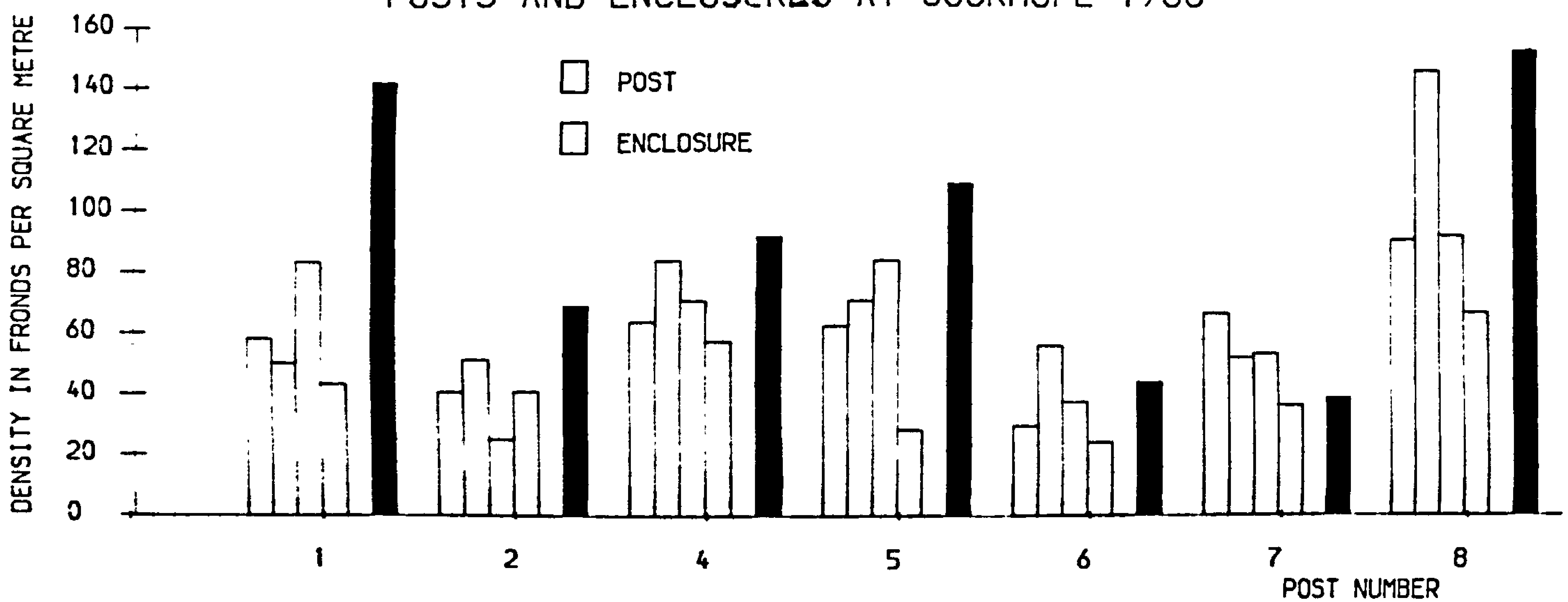


FIG. 7.3 COMPARISON OF FROND DENSITIES BETWEEN POSTS AND ENCLOSURES AT SOURHOPE 1986



of the post plots). Frond density is greater in the enclosures than in adjacent plots except at Posts Six and Seven.

Fig 7.2 shows up to 50 percent difference in height between grazed and ungrazed bracken, the shorter stands of Posts Two and Eight showing the greatest difference. These findings concur with the work of Lee et.al (1986) who found similar differences of frond height after exclusion of grazing. Both cattle and sheep are grazed at Sourhope and it is difficult to distinguish which are affecting frond vigour. Lee et.al. dealt with sheep at only a slightly higher stocking rate (3.2 ewes per hectare) than at Sourhope and therefore it is possible that the differences in vigour at Sourhope could have been caused by sheep alone.

Lee et.al. found that frond mortality decreased in ungrazed bracken, but no data are given on the effect of are/ this on frond density. Numbers of fronds broken through trampling (actual grazing of the frond being rare) in one plot at each post is shown below in Table 7.1. (Percentage mortality will only be meaningful for comparisons between posts if it represents percentage of numbers present at the time of breakage).

Table 7.1 Numbers of fronds broken during the whole growing season at Sourhope, (one plot per post)

	Post No.						
	1	2	4	5	6	7	8
1985	42	12	2	3	4	2	27
1986	38	-	5	-	-	-	5

The indications are that grazing is heaviest at Posts One and Eight and this is reflected in Fig. 7.3 which shows these two enclosures to have the greatest increase in frond density. The increase in frond height at Post Eight is quite marked, but less so at Post One although enclosure height is still greater than both the post plots. This is in contrast to Post Six which is of similar height, but which showed no obvious increase in frond height or density. Both Post One and Six are located on similar soils on north facing slopes in sheltered stream valleys on either side of Dodd Hill. However, Post Six is much less accessible from the main valley and has a slope of 20° in contrast to the slope of 14° at Post One. Post Seven on the opposite side of the valley to Post Six and with a slope of 26° also shows little or no increase in frond height or density. The most accessible post at the site, Post Eight, located on the lower valley slopes with a slope of only 9°, showed the greatest increase in both height and density. The indications are that accessibility is important in determing the degree of grazing pressure on a bracken stand.

Lee et.al (op.cit) found grazing to have most effect on shorter bracken, which implies that intrinsically taller stands are less liable to grazing in the later season, in contrast to the continuous grazing in the shorter stands. Bracken that is stressed by other factors (and is therefore relatively short) is more accessible to animals and more heavily grazed than unstressed bracken, creating a negative feedback effect. For example, the stand showing the greatest increase in height after Post Eight was at the most exposed post, Post Two. The amount of grazing pressure on a stand is therefore not only determined by accessibility in terms of location, but also in terms of the stand's intrinsic vigour. This interaction of factors is further demonstrated by the generally later senescence of the enclosure bracken, occurring up to a month after adjacent unenclosed bracken. Braid (1947) reported later senescence in bracken experimentally screened off from the wind. The very open mesh of the enclosures makes it more likely to be the increased height and density of the bracken that is reducing the effect of wind by creating a wind break effect (see Pears 1967) within the stand. Smith (1986) hypothesised that soil water stress could cause early senescence. It may be that moisture stress of the enclosure bracken is reduced by the reduced exposure, thus the later senescence.

The other factor that is likely to determine the degree of grazing pressure will be the sward type under the bracken. Ground flora under the more vigorous crests is generally of less desirable acidic species. This may either be a result of the greater amount of bracken litter or of the fact that the mor humus layer is better developed in the crests. Whatever the reason, a positive feedback effect is created with the animals grazing the crests more lightly than the Agrostis-Festuca hinterland bracken. Lee et.al. (1986) describe a similar effect between bracken on Deschampsia flexuosa and Agrostis dominated grassland. Whether or not differential grazing could have created the differences in vigour between crest and hinterland is discussed in Chapter Eight. The fact that Post Eight, (a crest stand) and Post One (one of the most vigorous stands at the site with a mor humus layer of up to 10cms depth) were both shown to be relatively heavily grazed, suggests that stand accessibility is the most important factor determining grazing pressure on bracken stands.

The other visible effect of enclosure was to produce generally closed and even canopies in contrast to the clumped distribution of the grazed bracken, especially of the shorter hinterland bracken. These clumps are often aligned on the runrig forming clear lines of bracken. This suggests the creation of paths in the stands by the grazing animals, possibly following the least line of resistance (thus the alignment with the runrig). The fact that the number of broken fronds counted at each post does not nearly account for the increases in frond density in the enclosures suggests that the paths are created by trampling of the emerging and even unemerged "hooks" just below the surface. This is supported by Hunter's finding that grazing in bracken stands is heaviest in early spring just before emergence (Hunter 1962). The early establishment of "paths" would explain why density seems to be more affected than height in the tall stands. Thus once the paths are established, the animals (including cattle) do not range into the tall bracken, the height of which is therefore relatively unaffected. This is supported by the observation that fronds in the taller stands remain relatively intact throughout the season, in contrast to the often very tattered fronds of the shorter stands where the animals range more freely. In both years cattle were put out to graze later than sheep, which suggests that sheep alone were responsible for the initial trampling and "path" creation.

The lack of increase in density at the lightly grazed Posts Six and Seven suggests that the large increases in density at the heavily grazed Posts One and Eight are merely short term responses to the cessation of grazing. This hypothesis is supported by comparison of bracken on either side of a plantation fence (Fig. 7.4) erected about thirteen years ago below Posts Three and Four. Density was found to be significantly lower ($p<0.05$) inside the enclosure using six randomly placed plots on each side of the fence. This suggests that in the long term relaxation or cessation of grazing pressure reduces frond density. However, height was found to be significantly greater inside the enclosure ($p<0.01$), indicating that increased height is not just a short term response to the cessation of grazing.

The response of bracken to grazing may be the compensatory production of more but shorter fronds, resulting in relatively high frond densities (despite the destruction of a certain proportion of the emerged

Fig. 7.4 Bracken after thirteen years of enclosure
at Sourhope

population). If grazing ceases, all the emerging fronds will survive, further increasing density. The increase in height may not be so immediate. For example, the increase in height in the first season at Enclosure Eight was only half that in the second season (shown by comparison of Fig. 7.5 with Fig. 7.1). Assuming height to be a better indication of vigour than density, it can be hypothesised that eventually an equilibrium between height and density will be reached with the concentration of biomass into tall robust fronds. Atkinson (1986) noted that frond density was increased and height decreased immediately after burning, but several years after the burn the reverse was true. The hypothesis that moderate grazing pressure may increase frond density and decrease frond height is supported by other work on bracken control. As discussed in Chapter Two, light cutting and burning was found to have the same effect (Institute of Terrestial Ecology 1979; New Zealand Forest Research Institute 1978), although more frequent treatments will eventually reduce stand biomass (I.T.E. op.cit; Preest and Cranwick 1978), as will heavy trampling.

At Glensaugh no visible differences were observed in bracken dimensions inside and outside the thermograph enclosures. However, "clumped" bracken does occur in the stands on *Agrostis* - *Festuca* grassland and there are visible lines of bracken on the runrig on the valley floor. This contrasts with the more even distribution of the fronds in the vigorous litter covered stands. Without adjacent enclosures it is impossible to determine whether the "clumped" pattern results from heavier grazing, as indicated at Sourhope, or whether it is an intrinsic feature of the stand. (Watt (1947) maintained that the effects of competition would produce a clumped pattern in the hinterland bracken). As will be discussed in Chapter Eight, the more vigorous litter covered bracken stands at Glensaugh are generally on the podsols, which again raises

Fig. 7.5 Bracken at Sourhope Eight, August 1986

the question of the effects of differential grazing. It is interesting that at Gatehouse, where the absence of Calluna and Nardus below the head dyke will result in more even utilisation of the grazing, the clumped pattern is not evident in the bracken-and-grass. No obvious differences in frond height or density between the two years were noted at Kilmartin after the site was fenced off in early spring in 1986. Indeed, comparison of plots that were used in both years shows height to be slightly greater in 1985.

It would seem therefore that grazing is having a significantly greater effect on bracken vigour at Sourhope than at the other three sites. As already suggested, this could cause a "site" effect in the analysis of bracken vigour and account must be taken of this. Frond height is adjusted if enclosure bracken was higher than in both of the post plots. The mean difference between enclosure height and mean plot height was added to the latter. Density was not adjusted because of the indications that increased density in the enclosures is only a short term response. Density should possibly be adjusted downwards as it is suspected that moderate grazing pressure actually increases density, but the lack of any "baseline" data makes it impossible to realistically do this. This problem, plus the fact that the Sourhope bracken is possibily intrinsically different from that of the other sites (as indicated by its xeromorphic frond morphology) made it prudent to carry out later analysis of vigour with and without the inclusion of the site.

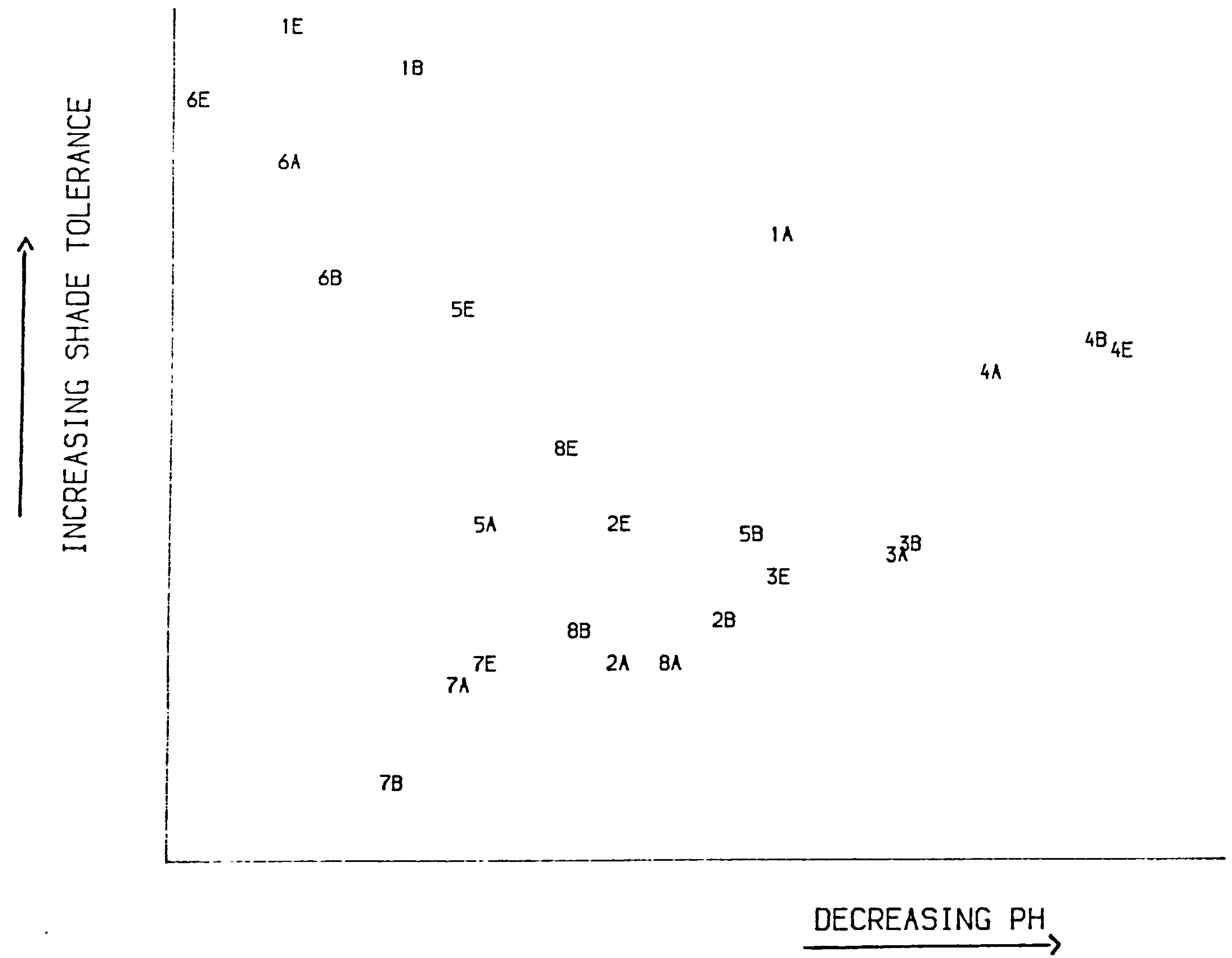
7.2 Effect on ground flora

Ground flora was recorded in the enclosure plots at the same time as the post plots at the end of the second growing season. Comparisons between post and enclosure ground flora are made by Detrended Correspondance Analysis. All the plots that were recorded at Sourhope (including the extra plots recorded in the investigation into bracken spread) were entered into the ordination. The two axes again reflected trends for pH and shade tolerance (as found in the ordinations of the post plots in Chapter Six). Fig. 7.6 shows the plot ordination with all but the post and enclosure plots omitted for clarity.

All the enclosure plots are placed to the left of their respective post plots (i.e. towards the less acidic end of the first axis) except at Posts Four and Seven. This reflects the reduction in Nardus as other more palatable species which would be normally eaten out become more abundant. The location of Enclosure Seven to the right of its respective post plots suggests that cessation of grazing had the opposite effect. The soil at Post Seven is colluvially flushed and supports a fairly diverse mesotrophic sward which includes Deschampsia caespitosa and Poa pratensis, but in which Nardus stricta is a minor element. Cessation of grazing resulted in the growth of the more vigorous tussock Nardus, thus the location of the enclosure plot towards the right of the axis. All except Enclosures Three and Four are placed above their respective post plots on the second axis (i.e. towards the shade tolerant end), reflecting an increase in abundance of shade tolerant species. Post Three is in bracken free Nardetum and no such movement up the second axis would be expected. The lack of movement to the right or up the second axis by Post Four is probably because the bracken, which has a complete litter cover and a very sparse ground flora, was unlikely to have been grazed much prior to enclosure.

The most obvious change in ground flora under the bracken after enclosure was the increase in abundance of Holcus mollis and Oxalis acetosella, not only under the relatively inaccessible bracken where these species were relatively abundant prior to enclosure, but also under the bracken on the old runrig. King and Nicholson (1964) also noted the increase in proportion of Holcus mollis in

FIG. 7.6 DETRENDED CORRESPONDANCE ANALYSIS OF GROUND FLORA PLOTS AT SOURHOPE (ONLY POST AND ENCLOSURE PLOTS SHOWN)



grassland under a closing bracken canopy. As discussed in Chapter Six, the presence of Oxa~~l~~is acetosella on old runrig demonstrates that bracken can provide a suitable habitat for recolonisation by certain woodland species as well as merely representing sites of woodland "refugia" .

Observations made during field work indicated that soils were probably the most important factor controlling bracken vigour within the bracken zone. The effect of soils is therefore considered first in the analysis of factors controlling vigour. In the next chapter a statistical analysis of the effect of soils on vigour is followed by examination of the types of soils and vegetation on to which bracken has or has not spread at each site in the past forty years.

Chapter Eight

Soils and bracken vigour

8.1 Soil and frond vigour

8.1.1 Soil and frond height

Frond height according to soil type is shown in Fig. 8.1. which shows that bracken is clearly able to grow vigorously on podsols. As discussed previously, sampling did not include sparse bracken in Calluna, which results in a narrower range of height and apparently greater vigour in the podsol class. The results of the correlation analysis are shown in Table 8.1 below. As discussed in Chapter Seven, correlations are also tried omitting Sourhope. (With the use of categorical data, distribution of the variables rather than the residuals is checked for normality).

Table 8.1 Correlation of soil type with frond height

	1985		1986	
	4 sites	3 sites	4 sites	3 sites
	n=29	n=22	n=29	n=22
Acidic brown earths	-0.130	-0.001	-0.063	0.039
Podsols	0.415* R^2=14.1	0.346	0.185	0.259
Mesotrophic brown earths	-0.257	-0.367	-0.212	-0.287

*p<0.02

FIG. 8.1 BOXPLOTS OF FROND HEIGHT BY SOIL TYPE

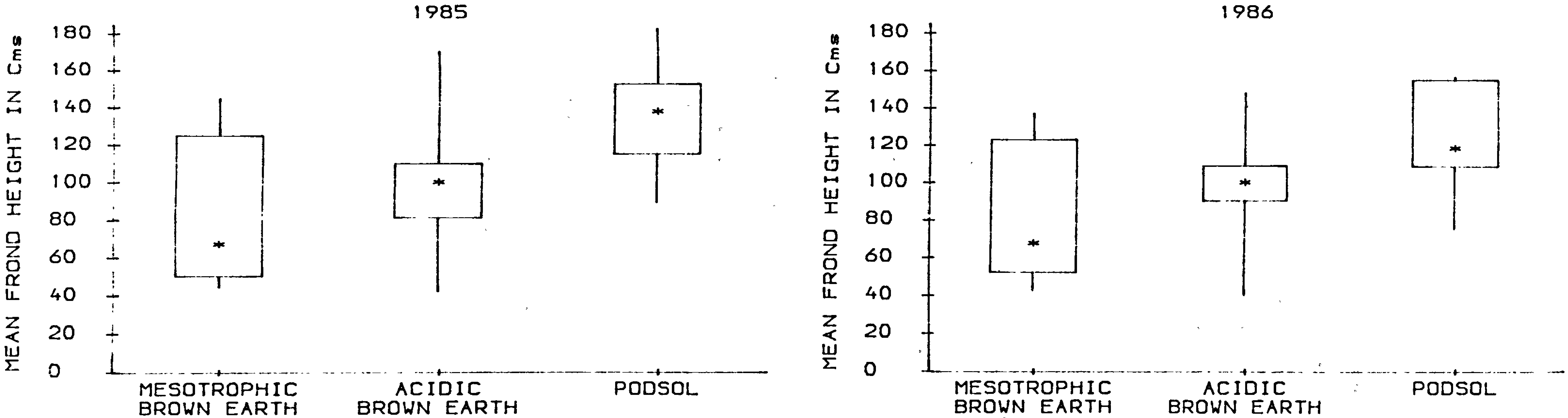
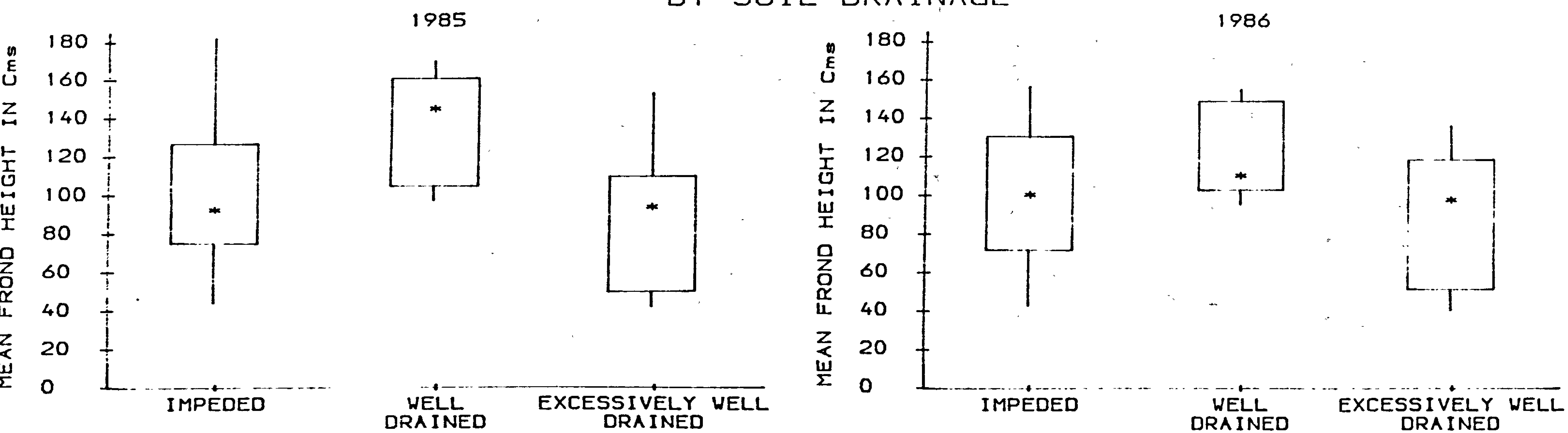


FIG. 8.2 BOXPLOTS OF FROND HEIGHT BY SOIL DRAINAGE



The only significant correlation is obtained on the podsols in 1985 when all four sites are included. The non-significant correlation with this soil type in 1986 reflects the relocation of posts. Thus when a a wider range of heights is sampled on the podsols, there is no relationship between soil type and vigour. The occurrence of vigorous bracken on both mesotrophic brown earths and podsols, supports the hypothesis that up to a certain limit, pH does not affect bracken vigour. (As discussed in the Literature Review, a high pH and/or high calcium levels may restrict vigour, but as yet there is no definitive work on this). It was observed that towards the end of the growing season, the tall bracken on the well-drained mesotrophic soils (e.g Gatehouse Five and Six and New Glensaugh One) tended to fall over under its own weight. Discussion with other bracken workers revealed that similar observations had been made when nitrogen was applied to growing stands.

Frond height according to soil drainage (impeded, well-drained and excessively well drained) is shown in Fig. 8.2. Height would seem to be greatest overall on the well-drained soil, although maximum height in this class is similar to that of the poorly drained soils. Vigorous bracken was recorded on both the periodically gleyed soils at Gatehouse and the permanently gleyed soils at Kilmartin. The lack of clear differences in frond height between the soil classes is confirmed by the correlation and regression results, shown in Table 8.2 below.

Table 8.2 Correlation of soil drainage with frond height

	1985		1986	
	4 sites	3 sites	4 sites	3 sites
Impeded	-0.053	-0.244	0.033	-0.163
Well drained	0.470** R^2 =19.2	0.402	0.317	0.251
Excessively well drained	-0.381* R^2 =11.3	-0.151	-0.281	-0.054

*$p<0.05$ **$p<0.01$

Significant correlations are only obtained for two soils in 1985 with all four sites, with height increasing on the well-drained soils and decreasing on the excessively well-drained soils. In both cases the correlation and amount of variation accounted for are low. This would suggest that drainage is not that important to frond vigour. However, as already observed at Gatehouse, fine roots do not penetrate far into the gleyed horizons in any of the profiles which must suggest otherwise. It was observed that the gleyed horizon occurred lower down the profile in soils supporting vigorous bracken than in soils supporting short weak bracken. Depth of gleying may therefore have to be taken into account in the analysis. A separate factor for depth of gleying would not be relevant to the non-gleyed soils and cannot therefore be used. Instead depth of gleying must be accounted for within the poorly drained soil class and to this end, soils are only classed as poorly drained if gleying occurs above a depth of 30cms. This is the depth of water table at which Smith (1986) found the limit of bracken growth to occur (although in the present study bracken was found to grow, albeit at reduced vigour, where gleying occurred at or above this depth).

The gradual increase in mottling down the profile of many of the Gatehouse soils makes determination of depth of the gleyed horizon difficult. An arbitary degree of mottling, i.e. 50 percent of the soil face, was therefore used to determine the gleyed horizon. Depth of profile above the gleyed layer has to be interpreted as depth of well aerated rooting substrate. Not only must the humus layer of the podsols thus be taken into account, but also the deep litter layers on some of the podsols and brown earths, fine roots being observed to grow vigorously in the F and L layers under vigorous bracken. Organic matter is usually considered to be poorly aerated. Watt (1976) contended that accumulating litter and humus may cause poor aeration. However, if this were the case, fine roots would be expected to be absent from the organic layers as they are from the gleyed horizons. As discussed in Chapter Two, other workers (e.g. Anderson 1961; Mitchell 1977) have commented on the ability of bracken to physically cultivate the soil, Anderson contending that the hollow bases of the dead fronds improve local soil aeration. The hypothesis that bracken can improve aeration in organic soils is supported by the observations in this study that the rhizomes and fine roots confer a blocky structure to the humus layer of the podsols.

The nature of bracken growth also has to be taken into account when considering the effect of excessive drainage on bracken vigour. It is not excessive drainage per se that is likely to affect bracken vigour, but rather the resulting low soil moisture content. (This is the opposite situation in poorly drained soils where it is poor aeration rather than water content per se that is detrimental to growth). All the mineral horizons of the excessively well-drained soils were either "slightly moist" or "dry" at the time of sampling (October-November) and throughout much of the summer. However the organic horizons of all but one of the podsols in this catergory were found to remain moist. Bearing in mind the concentration of the rooting systems in this horizon, it is unlikely that soil moisture will be limiting to the bracken on these soils. The mor humus at Station Two (not included in the correlation analysis) was found to be very dry and friable during the summer. This profile was one of the two podsols examined that did not have complete bracken litter cover (the other being Glensaugh Eight where the surface water gley prevented the humus horizon from drying out). Contrary to Smith's (1986) contention that a deep litter will result in soil moisture stress, this suggests that a litter cover is instrumental, at least on peaty soils, in maintaining soil moisture levels.

Rooting depth will also be important in dry soils. Lockwood et.al (1986) found that 70 percent of total soil moisture loss down to a depth of 150cms occurs in the top 50cms under bracken, while Watt (1964) found a positive correlation between soil depth and bracken vigour and related this to soil moisture availability. Account should therefore be taken of available rooting depth, but a separate factor for soil depth will only be relevant to bracken on dry soils. Soils in which the rooting susbstrate is either classified as slightly moist or dry and in which rooting depth is physically restricted to less than 50cms are therefore separated from those with a dry mineral soil but with either a thick moist organic layer or unrestricted rooting depth. Restrictions to rooting depth include, shallow and excessively stony soils, relict iron pans (i.e. in the podsolic brown earths at Kilmartin Four and Five) and fragipans.

The analysis now takes into account conditions of bracken growth. There are three classes of soil as follows:

"Poorly aerated" - in which there is less than 30cms well aerated rooting substrate

"Very well aerated" - in which the rooting horizons are only slightly moist or dry and in which rooting depth is physically restricted to less than 50cms.

"Well aerated" - all remaining soils.

(Nomenclature does not follow any standard system and the the soil classification is termed "soil aeration" from hereon). Classification of the posts according to "soil aeration" is shown in Table 8.3 below.

Table 8.3 Classification of soils by "soil aeration"

"Poorly aerated"			"Well aerated"				"Very well aerated"		
GS3	KM6	NGH1	OGS1	KM1	OGH1	SH1	GS6	KM4	SH2
GS8		GH4	NGS1	KM2	GH2	SH6		KM5	SH4
		GH8	GS4	KM3	GH3				SH5
			GS5	KM7	GH5				SH7
			GS7	KM8	GH6				SH8
					GH7				

GS=Glensaugh KM=Kilmartin GH=Gatehouse SH=Sourhope
O=Old post N=New post

Frond height in the three classes is compared in Fig. 8.3. Height is clearly greatest on the "well aerated" soils and there is very much less variation within the classes than in the previous two analyses. Correlation and regression results are shown in Table 8.4 below.

FIG. 8. 3 BOXPLOTS OF FROND HEIGHT BY "SOIL AERATION"

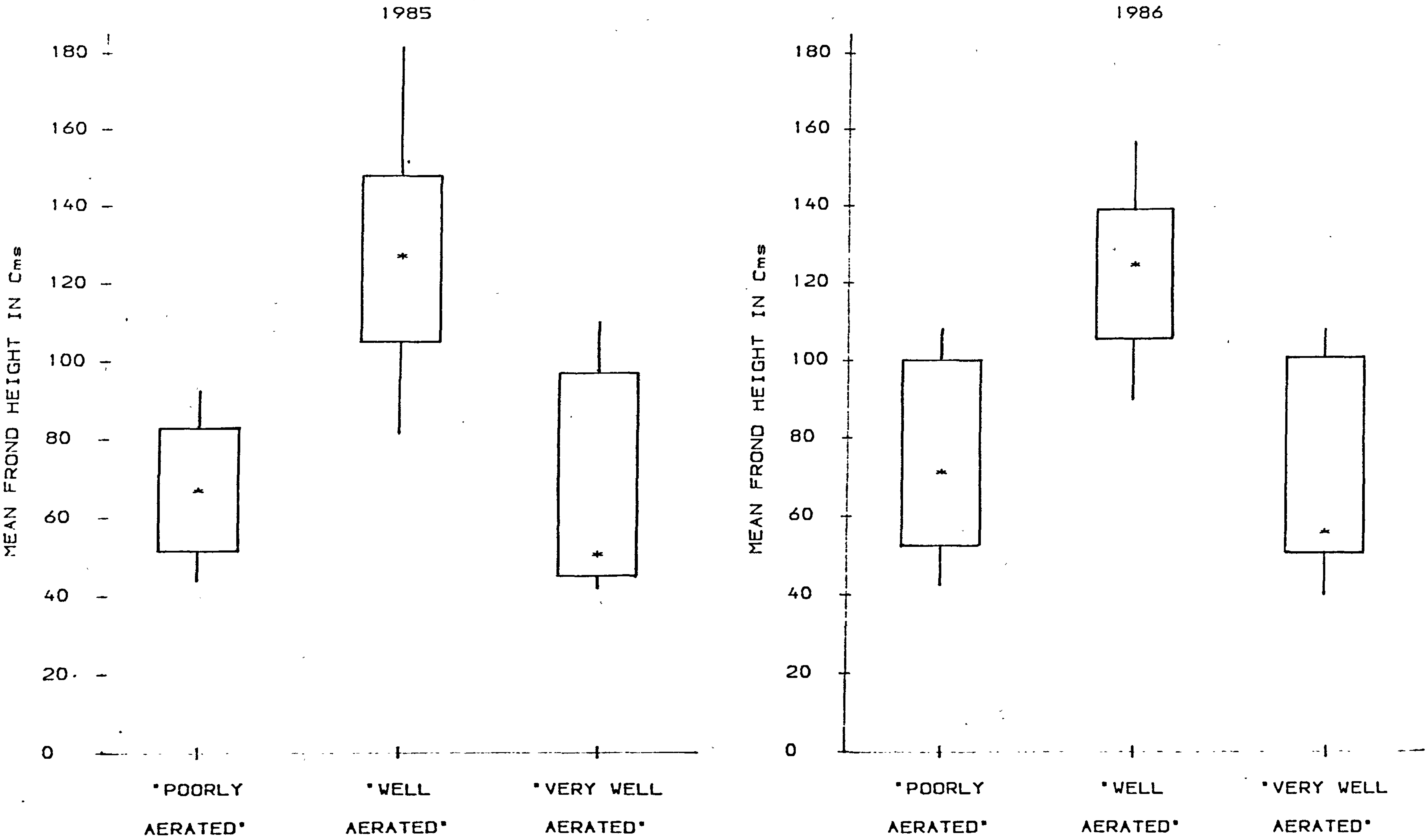


Table 8.4 Correlation of "soil aeration" with frond height

	1985		1986	
	4 sites	3 sites	4 sites	3 sites
"Poorly aerated"	-0.356* R^2=9.5	-0.600*** R^2=32.8	-0.353* R^2=9.3	-0.591*** R^2=31.7
"Well aerated"	0.744*** R^2=57.0	0.731*** R^2=51.1	0.730*** R^2=51.5	0.749*** R^2=54.0
"Very well aerated"	-0.545** R^2=27.1	-0.318 R^2=5.6	-0.495* R^2=21.7	-0.307 R^2=4.96

*p<0.05 **p<0.01 ***p<0.001

All three classes are significantly correlated, with over 50 percent of the variation accounted for by the "well aerated" catergory in both years. As in the analysis of soil drainage, the "poorly aerated" class has the lowest correlation with less than 10 percent of variation accounted for when four sites are used. However the correlations improve when Sourhope is omitted with the class now accounting for over 30 percent of variation in both years. This contrasts with the lack of significant results when height is correlated with the "poorly drained" class, supporting the hypothesis that depth of gleying rather than gleying <u>per se</u> is important to frond vigour.

As discussed above, the organic horizons have to be taken into account when calculating the depth of the gleyed horizon if these contain part or all of the rooting system. Depth of gleying may therefore be deeper in a podsol than in a brown earth when the gleyed layer is at an equivalent depth in the mineral profile. For example, the gleyed horizon occurs at the same depth in the mineral soil at Kilmatin Six and Seven (located within ten metres of each other). The available rooting depth at Kilmartin Six, a brown earth, is only a third of that at Kilmartin Seven, a peaty podsol. Mean frond height at Kilmartin Seven is twice as high as that at Kilamartin Six.

The lowering of the correlation in the "very well aerated" class on omission of Sourhope demonstrates that to some extent the site creates a "site effect". It is therefore difficult to determine the effect of soil moisture deficit on frond vigour because of the small number of posts remaining after Sourhope is omitted. However observations at Glensaugh would seem to support the hypothesis that a relatively dry soil reduces vigour if rooting depth is restricted. At the two posts with dry soils but unrestricted rooting depth (Post Four and New Post One), fine roots penentrate to nearly one metre depth. These two soils are brown earths with deep almost undifferentiated profiles, located in small gulleys on the steep lower slopes. (Nicholson and Robertson (1958) also described deeply penetrating bracken in such soils at Glensaugh). In contrast, fine root penetration is more limited at the shallower stonier brown earth at Post Six on the gentler slopes above. Mean frond height at Posts One and Four in 1986 was 126cms (152 cms at Post One), but only 93cms at Post Six. Both the deep soil posts have a complete litter cover, but Post Six, an <u>Agrostis</u> ground cover. The rest of the extensive stand of Post Six is of similar character and exploratory pits revealed the same shallow stony soil throughout.

The highly significant correlations and high percentage variation accounted for by the "well aerated" class confirm the importance of depth of gleying, soil moisture content and rooting depth to bracken vigour. A "t" test between the peaty soils and the brown earths in the "well aerated" class showed no significant difference in frond heights, confirming the ability for vigorous growth on peaty soils once the substrate has been opened up and aerated by the rhizomes. This process of rhizome colonisation and "cultivation" is further discussed in Section 8.2

The use of fixed arbitary depths of gleying and of rooting in dry soils can only demonstrate the approximate relationship between these factors and bracken vigour. The relationship between bracken vigour and depth of gleying and soil moisture deficit is likely to be linear rather than one determined by a sharp cut off point. Determination of these relationships would require quantification of oxygen diffusion rates and of soil moisture contents.

8.1.2 Soil and litter depth

Table 8.5 shows correlation and regression results for the three catergories of soils. As found in the analysis of frond height, the most significant results are obtained with the "soil aeration" catergory. Fig 8.4 compares litter depths according to this catergory. The greatest depth clearly occurs on the "well aerated" soils, although there is wide variation within the class. As discussed in Chapter Six, other factors such as different rates of decomposition and wind removal will also affect litter depth.

Watt (1976) maintained that as litter accumulated, so would the rhizomes have to progressively rise up the profile and eventually grow in the litter, leading to eventual degradation of the stand through nutrient deficiency and increased susceptibility to frost. However he only observed fine roots and not rhizomes in the litter and in the present study rhizomes were not observed above the F layer. Table 8.6 below shows depths of the shallowest and deepest rhizomes and the range of the main concentration of rhizomes in mature stands (i.e. with a complete litter cover) on brown earths.

Table 8.5 Correlation of litter depth with soil type, drainage and "aeration"

a). Soil type

	1985		1986	
	4 sites	3 sites	4 sites	3 sites
Brown earth	0.017	0.155	-0.001	0.134
Podsol	0.331	0.215	0.154	0.243
Mesotrophic brown earth	-0.376* R^2=10.8	-0.413	-0.186	-0.371

b). Soil drainage

	1985		1986	
	4 sites	3 sites	4 sites	3 sites
Impeded	-0.046	-0.161	0.073	-0.079
Well drained	0.411* R^2=13.8	0.385	0.381* R^2=11.5	0.375
Exccessively well drained	-0.369* R^2=10.4	-0.225	-0.392* R^2=12.3	-0.285

c). "Soil aeration"

	1985		1986	
	4 sites	3 sites	4 sites	3 sites
"Poorly aerated"	-0.455** R^2=17.7	-0.571*** R^2=29.3	-0.329	-0.534** R^2=25.0
"Well aerated"	0.704*** R^2=47.6	0.690*** R^2=45.1	0.582*** R^2=31.5	0.659*** R^2=40.0
"Very well aerated"	-0.449* R^2=17.1	-0.295	-0.353	-0.252

*$p<0.05$ **$p<0.02$ ***$p<0.01$

Data transformation: 4 sites-logten 3 sites-square root

FIG. 8.4 BOXPLOTS OF BRACKEN LITTER DEPTH BY "SOIL AERATION"

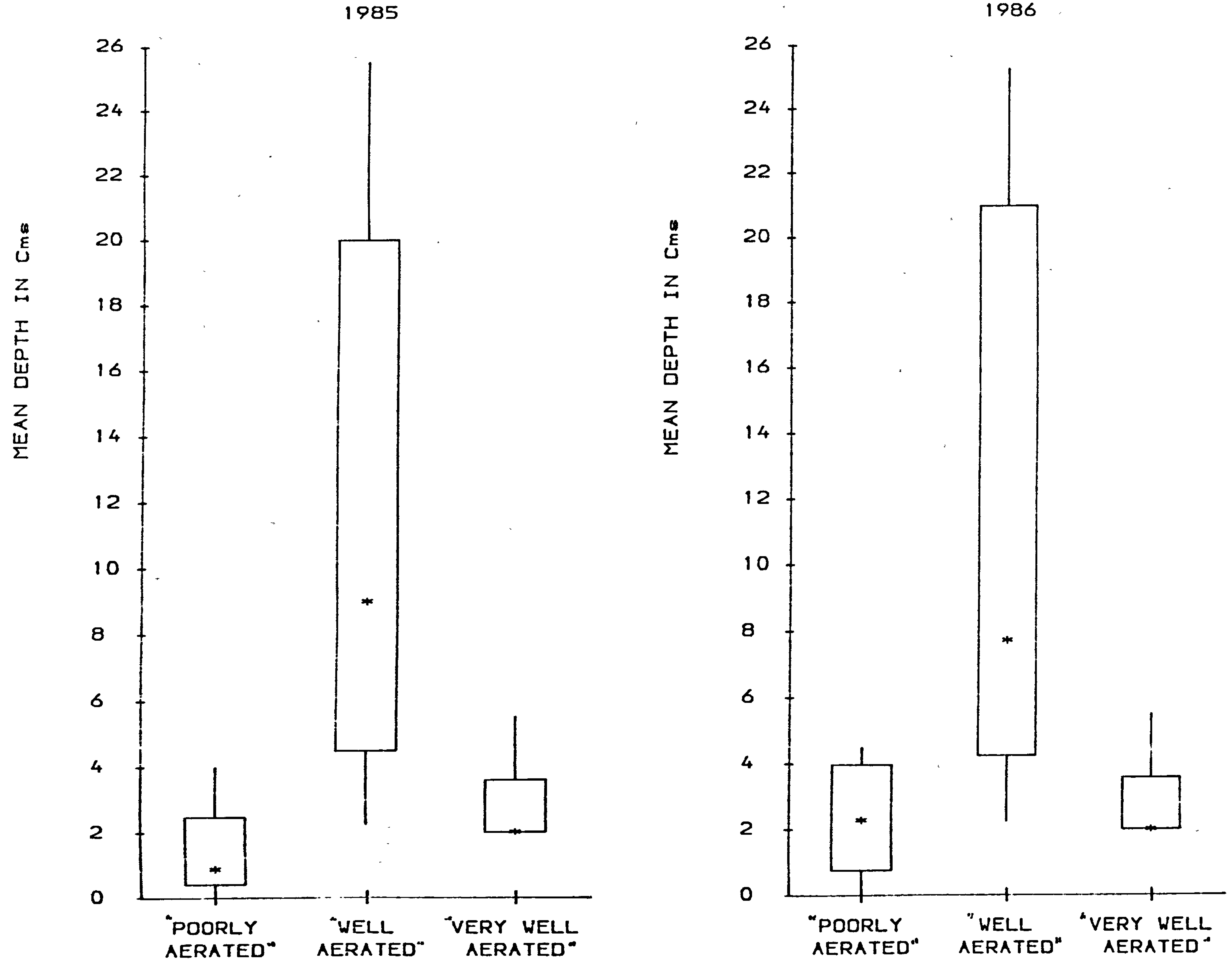


Table 8.6 Rhizome and fine root depths (cms) in mature stands on brown earths, depths from top of mineral soil.

	KM2	OGH1	GH2	GH3	GH5	GH6	GS4
Shallowest rhizome	5.0	2.0	0.0	0.0	4.0	6.0	8.0
Deepest rhizome	26.0	28.0	23.0	32.0	26.0	28.0	50.0+
Area of rhizome concentration	5-26	5-18	0-12	5-24	4-26	8-20	15-38
Deepest fine root	25.0	36.0	28.0	37.0	35.0	40.0+	75.0+

All the soils have a relatively unrestricted rooting depth and a fine root network in the lower litter layers. The "Deepest" rhizomes in the above table are also the deepest at all the posts, which suggests that it is only the upper frond bearing rhizomes that rise up the profile. Meaningful comparisons with stands of equivalent character to Watt's colonising and building phases are not possible as bracken at all but two of the litter-free posts is soil stressed. Soil factors rather than stage of stand succession therefore probably determine stand type and rhizome depth. Rhizome depth in the degraded podsols is generally shallower than in the brown earths (Sourhope excluded), but as already discussed, the indications are that rhizomes (and fine roots) are concentrated in the mor humus horizon for reasons other than stage of stand succession. However, even without the opportunity to compare depths in earlier stages of succession, the depths of "deepest" rhizome and area of rhizome concentration in Table 8.6 can be considered as being relatively deep.

The situation is less clear as to what extent the upper rhizomes rise up the profile as litter accumulates. The depths of the shallowest rhizomes suggest that this has happened at some of the posts. More samples are needed to determine this question. However it is clear that far from becoming isolated from the mineral soil as Watt suggests, much of the rhizome system in brown earth soils remains deep in the profile.

8.1.3 Soil and frond density

Table 8.7 shows correlations of frond density with all three soil catergories to be low. Density according to "soil aeration" is shown in Fig. 8.5. Poor soil aeration accounted for over 20 percent of variation in 1986 (with and without Sourhope), density being decreased by poor aeration. The indications are that density is increased on the dry soils, with significant correlations occurring using both the soil drainage and "soil aeration" catergories. The non-significant correlations obtained when Sourhope is omitted again demonstrates a "site effect". As discussed in Chapter Seven, the moderately heavy grazing at Sourhope may result in higher than usual densities. With only three soils in the "very well aerated" soil class after Sourhope is omitted, it is impossible to separate the effects of grazing and dry soils on density. The effects of soil moisture stress and exposure upon frond morphology are reputed to be similar (and this would seem to be the case at Sourhope where the xeromorphic frond morphology is unlikely to be caused by exposure, as discussed in Chapter Six). It may therefore be logical to assume that the effects of dry soils and exposure upon frond height and density are also the same. The analysis of the effects of exposure may therefore be useful in this respect.

Further examination of the relationship between height and density is important to the question of density control. As discussed in Chapter Six, correlations of frond density with height at the posts were non-significant as were correlations using all the plots sampled. When Sourhope was omitted from the larger sample the correlation became positive and significant, but still relatively weak. Fig. 8.6 shows the scatter of plots of the larger sample with and without Sourhope. An inverted 'V' shape is apparent in both graphs, although the

Table 8.7 Correlations of frond density with soil type, drainage and "aeration".

8.7(a) Correlation of frond density with soil type.

Soil type	1985 4 sites	1985 3 sites	1986 4 sites	1986 3 sites
brown earth	0.274	0.114	0.416* R^2=14.3%	0.376
podsol	-0.161	0.024	-0.225	-0.246
mesotrophic brown earth	-0.172	-0.162	-0.217	-0.191

8.7(b) Correlation of frond density with soil drainage.

Soil drainage	1985 4 sites	1985 3 sites	1986 4 sites	1986 3 sites
impeded	-0.399* R^2=12.8%	-0.483* R^2=19.5%	-0.447** R^2=17.0%	-0.464* R^2=17.6%
well drained	0.034	0.267	0.106	0.434* R^2=14.7%
excessively well drained	0.369* R^2=10.4%	0.254	0.375* R^2=10.9%	0.113

8.7(c) Correlation of frond density with "soil aeration".

"Soil aeration"	1985 4 sites	1985 3 sites	1986 4 sites	1986 3 sites
"poorly aerated"	-0.437* R^2=16.1%	-0.465* R^2=17.7%	-0.491*** R^2=21.3%	-0.547*** R^2=26.4%
"well aerated"	-0.020	0.304	-0.028	0.407
"very well aerated"	0.359	0.110	0.476** R^2=19.8%	0.270

* $p<0.05$ ** $p<0.02$ *** $p<0.001$

Data transformation (density): 1985 only, 4 sites - square root, 3 sites - log

FIG. 8.5 BOXPLOTS OF FROND DENSITY
BY "SOIL AERATION"

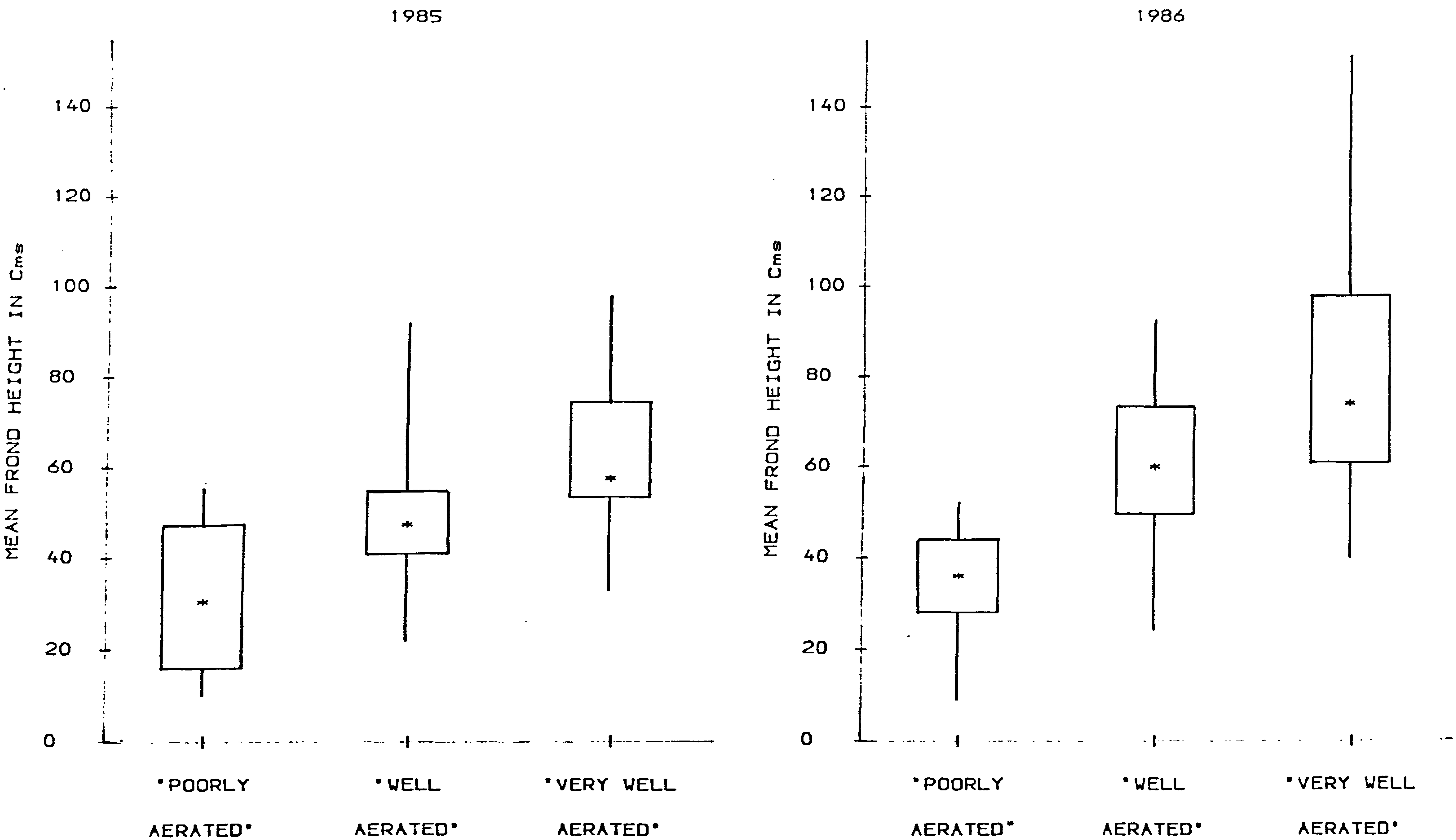
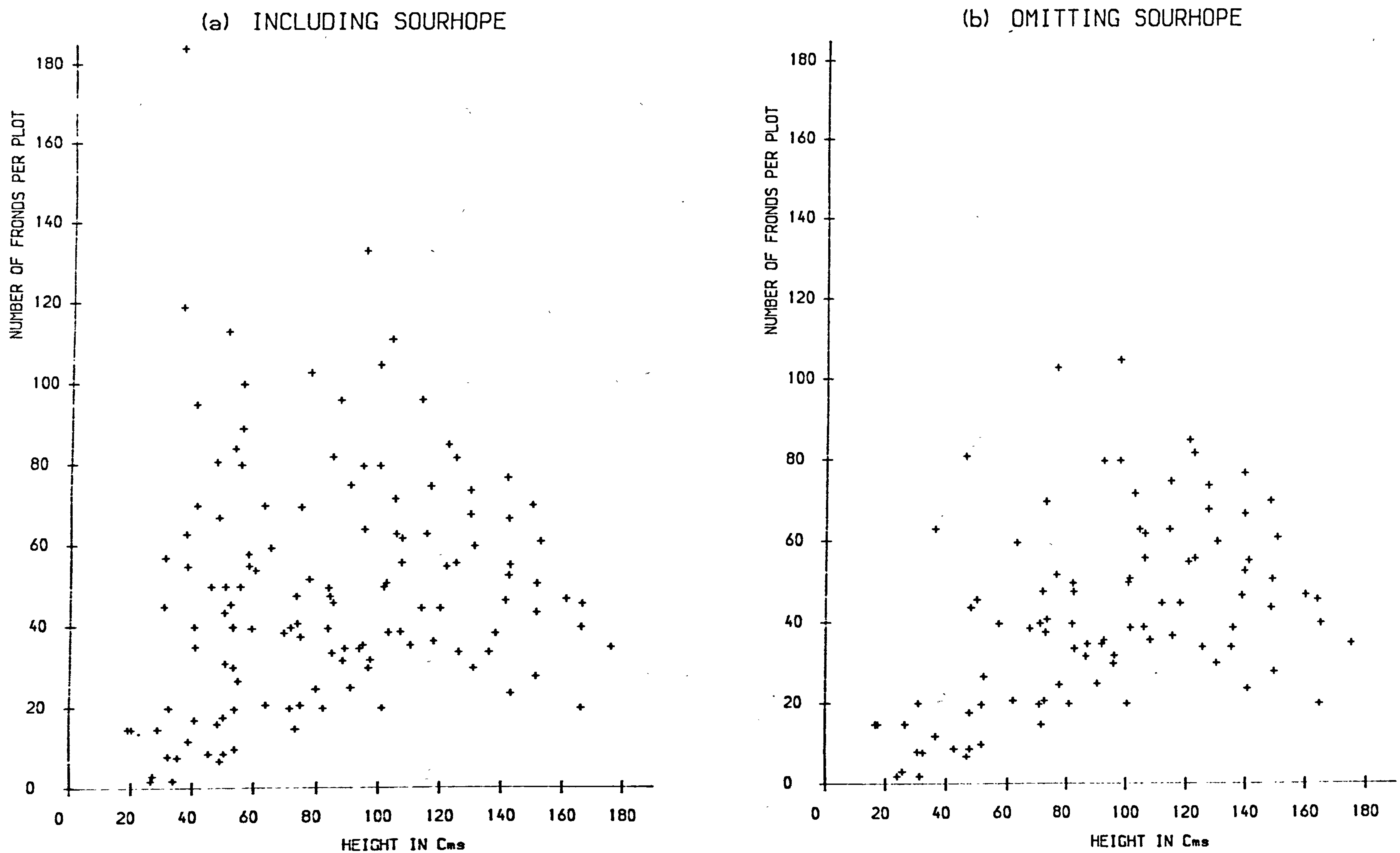


FIG. 8. 6

SCATTER PLOT OF FROND DENSITY AGAINST
HEIGHT AT ALL PLOTS



Sourhope plots do not generally fit in to this, demonstrating the different nature of the bracken at the site. When Sourhope is omitted, density clearly increases up until a height of about 110 cms, whereafter it starts to decrease. Whether a positive or negative or a significant or non-significant correlation is obtained therefore depends upon the relative number of plots on either side of the point of inversion. The systematic sampling of the post plots resulted in nearly equal numbers of plots with heights above and below 110cms and with only approximately a quarter below 80cms, thus the non-significant correlation. The greater proportion of plots below 110cms in the larger sample results in the significant positive correlation when Sourhope is omitted. Smith (1986) obtained a similar density-height distribution with the point of inversion occurring at about 100cms, but did not examine the implications of this pattern.

If all the plots on the "poorly aerated" and "very well aerated" soils are removed from the correlation of post plots, the correlation becomes negative and significant ($r=-0.568$, $p<0.001$, $n=30$) and 30 percent of the variation in density is accounted for. Thus the plots on the left hand side of the graph are removed. A similar analysis on the larger sample (using ground flora to indicate poorly drained soils) also results in a significant negative corelation with the omission of Sourhope ($r=-0.560$, $p<0.001$, $n=43$). Thus when soil factors are strongly influencing frond vigour, the relationship between density and height is not linear.

8.1.4 Bracken vigour and slope

The effect of slope on frond height and litter depth is examined here as slope will partly determine soil drainage status and soil depth. Neither height nor litter depth were found to be significantly correlated with slope. This is not unexpected as the adverse effects of poor drainage and shallow soils are likely to occur where slope is gentle and steep respectively and thus the relationship between vigour and slope is unlikely to be linear.

8.1.5 Summary of results of effect of soil on bracken vigour

1. Soil type <u>per se</u> (i.e. whether a podsol or brown earth) has little effect on bracken vigour (in terms of frond height and litter depth). Bracken is able to grow as vigorously on a peaty soil as on a brown earth.

2. Bracken does seem to be capable of "cultivating" organic soils and thus improving aeration, as evidenced by the abundant rhizomes and fine roots (which are absent from gleyed horizons) in normally poorly aerated mor humus.

3. The depth of gleying determines whether or not bracken vigour is affected by poor soil aeration. Organic horizons which have been aerated by the rhizome system provide additional rooting depth, possibly allowing greater vigour than on adjacent gleyed brown earths.

4. Dry soils affect vigour if rooting depth is physically restricted. Bracken may be less soil moisture stressed on podsols with a thick humus layer than on adjacent brown earths, although a complete litter cover seems to be necessary to prevent the humus from drying out.

5. Frond density is reduced on poorly aerated soils, but may be increased in soil moisture stressed bracken. Most plots below 110cms height were shown to be either poorly aerated or soil moisture stressed. On well aerated soils, density increases with decreasing height.

6. The indications are that in soils of unrestricted rooting depth only the uppermost rhizomes rise up the profile to lie in the litter-mineral soil interface.

The fact that stand type and therefore vigour seems to be largely determined by soil, may result in the effects of climate on vigour being masked in the subsequent analysis. Analyses in Chapter Nine are therefore tried with the omission of the soil stressed posts as well as Sourhope.

This determination of stand character and rhizome depth by soil makes investigation into Watt's hypothesis on stand succession difficult and even questions the validity of such a theory. The observation that much of the rhizome system remains relatively deep in the soil profile of the mature stands would suggest that degeneration through nutrient stress as the roots grow into the litter (as hypothesised by Watt) is unlikely. Watt also suggests that disturbance of the litter would precipitate degeneration by exposing the shallow fronds and rhizomes to frost. However in view of the extent of many of the mature stands, especially for example at Gatehouse, this would also seem unlikely except in localised areas. Rhizome "succession" in dry shallow soils, (such as Watt worked on) may be different to that in moist soils. Bracken crests, which represent somewhat foreshortened building and mature stages of Watt's successional model, only generally occur in the east of Scotland, particularly the southeast.

The other problem with Watt's hypothesis of stand degeneration is that it assumes nutrients to be limiting in the litter layers. If this were so, it is unlikely that roots would grow very vigorously into the litter while there is still a deep root system in the profile below (as was shown to be the case). The very occurrence of vigorous roots in the lower litter layers in fact suggests a plentiful supply of nutrients. Furthermore, the maintainance of bracken almost solely from the mor humus horizon in podsols demonstrates that the plant is well able to thrive in organic matter. Increased aeration of the humus may result in increased rates of humification and therefore increased nutrient availability. Miles and Young (1980) showed that old Calluna mor under birch is broken down and converted to a mull like form. Rates of cellulose decomposition and nitrogen mineralisation increase resulting in decreased carbon/nitrogen ratios. Examination of Mitchell's (1977) data from Sourhope and Conic Hill reveals that C/N ratios taken from old mor humus supporting bracken are below 20, that is, within the moder range. Only two such records are available from this source, but soil data recorded by the Macaulay Institute in 1956 from a degraded peaty podsol under bracken at Glensaugh (thought to be from the stand of Post Seven) shows a similar characteristic. In all three cases, pH and percentage base saturation remain low, because of the large cation exchange capacities.

Frankland (1976) found the majority of nutrients to be lost in the early stages of frond decay and Williams et.al. (1987) showed large increases in soil nutrients soon after frond senescence in autumn. Mitchell (op.cit) demonstrated that nutrients were relatively tightly cycled within the bracken ecosystem. The presence of vigorous fine roots in the litter may therefore increase the efficiency of cycling by the absorbtion of nutrients as they are released. The possibilty of utilisation of organic nutrients cannot be ignored, as also suggested by Mitchell (op.cit.). Thus far from being a disadvantage, a thick litter layer may aid the efficient cycling of nutrients with the upper rhizomes rising up the profile to allow the fine roots to penetrate the litter.

Examination of bracken spread at the sites now follows;

to further investigate the question of stand succession and degeneration; to determine the conditions in which bracken can spread on to organic soils; and to determine the potential for further spread.

8.2 Soils and bracken spread

8.2.1 Kilmartin

The northern two thirds of the site were surveyed by the Macaulay Land Use Research Institute in their study in to rates of bracken spread in Scotland (see Birnie and Miller 1986). There was no net increase in bracken in this area between 1947 and 1967 although increases and decreases occurred in many discrete stands. These are very fragmented and are therefore difficult to pinpoint on the ground. However it was possible to locate several areas (within all the site) of sustained spread between 1947 and the present day by comparison of 1947 and 1985 aerial photographs. Ground flora sampling showed that in all cases vigorous bracken is invading mature *Calluna* which is being shaded out under the tall bracken canopy. These *Calluna* stands are all located on relatively steep slopes on the sheltered east side of the small ridges that characterise the site. The underlying soils are peaty and humus-iron podsols.

Exploratory pits and vegetation mapping reveals that there are few areas of brown earths without a bracken cover. Most of the larger stands on the brown earths were already present by 1947 and the fluctuation in bracken cover has occurred largely in areas characterised by a small scale mosaic of *Calluna*, wet heath and bracken grassland. Here the soils are a mosaic of iron-pan gleys and podsolic brown earths. Within the rather fragmented bracken stands on the northern slopes of Bar a Chuirn are small pockets of wet grass heath characterised by *Nardus stricta*, *Deschampsia caespitosa* and *Sphagnum palustre* which support only very sparse short bracken. In contrast the bracken grows relatively vigorously from adjacent cushions of Sphagnum palustre (Fig. 8.7). The lowest areas of Molinia valley bog are bracken free. However the relatively vigorous bracken at Post Eight on very humified peat (depth of over 30 cms) demonstrates that invasion of relatively wet organic soil is possible. The adjacent vegetation to post Eight is wet Calluna and Erica tetralix heath rather than wet grass heath or Molinia bog. The most interesting feature to emerge from this investigation was that most of the vigorous bracken stands are located on the podsols rather than the brown earths. The noticable exception to this is the stand of Post Two adjacent to the head dyke, which may have been formerly cultivated.

It would seem therefore that most of the "optimal" soils, the brown earths, had already been colonised by bracken by 1947. Spread since then has been onto the adjacent podsols. The indications are that this is mainly onto Calluna communities rather than onto damp grass heath or grassland. That there has been no net increase in bracken suggests cycling between Calluna and bracken but it is difficult to determine any kind of time scale for this. The vigorous bracken stands on podsols are shown by the photographs to have been present and relatively vigorous forty years ago. The occurrence of a relict iron pan in the podsolic brown earths under much of the bracken grassland on top of and on the northeastern slope of Bar a Chuirn bears witness to the changing vegetation. As described for Posts Four and Five in Chapter Six, these soils now support a sward dominated by Poa pratensis, Holcus lanatus and Agrostis tenuis. There is no trace of any former layer of mor humus or of any of the other features of podsolisation.

The Macaulay Institute also mapped bracken change on the old fields to the north of the site. This area provides a useful comparison with the area above the head dyke. It comprises gently sloping areas of old runrig supporting damp herb rich Agrostis tenuis - Holcus lanatus

Fig. 8.7 Bracken growing on Sphagnum cushion, Kilmartin

Fig. 8.8 Fields below the head dyke, Kilmartin (centre of picture)

swards, separated by short steep slopes with drier herb poor Agrostis. Old wall lines run along the top of many of these slopes (Fig. 8.8). The fields were probably cultivated or at least the bracken controlled until the 1920s when the croft to which the land belonged was abandoned (Robin Malcolm, Pers. Comm. 1986). Net annual increase in bracken in this area from 1947 to 1967 was found to be 2.2 percent and was concentrated along the drier steeper slopes and old wall lines. Comparison of 1967 and 1985 photographs showed recent spread to have been from these areas onto the flatter damp pasture of the old runrig. Bracken has also colonised mounds of stones and slight ridges within the pasture where it is co-dominant with Juncus conglomeratus and J.effusus.

Ground flora plots showed there to be little difference in species composition between the recently established (post 1967) bracken stands and the adjacent pasture, with species indicative of impeded drainage and relatively mesotrophic conditions in both. Exploratory pits in the frond free pasture revealed a network of rhizomes extending well beyond the bracken front, but which are still supported by the parent colony. Poel (1951) made similar observa~~t~~tions in poorly aerated soils. As discussed in Chapter Two, he considered these rhizomes to be a potential source of spread if drainage should improve. It can be hypothesised that these colonising rhizomes may improve soil aeration in advance of the bracken front by their "cultivating" effect in the soil.

8.2.2 Gatehouse

Comparison of aerial photographs from 1946 and 1984 showed bracken spread to have been mainly below the head dyke. Spread has been over relatively large continuous areas from "core" areas of bracken (that existed in 1946) onto damp pasture. Exploratory and post pits revealed that the soil under the pasture is subject to periodic gleying in the lower A and/or B horizon. The ground flora of the "recent" bracken (i.e. post 1946) is Agrostis tenuis dominated with high values of Anthoxanthum odoratum, Holcus lanatus, Ranunculus acris and Cirsium palustre. In contrast, the older "core area" stands generally have a complete litter cover and sparse ground flora. (At Kilmartin, it is possible to discern that stands which appeared between 1947 and 1967 now have almost complete litter cover). The time scale of bracken spread from colonisation to maturity would therefore seem to be in the region of 20-30 years.

Bracken cover on all but the lowest field at the site (adjacent to the gorge) is very much more extensive than on the fields at Kilmartin and there are few bracken free areas that are not obviously poorly drained, suggesting that further spread below the head dyke is limited. The bracken free and sparse areas of bracken are either characterised by organic soils with Myrica gale communities or by flushed brown earths supporting herb rich swards. Unlike the situation at Kilmartin there are therefore clear differences between the ground flora in the recent bracken stands and on the adjacent flushed pasture. The pit at Post Eight (in a very sparse bracken area) and exploratory pits in bracken free areas showed the orange mottling to be more extensive and shallower than under the adjacent bracken. Mottling increases towards the centre of the larger linear flushes where the soils are permanently gleyed. It would seem that the degree of gleying in much of the remaining bracken free pasture is too great for further bracken spread. Grazing is concentrated onto the more accessible flushes (Fig. 8.9) which have short cropped turf, while those flushes surrounded by vigorous bracken are largely ungrazed in the growing season (Fig 8.10). The former areas are bracken free while the latter sometimes support sparse bracken. Heavy grazing on much of the remaining bracken free pasture may therefore also prevent further spread.

The lowest field at the site (but not on the hillside)

Fig.8.9 Grazed flush at Gatehouse (note bracken on stones)

Fig. 8.10 Ungrazed flush amidst dense bracken, Gatehouse

was reseeded in 1972, but has since lain as semi-improved pasture with a sward indicative of damp mesotrophic conditions. However bracken spread onto the field seems to be slow with only a few scattered fronds on drier areas and adjacent to the wall separating the field from the vigorous bracken at the top of the gorge (Fig. 8.11). Colonisation would therefore seem to be slow in the absence of vigorous parent colonies from which the colonising rhizomes can be supported.

Above the head dyke the outlines of many of the bracken stands have not changed since 1946. The vegetation adjacent to these particular stands is commomly damp Nardus - Molinia - Agrostis canina montana grassland on peaty podsols and peaty gleys. Wetter areas of bog characterised by Myrica gale and Eriophorum spp. make up most of the remaining bracken free areas. This failure to colonise peaty soils of acidic grassland was also observed on a smaller scale above the head dyke at Kilmartin. The only clear areas of bracken spread have been on to the podsols of small areas of former Calluna on rocky outcrops and the steeper slopes. The Calluna is shown to have been very fragmented by 1946 and there are no remaining stands today, being only represented by short grazed shoots in grass heath where bracken has not yet invaded. This indicates that bracken has not actively invaded and killed out the Calluna as observed at Kilmartin, but has merely replaced it.

The lack of spread above the head dyke demonstrates that most of the potential bracken areas, that is the brown earths, were already occuppied by 1946. Unlike the situation above the head dyke at Kilmartin where bracken is cycling with Calluna, there is little fluctuation in the stands due to the absence of Calluna and the apparent inability of the bracken to invade the peaty soils under the Nardus - Molinia grassland.

Fig. 8.11 Bracken spreading onto reseeded pasture from gorgeside at Gatehouse

8.2.3 Glensaugh

Comparison of photographs from 1947 and 1984 showed widespread bracken invasion into Calluna on the steep lower slopes (Fig. 8.12), where the pits at Old Post One and Station One revealed shallow, excessively drained degraded peaty podsols. The invading bracken stands are the only clear examples of Watt's succession sequence at the four sites apart from the foreshortened building and mature phases in the crests at Sourhope. However unlike Sourhope, there are no hinterland areas behind the fronts. Areas of mature bracken (with a complete litter cover) such as at Station One (see Fig. 8.12) are shown to be only in the colonising stage in 1946. As at Kilmartin, bracken is actively invading mature Calluna rather than merely replacing degenerating stands. Further up the hill on the gentler slopes, areas of bracken-and-grass and mature bracken stands have remained relatively unchanged. Stands have become more vigorous on small areas of brown earths surrounding the large marsh area and there has been some spread onto the upper part of the marsh where it grows from the bases of Polytrichum commune cushions. Areas of damp acidic grassland and grass heath which have a high proportion of Nardus in the sward, have remained relatively bracken free whilst being surrounded by bracken (Fig. 8.13).

As found above the head dyke at Kilmartin, exploratory pits showed most of the vigorous stands to be on degraded podsols and the bracken-and-grass stands to be on the dry brown earths. Current bracken invasion into Calluna and the inability of the bracken to invade the Nardus grass heath would suggest that the podsols supporting the bracken stands were formed under Calluna.

8.2.4 Sourhope

Comparison of aerial photographs from 1946, 1965 and 1985 showed very little change in the bracken stands in forty years. In ~~Watt~~'s theory of succession, the

Fig. 8.12 Bracken spread into <u>Calluna</u> on the lower slopes, Glensaugh. (Station Two with flag, centre of picture).

Fig. 8.13 Bracken-free <u>Nardetum</u> (upper centre) and marsh (foreground), upper slopes, Glensaugh

colonising and building fronts are supposed to advance while the mature phase degenerates. However, this is only evident in four very localised areas. The greatest area of spread has been on the northern side of the stand of Post Eight where the crest is least developed (Fig. 8.14) and where the ground flora of the adjacent pasture is Agrostis - Festuca dominated. It would seem that (as at the other three sites) the bracken has been unable to spread onto swards with a high proportion of Nardus, which at Sourhope includes most of the surrounding vegetation.

A series of soil pits across three different bracken fronts, from Nardetum, through the crest and into the hinterland, revealed that all the soils were acidic brown earths, but those in the hinterlands had a better structure, were less stony and were generally deeper than in the crests (Figs. 8.15 and 8.16). Soil structure under the crests was very similar to that under the adjacent Nardetum (Fig. 8.17). This is unexpected in view of the greater vigour of the crests. If the bracken were advancing it could be envisaged that the soil structure would be better where the bracken had been growing the longest (i.e. in the hinterlands). However as discussed, the fronts have not moved for forty years and there is therefore no evidence that the crest bracken is the most recent. Furthermore, there will be a limit to the the amount improvement possible in a bracken soil. Excessive stoniness and shallowness are intrinsic features that are unlikely to be ameliorated by bracken "cultivation". Thus it would seem that most of the bracken (that is, the extensive hinterlands) occupies the deeper and slightly less stony soils. Viewing the site from a distance it becomes clear that the bracken occupies the concave areas of the hillside with Nardetum occupying the slight convex spurs and uphill slopes (see Fig. 3.8). The crests generally occupy the transitional slope between the two communities.

The other feature revealed by the soil pits was the concentration of rhizomes in the mor humus layer under the

Fig.8.14 Stand of Post Eight Sourhope showing less well developed crest in area of recent spread onto <u>Agrostis-Festuca</u> grassland (right of stand).

Figs. 8.15, 8.16 & 8.17 - Soil pits under hinterland, crest and Nardetum respectively near Sourhope Eight

.15

.16

.17

crests. Though better developed than that under the hinterland, the maximum depth of this layer was never more than 4cms. (See Fig. 8.16). Thus the "mature" stands (i.e. the crests) have a shallow rhizome system, as would be expected from Watt's theory. Similar soil and rhizome characteristics were observed under the crests and hinterlands of the two bracken rings at the site, where the adjacent vegetation is Molinetum. (Fig 8.18) The rings occupy slight depressions on the hillside and the crests again mark the transition between convex and concave slopes. The mature stand type (i.e. relatively vigorous with a complete litter cover) also occurs at Posts One and Six where the rhizomes are again concentrated in and just below the thick mor humus (up to 10cms) of the slightly gleyed podsolic brown earths.

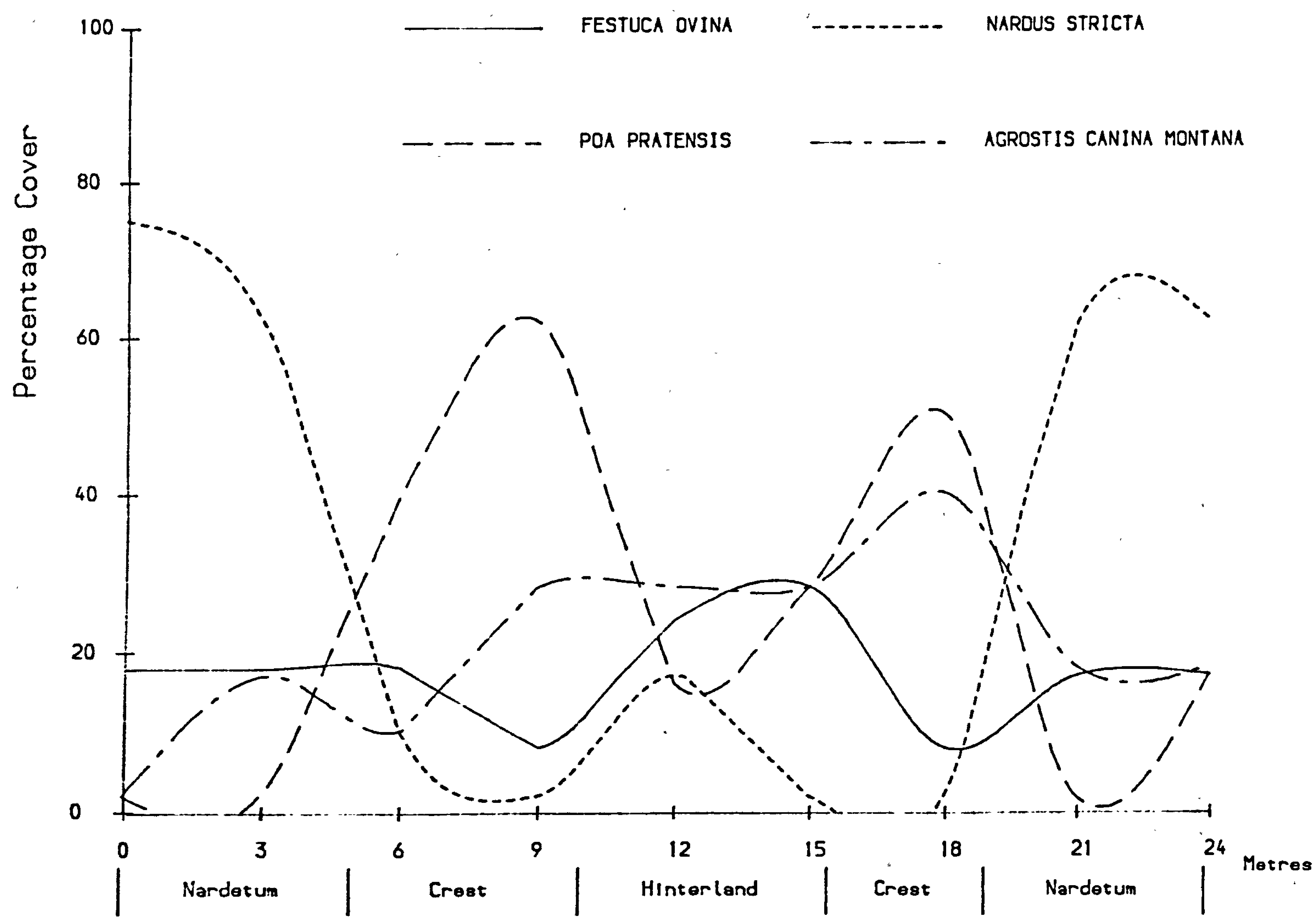
From the silmilarities between crest and Nardetum soils it would seem that the bracken has invaded the former ecotones between the Agrostis - Festuca hinterlands and the adjacent Nardetum or Molinetum, where for some reason it is more vigorous than on the better soils of the hinterlands. As discussed, where spread has been onto Agrostis - Festuca grassland (where the soil is similar to that of the hinterland) crest development is less marked. Most of the crests have a complete litter cover and a sparse ground flora. However, the crests at the heavily grazed stand of Post Eight are litter free. The composition of the sward under these crests is more indicative of mesotrophic conditions than in the adjacent hinterland, despite the better developed mor humus and the poorer soil of the former. Fig. 8.19 shows the change in percentage cover of selected species in plots taken every three metres from Nardetum, across the crests and into the hinterland. Clearly Poa pratensis increases in the crests and decreases in the hinterland.

8.2.5 Summary of bracken spread at the sites

1. Little net increase in bracken area in the past forty

Fig. 8.18 Bracken rings at Sourhope

FIG. 8.19 SPECIES COMPOSITION ACROSS BRACKEN CREST AND HINTERLAND



years above the head dykes at Kilmartin and Gatehouse, where most of the brown earths were already bracken covered by the 1940s. Thus "potential" bracken soils are already occupied, although there is cycling between Calluna and bracken on the podsols at Kilmartin. The small amount of bracken spread above the head dyke at Gatehouse has also been into Calluna soils, but there is no evidence of cycling between the two communities as the Calluna had almost disappeared from the site by 1946.

2. Large increases of bracken cover on the fields at the two west coast sites since the mid 1940s. Spread has been onto damp pasture from core areas of vigorous bracken. At Gatehouse spread is nearing its limit with only the wettest soils remaining bracken free, but at Kilmartin (where the fields were probably cultivated until the 1920s) there would seem to be potential for further spread. At both sites spread has been onto periodically gleyed soils. The indications are that soil aeration may be improved by colonising rhizomes supported by the parent colony prior to spread of the bracken front.

3. Large increases of bracken cover since 1947 on the steep lower slopes of Slack Burn valley at Glensaugh where bracken is actively invading mature (but not degenerating) Calluna.

4. Very little increase in bracken cover at Sourhope or change in the distinctive stand types of the crests and hinterlands. Where spread is onto Agrostis - Festuca grassland crest formation is less marked.

5. Greater physical affinities between soils of the crests and Nardetum than of the hinterlands, the latter being generally deeper and less stoney. Rhizomes are concentrated in the relatively thin mor humus layer under the crests.

6. No evidence of bracken spread onto vegetation with a high proportion of Nardus or Molinia at any of the sites.

7. The most vigorous bracken generally occurs where rhizomes are concentrated in mor humus at Glensaugh, Sourhope and above the head dyke at Kilmartin.

8. Little evidence of large scale degeneration of stands that were shown to be relatively vigorous (that is, representative of the "mature" stand type) in the 1940s. Decreases in bracken cover were most obvious in the very fragmented marginal stands above the head dyke at Kilmartin.

The lack of degeneration of mature bracken stands and the unchanging nature of many of the bracken hinterlands over the past forty years reinforces the view that soil factors rather than stand succession are largely determining stand type. There is therefore little evidence of the complete bracken cycle, succession apparently only occurring up to the mature stage. Bracken was found to cycle with Calluna at Kilmartin, but this is where the bracken is least vigorous and no such cycling was observed in the larger vigrous bracken stands on the degraded podsols at the site or at Glensaugh. Marrs and Hicks (1986) observed degeneration to grass heath over twenty years on the dry soils of Lakenheath Warren. It may be that stand degeneration does occur, but only where conditions are more marginal. It may only need a one or two years of sub-optimal weather conditions to trigger the process of stand degeneration in marginal stands.

The crests and hinterlands at Sourhope are the only examples in which relative rhizome depth corresponds to Watt's theory of rhizome "succession" up the profile. However there was no evidence in the profiles that rhizomes had previously occurred lower down the profile under the crests. It is more likely that rhizome depth is limited by the excessively stony soil and/or that rhizomes are concentrated in the humus horizon to take advantage of the moister conditions, especially under litter.

The failure of bracken to colonise Nardus and Molinia was also observed by Poel (1951). As discussed in Chapter Two, Poel found oxygen diffusion rates to be as high under these two vegetation types as under bracken and suggested that the thick impenetrable nature of the root mats and tussocks prevent bracken invasion. The ability of bracken rhizomes to colonise Calluna mor humus and peat and also lightly gleyed mineral soils, demonstrates that poor aeration is not an initial barrier to spread as long as the rhizomes are then able to sufficiently open up and aerate the upper horizon.

The findings of this and the previous section support the contentions made by various workers (see Chapter Two) that bracken now seems to be spreading beyond its "optimal." (but not ecological) range. The field evidence shows the brown earth areas to be colonised above the head dyke with most spread now onto peaty soils, which by their nature are less well aerated than brown earths. Below the head dyke at Kilmartin and Gatehouse bracken clearly colonised the drier areas first and is now spreading onto the wetter soils. It would seem that the prerequisite for spread onto the wetter soils is that there should be an adjacent parent colony which can sustain the pioneer rhizomes in the early stages of colonisation.

The greater vigour of the bracken on podsols at Kilmartin and Glensaugh and on the mor humus of the crests at Sourhope may be due to several reasons. These include; the additional rooting depth above a gleyed layer; the provision of "additional" moisture in litter-covered organic horizons and differential grazing. However, as demonstrated in Chapter Seven, the light grazing at Kilmartin and Glensaugh does not greatly affect bracken vigour. Furthermore, the heavier grazing at Sourhope was shown to affect the vigour of the crests at the very accessible stand of Post Eight to the extent of preventing the formation of a litter cover. Differences in nutrient levels may be another explanation. By their nature the upper mineral horizons of podsols are usually less fertile than those of acidic brown earths. However, bracken growth is mainly from the organic horizon which must therefore be considered in any comparison of fertility. As suggested, aeration of the organic horizon by the rhizomes may increase humification. This would result in greater nutrient availability, which may be greater than in the adjacent infertile acidic brown earths. The occurrence of the Poa pratensis dominated sward growing from what physically resembles a mor humus at the crest of Post Eight would seem to support this theory. Gregor and Watson (1953) noted the effect of nitrogen in increasing the contribution of Poa pratensis to the sward, while Helgadottir and Snaydon (1985) showed that applications of nitrogen fertilizer increased Poa pratensis and reduced Agrostis tenuis content when grown in competition. Applications of calcium alone and of calcium, phosphorous, potassium and nitrogen in combination have been shown to cause floristic succession from species poor Agrostis - Festuca and Molinia grassland to Poa pratensis rich grassland in conditions of controlled grazing (Milton 1940; Milton and Davies 1947).

King (1962) describes a Poa pratensis rich sward between the upper limits of bracken and the lower altitudinal limits of Nardetum and between bracken and Nardetum on the lower knolls at Sourhope. He describes these as night bedding areas for sheep and considered the mor humus to be enriched with faecal nitrogen. King did not include the bracken communities in his study, but it is interesting that the location of his Poa enriched areas almost corresponds to the position of the crests. Clearly there is scope for further research into the question of nutrient availability on organic soils under bracken.

Chapter Nine

Climate and Bracken Vigour

The effects of minimum and maximum temperature on bracken vigour and of soil temperature on bracken emergence are examined first, followed by examination of the effect of exposure. This is followed by a brief examination of the effect of altitude and aspect although most emphasis is placed on the preceeding analyses. A stepwise regression analysis comprises the final analysis.

9.1 Minimum temperature

Results of the correlation and regression analysis of frond height and air minima are shown in Table 9.1. below. (Residuals in all the regression analyses in this chapter are checked for normality and data transformed accordingly).

Table 9.1 Correlation of frond height with air minima

	1985		1986
Period 1 (May)	-0.317	Period 5 (Nov-April)	-0.235
Period 2 (May-mid June)	-0.369* R^2=10.4	Period 6 (Apr-June)	-0.397 R^2=12.7
Period 3 (May-mid Aug)	-0.338	Period 7 (Apr-July)	-0.455* R^2=17.8
	*p<0.05	Period 8 (Apr-Aug)	-0.395* R^2=12.5

In all the correlations in 1985 and those in Periods Seven and Eight of 1986 certain outlying predictors are influencing the correlation. In every case these posts are either the highest at their respective sites or are the frost hollow posts at the west coast sites. These "anomalous" posts are shown in the scatter plot of frond height against air minima for Period Two in Fig.9.1. Data transformation (achieved by adding values to the minima data to rid of the minus values) did not ameliorate their influence. Table 9.2 below shows the results with these outlying predictors removed (significant correlations only). Except for Kilmartin Eight, which affected nearly every correlation, different posts are omitted in different correlations.

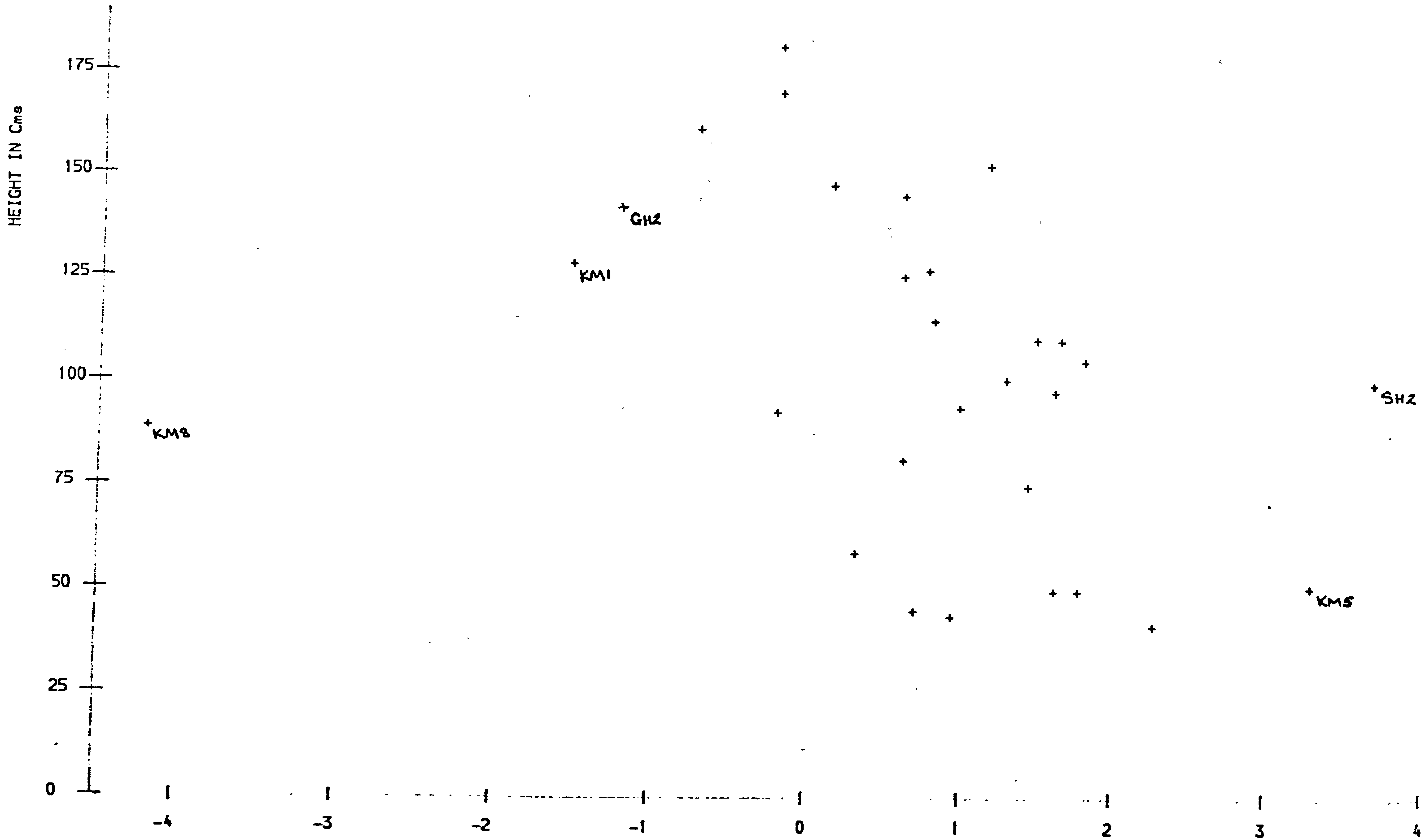
Table 9.2 Correlation of frond height with air minima omitting "anomalous" posts

	1985		1986
Period 1	-0.477*	Period 7	-0.489**
(May)	R^2 =19.4	(Apr-July)	R^2 =21.0
	4 posts omitted		1 post omitted
Period 2	-0.611**	Period 8	-0.417*
(May-mid June)	R^2 =34.5	(Apr-Aug)	R^2 =14.2
	5 posts omitted		1 post omitted
Period 3	-0.589**	*p 0.05	
(May-mid Aug)	R^2 =32.0	**p 0.02	
	2 posts omitted	***p 0.001	

Data transformation - heights squared in 1985.

Clearly the correlations increase when the anomalous data are removed. Analysis omitting Sourhope and the soil stressed posts also produces negative correlations. No

FIG. 9.1 SCATTER PLOT OF FROND HEIGHT
AGAINST AIR MINIMA IN PERIOD TWO
(MAY TO MID JUNE 1985)



significant correlations are obtained between ground minima and frond height in either analysis. Only one significant correlation between minima and litter depth is obtained with all the posts, but omission of Sourhope and the soil stressed plots increases the correlations, shown below in Table 9.3. below.

Table 9.3 Significant correlations of air and ground minima with litter depth, omitting Sourhope and the soil stressed plots

1985		1986	
Period 2 air	-0.050	Period 7 ground	-0.612**
(May-mid June)		(Apr-July)	R^2=37.0
omitting 2 posts	-0.549*		
	R^2=23.8		
		Period 8 ground	-0.548*
			R^2=23.6

*$p<0.05$ **$p<0.01$

The negative correlations obtained for both height and litter depth are unlikely to demonstrate a direct relationship between minima and bracken vigour. They more likely reflect a conicidental relationship resulting from the effect of temperature inversion and shelter as demonstrated in Chapter Five. Thus the lower and,or more sheltered stands, which tend to be the most vigorous, experience the lowest minima. The fact that significant correlations are still obtained when Sourhope is omitted demonstrates that it is not merely a "site effect" caused by the shorter bracken and higher minima of the site. This coincidental relationship breaks down in Period Five (winter) because of the extreme winter at Glensaugh.

The absence of results showing the effect of frost on bracken can be explained by the limitation of frost damage to a few posts at Kilmartin and Gatehouse. Furthermore, in some periods the mean temperature of many posts did not fall below 0 °C. The effect of frost on the bracken is therefore largely overridden by the effect of temperature inversion in the analysis. The heavily frosted posts, Kilmartin One and Eight, suffered significant frost damage in the first growing season and therefore have a lower frond height than would be expected from the general negative relationship between height and minima (thus their influence on the correlation).

The results of the analysis of air minima and frond density are shown in Table 9.4 below. The same posts are again inflencing the correlation. This influence cannot be removed by data transformation and results with and without these posts are therefore shown.

Table 9.4 Correlation of frond density with air minima (showing significant correlations only)

	1985		1986
Period 1	0.317	Period 5	0.426*
omitting 4 posts	0.526*		R^2=15.1
	R^2=24.5		
Period 2	0.508**	Period 6	0.422*
omitting 5 posts	0.564**		R^2=14.8
	R^2=28.7		
Period 3	0.500*	Period 7	0.446*
omitting 2 posts	0.663**		R^2=17.0
	R^2=41.7	omitting 1 post	0.516**
			R^2=23.9
		Period 8	0.455*
		omitting 1 post	0.522**
			R^2=24.4

*p<0.05 **p<0.01

Again the correlations increase when the anomalous data is omitted. Omission of both Sourhope and the soil stressed posts also results in significant positive correlations. A positive relationship between density and minima would be logically expected, in that the less frosted the bracken the more fronds will survive. Watt's (1950) significant correlations between frond numbers and percentage mortality of fronds killed by frost (used as an indirect measure of spring frost) would seem to indicate that in the short term spring frost increases density. However, Watt included frosted as well as healthy fronds in the total frond number and assumming the growth of replacement fronds, a positive correlation is inevitable. The overall lack of frost kill in the present study would suggest that the correlation is again merely reflecting a coincidental relationship.

Clearly frost damage was not extensive enough to allow an insight into the effect of frost on the correlation results. Examination of the effects of frost on bracken at individual posts is therefore necessary.

Spring frosts were recorded until the end of June at Gatehouse and Kilmartin and until the second week of June at Glensaugh and Sourhope in both years. Significant frosting of bracken was only observed at Kilmartin and Gatehouse and only in 1985. Frosts were generally lighter in 1986, but the Period means for that year are as low as those of 1985 because of the inclusion of April in the second growing season. The heavy frosts of this month did not affect above ground bracken vigour as few fronds had emerged by then.

Tables 9.5 and 9.6 show the number of healthy fronds and the number of newly frosted fronds (partially and completely frosted) at each frond count at each post at Kilmartin and Gatehouse in 1985. The temperatures recorded between frond counts are also shown. (At Gatehouse this amounts to only one reading per frond count interval). The numbers of healthy fronds do not necessarily represent the

Table 9.5 Number of healthy and frosted fronds at each frond count, with intervening minima readings:- Kilmartin 1985.

date of reading		1	2	3	4	5	6	7	8
		post number							
8.5.85	air	-1.5	-0.5	1.0	1.0	1.0	-0.5	-1.0	-2.5
	ground	-2.5	-1.5	-1.0	-0.5	-2.0	-3.5	-0.5	-3.0
	healthy fronds	33	11	0	0	0	3	11	8
	partially frosted	0	0	0	0	0	0	0	0
	completely frosted	6	0	0	0	0	0	0	0
14.5.85	air	-1.5	0.0	2.0	1.5	5.5	0.0	-0.5	-4.0
	ground	-2.5	-4.5	-2.0	-2.0	-1.0	-2.5	0.5	-4.5
	healthy fronds	76	23	1	0	0	18	16	0
	partially frosted	0	0	0	0	0	0	0	0
	completely frosted	3	1	0	0	0	3	0	14
21.5.85	air	5.5	6.0	5.5	5.0	5.0	4.5	4.5	4.0
	ground	2.5	4.0	3.5	3.0	4.0	1.5	4.5	2.5
	healthy fronds	82	ND	ND	ND	ND	ND	ND	ND
26.5.85	air	2.0	1.5	4.0	3.0	3.5	2.0	2.0	-0.5
	ground	-0.5	-2.5	0.0	0.0	0.0	0.0	2.0	-2.5
31.5.85	healthy	107	80	23	30	8	33	38	0
	partially frosted	0	0	0	0	0	0	0	68
	completely frosted	0	0	0	0	0	0	0	21
3.6.85	air	-0.5	0.5	2.5	3.0	3.5	1.0	1.0	-2.5
	ground	-3.0	-2.0	-2.0	0.0	-1.5	-2.5	0.0	-3.5
10.6.85	air	-2.5	-1.0	1.0	0.5	5.0	-1.5	-1.0	-3.5
	ground	-3.0	-2.0	-3.0	-2.5	-1.5	-5.5	-1.0	-4.5
17.6.85	air	-2.0	0.0	2.0	0.5	2.0	-1.0	-0.5	-3.0
	ground	-1.5	-1.5	-2.0	-0.5	0.5	-4.0	0.5	-3.5
24.6.85	air	-0.5	1.0	4.0	3.0	4.5	1.0	1.0	-1.5
	ground	0.5	0.5	0.5	0.5	-2.0	-2.0	2.0	-2.5
29.6.85	air	7.5	7.5	7.5	7.0	9.0	7.5	11.5	7.0
	ground	7.0	7.5	6.0	7.0	7.0	7.0	10.5	6.5
	healthy fronds	24	93	70	77	87	28	44	48
	partially frosted	82	0	0	0	11	14	0	0
	completely frosted	0	0	0	1	1	0	0	0
15.7.85				no frost					
22.7.85				no frost					
	healthy fronds	32	97	75	78	109	31	44	71

Table 9.6 Number of healthy and frosted fronds at each frond count, with intervening minima readings:- Gatehouse 1985.

date of reading		post number 1	2	3	4	5	6	7	8
14.5.85	air	0.0	-1.0	1.5	0.5	0.5	0.0	0.5	-0.5
	ground	-1.0	-4.5	-1.5	0.5	0.0	0.0	0.0	-1.5
	healthy fronds	1	0	6	0	1	6	34	0
30.5.85	air	0.0	0.0	2.0	2.0	2.5	3.0	3.5	2.5
	ground	0.5	-3.5	-1.0	1.0	0.0	2.0	0.5	-1.0
	healthy fronds	7	4	47	46	30	45	149	0
19.6.85	air	-2.0	-2.5	-1.0	2.0	-1.0	-1.0	1.0	-1.0
	ground	-1.0	-4.5	-4.5	-3.5	-4.5	-1.0	-1.5	-4.0
	healthy fronds	53	31	99	71	64	104	170	2
	partially frosted	4	3	1	7	0	0	0	0
	completely frosted	4	18	4	9	17	1	1	0
20.7.85	no frost								
	healthy fronds	61	54	106	108	77	112	182	94

proportion of fronds that survived frosting as fronds may have emerged after the last frost before each frond count. However, where the number of newly frosted fronds is less than the total number of healthy fronds recorded at the previous frond count, a certain proportion of fronds have obviously escaped frosting. Tables 9.5 and 9.6 show that there are often no frosted fronds recorded despite sub-zero temperatures in the intervening weeks. This is particularly noticable at Kilmartin Two, Three, Four and Five and Gatehouse Three, Six and Seven.

There are three possible explanations for this apparent resistance of the fronds to frost:

1. the duration of frost is too short to be effective (assuming there to be a time lag between the onset of frost and the onset of damage to the bracken tissue)
2. a light frost is not cold enough to damage bracken tissue
3. the more robust fronds can withstand a colder frost than the weaker fronds.

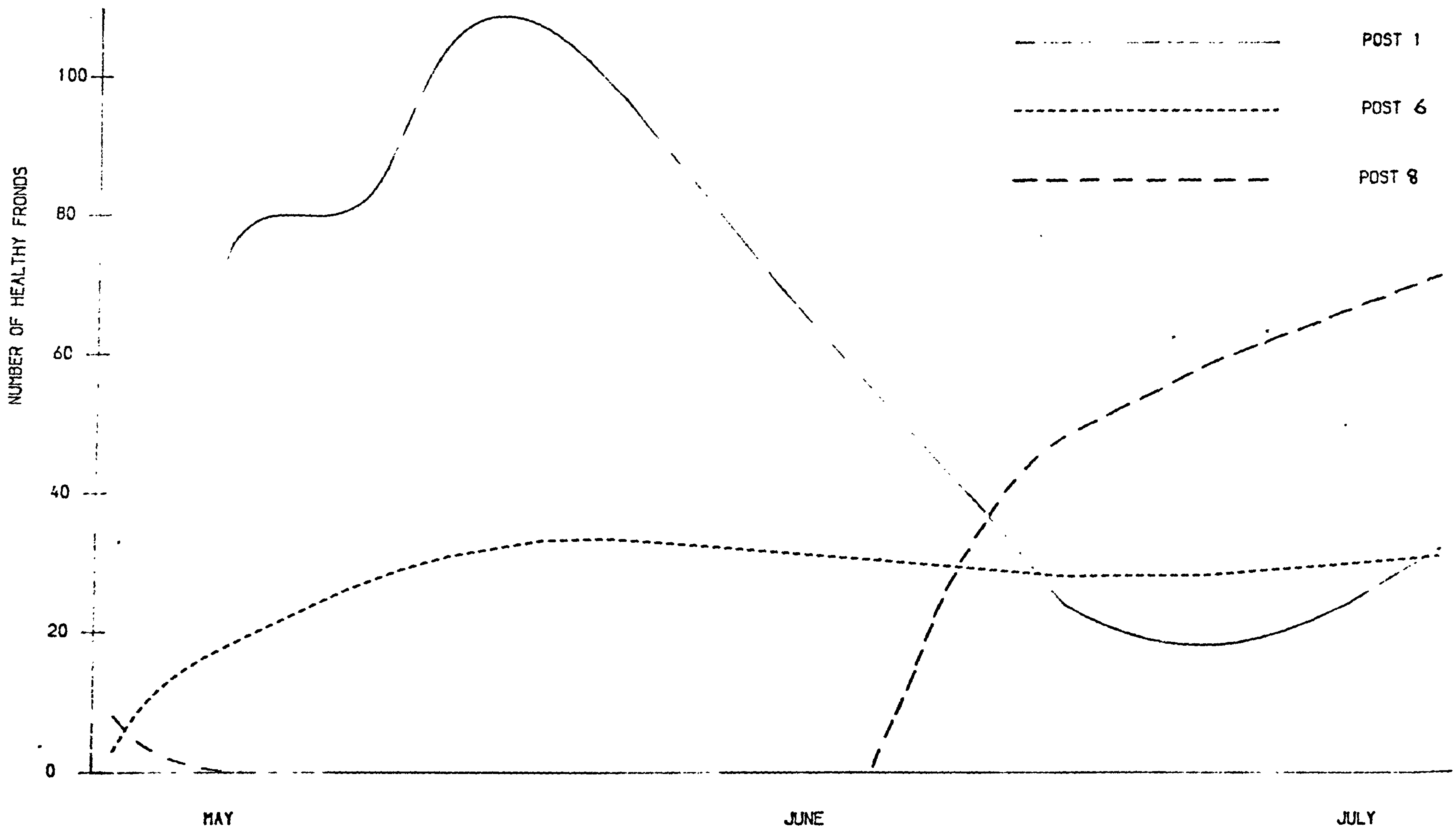
All three explanations are interlinked for a light frost is more likely to be of shorter duration than a heavy frost and may only affect the weakest fronds. Tables 9.5 and 9.6 show that as expected, frost was less frequent and lighter at the posts where it had the least impact on the bracken. This tended to be at those posts located on the open hillside. It would seem that bracken was less frosted where minima did not generally fall below -2.0 ^{o}C and where air frosts were less frequent than ground frosts. However, it is impossible to determine the exact temperature at which frost began to affect the bracken because, as already suggested, this may to some extent depend on the duration of frost and robustness of frond. For example, Table 9.6 shows that in June, Gatehouse Three experienced as cold a frost as Gatehouse Five but suffered less frost damage. Gatehouse Three was located on the open hillside and Gatehouse Five in a sheltered hollow in a corner of the upper field. Both have relatively robust fronds. Duration of the frost was therefore probably the crucial factor in determining extent of damage in this particular case.

Stage of emergence and timing of frost will also determine the extent of frost damage. Apart from fronds at the heavily frosted posts, most frosted fronds were observed to be at the hook or crozier stage with older more robust fronds remaining unscathed. On the other hand, late emerging bracken can miss frost altogether as is the case at Sourhope where bracken emergence did not begin until the end of May in either year. Watt (1950) found that bracken which emerged later because it had been affected by winter frost had less chance of being affected by spring frost.

Tables 9.5 and 9.6 serve to show the limited effect that frost had on the bracken overall. It was only at those posts experiencing frequent frosts down to about -3^{o} to -4.0^{o}C that significant numbers of fronds were damaged or killed. In most cases replacement fronds were observed to grow, but as Watt (1950) points out, it is difficult to draw a dividing line between regrowth and merely late emerging fronds. However when a large proportion of fronds are frosted well into the season and the number of fronds emerging thereafter is quite large relative to the original number of fronds, it can be assumed that most of these will be regrowth.

Table 9.5 shows that Kilmartin Eight suffered heavy frosting with complete frond kill early on in the season, while Kilmartin One and Six were frosted later on in June when many fronds were only partially frosted. Partial frosting usually resulted in damage to just the growing tip and/or the upper pinnae. In some cases one of the side pinna would extend upwards to become the new leading shoot. The pattern of emergence and regrowth of these three posts is shown in Fig. 9.2. which shows the number of healthy fronds at each post through the season. The effect of continuous frosting at Post Eight in May is

FIG. 9.2 TOTAL NUMBER OF HEALTHY FRONDS
AT POSTS 1,6 AND 8, KILMARTIN, 1985



clearly seen, as is the substantial regrowth thereafter. (Although fronds were not counted between the end of May and the end of June, the regrowth was only in the hook and crozier stage at the latter count, indicating that emergence could only have occurred in the previous week. Thus regrowth took three to four weeks to emerge). In contrast, regrowth at Post One and Six was very limited. The capacity for regrowth would thus seem to depend either on the timing of the frost or on whether partial or complete frosting occurred. Regrowth will only occur if frosting is early in the season and/or if all fronds are affected. It can be hypothesised that some form of growth hormone control mechanism operates which determines whether or not regrowth occurs.

The average frond height at frosting at Post One was 75cms. By the next count in mid July, the fronds that had escaped frosting were an average of 115 cms high while those that had been partially frosted were only 85cms. high. Thus partially frosted fronds were still growing but with very much reduced vigour. It was observed that these frosted but slowly growing fronds often developed soft stems later in the season, which must hinder if not compleletly halt translocation of metabolites to the rhizome.

Frond height and density at Kilmartin Six and Eight were greater in 1986 (the comparison not being possible for Kilmartin One which was ploughed up in spring 1986). This indicates that the short term effect of frost (that is, within the same year)is to reduce vigour. Watt (1950) found a negative correlation over a number of years between spring frost (measured in percentage frond mortality) and frond height and also length of lamina. It can be hypothesised that the long term effect of frost will be to permanently depress vigour (that is height and biomass). The long term effect on density is less clear, although in the short term frond numbers are reduced. Watt (1950) found that in a decade characterised by heavy spring frosts, bracken was generally shorter and denser than in the proceeding decade which was characterised by light spring frosts.

Perhaps the most important feature to emerge from the results is the fact that spring frost had little overall effect on the bracken, particularly at the eastern sites. Short term vigour was only obviously affected at a few posts at the west coast sites, but even here there is little evidence of large reductions in long term vigour. Three of the four frosted posts, Kilmartin One and Eight and Gatehouse Two are all relatively vigorous (Gatehouse Two being the most vigorous post of all thirty two posts). Thus if other factors are optimal, spring frost has minimal effect, although continual frosting may depress vigour to slightly below its maximum.

The final point of the effects of minima and frost relates to end of season senescence which in the literature is sometimes quoted to be brought on by the first autumn frosts. In both years the first frosts had occurred by mid-September at Kilmartin, Gatehouse and Glensaugh and by the beginning of October at Sourhope. There was no evidence of frost kill at the end of the season at any of the sites, the mature fronds therefore withstanding the mainly light ground frosts. Furthermore, senescence was observed to start before the first frosts in the more stressed bracken stands, as discussed in Chapter Seven.

9.2 Maximum temperature

Table 9.7 below shows results of correlation and regression analysis of air maxima with frond height and litter depth. Correlations with ground maxima (three sites only) or for litter depth in 1986 were not significant.

Table 9.7 Correlation of frond height and litter depth with air maxima

	1985 Height (square)	1985 Litter (square rt.)		1986 Height (square rt.)
Period 1 (May)	0.544** R^2 =27.0	0.416* R^2 =14.2	Period 5 (Nov-Mar)	0.222
Period 2 (May-June)	0.566** R^2 =29.5	0.488** R^2 =20.9	Period 6 (Apr-June)	0.300
Period 3 (May-Aug)	0.551** R^2 =27.7	0.501** R^2 =22.3	Period 7 (Apr-July)	0.364* R^2 =10.0
			Period 8 (Apr-Aug)	0.305

*p<0.05 **p<0.01

Bracken vigour will vary from year to year in response to short term fluctuations, but overall vigour will be determined by long term trends. The significant correlations in 1985 are therefore unexpected in view of the atypical maximum temperature pattern of the sites in that year. However, as discussed in Chapter Five, the maximum temperature pattern of the sites in 1985 follows that of the predicted mean temperature pattern and it is therefore possible that the correlations for this year are reflecting the long term effect of mean temperature.

Correlations omitting Sourhope and the soil stressed posts are shown below in Table 9.8.

Table 9.8 Correlation of frond height with air and ground maxima, omitting Sourhope and the soil stressed posts

	1985			1986	
	Air	Ground		Air	Ground
Period 1	0.387	N.S.	Period 5	N.S.	N.S.
Period 2	0.527* R^2=22.2	N.S.	Period 6	0.266	0.8.00** R^2=60.3
Period 3	0.326	N.S.	Period 7	0.270	0.590* R^2=28.9
			Period 8	0.321	0.469

*$p<0.05$ **$p<0.01$

Data transformation - air maxima logten in 1985.

There is now a strong correlation with ground maxima in Period Six (begining of the 1986 growing season) with 60 percent of the variation accounted for. The decreasing correlations with ground maxima in Periods Seven and Eight reflect the decreasing influence of the early season temperatures in the cumulative period means. The earlier relative reduction in air maxima at Kilmartin (see Chapter Five) results in the non-significant correlations in 1986.

Bracken vigour therefore increases with increasing early season maxima and/or mean temperature. Mean temperature would, logically, be expected have a greater influence on growth than maxima (which is a measure of extreme temperature). It is not possible to tell from the results whether mean temperature will influence growth throughout the season or in the early period only. The predicted mean site temperature pattern remains the same throughout the season. The significant correlations obtained for Periods Two and Three may therefore merely be reflecting early season effect.

Table 9.9 below shows the results of correlation and regression analysis between air maxima and frond density. Correlations in 1986 and for ground maxima in 1985 were not significant and are therefore not included

Table 9.9 Correlation of frond density with air maxima, 1985

	All posts	Omitting Sourhope and soil stressed posts
Period 1	-0.566**	-0.569*
	R^2=28.4	R^2=27.1
		(log of density)
Period 2	-0.533**	-0.536*
	R^2=25.7	R^2=23.3
		(log of density)
Period 3	-0.524**	-0.512
	R^2=24.8	R^2=20.5
		(log of density)

*p<0.05 **p<0.01

Analysis using all the posts except those at Sourhope results in non-significant correlations, demonstrating the "site effect" of Sourhope on the correlation. However, the significant correlations obtained when the soil stressed posts are also omitted shows that this relationship between maxima and density does exist. That non-significant correlations are obtained if all the posts except Sourhope are included, demonstrates that this mechanism of density regulation either does not operate or is masked when bracken vigour is largely determined by soil factors.

9.3 Temperature and frond emergence

In both years frond emergence began in late April at Kilmartin, Gatehouse and Glensaugh, but not until mid to late May at Sourhope. The threshold temperature for plant growth is commonly held to be $5.5^{\circ}C$ (see for example, Alcock et.al. 1967, Birse and Dry 1971, Hogg 1965, Hunter and Grant 1971 and Manley 1945). The predicted mean April temperature at Sourhope is only $4.8^{\circ}C$ in contrast to $6.6^{\circ}C$ at the two west coast sites. (Mean temperatures at Glensaugh are probably similar to the west coast sites as discussed in Chapter Five). The predicted mean May temperature of $8.1^{\circ}C$ at Sourhope indicates that temperatures at the site rise rapidly at the end of April. The indications are therefore that the low mean temperature at Sourhope in the early season may delay frond emergence.

Watt (1940) found that the current year's fronds were mostly differentiated as frond buds in the preceeding summer, but growth of both bud and rhizome is very slow during the winter. The thermograph stations were set up to investigate the effect of spring soil warming on frond emergence and growth. Before discussion of the results proceeds, it is necessary to briefly review the character of the bracken and soils at the four stations as this is important to interpretation of the results. The bracken characteristics are shown below in Table 9.10.

Table 9.10 Frond density (numbers per 1.5x1 metre plot), height (cms) and litter depth (cms) at the thermograph stations

	1985				1986			
	S1	S2	S3	S4	S1	S2	S3	S4
Density	39	32	68	71	42	32	85	80
Height	155	70	85	120	155	100	90	120
Litter	--	--	--	--	18.75	3.5	1.0	14.5

Stations One and Four have the most vigorous bracken with deep litter and sparse ground flora. Both are located on degraded podsols. Station Two, also located on a podsol, has less vigorous bracken and a grass heath ground flora of nearly 100% cover. As previously discussed, unlike the podsols under the other stations and posts at the site, the mor humus at Station Two becomes very dry in summer. Station Three is located on a flushed brown earth with ocherous mottling in the B horizon. Bracken is again less vigorous than at Stations One and Four and there is a complete ground flora which includes species indicatve of the damp, mesotrophic conditions. Stations One and Two are located on the steep lower slopes and Stations Three and Four about ten metres apart from each other just below the Calluna marking the edge of the plateau. Station Three is flushed by a spring arising at the break of slope below Station Four.

Figs. 9.3 and 9.4 show mean weekly air temperature and soil temperature at 10cms depth respectively during the two growing seasons and intervening winter. Data for Station Four in 1985 and from December to March and for Station One from March to April are not available because of malfunctioning equipment. The probes in the three podsols were all located in the mor humus horizon.

Peaks and troughs in soil temperature are either synchronised with air temperature or are one week behind. Air temperature does not vary much between stations but

FIG. 9.3 MEAN WEEKLY AIR TEMPERATURES

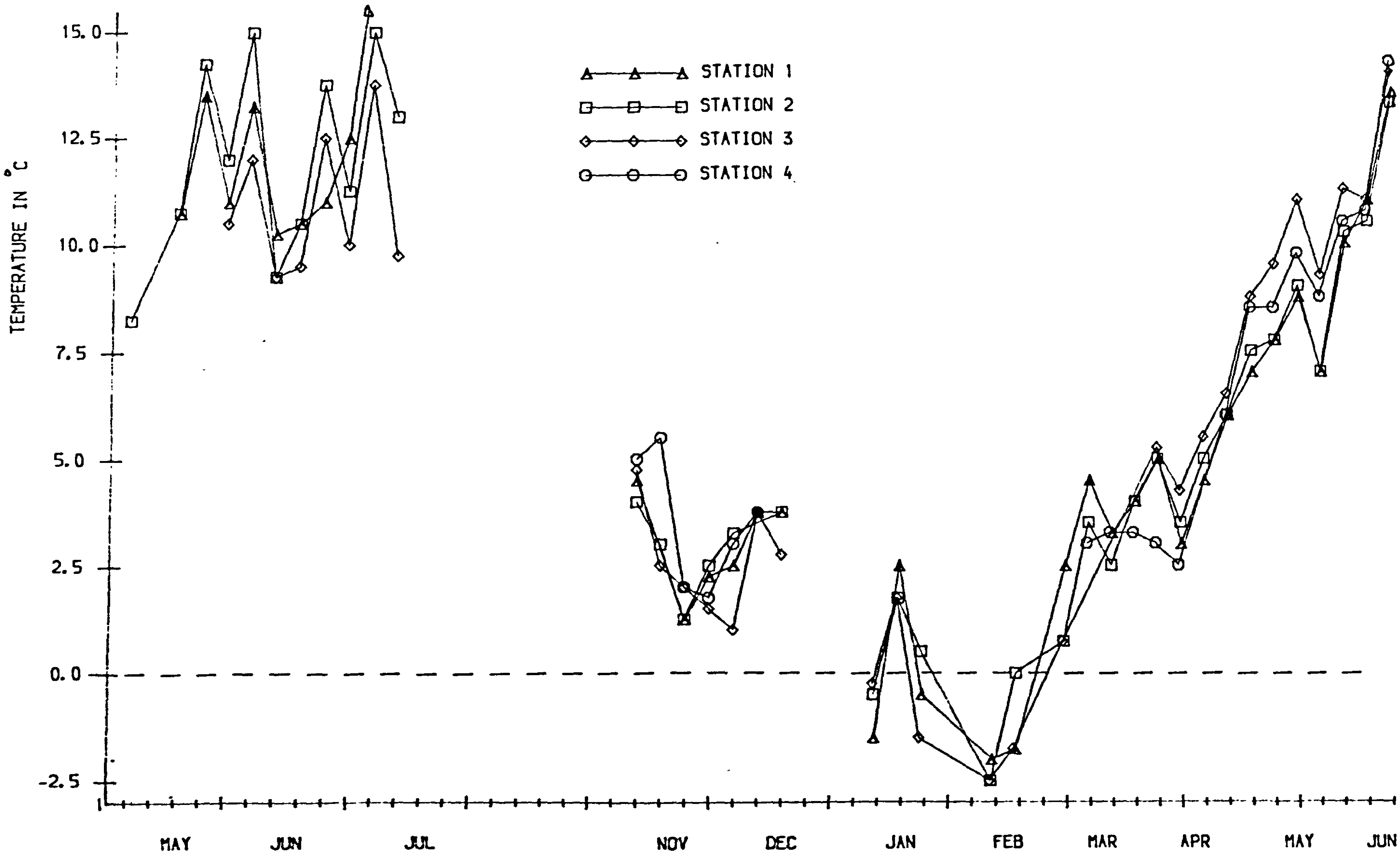
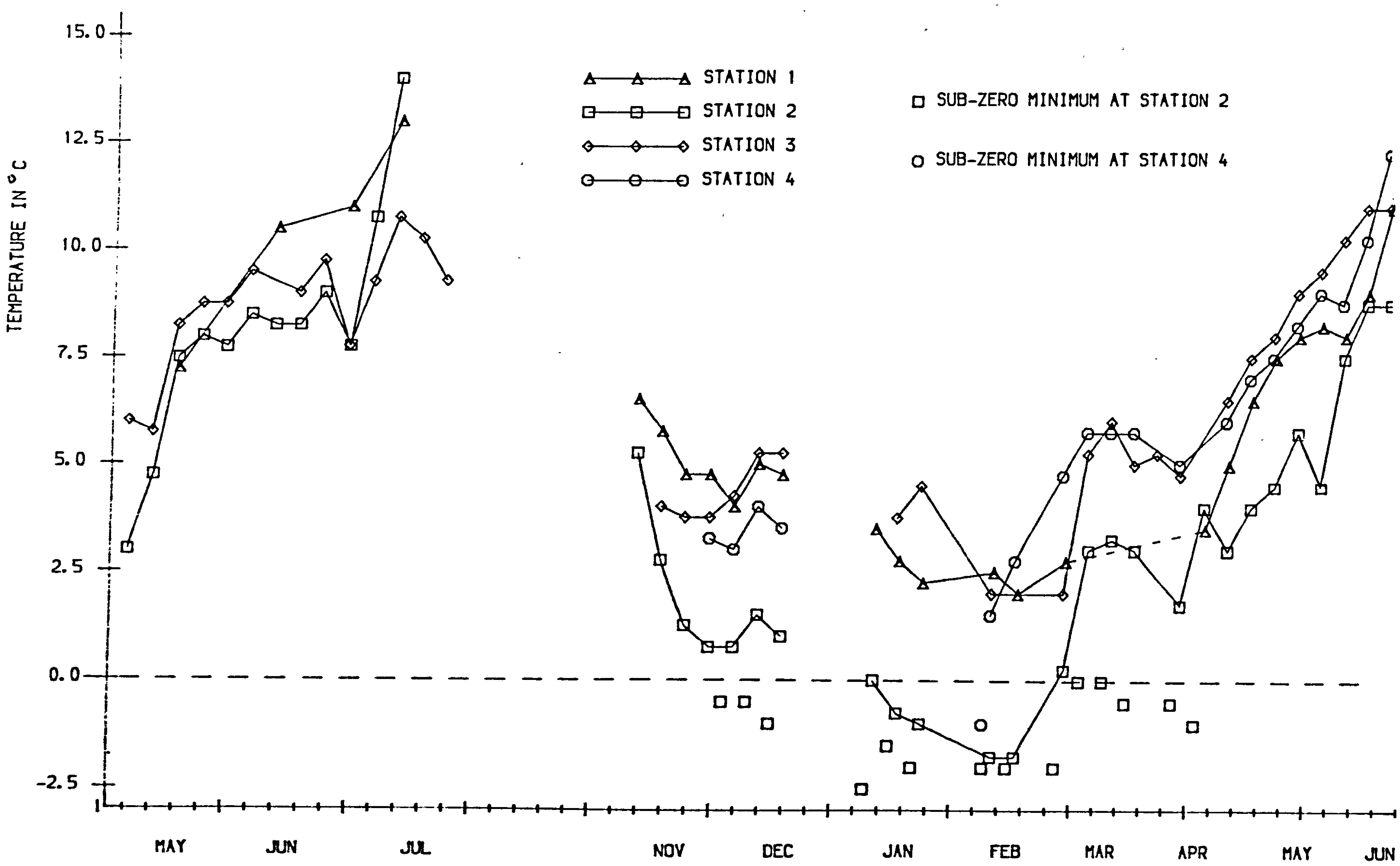


FIG. 9. 4 MEAN WEEKLY SOIL TEMPERATURES

AT 10cms DEPTH



soil temperature clearly does. Soil temperatures at Station Two are markedly different from the other three stations with mean temperatures remaining below 0 °C from mid-January to early March. Weekly minima remained below 0 °C from the end of November to the beginning of April. In contrast, mean soil temperature at the other stations remained above 0 °C all year with minima only falling below 0 °C at Station Four in mid-February. Snow lay for the same length of time at Stations One and Two which suggests that litter cover rather than snow cover prevented soil freezing at Stations One and Four. Station Three lacks a litter cover but flushing by spring water probably explains the absence of soil frost. The influence of this flushing was also seen in the relatively narrow diurnal variations in temperature recorded at the station. A wet soil would normally be expected to be relatively cold in spring, but clearly this is not the case, suggesting that the temperature of the spring water must be relatively high. Because of the flushing, comparison of soil temperatures between the relatively litter free podsol and brown earth (i.e. Stations Two and Four) is not possible.

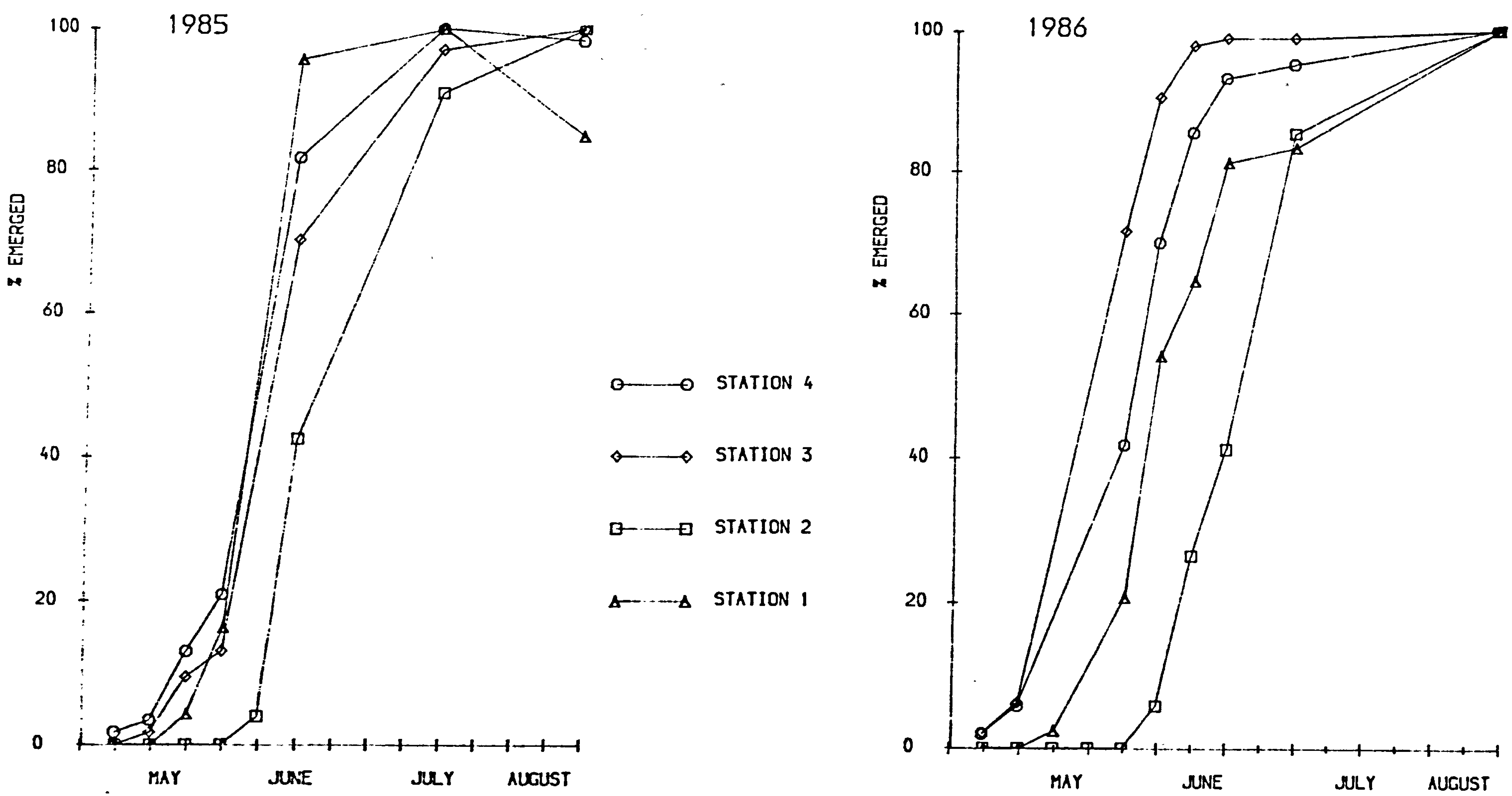
The drier mor humus with only a thin litter cover at Station Two would be expected to warm up faster than the wetter litter covered humus at Stations One and Four. However, soil temperatures at Station Two remained the coldest until late June in 1985 and had not caught up by the time recording ceased in mid-June in 1986. In both years there was a rapid rise in soil temperature in May after the last frosts at Station Two. Spring frost may therefore delay soil warming, resulting in higher temperatures in the litter covered, frost free soils. (This may not necessarily be true of mineral soils. Mineral soil characteristically has lower minima than humus, but has shorter frost persistance in spring (Shanks 1956). The difference in soil warming times between a litter covered and a litter free mineral soil may not therefore be so marked). It can be hypothesised that a litter free soil that is only lightly frosted in winter and is frost free in spring will warm up more rapidly than a litter covered soil, whether it be an organic or mineral soil.

Fig. 9.5 shows the pattern of frond emergence at the stations in 1985 and 1986 respectively, using percentage of total fronds emerged by the final frond count (including fronds that were lost before the final count). Comparison with Fig. 9.4 shows that emergence patterns are similar to soil temperature patterns. In both years the order of emergence and the rank order of the emergence curves are the same as those for temperature. Emergence at Station Two did not start until June in either year, when its soil temperature approached that of the other stations. Higher temperatures were recorded in early spring in 1986 than in 1985 and accordingly, frond emergence was earlier at Stations One, Three and Four in 1986 than 1985. The rate of emergence was also greater during the first few weeks of emergence at Stations Three and Four in 1986 than in 1985. In 1986 the rate of emergence was greater at Station Three than Station Four during May, reflecting the higher May temperatures of Station Three. The increased rate of emergence at Station One in late May 1985 coincides with a marked rise in temperature at the station.

Such responses to temperature are only evident until early to mid June. Temperatures at Station Two increase markedly at the beginning of July in 1985 but there is no corresponding change in the rate of emergence. Likewise, in 1986 temperatures at Station Four overtook those at Station Three at the beginning of June, but there was no corresponding response in emergence.

It should be possible to determine the threshold temperature for commencement of spring growth from the data. The mean temperature at emergence will not equal the threshold temperature for growth because the frond buds grow in the soil and litter prior to emergence. It was not

FIG.9.5 FROND EMERGENCE AT THERMOGRAPH STATIONS IN 1985 AND 1986 - PERCENTAGE OF ACCUMULATED TOTAL OF FRONDS EMERGED, INCLUDING FRONDS LOST PRIOR TO FINAL COUNT



possible to record the exact time of the onset of spring growth, but by removing the overlying litter and soil at 20 extra plots in spring 1986 (five per site) it was observed that growth began about three weeks before emergence. (Spring growth is indicated by the curling of the tip of the frond bud into the beginnings of the "hook"). The mean soil temperature of the four weeks prior to emergence in 1986, including the week of emergence, are shown below for each station.

Table 9.11 Mean soil temperature at 10cms in the four weeks prior to emergence (including week of emergence) at the stations in 1986.

Station One	14th April to 12th May	5.69°C
Station Two	5th May to 2nd June	5.43°C
Station Three	31st March to 28th April	5.52°C
Station Four	31st March to 28th April	5.50°C
	Mean	5.53°C

Clearly temperatures prior to emergence are very similar at all four stations and the mean temperature for growth (5.53°c, 95 percent confidence intervals, 5.36°c,5.71°C) is very similar to the generally used threshold temperature for growth (5.5°C). Temperatures at Station Two did not reach this required threshold temperature until around the beginning of May, which supports the hypothesis that later frond emergence is due to delayed soil warming.

Watt did not recognise the effect of late spring frost in delaying soil warming and therefore frond emergence. He did however find that heavy winter frosts delayed emergence by killing the underground frond buds, particularly in litter free bracken. In years of light winter frost he found that litter free bracken usually emerged before litter covered bracken and the opposite to be the case in years of heavy frost (Watt 1953). Winter frosting may therefore also explain the later emergence at Station Two and certainly this was the only station at which frosted rhizomes and frond buds were observed. Frosted rhizomes and buds were also commonly observed at Sourhope, particularly under the hinterland litter-free bracken. Emergence in the enclosure bracken that was litter-free prior to enclosure began earlier than the adjacent bracken outwith the enclosures (Fig. 9.6). After the first season there was observed to be a marked increase in litter inside the enclosures, which will be due to the increased vigour of the bracken and to reduced wastage by wind and trampling. It would seem therefore that the increased litter cover effectively insulated against the effects of winter frost. Thus grazing not only directly affects vigour by reduction of frond height, but also indirectly by reducing the amount of protective litter.

A Chi squared test (using a 2x2 table) on all the posts and stations showed emergence in litter covered plots to be significantly earlier than in litter free plots in both years (e.g. 1985 χ^2=9.192, p<0.01) . (The mid-May frond count was used to distinguish "early" and "late" emerging bracken in the test).

Fig. 9.7. shows the emergence pattern of litter covered and litter free plots and also of the two springline plots at Glensaugh in 1986 (including the Stations). The early emergence at both of the spring flushed plots supports the hypothesis that the temperature of the spring water is relatively high. Under normal circumstances soil warming would be retarded in wet soils and accordingly, emergence from the "poorly aerated" soils was generally later than from the other "well aerated" soils. However it is impossible to tell whether this is due to the absence of litter (and therefore the effect of winter frost) or to delayed soil warming without examining the frond buds in spring. It is likely that both factors

Fig.9.6 Early emerging enclosure bracken at Sourhope Eight, 1986

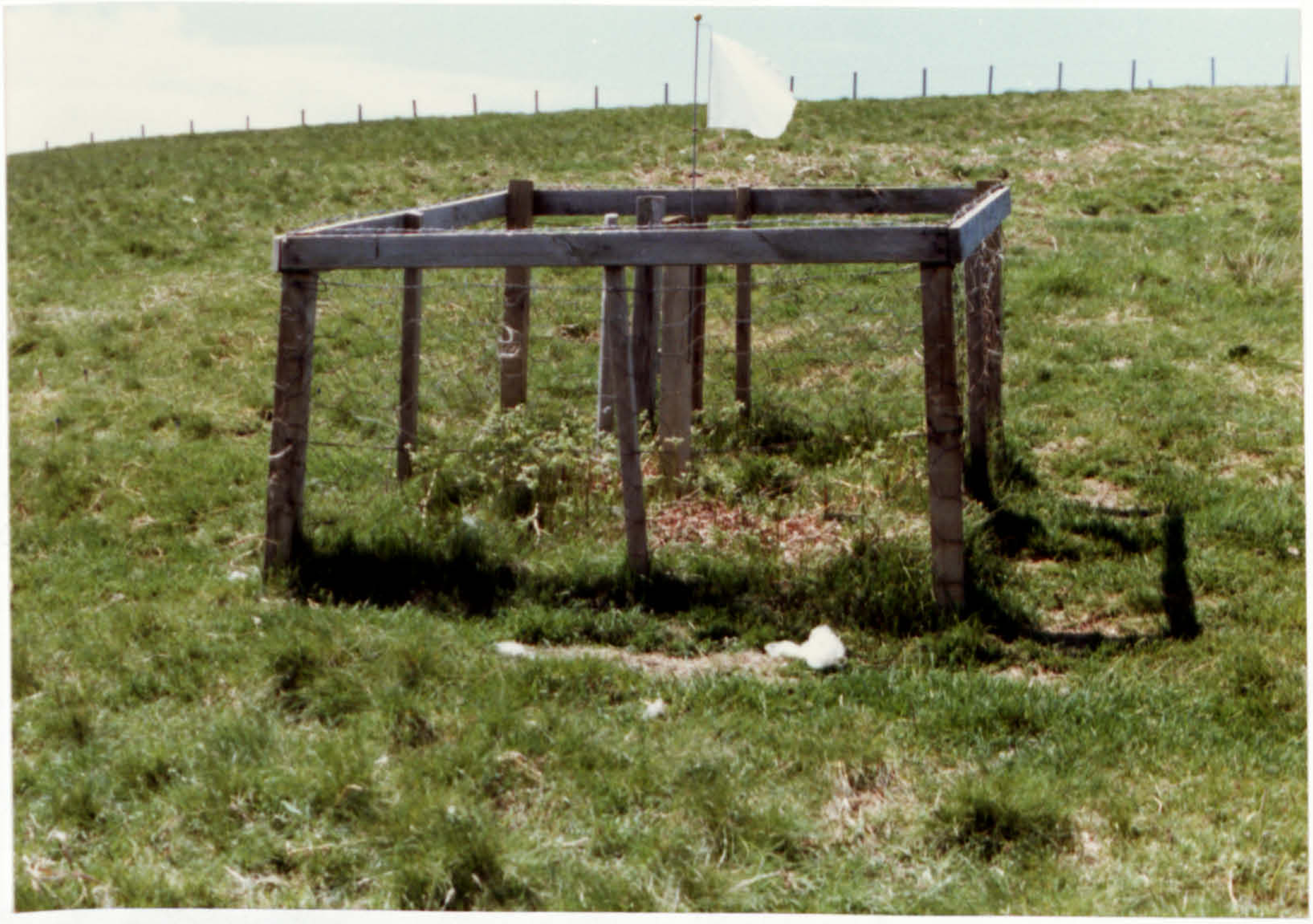
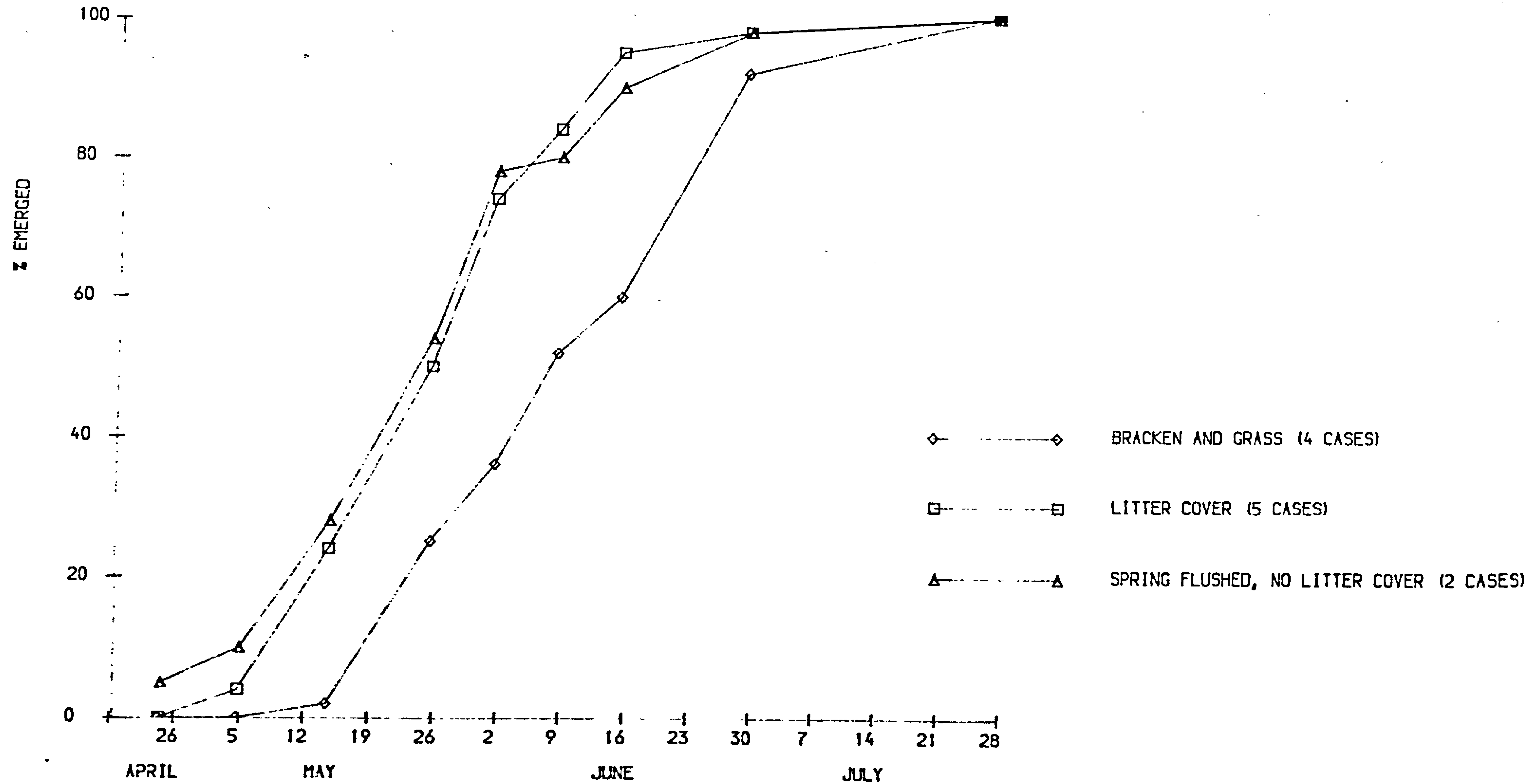


FIG. 9.7 FROND EMERGENCE AT GLENSAUGH IN 1986 – PERCENTAGE OF ACCUMULATED TOTAL OF FRONDS EMERGED, INCLUDING FRONDS LOST PRIOR TO FINAL COUNT



are important to emergence. Thus although litter covered bracken emerged before litter free bracken at Sourhope, emergence of litter covered bracken was still later than at the other sites. Effects of both winter frost (on the litter free bracken) and later soil warming (on the litter covered bracken) are therefore evident. As discussed, the predicted mean April temperature is markedly lower for Sourhope than for the other sites and thus it is reasonable to suppose that mean soil temperature is likewise lower.

9.4 Temperature and the rate of growth

It should be possible to correlate the rate of growth (increase in frond height) and the rate of development of the frond (stage of unfurling) with temperature. However, the data cannot be used for this purpose because only mean frond height and mean stage of unfurling per plot were recorded. The effect of the late emerging fronds is therefore to depress mean height and stage (which can decrease after the first couple of weeks of emergence as more fronds emerge). At some plots early emerging fronds were observed to remain the tallest throughout the season, but at other posts they were overtaken by later emerging fronds. Only by monitoring individual fronds will it be possible to accurately correlate rate of growth and development to temperature. However, the effect of temperature on the rate of emergence in the early season suggests that temperature does influence rate of growth at least in the early season. This hypothesis is supported by the strong correlation between maxima and frond height in the early season.

In most cases the stage of development of the later emerging plots was equal to, or ahead, of the earlier emerging plots at the final frond count, which suggests that temperature is not important to unfurling, at least not in the late season. The later emerging bracken is generally the less vigorous bracken (that is, litter free). This suggests that in relatively stressed short bracken the lack of height and frond area are partly compensated by rapid unfurl . Atkinson (1986) observed rapid unfurl in short, litter free early emerging bracken in the Malverns (where winter frosting of underground parts was probably minimal). This suggests that it is the vigour of the bracken rather than time of emergence that determines rate of unfurl .

9.5 The review of the effect of temperature on bracken vigour has revealed the following points:

1. Bracken vigour was significantly affected by spring frost at only two posts both at Kilmartin where frosts were the most frequent and the heaviest. Frosts down to about -2.0^{o}C generally inflicted little damage, especially if a ground frost only had occurred.

2. Timing of spring frost and frond emergence largely determines the extent of frost kill. Duration of frost may also be important, with bracken surviving frosts of -4.0^{o}C where posts were located on the open hillside.

3. The overall lack of frost kill results in a negative correlation between frond height and minima because of the coincidental relationship between frond height and minima arising from the effect of temperature inversion.

4. Complete and/or early frost kill induces substantial regrowth. Partial and/or late frost kill induces very limited regrowth. Side pinnae may extend to replace the frosted growing apex in partially frosted bracken.

5. Frond height and density are reduced in heavily frosted stands in the current season. Growth in partially frosted

bracken proceeds only slowly, while height and density of regrowth bracken is less than that of unfrosted bracken. The long term effect of regular frosting on density is not clear.

6. Autumn frost does not affect bracken in the late season and does not therefore directly cause end of season senescence.

7. Emergence in the litter-free bracken was significantly later than in the litter-covered bracken.

8. A cover of bracken litter insulates the soil from frost, which (in organic soils, at least) results in faster soil warming in spring and therefore earlier frond emergence than in litter-free bracken. In years of lighter frost, a litter-free soil may warm up faster than a litter-covered soil and emergence will probably be later in the latter. Delayed emergence in the litter free stands will also be due to winter frosting of the underground buds and rhizomes.

9. The threshold mean temperature for the onset of growth of the frond buds would seem to be approximately 5.5 ^{o}C.

10. Mean soil temperature affects the rate of emergence up until about early June and it is therefore likely that temperature also largely determines the rate of growth. This hypothesis is supported by the positive corelations obtained between maxima and frond height. Significant correlations obtained with all the posts in 1985 may reflect the effect of mean temperature rather than maximum, (as may the strong correlation obtained for the early season when the soil stressed posts and Sourhope are omitted from the analysis in 1986).

11. There is no evidence that temperature affects rate of

unfurling .. Stressed bracken is observed to unfurl relatively rapidly.

13. Frond density increases with decreasing air maxima.

Temperature therefore has three main controls on bracken vigour at the sites; by determination of time of emergence (and therefore length of the growing season); by determination of the rate of growth in the early season, and by winter frosting of unprotected frond buds. Clearly the three are interlinked for the more vigorous the bracken the greater the protection against winter frost. This interaction of factors is further discussed at the end of the chapter. Whether temperature determines the end of the growing season is not clear, although frost has been shown to have no part in this. The possibility that moisture stress causes early senescence is discussed in Chapter Seven. However such a mechanism is unlikely to occur in bracken on moist soils and some form of temperature or photoperiodicity control is therefore a possibility.

The hypothesis that temperature has most effect on growth in the early season is supported by work on other plant species. Hunter and Grant (1971) and Alcock et.al. (1967) established the importance of early season temperature for grass which Alberda (1965) showed to have an upper threshold temperature of $10^{o}C$ after which temperature ceases to influence growth. The hypothesis that an upper threshold temperature exists for bracken is supported by Watt's (1950) finding that there is no correlation between mean temperature and frond height after late May (although he did not investigate the effect of early season temperature). The rate of growth of late emerging bracken at high altitudes (where the mean temperature does not remain above the upper threshold temperature for very long) may therefore be influenced by temperature well into the season.

9.6 Exposure and bracken vigour

Negative correlations were obtained between exposure (that is, mean tatter rate) and frond height in both years. However, the three posts that were shown in Chapter Five to be disproportionately exposed strongly influence the correlation. Omission of these three posts from the analysis weakened the correlation as shown below in Table 9.12.

Table 9.12 Correlation of frond height with exposure - a). with all posts b). omitting the three most exposed posts

	1985	1986
a).	-0.478**	-0.517** R^2 =24.0
b).	-0.361	-0.405 R^2 =13.2

**p<0.01

The weaker correlations in 1985 probably reflect the use of 1986 tatter data in 1985. Omission of Sourhope and the soil stessed posts improves the correlations in 1986 ($r=-0.679$, R^2 =41.2, $p<0.02$) although the one remaining very exposed post, Gatehouse Seven, still affects the correlation. Its removal gives a lower but still significant correlation ($r=-0.653$, R^2 =37.4, $p<0.05$). If Sourhope is included but the soil stressed posts still omitted, the correlation becomes non-significant, supporting the hypothesis that exposure does not account for the reduced vigour of the bracken at the site.

Positive correlations were obtained between exposure and frond density, although again the three very exposed posts strongly affect the correlation. Their omission increases the correlation in 1986 (although the regression coefficients are still low), but has little effect in 1985 as shown below.

Table 9.13 Correlation of frond density and exposure - a). with all posts b). omitting the three very exposed posts

	1985	1986
a).	0.396 $p<0.05$ $R^2=12.6$	b). 0.337 N.S
b).	0.391 $p<0.05$ $R^2=11.7$	0.405 $p<0.05$ $R^2=15.2$

Omission of Sourhope and the soil stressed plots results in stronger correlations, shown in Table 9.14 below, in which the remaining very exposed post only affects the correlation in 1985.

Table 9.14 Correlation of frond density and exposure omitting Sourhope and the soil stressed posts

	1985	1986
Including GH7	0.772 $p<0.01$ $R^2=56.5$	0.671 $p<0.05$ $R^2=32.4$
Omitting GH7	0.448 N.S.	

Data transformation - logten both variables

If Sourhope is included but the soil factor still omitted, the correlations become non-significant, indicating that exposure does not account for the high frond densities at the site.

The effect of increasing exposure is therefore to reduce frond height and increase frond density. The correlation obtained on omission of Sourhope and the soil stressed posts in 1986 is not as high as the correlation between frond height and ground maxima in Period Six (1986) when the same posts are omitted (r=0.800, R^2=60.3), p<0.01). This suggests that (within the sites) temperature per se is more important than the temperature element of exposure to bracken vigour and also demonstrates that other effects of exposure (such as mechanical stress and moisture stress) must be important as well. The strong influence of the very exposed posts on the correlations confirms the hypothesis that the effect of exposure on bracken increases markedly at the upper bracken limit. Thus it can be hypothesised that the upper bracken limit is determined by exposure rather than temperature per se.

It is not possible from the data to determine the upper exposure limit for bracken and a series of tatter flags across the upper bracken limit and beyond would be necessary to do this. However the limit will be greater than the maximum tatter rate recorded which was 11.50 cms/day at Kilmartin Five in 1985. The limit will vary depending on the influence of other factors. For example, Kilmartin Five had a tatter rate of 11.5 and 10.75 cms/day and a mean frond height of 44 and 50 cms in 1985 and 1986 respectively. In contrast, frond height in 1985 at Gatehouse Seven was 95 cms but the tatter was only approximately 2cms lower than at Kilmartin Five. Rooting depth at Kilmartin Five is restricted by a relict iron pan and the soil can become fairly dry in summer, but the soil at Gatehouse Seven has no such restrictions. Soil depth generally becomes shallower with increasing altitude and therefore increasing exposure. The effect of the two factors upon bracken are therefore interlinked.

The effects of temperature and exposure are therefore similar, in that frond height decreases and density decreases with increasing environmental stress. As discussed in Chapter Seven, the effect of soil moisture may be similar to the effect of exposure. The relatively short and dense bracken at Sourhope could therefore be due to soil moisture stress. As discussed in Chapter Two, past work has shown that cutting and burning produces similar effects (i.e. increased density and decreased height). It would therefore seem that bracken produces fewer and more robust fronds in optimal conditions than in stressed conditions. Thus the short dense character of the Sourhope bracken could be the result of relatively heavy grazing pressure and the low spring temperatures, as well as the dry soils. All three factors are probably influential. Density was found to decrease on poorly aerated soils (i.e. those in which gleying is near the surface), which suggests that extreme stress may reduce density.

9.7 Aspect and altitude and bracken vigour

In both years correlations of aspect with frond height are positive and with frond density are negative, as would be expected from the maxima results. However, none are significant even after omission of Sourhope and the soil stressed posts. A larger sample would probably need to be taken to obtain significant results because of the indirect nature of the factor in relation to bracken growth. It follows that aspect must be important in view of the significant results obtained for maximum temperature and of the results of the soil temperature investigation.

As expected, altitude was negatively correlated with frond height and positively with frond density, mirroring the results of maxima and exposure. The correlations are not significant if Sourhope and/or the soil stressed posts are removed. Thus the altitudinal range of the three remaining sites is not great enough to show the effect of altitude in the smaller sample. (In contrast, the correlations with exposure improved in 1986 in the smaller sample, demonstrating that local topography rather than altitude determines exposure within the bracken zone).

9.8 The interaction of factors

The value of a multi-variable approach to analysis is limited for several reasons. Without individual analysis of each factor it may be impossible to interpret the results properly. For example, the anomalies in the minima results, the strong influence of the very exposed posts on the correlations, and the influence of the soil factor and Sourhope in masking the effect of the other factors, are likely to be missed. One of the purposes of a multi-variable analysis is to determine the most important variables. However, the importance of a factor will vary according to the study area and a multi-variable analysis in this study will therefore only indicate the most important factors within the main bracken zone. Furthermore, most muti-variable analyses cannot determine the interaction of factors. However, Stepwise Regression Analysis overcomes this problem to some extent by selecting factors at each step on the basis of their partial correlation and this method of analysis is therefore used while bearing in mind the limitations of a multi-variable approach. The minimum temperature factor is not included in the analysis because of its coincidental correlation with bracken vigour. Only the "soil aeration" classification is included (the use of catergorical data excluding the use of more than one soil classification). It is impossible to omit posts from the analysis for one factor alone and therefore the strong influence of the very exposed posts on the results has to be borne in mind. Winter frost cannot be included as a factor because its effect is impossible to statistically analyse with the present data. It was shown that litter free bracken is most suseptible to winter frost and separate analysis would therefore have to be carried out on the two bracken stand types. The analysis was also tried omitting Sourhope and the soil stressed posts. The results are shown below in Table 9.15.

Table 9.15 Results of Stepwise Regression Analysis of factors affecting frond height

a). All posts

	1985		1986	
Step	1	2	1	2
	"Well aerated" soil	"Well aerated" soil	"Well aerated" soil	"Well aerated" soil
		Air maxima Period 2		Exposure
R^2	55.4	66.55	53.23	64.49

b). Omitting Sourhope and soil stressed posts

	1985	1986
Step	1	1
	Air maxima Period 2 (May-June)	Ground maxima Period 6 (April-May)
R^2	28.9	63.92

The results merely confirm the results of the analysis of individual factors. The soil factors covered by the "soil aeration" classification (drainage, moisture content and depth) are therefore the dominant factors controlling bracken vigour at the sites, (that is, within the main bracken zone). Exposure was not significantly correlated with frond height in the individual analysis in 1985 and does not therefore appear in the above results in that year. The exclusion of maxima in the first analysis in 1986 reflects the fact that maxima were only significantly correlated with height after Sourhope and the soil stressed posts had been omitted. The exclusion of exposure in the second analysis in 1986 demonstrates the correlation between temperature and exposure in Period Six (when Sourhope and the soil stressed posts are omitted)

Although the analyses of the past two chapters have examined the effect of factors in isolation, in reality there will be interaction between factors. The interaction between soils and exposure has already been discussed. The effect of a litter cover in protecting against winter frost has also been shown to be important. If other factors are optimal, the bracken may produce enough litter to achieve this protection, resulting in a system of positive feedback. Thus vigorous bracken at Glensaugh is unaffected by the extreme winters that characterise the region. That it is able to do this demonstrates that the other factors controlling vigour must be fairly optimal. A negative feedback mechanism can be seen to exist at Sourhope in which grazing reduces vigour and therefore litter production, resulting in later frond emergence. The importance of the interaction of factors is also demonstrated by the ability of bracken to overcome the affects of spring frost. Thus bracken at the two most heavily and regularly frosted posts is relatively vigorous, underlining the effectiveness of regrowth. It is likely that all the other factors must be optimal for bracken to overcome the effects of frost. Thus exposed or soil stressed bracken is unlikely to become vigorous enough to build up a protective litter cover, or to produce vigorous regrowth, regardless of the temperature regime.

In the final chapter, the main findings of the thesis are summarised and discussed in relation to the hypotheses put forward in Chapter Six and in relation to the distribution and spread of bracken in Scotland as a whole.

Chapter Ten

Conclusions

The main findings of the study can be summarised as follows:

1. The main bracken zone has a higher altitude in the east than in the west.

2. Exposure is relatively low and uniform within the main bracken zone, but increases rapidly at the upper bracken limit.

3. There is greater inter-site variation in maxima and predicted mean temperature than in exposure, with relatively low predicted mean and early season maxima at Sourhope.

4. Glensaugh has a relatively warm local climate in the early growing season which is atypical of the region.

5. The lower western sites have the coldest minima due to temperature inversion, except in winter when Glensaugh is the coldest site.

6. Frond emergence is largely determined by soil temperature, the threshold temperature for frond bud growth being approximately 5.5^{o}C.

7. There is only limited spring frost kill in the main bracken zone and this is mainly in the west. Frost depresses frond height and density in the short term.

8. Vigorous bracken is able to withstand winter frost because of the insulation of its litter cover. The effects of spring frost are partially offset by regrowth.

9. Frond height (and therefore frond vigour) decreases and frond density increases with increasing stress. This includes exposure, low early season temperature, and possibly dry soils and grazing. Density decreases on poorly aerated soils and extreme stress may therefore decrease density.

10. The effect of exposure on frond vigour increases markedly at the upper bracken limit.

11. Moderately heavy sheep grazing (i.e. approx. 3 ewes per hectare) depresses frond vigour. The accessibility and intrinsic vigour of the stand determines the degree of grazing.

12. The depth of gleying determines whether or not bracken vigour is affected by poor soil aeration. A thick "aerated" organic layer provides extra rooting depth above a gleyed layer.

13. Soil depth determines whether or not soil moisture stress will occur on dry soils. A thick litter covered organic layer probably offsets soil moisture deficit in the mineral horizon.

14. Soil largely determines stand type and rhizome depth, therefore masking stand succession. There is little evidence of rhizome "succession" up the profile or of stand degeneration through nutrient deficiency with increasing litter accumulation.

15. Soils under the crests at Sourhope are physically similar to soils under adjacent <u>Nardetum</u>, rather than to the soils of adjacent bracken hinterlands. Rhizomes are

concentrated in the mor humus of the crests. There is no evidence that the crests are the advancing front of Watt's successional sequence. The greater vigour may be due to greater moisture or nutrient availability in the humified mor humus.

16. Vigorous bracken at Glensaugh, Sourhope, and above the head dyke at Kilmartin mainly occurs on peaty soils. Rhizomes are concentrated in the mor humus horizon.

17. Colonisation of the brown earths by bracken above the head dyke had occurred by the 1940's. Spread above the head dyke is now on to peaty soils, particularly Calluna soils. Spread below the head dyke is now onto the wetter brown earths.

18. There has been little spread on to Nardus or Molinia soils, and therefore there has been little spread at Sourhope (where most adjacent vegetation is Nardetum) since the 1940's.

19. There has been no large scale degeneration of bracken since the 1940s and most degeneration has been in marginal rather than mature stands.

The hypotheses put forward in Chapter Six can now be reappraised. Comparison of maxima patterns and bracken vigour between the sites suggested that early season maxima are important to vigour. The results of the maxima analysis supports this hypothesis and as discussed, mean temperature is probably as important as maxima, if not more so. (The importance of mean soil temperature to frond emergence supports this latter view). Clearly, concentration of bracken along the southern slopes of the Southern Uplands and the Highlands is related to temperature and length of the growing season.

Low spring temperature, due to the higher altitude of the bracken zone, will partly account for the lesser vigour of bracken at Sourhope and in the south-east generally. (At sea level the region is the warmest in Scotland in the growing season). The importance of temperature also supports the hypothesis that the relatively warm local spring climate at Glensaugh allows vigorous bracken growth in a region where prolific bracken is not commonly observed. The low mean spring temperatures in the region generally will partly account for the poor vigour of bracken in the north-east. Vigorous bracken at Glensaugh is protected from the extreme winter frosts by its litter layer, but this protection will be very much reduced elsewhere in the region. Warmer spring temperatures (and therefore a longer growing season) must largely account for the prolific vigorous bracken that characterises the west of Scotland.

Comparison of bracken vigour and minima between sites suggested that frost is not important to bracken vigour at the sites. This is certainly true for spring frost which inflicted only limited damage. However it is clear that winter frost is important to less vigorous bracken that does not have a protective litter cover. Bracken at Sourhope is largely litter-free and winter frost will therefore have more effect at this sites than the others. As discussed above, winter frost will also be important in most of the north-east where low temperatures restrict bracken vigour. The same will be true for bracken at high altitudes and on north facing slopes.

It could be argued that the limitation of spring frost damage is due to avoidance by bracken of the most frosted areas. Vigorous bracken is largely able to overcome the effects of spring frost in the west, but in the east where frosts are colder at comparable altitudes, this may not be possible. The higher altitude of the bracken zone in the east may therefore be a response to colder frosts at lower altitudes. However, soil moisture deficit will be greater at lower altitudes in the east and this may also restrict the bracken zone to higher altitudes where temperature is suboptimal. The generally reduced vigour of bracken in the east will result in lower resistance to frost than in the west. Bracken in the east may therefore require less frosted locations and this would explain why spring frosted bracken is generally a rarer phenomena in the east.

The findings support the hypothesis that the xeromorphic frond morphology at Sourhope is due to soil moisture stress rather than to exposure. The relatively uniform exposure but varying temperature regimes of the sites suggest that temperature _per se_ is more important than exposure within the site. However, the increasing effect of exposure on vigour at the upper bracken limit indicates that exposure determines the altitudinal limit for bracken. Thus the greater exposure in the west results in a lower altitudinal limit for bracken than in the east.

Climatic controls, soil moisture deficit and land use are therefore largely responsible for the pattern of bracken distribution in Scotland. Poor soil aeration will be of more importance to distribution on a local scale. Bracken has been shown to be able to colonise _Calluna_ peat, but rarely other kinds of peat, (such as _Molinia_ or _Nardus_ peat). In the north-east where _Calluna_ peatland is dominant, the cold temperatures and high exposure of the Cairngorm plateau militate against spread. In the far north the cold temperatures and exposure will again be important, but the dominance of peat communities of other than _Callunetum_ will also restrict the spread of bracken. In the Southern Uplands and particularly in the east, the relatively long history of sheep grazing and high stocking rates has resulted in a decrease in the _Calluna_ area and an increase in _Nardus_ (King and Nicholson 1964). Thus the failure of bracken to spread at Sourhope can be partly attributed to the lack of suitable soils (or possibly the lack of suitable vegetation type, it being suspected that it is the _Nardetum_ itself rather than the soil type that is preventing spread). Furthermore, the lesser vigour of the bracken at the site and in the east generally will weaken bracken's competitiveness.

The finding that most of the brown earth areas are already colonised above the head dyke suggests that most future spread will be restricted to below the head dyke in the south of Scotland because of the lesser extent of Calluna soils and therefore, potential sites for spread. This is already seen at Gatehouse and to some extent at Kilmartin. Agriculture is more intensive below the head dyke in the east than in the west due to the smoother topography and drier soils. Bracken is therefore less likely to spread very much below the head dyke in the east, unless agriculture should become less intensive. However, the possible effect of frost and soil moisture deficit at lower altitudes in the east may somewhat limit downhill spread regardless of the agricultural system. The cold temperatures of the plateau and less sheltered slopes will restrict further bracken spread in the north-east to sheltered valleys on the southern edge of the plateau.

Future bracken spread is therefore likely to be limited to the brown earths below the head dyke in the west and to the more sheltered Calluna soils generally. This excludes much of the north-east and the south-east, although future farming practices could change this scenario. As discussed in Chapter One, estimations of rates of bracken spread for Scotland have been taken from the studies by the Macaulay Institute at Kilmartin and Glensaugh. Both areas are optimal for bracken growth and Glensaugh is atypical for the north-east. It is therefore unrealistic to apply similar rates of spread to Scotland generally. Present and potential restrictions to bracken spread, such as those outlined above, have to be taken into account. Failure to do so will result in gross over-estimates.

While future bracken spread may be somewhat limited, the findings of this study suggest that there is unlikely to be any large scale degeneration of bracken in the near future. The lack of tree regeneration in the uplands of Britain, due primarily to grazing, ensures that bracken will remain a dominant feature of our upland landscape for some time to come.

Appendix One - Topographic Characteristics and Stand Types at Monitoring Posts

Kilmartin

	post number							
	1	2	3	4	5	6	7	8
aspect	N	N	E	N	E	W	S	E
altitude(m)	112	110	123	169	174	130	130	110
slope(°)	20	0	15	8	5	12	15	5
stand type	1	1	2	3	2	2	1	1

Gatehouse

	post number								
	01	N1	2	3	4	5	6	7	8
aspect	S	S	W	S	SW	SE	E	S	S
altitude(m)	60	60	65	140	150	150	180	210	138
slope(°)	35	6	10	10	5	14	14	20	10
stand type	1	2	1	1	2	3	1	2	2

Glensaugh

	post number								
	01	N1	2	3	4	5	6	7	8
aspect	S	SE	W	S	SE	SE	SE	SE	SE
altitude(m)	225	1	183	153	183	205	220	235	232
slope(°)	32	34	44	1	35	33	19	20	7
stand type	1	3	-	2	1	1	2	1	2

Sourhope

	post number							
	1	2	3	4	5	6	7	8
aspect	NW	W	W	W	W	N	SW	SE
altitude(m)	320	380	310	315	315	325	325	270
slope(°)	14	24	18	17	15	20	25	10
stand type	1	2	-	1	2	1	2	2

key: stand type 1 - litter covered
2 - litter free
3 - litter-grass mosaic

Appendix Two - Details of Meteorological Stations used in Chapter Five

	altitude	location from site
Lochgilphead	5m	9 miles SW
Threave	73m	10 miles E
Fettercairn (Craigmoston)	95m	3 miles SW
Floors Castle (Kelso)	59m	15 miles N

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