The morphology and physiology of moorland bracken (*Pteridium aquilinum* (L.) Kuhn) and their implications for its control.

A thesis submitted in part examination
for the degree of D.Phil. by
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April, 1993.

"To place it in perspective as succinctly as possible, bracken
is one hell of a plant".

I.A. Evans (1987).

TABLE OF CONTENTS

Appendices

LIST OF TABLES AND FIGURES

Acknowledgements

I would like to thank my supervisor, Dr. John Digby, for all his help, support and guidance during the course of this project.

Thanks also Harry Vallack and James Merryweather for their help in teaching techniques and allowing me to use their equipment and to Colin Abbot for all his help in the greenhouses. Jacqueline Hattee and Paul Longhurst, both experts in the art of digging, have also been of very great help with fieldwork.

Work in the field would not have been possible without the kind permission for access to field sites granted by the Farndale and Goathland Estates for which I am grateful. Thanks must also go to A.D.A.S. for access to their experimental site at Spaunton Knowl. The North York Moors National Parks Department, especially Sue Rees, have also provided valuable support in finding suitable field site and providing access to maps and aerial photographs.

The work was funded by a grant from S.E.R.C. to whom I am grateful.

Lastly I would like to say a big thankyou to my family, the members of U.Y.W.R.U.F.C. and my friends Laura, George and Jo who have managed to keep me almost sane throughout the past 3 years!

1. ABSTRACT

A study of the morphology and physiology of bracken, specifically the requirements for its advance into heather moorland has been carried out. These studies have suggested ways in which bracken physiology might be manipulated to improve control methods. Three experimental systems have been employed - rhizome segments grown in boxes, bracken grown from blocks of moorland peat containing relatively undisturbed rhizome, and bracken in the field.

Morphological studies have revealed several differences between advancing fronts and the mature bracken stand. When compared with the mature stand, advancing fronts are found to have a greater density of fronds close to the stand before declining in number towards the outermost margins. Shorter fronds, earlier frond emergence, a greater proportion of 'transitional' relative to 'short' and 'long' rhizome shoots and a greater proportion of rhizome buds which are active also occur at the margins. These findings have control implications supporting the treatment of stand edges where bud activity is greatest, litter shallowest and the availability of vegetation to initiate *Calluna* / grass recovery greatest. Earlier emergence of margins suggests that the timing of herbicide applications should be earlier here.

The margins of bracken stands are seen to show drought effects before the mature stand and also have lower phosphate concentrations. Radiotracer experiments have shown that nutrients are able to move through the rhizome towards active growing points. However, severing of rhizome in order to isolate the margins of the plant has demonstrated that the margins are not dependent on such transport of resources for their survival.

The control of rhizome bud dormancy can be manipulated by both fertiliser and cutting treatments, resulting in increased rhizome bud activity and providing scope for the use of stimulatory pre-treatments before herbicide application. Plant growth regulators and sub-lethal herbicide doses did not increase this activity.

2. INTRODUCTION

2.1 THE IMPORTANCE OF BRACKEN AS AN UPLAND WEED

2.1.1 Distribution

Bracken (*Pteridium aquilinum* (L.) Kuhn) is a highly successful perennial plant which is present throughout the world in a wide variety of climates, altitudes and latitudes with the only exceptions of the hot and cold desert regions. Page (1976) describes bracken as having a "notoriously plastic morphology", showing a number of morphological differences in response to the particular environment in which it is found.

2.1.1a Estimated U.K. bracken cover

Pteridium aquilinum var. *aquilinum* is widespread throughout Britain from sea level to over 600m, but is most successful in areas including uplands and steep slopes where intensive agriculture is impossible or not economically viable. Within Britain, bracken is therefore most abundant above 360m in the uplands of the North and West although it reaches the limit of its altitudinal range at around 600m (Hopkins *et al.*, 1988).

The total U.K. land loss to bracken has proved difficult to estimate because of the tendency to underestimate areas of sparse bracken cover and the area of slopes covered by bracken when using remote sensing methods, and the inaccuracies involved in the extrapolation of local information to a national scale. Taylor (1986) estimated total U.K. bracken cover at 6720km^2 (an area equivalent to that of the county of Devon) and suggested that this figure was likely to have been an under-estimate since it was based on relatively old data from 1961-1966, and because of difficulties in estimating the area covered on sloping terrain from aerial photographs. In this estimate the figure for bracken area in Scotland (4720km^2) was extrapolated from that for Wales and was highly speculative.

Other estimates for Scotland based on questionnaires sent to farmers (Hendry, 1958) and remote sensing techniques (Miller and Whitworth, 1990) gave figures of 180,000ha and 63,250ha respectively, with bracken found mostly on the western side of the country. Subsequently, Taylor (1990) has revised his estimate to 2360km^2 for Scotland and hence 4005km^2 for the U.K.. Alternative estimates of U.K. bracken cover include 3000km^2 (Lawson et al., 1986) and 2880km^2 in the I.T.E. land use survey (Bunce et al., 1980).

2.1.2 Rates of encroachment

The annual rate of bracken encroachment in the U.K. has also been the subject of debate. Taylor (1986) gives figures of between 0.65% and 3.3% p.a.. In a 1986 survey of upland grassland in England and Wales (Hopkins *et al.*, 1988) an increase in bracken cover from 4.8 % to 6.3% of the land surveyed was reported between 1970-1972 and 1986. This translates to an increase of 30% in 14-16 years or approximately 2% p.a.. The increases were usually localised and confined to steeper slopes. Twenty-five per cent of the land surveyed with gradients in excess of 13^{o}was affected by bracken whilst only 4% of less steep slopes were affected. Miller and Whitworth (1990) estimate mean annual increase of bracken in Scotland at around 1%. Again there is much variation between localities and it is difficult to extrapolate from local rates of encroachment to a national scale. However, some studies (Watt, 1971, 1976; Smith, 1990; Marrs and Hicks, 1986) have reported a reduction in the amount of bracken present in some localities. Varvarigos and Lawton (1991) reported that farmers in the uplands of England and Wales actually perceived the rate of bracken encroachment as well below other estimates. The questionnaire resulted in an estimated increase of only 2.5% over the past 10 years in England and a decline of 1.8% over the same period in Wales. However, the collection data from the questionnaire was based on visual estimates of the area of land covered by bracken and no actual measurements were made. This information may therefore be less reliable than estimates involving quantitative surveys of bracken cover.

2.1.3 Bracken in the North York Moors

Within the North York Moors bracken represents a specific threat to heather moorland. The North York Moors National Park contains the largest single area of heather (*Calluna vulgaris*) dominated moorland in England and Wales (approx. 500 km^2), a feature which, within Europe, is unique to Britain (North York Moors National Park, 1991). The moors have a relatively mild climate, which favours bracken encroachment, with a maximum altitude of less than 500m and a rainfall of less than 1000mm per annum (Barber, 1986). Much of the unenclosed moorland is used for hill sheep farming under long-standing common rights agreements and

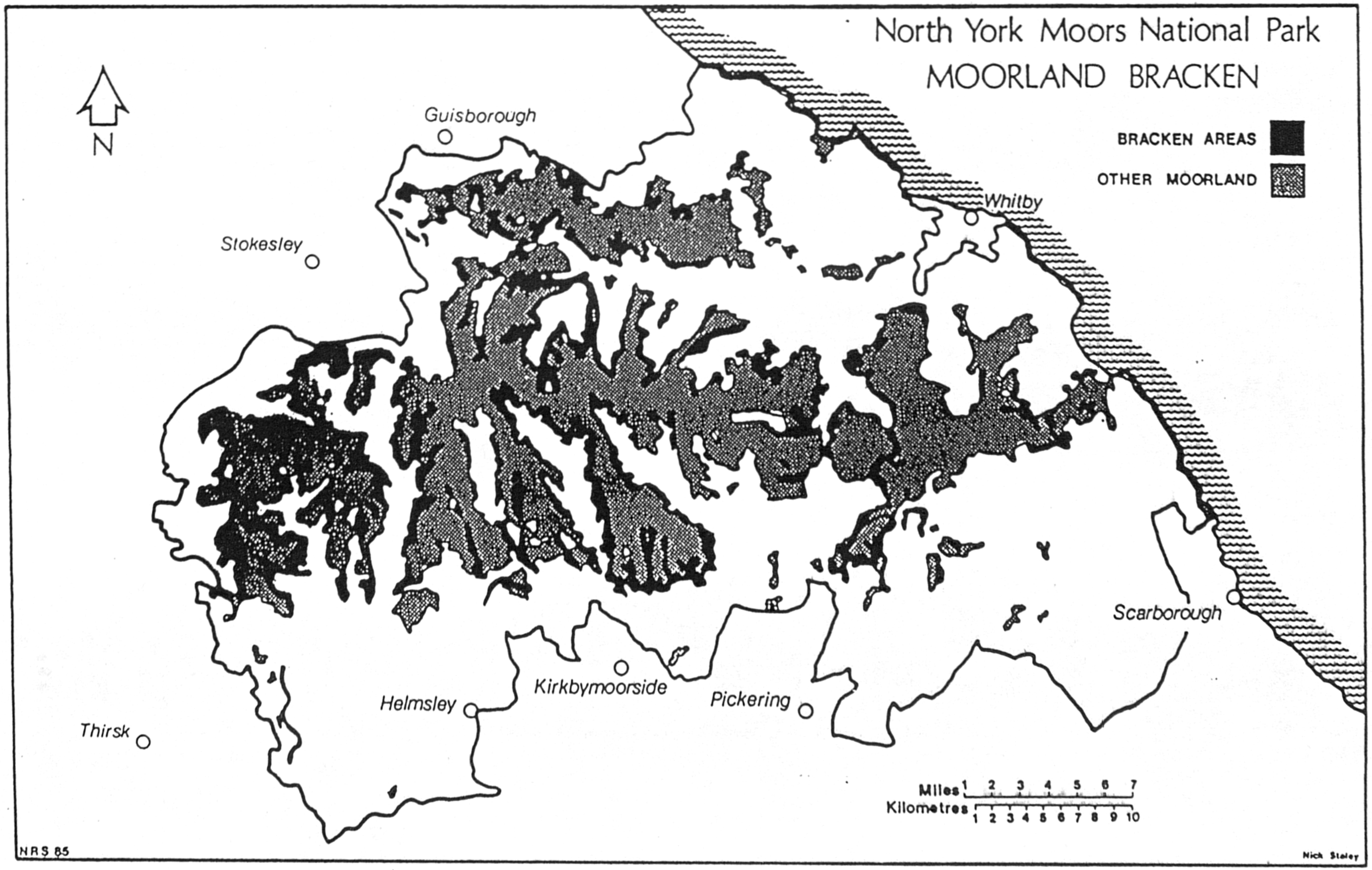


Fig.1 The extent of bracken encroachment within the North York Moors National Park. Taken from Brown (1986).

is managed by rotational *Calluna* burning to maintain high densities of red grouse (*Lagopus lagopus*) for sport. The moorland is also valued for its upland bird communities and for its amenity value.

Weaver (1986), using a remote sensing technique, estimated that 120km^2 of moorland in the North York Moors National Park was dominated by bracken. Bracken formed a "more or less continuous belt on slopes between agricultural valleys and moorland plateaux". This figure is in agreement with the national park committee's estimate of 140 km^2 (28% of the total moorland area) dominated by bracken in 1988 (North York Moors National Park, 1991).

2.1.4 Explanations for the encroachment of bracken

The fossil record shows that bracken has been present as an understorey species of deciduous woodland for the last 2 million years and has increased since competition from trees was first removed by deforestation (Rymer, 1976). The presence of bracken itself results in the formation of soils which are favourable to bracken growth (Taylor, 1986). Soil aeration is improved, nutrient cycling enhanced and the formation of litter layers results in smaller fluctuations in soil temperature and reduced risk of frost damage to the rhizome system. Competition from other plant species is hindered by the production of allelopathic chemicals by bracken (Gleissman, 1976; Gleissman and Muller, 1978).

Many factors may have contributed to the success of bracken, including a reduction in moorland management and changing agricultural practices. The depopulation of the Scottish highlands and resulting reduction in management has been given as a major reason for bracken encroachment in Scotland (Braid, 1934). In the past the right of commoners to cut bracken for thatching, animal bedding and the manufacture of potash and soap was considered valuable (Rymer, 1976). The reduction in total labour expended in the moors has undoubtedly contributed to the expansion of areas dominated by bracken. However bracken was most often cut late in the growing season (at a time when the fronds are least toxic to animals (Rymer, 1976)) and it is difficult to see how cutting at this time could greatly deplete rhizome mass. Changes in agricultural practise have led to a decline in the number of cattle found in the uplands, while sheep have increased. Trampling by animals (particularly cattle) is an effective method of reducing the amount of bracken present. Hopkins *et al.*, (1988) found bracken on none of the land grazed only by cattle, 4% of land grazed by cattle and sheep and 24% of the land grazed only by sheep. They suggested that the switch towards hill sheep production could be responsible for the increase of bracken in upland areas. However, these data may simply indicate that sheep are more frequently grazed on poorer land where bracken is abundant.

Two factors which seem to be particularly important to bracken encroachment in the North York Moors are the practice of *Calluna* burning and the problem of overgrazing by sheep, both of which result in the removal of competition from *Calluna*. Rotational *Calluna* burning is extensively carried out on the moors in order to produce a mosaic of young, rapidly growing *Calluna* shoots, together with older *Calluna*. Both grouse and sheep graze on young shoots, whilst older shoots provide both a habitat for the insects important to the diet of young grouse and cover for these birds. *Calluna* recovery after a burn at too high a temperature is often delayed until seedlings are established, since regrowth from surviving stem bases has been prevented. Full re-establishment of *Calluna* cover may require 5-6 years under such circumstances (Gimingham, 1960). However, bracken rhizome present deep in the mineral soil is able to survive high temperature burns and exploit the area from which competition has been removed (Whittaker, 1960; Flinn and Pringle, 1981). Nutrients are also released from plant tissue into a more mobile mineral form during the burn further encouraging bracken encroachment (Allen, 1964). The burnt ground also provides highly suitable conditions for the germination and establishment of bracken spores. This problem is particularly serious when a burn takes place close to or in to an existing bracken stand, especially when bracken rhizome is already present under the *Calluna* prior to burning.

Within the North York moors the rights of commoners make it very difficult to fence areas of moorland in which *Calluna* is recovering after burning or bracken control. Grazing pressures on common land are often very intense locally and overgrazing has become a serious problem preventing rapid *Calluna* regeneration and encouraging the spread of bracken. Perhaps the most important problem affecting the spread of bracken is lack of investment in moorland management resulting in lack of money for control programmes and labour input into the burning of over-age *Calluna* producing high temperature burns and poor regrowth.

2.1.5 Bracken encroachment and the changing environment.

Smith (1990) suggests that the greatest rates of bracken encroachment due to changes in management techniques are now over. However climatic change could encourage further spread in the future. Increasing temperatures due to global warming might result in a reduction in frost damage, earlier emergence of fronds and therefore a longer growing season (Pakeman and Marrs, 1992b), and the drying of waterlogged land previously inaccessible to bracken.

Dyer (1990) suggests that sporeling establishment is a more important source of bracken encroachment than is generally thought. Increased temperature and reduced rainfall result in the formation of conditions which are ideally suited for increased bracken spore production.

Increased soil acidification as arising from atmospheric pollution would also favour plants, including bracken, which flourish on acid soils.

2.1.6 Problems associated with the presence of bracken

In the past bracken was widely cut for thatching and animal bedding. Other valuable uses have been found including the manufacture of glass, soap and bleaches which are extensively reviewed by Rymer (1976). During both world wars work was carried out to investigate the value of bracken as a foodstuff principally for animal feed (Hendrick, 1921; Moon and Pal, 1949; Hunter, 1953) and interest is still being shown in the possibility of using bracken as a biofuel (Callaghan *et al.*, 1981; Lawson *et al.*, 1986). In spite of these uses the problems caused by the presence of bracken greatly outweigh the benefits.

2.1.6a Economic losses

Varvarigos and Lawton (1991) give an estimate of £9 million p.a. as total net losses to upland agriculture in England and Wales based on information gathered in questionnaires sent to farmers. The largest part of these losses are an estimated £5.9 million p.a. due to the opportunity costs of reduction in stocking rates. As bracken advances, there is a significant reduction in the amount of *Calluna* and grass available for both stock and game usually at the expense of better quality grazing (Brown, 1988). The resulting reduction in winter fodder and hence carrying capacity of the hill is of great significance in the marginal economics of hill sheep production.

The presence of tall bracken stands also result in increased shepherding problems on the moor. Shepherding costs and stock mortalities account for a further £1.6 million p.a., veterinary costs £0.16 million p.a. and bracken control costs £1.3 million p.a.. Financial benefits from the use of bracken for bedding are estimated at £46,000 p.a.. Additional economic losses centred on the shooting of red grouse for sport have proved difficult to estimate.

Bracken itself is of very little value as a feedstuff, being both toxic and carcinogenic to livestock (Fenwick, 1990). Grazing of bracken by livestock results in two acute diseases. Firstly a form of avitaminosis B_1 in simple stomached animals and secondly an acute cumulative poisoning in ruminants. Avitaminosis B_1 is caused by the presence of the enzyme Thiaminase I which catalyses the decomposition of thiamine. Symptoms include loss of condition, lack of co-ordination and muscle tremors ("staggers") (Evans, W.C., 1976). These symptoms can usually be reversed by feeding with vitamin B_1 and are not found in ruminants whose rumen microflora produce enough thiamine to meet the animals needs.

Ruminants, especially cattle, suffer acute bracken poisoning as a cumulative effect of continued bracken grazing. The active toxin involved in this disease, identified by Hirono (1990) as ptaquiloside, a norsequiterpene glucoside, gives rise to a severe depression in bone marrow activity and loss of white blood cells. This results in weakness, anaemia and internal haemorrhaging from which animals rarely recover (Evans, 1986). Sheep suffer from degeneration of the neuroepithelium of the retina ("bright blindness"), which is also associated with low blood platelet and white blood cell counts (Hannam, 1986).

Chronic bovine enzootic haematuria is a further disease associated with the ingestion of bracken by cattle which is characterised by haemorrhages in the urinary bladder mucosa and in advanced cases by tumours of the bladder wall (Villalobos-Salazar *et al.*, 1989).

Of the tumours resulting from ingestion of bracken, fibrosarcomas of the lower jaw in sheep are the most common (Hannam, 1986). In laboratory experiments on mice and rats however, a wide variety of tumours have been produced including intestinal adenocarcinomas, leukaemias and gastric carcinomas (Evans, 1987). In addition to ptaquiloside (also identified by Hirono (1990) as a powerful bracken carcinogen), shikimic acid and other carcinogens and mutagens have been identified in bracken (Evans, I.A., 1976) and it is likely that different varieties and developmental stages of bracken produce different carcinogens and mutagens (Fenwick, 1988).

The loss of sheep and grouse chicks due to tick-borne diseases including louping ill, tick-borne fever and tick pyeamia, are probably more significant than losses due directly to bracken poisoning. The presence of bracken increases the incidence of sheep ticks (*Ixodes ricinus*) because the humid habitat provided by bracken and bracken litter is required for the survival of the early life stages of the tick. Hudson (1986) found that within bracken stands the degree of tick infestation on grouse chicks were increased and their survival chances decreased in comparison with chicks found in *Calluna*.

2.1.6b Human health risks

There is growing concern about the risk which bracken poses to human health. Concern has been expressed regarding the cancer threat of ingestion of bracken spores from the air in bracken infested areas, and of ingestion of spores or exudates from water supplies or diary products which originate in bracken infested areas (Trotter, 1990). The warm, dry summer of 1989 gave rise to bracken sporing on an unusually large scale and prompted the release of a statement by the International Bracken Group regarding the carcinogenic risk of inhaling spores in bracken infested areas and encouraging people working in bracken areas to wear face masks.

Ingestion of both bracken spores and fronds have been repeatedly shown to induce many different cancers in a wide variety of species (Evans and Mason, 1965; Evans, 1987; Evans, 1986). In Japan, where 13,000 tonnes of bracken is imported annually for human consumption (Fenwick, 1988), oesophageal carcinomas have been shown to be 2.7 times more common in those who regularly eat bracken when compared with those who do not (Fenwick, 1990). Evans and Galpin (1990) have suggested that ingestion of bracken spores might be the cause of leukaemia clusters usually associated with nuclear power stations since such stations are invariably found in remote areas where bracken is common.

There is also correlative evidence from studies in Gwynedd, Wales, to suggest that there is a relationship between gastric cancer, which has an unusually high incidence in this area, with exposure to bracken in childhood, with consumption of buttermilk from cattle grazing or with drinking water from wells dug in bracken infested areas (Buckley, 1989; Galpin, Whittaker and Kassab, 1990). The carcinogenic effects of milk taken from cattle fed on bracken have been demonstrated in experiments on mice (Villalobos-Salazar *et al.*, 1989).

The tick-borne diseases to which man is susceptible include Lyme disease which is well-known in the U.S. and becoming increasingly frequent in Europe. The disease, caused by the spirochete *Borrelia burgdorferi* has symptoms ranging from an initial rash around the site of the tick bite, through fevers, flu-like symptoms and painful joints to severe nervous disorders (including facial nerve palsies), heart disorders, meningitis and encephalitis. Early treatment with antibiotics is essential to stop the progression of the disease (Parke, 1987; Habicht *et al.*, 1987).

2.1.6c Ecological and amenity implications

In general, the diversity of species found in bracken covered areas is less rich than in the *Calluna* moorland it replaces. Bracken's tall, dense foliage, deep litter layers and allelopathic chemical production make a bracken stand inhospitable to other plant species (Glass, 1976; Gliessman, 1976). Bracken can, however, sometimes substitute for a woodland canopy, providing shade cover for woodland plant species such as bluebells (*Hyacinthoides non-scriptus*) and wood sorrel (*Oxalis acetosella*). Some rare plants including climbing cordalis (*Cordalis claviculata*), chickweed wintergreen (*Trientalis europaea*) and dwarf cornel (*Cornus suecica*) are associated with bracken (Pakeman and Marrs, 1992b).

In a survey of upland areas Radcliffe (1977) found only 15 bird species breeding in bracken as opposed to 33 in *Calluna*. Several rare species including hen harrier (*Circus cyaneus*), twite (*Acanthis flavirostis*) and greenshank (*Tringa nebularia*) did not breed in bracken. Ground nesting birds such as merlin (*Falco columbarius*), curlew (*Numensius arquata*) and golden plover (*Charadrius apricaria*) and heathland species such as the Dartford warbler (*Sylvia undata*) are particularly susceptible to loss of breeding habitat. However, bracken stands provide an important habitat for birds such as whinchats (*Saxicola rubetra*), nightjars (*Caprimulgus europaeus*), tree pipits (*Anthus trivialis*) and yellowhammers (*Emberiza citrinella*).

Bracken also provides cover for several small mammals including shrews (*Sorex araneus*) and hedgehogs (*Erinaceus europaeus*), though herbivorous species such as voles (*Microbus agrestia*) and woodmice are more likely to be found in discontinuous bracken (Nicholson and Patersen, 1976). In addition there are some 40 invertebrate species which live on bracken, 11 of which depend exclusively on bracken. Again this represents a species poor invertebrate community when compared with that found in *Calluna* dominated vegetation (Lawton, 1976).

Bracken is often considered to be an attractive landscape feature, particularly in the autumn and winter, but its domination can also reduce the diversity of the landscape in infested areas. The recreation value of moorland infested with bracken is also frequently reduced as access becomes difficult for walkers, orienteers etc..

2.2 THE TAXONOMY OF BRACKEN

Given the antiquity of the genus *Pteridium* which has been present since the late Jurassic period in South West China there has been ample time for the evolution of local forms and races of bracken (Page, 1990) and hence the taxonomy of bracken is not straightforward.

Until recently *P. aquilinum* has been regarded as a single species world-wide with subsp. *aquilinum* (composed of 8 varieties) occurring in the northern hemisphere and in Africa, and subsp. *caudatum* (composed of 4 varieties) occurring in the southern hemisphere (Tryon, 1941). Studies on the variation in flavonoid content of fronds (Cooper-Driver, 1976) and nuclear DNA content (Tan and Thompson, 1990) support this classification suggesting that all the varieties belong to the same species. Varieties often overlap in geographical range with a range of intermediate forms occurring. Also, within areas occupied by a single variety local populations can occur which exhibit one or more characteristics of the other varieties (Tryon, 1941).

However, Page (1990) recognises the existence of 3 subspecies of bracken which are native to Britain. The most common and vigorous form, *Pteridium aquilinum* subsp. *aquilinum*, which is itself both genetically polymorphic and phenotypically plastic, accounts for the vast majority of British bracken (over 95%). This subspecies is able to occupy the widest range, has the highest spore output and the greatest potential for vegetative spread of any British bracken. The 2 other subspecies identified by Page (1989) are not so widespread, less vigorous and have more specific habitat requirements. *P. aquilinum* subsp. *latiusculum* (Desv.) C.N. Page is found as an understorey species of native Scot's pine (*Pinus sylvestris* L.) woods in the Cairngorms and is also found in Northern Eurasia where it is adapted to cold winter climates. *P. aquilinum* subsp. *atlanticum* occurs at low altitude on base-rich soils in the western-most parts of Scotland. This sub-species seems able to survive only the mildest most oceanic climates in Europe.

The morphology of the 2 less common subspecies suggest the possibility that the most common form *P. aquilium* subsp. *aquilinum* could be a hybrid of these 2 taxa. This hypothesis explains the high degree of variation found within the subspecies *P. aquilium* subsp. *aquilinum* but does not explain the wide distribution of this subspecies within Britain.

2.3 LIFE CYCLE.

The more familiar form of bracken, the sporophyte generation, spreads vegetatively by the expansion of the rhizome system often dominating large areas of moorland. However bracken, like all ferns, is also able to spread by spore production and sexual reproduction in the gametophyte generation. In most years spore production by the sporophyte is generally poor in the U.K. but some populations produce spores every year (Dyer, 1990) and under suitable conditions can produce up to 30 million spores per frond (Conway, 1952).

The extent to which bracken reproduces sexually has almost certainly been underestimated in the past (Oinonen, 1967; Page, 1976). Wolf *et al.* (1988, 1990) report a high gene flow among British populations of bracken which appear to be acting as a single random-mating population. The high level of genetic variability found allows for the presence of genes for resistance to chemical and biological control within the population and may explain how bracken is able to recover following herbicide treatments (Wolf *et al.*, 1988).

During warm, dry summers spore production is encouraged and if conditions are suitable the spores germinate forming a small, disc-like prothallus (or gametophyte) (fig. 2). The prothallus produces both male and female gametes and in moist conditions the mobile male gamete is able to travel to and fertilise the female gamete, usually on a different prothallus. The sporophyte resulting from this fertilisation eventually becomes independent of the prothallus, and gives rise to a large clonal plant.

The apparent scarcity of bracken gametophytes observed in the field in Britain may be explained by several factors, including the sporadic nature of spore production (Conway, 1957; Schwabe, 1951), competition (Conway and Stephens, 1956), grazing (Conway, 1952) and drought (Schwabe, 1951). Gametophytes are rarely established under the sporophyte generation where deep litter layers surpress development (Conway, 1957) and are most frequently found in moist conditions in disturbed, open situations (Dyer, 1990) with the establishment of sporelings on cooled volcanic lava slopes and following fire being well documented (Oinonen, 1967; Beard, 1945).

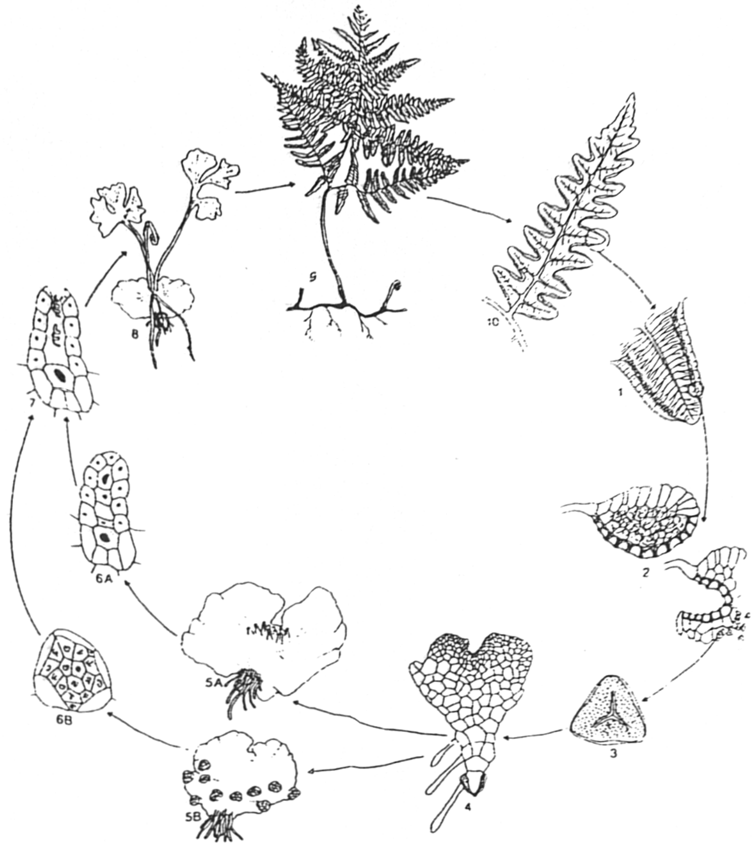


Fig. 2 Life cycle of Pteridium (generalised). **1**, lower surface of a fertile leaf segment (here a pinnulet) showing a single continuous marginal sorus (coenosorus) producing sporangia; **2**, a mature sporangium (above) and sporangium after release of spores (below); **3**, spore ; **4**, germinated spore to show developing prothallus with rhizoids; **5**, cross-fertilisation is normal in *Pteridium*, archegonia and antheridia are not normally formed simultaneously on one prothallus; 5A, larger older prothallus bearing archegonia (6A); **5B**, smaller, younger prothallus with antheridia (**6B**); 7, spermatozoids released from antheridia move towards mature egg cell; **8**, developing sporeling (sporophyte) growing *in situ* on gametophyte. Normally only a single zygote develops from each prothallus. The first leaf of the sporeling is bipinnate; successive leaves are more complexly divided (illustrated by Gottlieb, 1958). The prothallus degenerates whilst the growing sporeling withdraws material from it and becomes increasingly independent. The rhizome of the sporeling then develops. The adult sporophyte (**9**) does not usually become fertile (**10**) before 3-4 years of age (Conway, 1957; Dasanayake, 1960). **Taken from the appendix to Thompson and Smith (1990).**

2.4 THE GROWTH AND STRUCTURE OF THE BRACKEN PLANT.

The work of A.S. Watt in the Brecklands of East Anglia looking at the interactions at margins between bracken and grassland, and between bracken and *Calluna*, is responsible for much of our knowledge of the growth and morphology of the bracken plant. Watt's work remains the only long-term exhaustive study of bracken ecology and growth. In comparison, little work has been carried out on the growth of upland bracken advancing into *Calluna* moorland.

2.4.1 Size and age of a bracken plant

Watt refers to the formation of many independent bracken plants (up to 46,500 ha^{-1}) by the fragmentation of existing rhizome (Watt, 1940). Such ramets would presumably originate from a single genotype. Looking at 14 isoenzymes with the use of electrophoretic techniques Sheffield *et al.* (1989) found considerable variation in the distance covered by a single bracken genotype ranging from less than 30m to at least 390m in a single dimension. A single stand however, may include several distinct clones (Wolf *et al*, 1990).

A single clone obviously requires a long period of time to spread to a distance of 390m. This was estimated by Sheffield *et al.* (1989) at between 400 and 1600 years. Such a figure is very close to estimates of the age of circular clones formed from a single sporeling following fire as 650 years (Oinonen, 1967). Once bracken has become established therefore, it is extremely persistent and likely to dominate the vegetation.

2.4.2 The fronds

Bracken shows a great variation in frond morphology in response to the habitat in which it is found. On fertile sites the dry weight of fronds can exceed $1.2Kgm^2$ and frond heights (especially on lowland sites) can be greater than 2m. In full sunlight the fronds form a many-layered dense canopy with high leaf area index. Shade fronds are seen to have a less upright lamina with relatively large, thin fronds (Woodhead, 1904; Daniels, 1986). Frond morphology also varies with altitude with increased biomass being found in the lamina and underground part of the stipe, as opposed to the aerial part of the stipe, at high altitude resulting in the formation of a short canopy with densely packed pinnae (Atkinson, 1989).

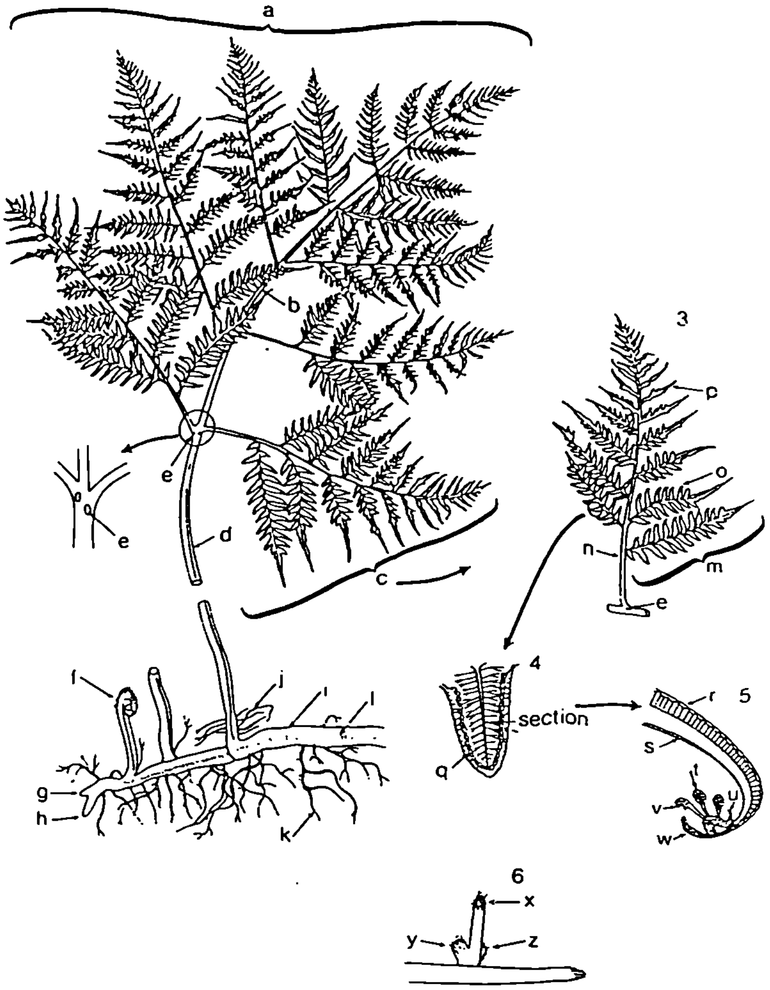


Fig. 3. Major morphological features of *Pteridium* (generalised). **1**a, frond lamina (blade); b, rachis; c, pinna; d, stipe; e, nectary; f, crozier with hairs; g, leaf primordium borne on short shoot; h, shoot apex; i, lateral line; j, petiolar roots; k, root; l, rhizome; **2**e, nectary (minor nectaries are usually present at the bases of the pinnae (3e) and even some pinnules; **3**, pinna, showing m, pinnule; n, midrib of pinna; o, pinnulet; p, midrib of pinnule; **4**, lower surface of pinnule, showing q, coenosorus continuous around margin; **5**, section through margin of pinnulet, showing r, upper surface; s, lower surface; t, mature sporangium; u, indusium; v, sporangium after discharge of spores; w, false indusium (margin of segment); **6**, rhizome, showing x, frond primordium; y, abaxial bud; z, adaxial bud. **Taken from the appendix to Thompson and Smith (1990).**

Watt (1940) reports that the height of the frond is primarily related to its position on the plant and to the size of the plant as a whole. Frond heights are generally short at the edge of a bracken stand rising to a maximum height and then falling slightly before finding a relatively uniform height further into the stand. Watt (1940) also found a correlation between the height of a frond and the diameter of the rhizome from which it grew.

Fronds begin to emerge and unfurl in late May and continue to do so throughout the growing season. The emergent frond first completes the extension of the stipe before the pinnae unfold (Watt, 1945a). The stipe makes up around 50% of the height of the frond and gives way to the rachis on which the pinnae are usually arranged in opposite pairs. The developing frond is totally reliant on rhizome carbohydrate reserves at least until the second pair of pinnae have unfolded and partially reliant until reaching 66-75% of its mature height (Williams and Foley, 1975). Later in the season carbohydrate reserves are replenished as the frond becomes a net exporter of carbohydrates to the rhizome. Late emerging fronds are able to compensate for the loss of earlier fronds through damage from cutting, wind, disease, grazing, desiccation or frost.

2.4.3 The rhizome

The rhizome is the horizontal, under-ground stem system of the bracken plant. Braid (1935) found up to 3 layers of rhizome, the deepest of which was found at 50-65 cm (fig. 4). On moorland soils, rhizome is generally found densely interwoven in the top 20cm of soil often under a deep layer of litter. Daniels (1982) gives a rhizome dry weight of 3Kgm^{-2}, a far greater mass than that of the above-ground foliage. The rhizome is responsible for the vegetative expansion of the plant and its ability to exploit available resources in the adjacent soil. The average annual rate of rhizome expansion at the stand margin in Brecklands was given by Watt (1940) as 33-74 cm, but distances as great as 210cm p.a. (Fletcher and Kirkwood, 1979) have been stated. Further into the established part of a bracken stand such high rates are not achieved because of intra-specific competition (Watt, 1940).

The morphology of bracken rhizome has been described by many workers with most schemes being based on Watt's (1940) description of "short" and "long" shoots.

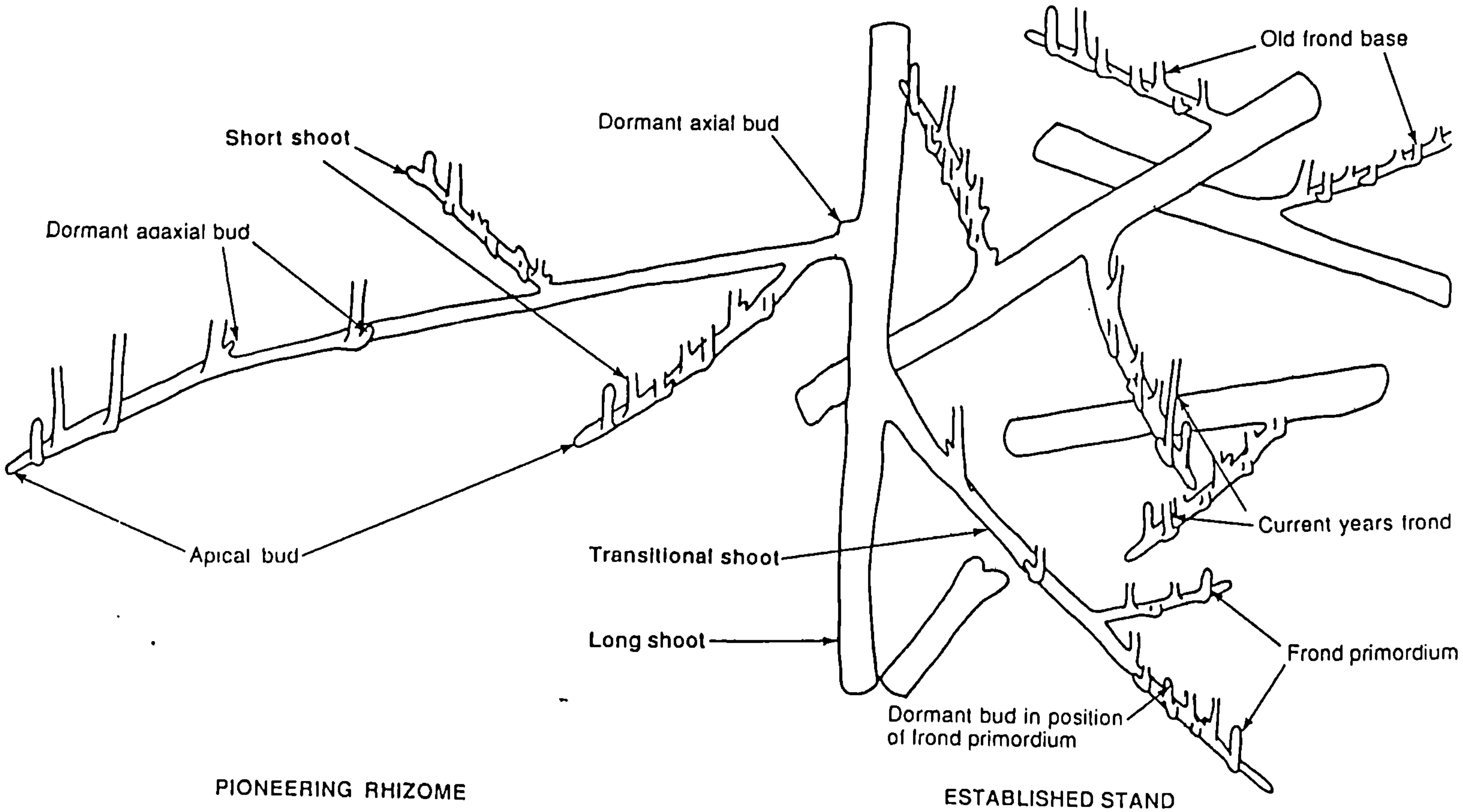


Fig. 4 The bracken rhizome system (generalised).

Long shoots are found at greater soil depths than short shoots and have longer internodes (30-40cm). They form the main axis of the rhizome system from which short shoots grow laterally and are responsible for the extension of the rhizome growing more rapidly than short shoots. They also make up 70-80% of the rhizome weight and are responsible for the bulk of carbohydrate storage (Lowday, 1984a). Watt (1940) maintained that these shoots are frondless and produce few lateral buds. He also recognised "intermediate" shoots which, like long shoots, do not carry fronds but grow relatively slowly and have shorter internodal lengths than do long shoots.

Subsequent authors have disagreed over the question of whether the long shoots are frondless. Dasanayake (1960) reported the presence of fronds on long shoots and after microscopic dissection of shoot apices found that frond primordia developed similarly on both long and short shoots. This view was supported by O'Brien (1963) working on var. *esculentum*. Gottlieb (1958) also found that young sporeling bracken developed fronds on the long shoots but that this tendency disappeared as the rhizome matured. The idea of "transitional" shoots resulting from the branching of a long shoot tip or from the transposition of a short shoot to a long shoot was introduced by Webster and Steeves (1958). Like Watt they believed the long shoot to be frondless but unlike Watt's intermediate shoot their transitional shoots formed fronds.

Short shoots are typified by a relatively short internodal length (0.5-2.0cm) and the production of usually one frond primordia immediately behind the apex in each season. Differentiation of the apex into next years frond bud and the next rhizome internode occurs at the end of June or during July. The bud grows slowly throughout the winter before increasing its growth rate and emerging the following spring (Watt, 1945b). The first bud on a new short shoot is formed on the adaxial side and buds thereafter alternate between left and right giving the characteristic zig-zag appearance. Some short shoots are relatively inactive and become dormant or even necrotic after the production of only 1 or 2 fronds. Other shoots remain active for many seasons and reach considerable lengths (Webster and Steeves, 1958).

At the base of each new frond is a dormant adaxial bud which is believed to grow to replace the frond if it becomes damaged (Dasanayake, 1960; Watt,1950). Alternatively such a bud may develop into a lateral short shoot (Conway and Stephens, 1954). How long these buds are able to remain viable and what causes them to become active is unknown, but Daniels (1982) quotes cases of such dormant buds becoming active 12 years after their formation.

The terminal bud produced each season does not always develop into a frond, and it too may remain dormant for one or more seasons after initiation. The number of young and unemerged frond buds present in the field also much exceeds the number of mature fronds formed and provide a large potential for further frond production (Conway and Forrest,1961). Braid and Conway (1943) argue that the growth of one frond and one internode per apex in each season is insufficient to account for the rapid rate of expansion seen in the field, especially at stand margins or in the early years of sporeling growth. More than one frond must therefore be produced per apex in each season at the stand margins or in young sporelings.

A shoot from each category may change its character under certain conditions. Deep long shoots may grow near to the surface and give rise to fronds or short shoots may grow deeper and become storage organs (Conway and Forrest, 1961). At the margin of a bracken stand there are a higher proportion of rapidly elongating long shoots than are found further into the stand (Watt, 1943). As time passes there is a relative increases in the lengths of short and intermediate shoots present (Watt, 1970). Watt (1945a, 1969) also noted that fronds produced by pioneer rhizome tended to emerge earlier than others (probably due to lack of deep litter layer) and thus suffered a high frost mortality (Watt, 1970). This is particularly true in Breckland where the risk of late frost is high.

2.4.4 Watt's cycle of change

Watt (1945a, 1945b) describes a 5 phase cycle: Grass-heath, pioneer, building, mature and degenerate through which individual plants in a bracken stand are passing independently of one another. Similar observations, involving bracken degeneration in localised areas have been observed in a *Calluna* moorland situation (Smith, 1990) though it is not known whether such a cycle is occurring on the North York Moors.

The pioneer phase involves the encroachment of bracken with small amounts of parallel rhizome shoots and short fronds into other vegetation. During the building phase the fronds become taller and the amount of rhizome present increases with short and intermediate shoots becoming more plentiful until the mature phase is

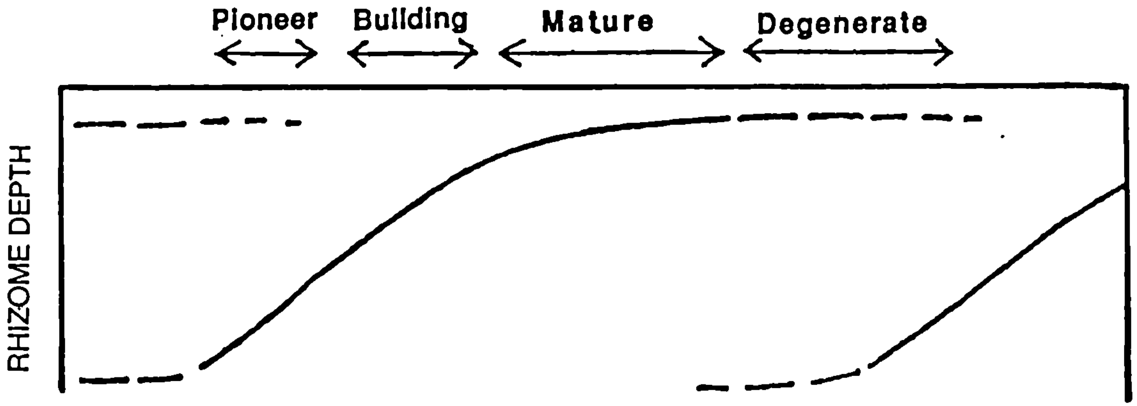
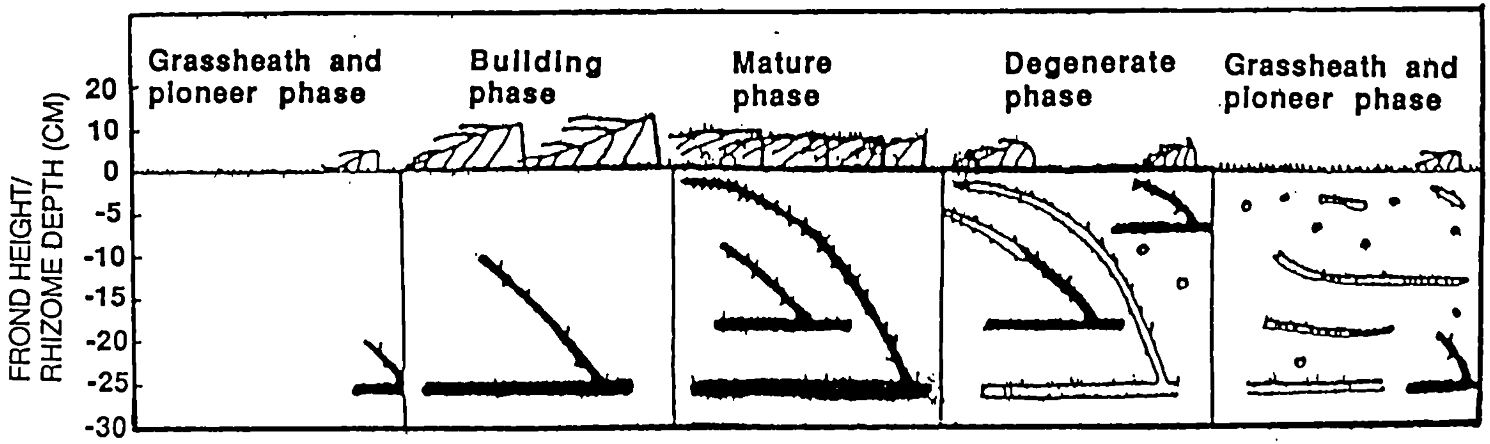


Fig. 5a) Diagrammatic representation of the general course of change in the depth of origin of the frond, in age of short shoots and the distribution of new and old rhizome. The broken line at the base indicates progressive invasion by new rhizome and at the top death and disintegration of old rhizome. After Watt, 1945.



b) A diagrammatic representation of the changes in the litter, and in the behaviour of the long and short shoots, across the marginal belt on the podsol on Lakenheath Warren. Black = live shoots. White = dead shoots. After Watt, 1976.

reached. Away from the margin the majority of the stand has slightly shorter, less dense fronds and the rhizome becomes fragmented as the plant enters the degenerate phase.

Degeneration is associated with the accumulation of large amounts of rhizome. This was thought to lead to increased competition and the accumulation of deep litter layers. The rhizomes become concentrated in the litter layers where they are more susceptible to damage from frost and drought (Watt, 1971). In a final phase vegetation other than bracken predominates though Watt did not suggest that bracken is totally absent in this phase. The mature stand may be made up of a mosaic of bracken plants in which all of the phases are in dynamic equilibrium (Watt, 1956).

Bracken cycling in this manner and the recession of bracken leading to the formation of grass heath in areas previously dominated by bracken (which in places has persisted for more than 5 years) has been confirmed to be still occurring on Watt's sites (Marrs, 1988; Marrs and Hicks, 1986).

2.4.5 The role of apical dominance in bracken rhizome.

The frond-bearing apex of short and intermediate shoots have been observed to grow only when the frond is dead or has been severely damaged (O'Brien, 1963). It is therefore likely that the presence of a growing frond has a dominant effect over the development of new buds at the apex and possibly also over dormant buds present on the rhizome.

Daniels (1985) carried out a series of pot experiments involving the ability of rhizome segments to regenerate. This ability was not affected by the presence or absence of an apex but more new lateral buds grew on segments which originally lacked an apex. A further experiment (Daniels, 1986) involving the effects of nutrient applications on the growth of bracken plants showed that the application of NPK fertilisers increased both rhizome growth and the number of fronds produced. Such evidence supports the idea of correlative inhibition by the apex and specifically the involvement of nutritive inhibition. Schwabe (1953) also found nutrient status to have an effect on apical dominance, with potassium deficiency limiting lateral bud production initially but eventually reducing dominance as the vigour of the apex is reduced by lack of potassium.

Extensive work has been carried out on the role of apical dominance in couch grass (*Agropyron repens* (L.) Beauv.), another rhizomatous weed. Leakey and Chancellor (1975) were able to effectively substitute plant growth regulators 1-napthylacetic acid (NAA) and 6-benylaminopurine (BAP) for the rhizome apex, preventing growth of lateral buds. This was achieved only in rhizome which remained attached to the parent plant and not in multi-node fragments unless hormones were also applied to the basal end. The maintenance of dominance in *A. repens* therefore seems to involve both apical and basal ("parental") factors.

There is strong evidence that nutrients (especially nitrogen) are involved in apical dominance in *A. repens* (Leakey *et al*, 1978). It was found that the application of nitrogen delayed the onset of dominance by any one lateral bud after the apex had been removed, and suggested that apical dominance can be explained in terms of competition for nutrients between shoots and the suppression of auxin-mediated dominance by the presence of high nitrogen levels. McIntyre (1964, 1965) found that nitrogen levels determined the number of developing rhizome buds with tiller initiation and development requiring high levels of nitrogen unless the apex had been removed. Competition for carbohydrate nutrients is also reported to have a role in the maintenance of apical dominance in *A. repens* with lateral buds being released from dominance after the provision of sucrose solution to the lateral buds or the cut basal end of the rhizome (McIntyre, 1969).

In the fern *Davallia* the removal of the apex also stimulates lateral bud growth, though auxins do not prevent bud growth when substituted for an excised apex. No auxin was detected in the rhizome tips of the fern, nor did the application of exogenous cytokinin to lateral buds result in their development. However, both application of the herbicide glyphosate and the ethene-producing compound ethrel did result in lateral bud expansion (Croxdale, 1976). The mechanisms controlling apical dominance in both *Davallia* and other ferns are therefore unclear but need not involve auxin.

2.5 ALLELOPATHIC CHEMICAL PRODUCTION.

Plants of other species are often excluded from bracken stands for reasons which cannot be adequately explained in terms of competition for water, nutrients or light, or in terms of physical factors (pH, organic matter content etc.) (Gliessman and Muller, 1978). The role of phytotoxins produced by bracken has therefore been examined as an explanation for this inhibition.

Water soluble extracts from bracken have been shown to reduce the germination of many plant species (Stewart, 1975) and several phenolic compounds have been isolated from bracken fronds and soil associated with bracken (Glass and Bohm, 1969; Glass, 1976; Gliessman and Muller, 1978).

Gliessman (1976) suggests that there is a complex relationship between bracken allelopathy and the environment resulting in the release of toxins at different stages in the development of the plant - roots, green fronds, senescent fronds, rhizome or litter; depending on the environment in which the plant is growing and the time at which competing vegetation is most susceptible. For example, in southern California toxin release is timed to match the germination of competitive plants at the beginning of the wet season with toxins largely being released by dead standing fronds. Alternatively, in the Pacific north-west of the U.S.A. release is timed for the breaking of dormancy in the spring and allelopathic chemicals are released largely from the litter, roots and rhizomes of the bracken plant.

The production of allelopathic chemicals by bracken could have an important role in allowing bracken to advance by inhibiting the growth of competing vegetation e.g. *Calluna*.

2.6 THE EFFECT OF THE ENVIRONMENT ON BRACKEN GROWTH.

The distribution of bracken is limited by altitude and latitude with frost probably being the most important influence in determining bracken's range (Watt, 1976). Serious winter frosts can kill rhizome apices and frond primordia whilst spring frosts damage the emerging croziers delaying the development of the full canopy and reducing the final frond height (Watt, 1950). Under sub-optimal conditions deep litter layers do not accumulate and the frost problem is compounded by the lack of protection afforded to the underground buds from litter (Ader, 1990). Ader (1990) also reports that exposure has an important role in determining altitudinal range of bracken whilst not exhibiting a great influence on bracken vigour.

Bracken is most abundant on well-aerated, loamy soils often on well-drained slopes and soil moisture is another factor which is important in limiting the growth of bracken (Thompson *et al.*, 1986). The rhizomes are unable to tolerate low oxygen concentrations (Poel, 1951; 1961) and bracken is therefore absent from waterlogged areas surviving only in areas which are irregularly wet. Since submergence in water prevents the aeration of elongating rhizome, it is possible that mature rhizome might be better able to withstand wet conditions than pioneering rhizome (Watt, 1979). A lateral line of raised tissue is found on both sides of long rhizome shoots which contains both stomata and highly aerated parenchyma which are presumed to be responsible for the aeration of the rhizome (O'Brien, 1990). Under drought conditions the presence of large amounts of mucilage in the vacuoles of rhizome parenchyma contribute to the water holding capacity of the rhizome (O'Brien, 1990). In common with many pteridophytes, bracken has a low level of stomatal control and is relatively insensitive to changes in air humidity though it does respond to changes in soil moisture content (Hollinger, 1987).

The association of bracken with poor soils of low pH (4.6-6.8), low exchangeable calcium and low nutrient status (Page, 1976) is probably largely due to agricultural economics rather than to the physiology of bracken itself (Watt, 1976; Thompson *et al.*, 1986). Bracken has no specific requirement for acidic soil and has been shown to grow with no significant deleterious effects over a pH range of 3 units (Schwabe, 1953). Soil depth is an important factor in the control of bracken biomass which increases together with increasing soil depth (Chen and Lindley, 1981).

The mineral requirements of bracken grown in pots were examined by Schwabe (1951; 1953). Nitrogen deficient plants show yellow fronds, reduced frond production, slowed growth and early frond senescence. Phosphate deficiencies resulted in the formation of brittle, small fronds which were dark green in colour and potassium deficiencies in the early senescence of fronds. The availability of potassium seems to be of importance in determining the starch content of the plant and the amount of material present in the rhizome. Starch increases if phosphate is deficient but decreases in the absence of potassium, deposition of material into the rhizome as the season progresses being dependent on the presence of sufficient potassium (Schwabe, 1951; 1953). The presence of high levels of nitrogen, phosphate, potassium and calcium all resulted in increased frond bud production. A similar result was observed by Conway and Stephens (1957) who found that lime acted as a stimulant to the growth of young sporelings, increasing both growth rate and the number of frond primordia per apex.

Hunter (1953) measured the mineral composition of bracken throughout the growing season and found that the concentration of major elements (except Ca and Na) decreased with age in the fronds whilst remaining fairly constant in the rhizome. There was also correlation between the concentrations of major elements found in the plant tissue and those found in soil analyses. Bracken soils are relatively high in phosphorus and the presence of bracken leachates has been shown to promote the mobilisation of phosphate from inorganic sources (Mitchell, 1973). The roots of bracken routinely contain mycorrhiza (Conway and Arbuthnot, 1949;) and experimental plants are known to grow poorly in the absence of mycorrhizal fungi (Cooper, 1975).

2.7 BRACKEN CONTROL STRATEGIES.

Bracken encroachment is not a problem on highly productive agricultural land where repeated cultivation and control treatments are possible both economically and in terms of accessibility for machinery. In upland areas, where agriculture is usually economically marginal, the most important problem in controlling bracken has been that of achieving adequate and maintained control without the need for frequent and expensive re-treatments.

The control of bracken within the North York Moors National Park is of major concern to the national park committee which established programme of grant-aid for bracken control as part of its Upland Management Scheme. The North York Moorland management programme 1985-89 (North York Moors National Park, 1991) states :

> *" A high priority will be given to the eradication of bracken from existing or potential heather moorland; the target will be to reduce the bracken area to less than 10% of the moorland area by the year 2000. To this end the National Park Committee will work closely with moorland owners through grant aid linked to management agreements for eradication and afteruse."*

Selection of suitable sites for bracken control is important, since if good control is achieved in areas where there is a good cover of surviving undergrowth, full sward cover can quickly result which helps to prevent bracken regrowth. Conversely, where a deep layer of litter is present, even when good control is achieved there is a tendency for land to remain derelict because of surface erosion and lack of seedling re-establishment.

The importance of post-control restoration and follow-up treatments have been stressed within the North York Moors bracken control programme. Following herbicide treatment the re-treatment of missed fronds is vital if they are not to act as a source of bracken recovery.

Litter dispersal following the treatment of dense bracken stands encourages re-establishment of *Calluna* (Lowday, 1984b; Marrs, 1987; Lowday and Marrs, 1992b) and the rapid re-colonisation of grass species such as *Holcus mollis* and *Agrostis* spp. (Sparke and Williams, 1986). Without the use of dispersal techniques Chen and Lindley (1981) calculated that the time taken for 95% litter standing crop to decompose was in the region of 10-13 years. Reseeding with more productive pasture grasses such as *Lolium perenne* and *Festuca rubra* which respond better than indigenous species to fertiliser and lime is most successful following litter removal or incorporation (Sparke, 1985; Sparke and Williams, 1986).

Management of stock numbers, a particular problem on common land within the North York Moors, is essential if vegetation is to recover adequately after bracken control (Soper, 1986).

2.7.1 Chemical control

2.7.1a Early bracken control herbicides

Many herbicides have been used in attempts to control bracken. During the 1960's amitriole (3-amino-1-H-1,2,4-triazole), picloram (4-amino-3,5,6-tricholopicolinic acid) and dicamba (2-methoxy-3,6-dichlorobenzoic acid) gave high levels of control and reduced carbohydrate levels in the rhizome (Farnworth and Davies, 1974). However, these herbicides are not translocated well from the foliage to the rhizome and are not able to achieve a direct affect on the rhizome. They are also relatively non-selective, interfering with the growth of pasture grasses and broad-leaved species and persistently active in the soil leading to problems with sward regeneration (Erskine, 1968). Following treatment, extensive regeneration of bracken frequently occurred within 3 years (Martin, 1968) and the herbicides were often prohibitively expensive (Mitchell, 1968).

Paraquat has been used with good results to control bracken but is more often used as a pasture improving herbicide prior to reseeding rather than exclusively for bracken control (Farnworth and Davies, 1968). At doses of above 2 Kg ha^{-1} glyphosate is active in reducing rhizome weight and carbohydrate levels (Kirkwood and Archibald, 1986; Williams and Foley, 1975) together with the number of active and viable dormant buds (Al Jaff *et al.*, 1982). Again glyphosate is non-selective and pasture grasses suffer severe damage. All of these non-selective herbicides are more frequently used in forestry to clear ground before planting than in a moorland environment.

2.7.1b The role of asulam in bracken control

By the mid-1970's asulam (Methyl (4-aminobenzenesulphonyl) carbamate) ("Asulox", Embetec Crop Protection) became the only bracken herbicide approved for aerial spraying and recommended for bracken control in a moorland environment. The compound was first described in 1965 and introduced commercially for the control of bracken in 1972. The recommended application rate is 4.4Kg ha^{-1} with non-ionic surfactants (Agral 90 (ethoxylated alkylnonylphenol, ICI); Triton X-45 (octylphenoxy polyethoxy ethanol polymer, Rohm and Haus; Silwet L-77 (organosilicone block polymer, Union Carbide)) often added to increase the retention and penetration of the spray (Holroyd and Thornton, 1978; Kirkwood, 1990). Large-scale aerial spraying of asulam allows the treatment of rocky areas and slopes where mechanical control and tractor application of herbicides are impossible.

Damage to species other than bracken is largely confined to other ferns and docks (*Rumex obtusifolia*) with damage to grass species and *Calluna* being minimal and usually limited to scorching (Williams, 1977; Williams and Fraser, 1979; Marrs, 1985). The timing of asulam application, late in the growing season, gives the underlying sward the benefit of frond canopy protection when the herbicide is applied (Cadbury, 1976).

Asulam is a systemic, phloem-mobile herbicide which is effectively taken up by the foliage and accumulates in the rhizome buds. Its mode of action involves the inhibition of folate synthesis which is at least partially responsible for the inhibition of protein and RNA synthesis observed in treated plants (Veerasekaran *et al.*, 1977b; Killimer *et al.*, 1980). The effects of asulam treatment are not normally visible until the time of frond emergence in the year following treatment, when, if good control has been achieved, frond numbers are reduced by more than 95% (Martin *et al.*, 1972; Veerasekaran *et al.*, 1978). Carbohydrate reserves are also depleted because of a reduction in the amount of photosynthates translocated into the rhizome in the weeks following treatment. However, not all the rhizome buds are killed and those remaining (often dormant buds found on the storage rhizome) remain and may later give rise to recovery and re-invasion of bracken (Veerasekaran *et al.*, 1978; Lowday, 1987).

The timing of asulam application is of vital importance to the success of the treatment. Application is timed such that net translocation is in a basipetal direction, i.e. frond growth is complete and rhizome reserves are being replenished by photosynthates from the mature fronds (Veerasekaran *et al.*, 1977a). If left too late, uptake is poor because the frond cuticle has thickened. At the time of spraying, fronds must therefore be fully emerged i.e. at least 3 pairs of fully developed pinnae are present on each frond. This situation is usually reached in late July or early August in the U.K. (Holroyd and Thornton, 1978; Veerasekaran *et al.*, 1978).

Following successful treatment of bracken with asulam some recurrence normally occurs after 4-6 years. Veerasekaran *et al.* (1978) report 50% cover in the 5th year after spraying. Where good livestock management is in place this period may be extended to 7-12 years (Soper, 1986). However, given deep litter layers and poor seedling re-establishment full bracken cover can be re-established within 6 years (Lowday, 1984b).

Grant aid of up to 50% is available for the control of bracken with asulam under the MAFF farm and Conservation Grant Scheme. In addition further financial help for asulam control of between 25% and 50% (depending on other sources) is available within the national park from the North York Moors National Park Moorland Management Scheme. This policy has resulted in the spending of £170,000 of National Park funds in the period 1988-92. Still the cost of asulam treatment is high at £170 - £190 ha^{-1} in 1992.

2.7.1c Development of new herbicides for bracken control

Much interest has been shown in the development of the sulphonyl-urea group of herbicides for the control of bracken (Oswald *et al.*, 1986; West and Richardson, 1987). Chlorsulfuron was marketed in a mixture with another sulphonyl-urea metsulfuron as "Finesse" (DuPont) and when used for bracken control achieved reductions of up to 100% in frond numbers with no damage to grass dry matter production at very low doses (15gha^{-1}) (Oswald et al., 1986). Chlorsulfuron is an inhibitor of cell division, specifically interfering with branched chain amino acid synthetic pathways by acting on the enzyme acetolactate synthease (Ray, 1984; Reynolds, 1986; Chaleff and Mauvais, 1984). It has now been removed from the market because of problems with selectivity and persistence in arable use. Because of these problems and their high toxicity at very low doses sulphonyl-ureas are unlikely to be cleared for bracken control by aerial spraying. However, new sulphonyl-urea herbicides are currently under development and may prove useful for the control of bracken by hand or tractor application in the future.

2.7.2 Mechanical control

Bracken rhizome is unable to withstand regular cultivation and wherever land is accessible can be efficiently controlled by ploughing or rotovating. Mechanical control of bracken more usually refers to cutting or rolling the fronds. Both of these treatments result in the depletion of carbohydrate reserves in the rhizome due to the removal of photosynthesising fronds and the additional drain of replacement frond production. This also has the effect of depleting bud reserves. An additional effect of cutting treatment is the early emergence of fronds in the season following cutting, possibly explained by warmer temperatures in the litter layer. This may cause an increase in frost damage and further bud reserve depletion in subsequent years (Lowday, 1983).

Cutting treatments must be continued for several years in order to obtain satisfactory control, because of the large reserves of carbohydrates in the rhizome. However, after cutting has been carried out for around 3 successive years a diminishing response to cutting treatments is observed (Daniels, 1982). Lowday and Marrs (1992a) found that bracken was not eradicated even after ten continuous years of cutting twice a year with fronds persisting at low densities. These trials also showed that rapid recovery of bracken cover occurred if cutting was stopped after 6 years. Only after cutting fortnightly for 3 successive summers did Santon (1990) reach a situation where there were no further fronds present in the fourth year.

The timing of cutting treatments are important if maximal carbohydrate depletion is to be achieved. Optimal timing in the U.K. is mid-June to late July with 2 or more cuts per year, with an interval of 5-6 weeks between cuts, accelerating control (Braid, 1935; Williams and Foley, 1976). Increasing the number of cuts to more than 2 per year increases the number of buds exhausted but does not achieve any great reduction in net flux of dry matter from the rhizome. This is due to a reduction in the amount of dry matter available for removal from the plant with each successive cut resulting from the smaller size of fronds produced after each cutting treatment. As the dry matter of the rhizome decreases there is also a net reduction in winter respiratory losses (Lowday, 1984a).

A combination of cutting and asulam treatments have been shown to be more effective than either approach alone. Cutting removes dry matter from the system but may fail to sufficiently reduce the number of viable fronds. Conversely, asulam causes severe depletion in the numbers of viable buds but does not substantially deplete carbohydrate resources (Lowday and Lakhani, 1987). Cutting prior to herbicide treatment may act to increase herbicide efficacy by increasing frond density and therefore the number of entry points available for the herbicide. Cutting also reduces canopy height and produces a more even stand to which herbicides may be applied. The number of buds which are active and acting as sinks for the herbicide also increases following cutting treatments. The effective dosage of the herbicide may also be increased due to a reduction in biomass resulting from the cutting treatment. Alternatively cutting pre-treatments could act to improve the cuticle penetration, translocation, metabolism or biochemical activity of the herbicide (Kirkwood *et al.*, 1982).

2.7.3 Biological control

The presence of stable insect populations feeding on bracken has stimulated interest in the possibility of using biological control agents against bracken. Up to 40 insect species feed on bracken in Britain alone, employing many different feeding strategies (Lawton, 1976; Lawton *et al.*, 1986). Work carried out by Lawton (1986) has shown that the populations of these native bracken-feeding insects are regulated by natural predators and parasites and that when these enemies are removed they are able to defoliate bracken. This would indicate that there is potential for the control of bracken by exotic insects on which native predators do not feed. The world-wide distribution of bracken gives scope for the identification of an exotic bracken herbivore which is able to survive in the British climate.

Several insects have been investigated as possible bracken control agents, the most promising of which are 2 South African moths *Panotima* sp. near *angularis* and *Conservula cinisigna* (Lawton, 1990). Both of these insects differ in their feeding habits from native bracken herbivores and would therefore exploit a vacant ecological niche. *C. cinisigna* feeds exclusively on bracken in its native environment by chewing on the pinnae and has been shown to be very host specific. The 3rd stage instars of *P. angularis* also feed on the fronds in addition to tunnelling into the rachis interfering with the vascular system. Again *P. angularis* looks like being very host specific, developing beyond the 1st instar stage only if fed on bracken rather than twelve other ferns. It seems likely therefore that both of these species could be safely introduced without risk of damage to non-target plant species. Lawton (1990) has also been able to overcome initial rearing problems of larval and pupal diseases and stubborn pupal diapause (exacerbated by the 6 month shift in season involved in bringing the insects from South Africa) experienced with *C. cinisigna*.

A number of other species have been investigated as bracken control agents including an *Eriophyid* gall-forming mite which badly distorts the fronds (Lawton, 1990). Work continues is continuing to find more exotic bracken herbivores which may be suitable for release in the U.K..

A small number of fungi parasitise bracken, including those associated with curl-tip disease (*Ascochyta pteridium, Phoma aquilina* and a species of *Stagonospora*) (Hutchinson, 1976; Burge *et al.*, 1986). These too are being investigated as possible control agents with particular interest being shown in the resistance mechanisms, including production of phenolic acids and lignification, shown by bracken to these fungi (McElwee and Burge, 1990). Fungal sprays could possibly be used together with herbicides which might act to increase the susceptibility of bracken to the pathogens (Burge *et al.*, 1986).

The prospect of the widespread control of bracken by biological means is not yet immediate. Whilst biological control has many advantages in terms of low cost, easy access to difficult terrain, high selectivity and self-sustainability there are still risks and problems involved. The problem of breeding sufficient numbers of insects for release still persist, especially in the case of *P. angularis* where there have been problems in providing sufficient food for the stem mining stages. The political and legal problems involved in the release of an exotic species are complex and as yet no proper legal structure has been put in place to deal with them. It is also difficult to limit the presence of a biological control agent to a specific area and control organisms could not be limited to land owned by a consenting landlord. Within the North York Moors problems with biological control may also arise where commoners have the right to cut bracken for bedding (Heads and Lawton, 1986). The presence of vegetation is essential in some areas, particularly steep slopes, in order to prevent soil erosion and in this case the total eradication of bracken could prove disastrous.

2.8 SUMMARY

Whilst debate over the extent of bracken cover and its rate of encroachment within the U.K. continues, it is certainly true that where bracken is dominant agriculture, sport and recreation and ecological diversity suffer. Within the North York Moors National Park the protection of heather moorland and the ecosystem it supports is a major priority and bracken encroachment represents one of the most serious threats. Increasing concern about the risks posed to human health by the presence of bracken may add to the need for bracken to be controlled.

Suppression of other vegetation is achieved by bracken through competition for light and other resources together with the production of toxic chemicals allowing bracken to become dominant. The presence of large rhizome reserves of carbohydrates and buds allow this dominance to be maintained and hence once established a bracken plant can survive for many hundreds of years.

Whilst good control can be achieved by aerial spraying of asulam on moorlands the process is expensive and follow-up treatments are required if bracken is not to return quickly. Total eradication of moorland bracken remains impossible in practice, despite the toxicity of existing herbicides, and is not desirable in many areas where alternative ground cover could not be easily re-established. More information on how the plant is able to maintain its advance and recover from control treatments seems essential if the effectiveness of existing and future control methods are to be increased. In the past, bracken research has tended to concentrate on the development of control techniques and on the restoration of grass or *Calluna* following control. Comparatively little effort has been expended in the study of the plant itself, especially on the rhizome system, particularly in a mooorland environment.

2.9 PROJECT OBJECTIVES

The project is concerned with the morphology and physiology of the bracken plant at its margin with *Calluna* moorland and the implications which these have for the control of bracken. The project aims to achieve a better understanding of the way in which bracken advances in terms of how the margin acquires resources, how the plant allocates its reserves of carbohydrates and rhizome buds and how bracken competes with the vegetation into which it is encroaching.

2.9.1 The morphology of bracken at the interface with *Calluna*

1. To identify morphological traits which can be used to identify advancing and stationary bracken margins.

Bracken has been observed to be advancing at some margins whilst remaining almost stationary at others over a period of many years. It is often difficult to determine whether or not a particular margin is advancing unless detailed long-term records have been kept. With the aid of aerial photographs made available by the North York Moors National Park Department and after discussion with farmers, gamekeepers and land agents it has been possible to identify advancing and comparatively stationary margins. This has allowed comparison of morphological characters of both frond and rhizome in advancing margins, stationary margins and bracken further into a mature stand.

Information which allows the identification of margins which are advancing, without the need for historical records, could be of significance in the selection of sites for control where financial resources are limited and advancing margins prioritised.

2. To assess the size of rhizome bud and carbohydrate reserves available to bracken both of which must be depleted if successful control and prevention of further front extension is to be achieved.

2.9.2 Resource acquisition at the margin

The objective of this section is to assess the level of dependence of pioneering bracken at an advancing margin on the remainder of the stand.

It is possible that pioneering rhizome is able to take up significant mineral nutrients to support its own growth without a requirement for mineral nutrients to be translocated from further back into the stand. However, rhizome at the margin frequently extends for distances of around a metre beyond its last frond and translocation of carbohydrates, if not mineral nutrients, towards the apex from further into the stand seems likely. Similarly the pioneering rhizome may be more or less dependent on the mature stand for water supplies.

An investigation has therefore been carried out to determine the extent to which the margin is reliant on the mature stand behind it and how great an area of bracken is involved in translocation of nutrients and water to, and possibly from, the margin. Again this information may prove useful when attempting to control bracken at the margins of the plant providing information as to how the margins will gain the resources necessary for any subsequent recovery.

2.9.3 Control of rhizome bud dormancy

The objective of this section is to investigate factors which may control rhizome bud dormancy. An improved understanding of these factors would have obvious implications for the improved success of available control methods since increases in the proportion of rhizome buds which can be activated corresponds to in increase an the proportion of buds vulnerable to herbicides.

The large numbers of inactive buds found on bracken rhizome play a vital role in the provision of replacement fronds following cutting, grazing or spring frost damage. These metabolically inactive sites have also proved very difficult to reach with herbicides when attempting to control bracken and have later been a source of bracken recovery (Kirkwood and Archibald, 1986; Lowday, 1987). It is not clear where the dormant buds which become active and are responsible for recovery in either of these situations are situated on the rhizome or how many buds have the potential to do so.

The positions of buds surviving asulam treatment have been investigated and the project includes an extensive study (carried out both under field and glasshouse conditions) of factors, including competition from *Calluna* which may influence rhizome bud dormancy.

3. EXPERIMENTAL SYSTEMS AND SITE DESCRIPTIONS

3.1 INTRODUCTION

The use of field experiments allows the study of bracken in a 'real-life' environment. The plant is growing in an undisturbed state and external factors such as interference from animals and other plants are taking place. Conditions of drainage, precipitation, soil nutrient availability, exposure, temperature etc. found in the field are also not reproduced accurately when bracken is cultivated in boxes, blocks or experimental plots. When studying the morphology and physiology of bracken it is important that the disturbance required to grow bracken under cultivated conditions has not taken place. Growth of bracken in boxes, blocks or pots necessitates the severing of the rhizome of this very large plant and major disruptions to both its physiology and morphology. For example, plants grown in boxes from rhizome segments show greater numbers of active buds and shorter fronds than undisturbed bracken in the field. Additionally any peturbation treatment designed to manipulate the growth or morphology of bracken must be effective under field conditions if it is to be of use in helping to control bracken.

For these reasons extensive field studies of bracken were carried out. These studies initially involved the morphology and physiology of bracken especially at its interface with *Calluna*. Later peturbation treatments designed to alter the rhizome bud activity of bracken were applied in the field.

The use of smaller bracken plants grown under greenhouse or small plot conditions does however offer several advantages which are not available when working on bracken in the field. Firstly they allow the plant to be grown under more uniform conditions. Under greenhouse conditions factors such as competiton, animal interference and localised climate or geography do not vary. Where rhizome is isolated and grown in commercial peat any differences relating to soil or intra-specific competition are also removed. Hence under the more standardised condition available in a greenhouse the effects of peturbation treatments can be recognised more easily above the background effects caused by differences in other factors.

Secondly, during the winter months active rhizome buds grow only very slowly in the field. Therefore in a project in which most of the summer months were taken up with fieldwork, it was of great advantage to use systems which, after a period of in a cold room, allow rapid bud growth and development of fronds in the greenhouse during the winter months. (fig. 6).

Because of the varying advantages of the various systems described below experimental work was carried out at four levels:

a) rhizome segments grown in boxes containing peat,
b) moorland soil blocks containing bracken rhizome,
c) bracken established in peat beds
and d) undisturbed bracken in the field.

3.1.1 Isolated rhizome segments

Rhizome segments were grown in Irish Moss Peat in wooden boxes of size 30cm x 60cm x 15cm. When rhizome was collected from the field in the autumn it was possible to encourage frond growth by chilling at 4°C for a period of 4-6 weeks before transferring the boxes to the greenhouse. The longer the period of chilling, the shorter was the observed time taken for fronds to emerge after transfer to the greenhouse. This system allows the rapid trial of experimental treatments in a small space and eliminates the greatest number of environmental variables of the 3 systems used. It is, however, the most invasive system as it involves the isolation of individual rhizome segments from the rest of the plant and thus greatly interferes with their physiology. For example, the isolation of rhizome segments was found to encourage rhizome bud activity and resulted in the formation of much shorter fronds than those found in the field.

3.1.2 Rhizome-containing blocks

Blocks of moorland soil of area 50cm X 50cm (and depth 15cm-25cm) containing bracken rhizome can be removed from the field and transported to the greenhouse (fig. 7). A dense mat of rhizome is found within the collection site, the mature bracken stand situated on the east side of Lowna Lund (described below), to a depth of around 20cm below the soil surface and blocks containing all the rhizome present within the 50cm X 50cm area can be levered out of the ground in an intact state.

The use of these blocks shares many of the advantages of isolated rhizome segments in that blocks can be collected in the autumn, chilled in a cold room and then grown up in a greenhouse over winter. Again this permits the trial of experimental treatments in the greenhouse before the field season begins and alternatively, the

Fig. 6 Bracken grown from isolated rhizome segments of 25cm in length taken from the field 15.3.90. (17.5.90).

Fig. 7 **Bracken growing in 50cm X 50cm soil blocks.** Collected from Lowna Lund mature stand 9.4.91. (4.7.91).

growing of blocks to which treatments have been applied in the field outside of the normal growing season. Whilst the rhizome is undoubtedly disturbed by separation from the rest of the bracken stand the level of disturbance in this system is small when compared with the use of isolated segments of rhizome and frond heights much closer to those found in the field are achieved.

3.1.3 Bracken in peat beds

A series of beds of size 50cm X 200cm, divided from each other by wooden boards and containing Irish Moss Peat were set up in the winter of 1989. In March 1990, a 50cm X 50cm block of moorland soil containing bracken rhizome was collected from a mature bracken stand on Harland Moor and was placed adjacent to a brick wall at one end of each of these beds. These blocks grew well with fronds reaching heights of 110cm in the first season after planting and rhizome rapidly advanced along the peat beds (fig. 8).

This system was used as a model of the advancing bracken margin for studies on movement of nutrients which involved the use of radiotracers. The system offers the advantages of being at a secure site. It also provides much easier access to bracken rhizome in beds of loose peat than can be achieved in the field in compact soil and the presence of *Calluna* roots. This was particularly valuable during experiments which involved feeding radiotracers to the rhizome through roots and returning the intact rhizome to the peat bed before harvesting after a period of some days.

3.1.4 Bracken in the field

A series of small experimental strips of 1m in width and 5m in length were pegged out at the margin between *Calluna* and bracken at several sites on the North York Moors (fig. 9). Each of these strips reached 2m into the area in which bracken was the dominant vegetation and extended 3m into moorland in which *Calluna* was dominant, but a varying number of bracken fronds were found.

Frond and rhizome data was collected from each of the five 1m^2 quadrats within each strip which will be described as quadrat A ,B, C, D and E with A being the quadrat furthest into the bracken stand as shown in fig. 10. A diagram of these plots is also available for easy reference in Appendix 4 at the back of this thesis.

Individual $1 m^2$ quadrats sampled in the same way as the strips at the margin were used to obtain data away from the stand margins in areas of dense bracken or bracken/*Calluna* mixtures.

During morphological studies in the 1st year of the project, frond data was collected for the whole of the quadrat but in later experiments it was felt that the collection of frond data from only $0.25m^2$ in each quadrat would allow a greater number of quadrats to be sampled and lead to more conclusive results. The top, left quarter of each quadrat was therefore used for collection of frond data. Throughout the project rhizome data was collected from a $0.25m^2$ quadrat in this same position in each strip which was dug up at the end of the growing season.

Fig. 8 **Model advancing bracken front in peat beds.** This system was formed by the spread of rhizome from 50cm X 50cm soil blocks from a mature bracken stand into beds of loose Irish Moss Peat (4.7.91).

Fig. 9 **Experimental strip at a bracken-*Calluna* interface in the field.** In this case a cutting treatment to remove competition from *Calluna* has been applied (15.10.90).

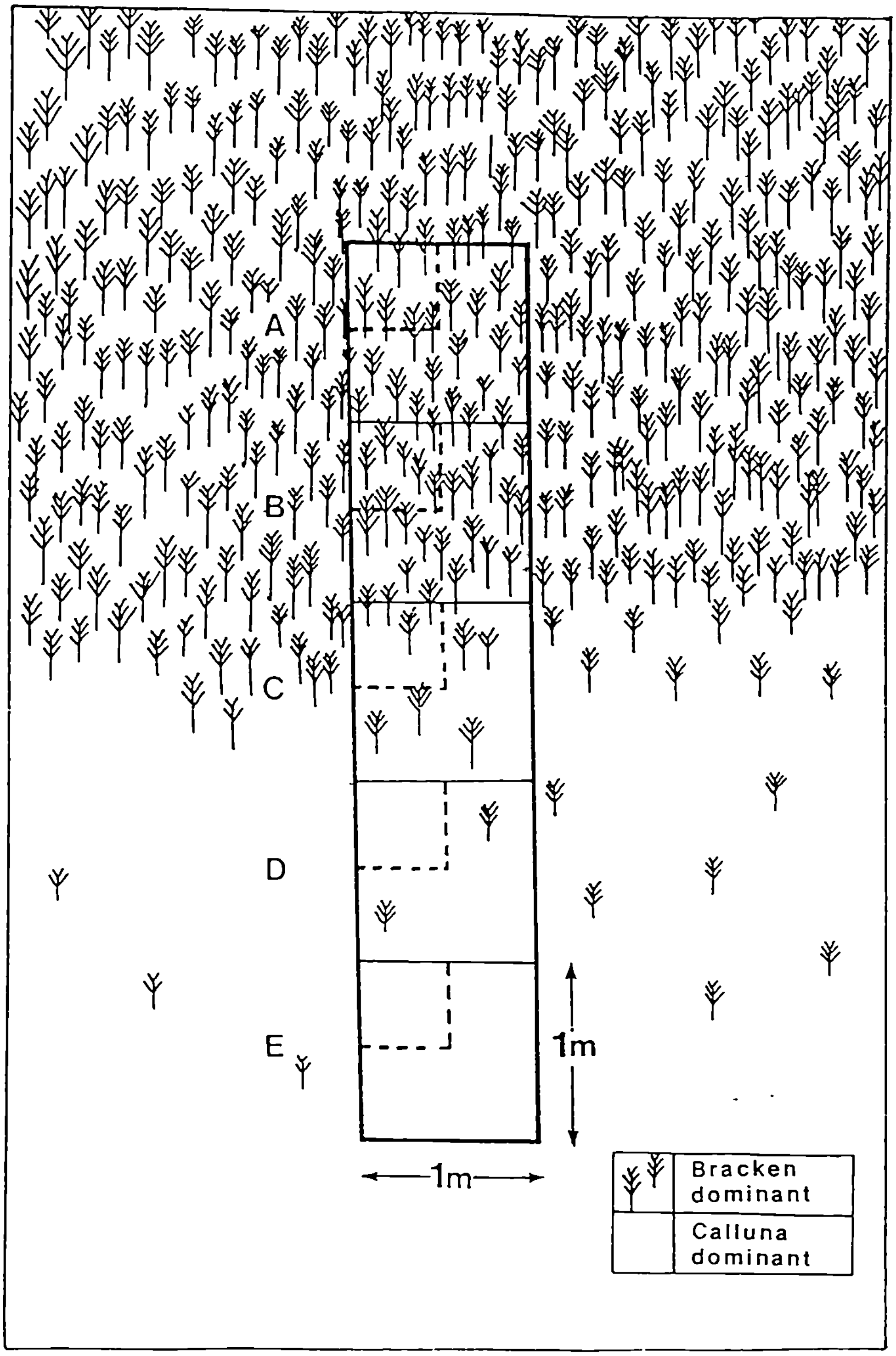


Fig. 10 Diagram of an experimental strip at the bracken-*Calluna* interface. Quadrats A and B are dominated by bracken whilst C, D, and E have predominantly *Calluna* as ground cover.

3.2 FIELD SITE DESCRIPTIONS

3.2.1 Criteria for site selection

Much of the first few months of the project were spent in locating suitable sites in which to work. Criteria for experimental sites included ease of access, the presence of as simple a flora as possible (with preference given to sites in which only bracken and *Calluna* were present) and bracken which had not been controlled in the recent past nor would be controlled during the course of the project. Difficulties were initially experienced in obtaining a comparison between margins which are advancing and those which remain relatively stationary. Studies using image analysis of aerial photographs taken in May 1973, the late summer of 1984 and the summer of 1988 (made available by the North York Moors National Park Department) made it possible to identify rapidly advancing margins and margins which had moved very little between 1973 and 1988. Subsequent discussion with farmers, game keepers and land agents have served to confirm these observations. A list of experimental sites, the abbreviations by which they are referred to, and the rate at which their bracken margins are advancing is given in Appendix 1 at the back of this thesis.

Soils on all experimental sites were acidic with pH varying in the range 2.8-3.3.

3.2.2 Lowna Lund

Lowna Lund is a south-west facing piece of gently sloping moorland at an altitude of 140-200m. It is part of the Farndale Estate and situated about 1.5km to the north-west of Hutton-le-hole (Grid ref. SE6991) bounded by Lowna Rd. to the south, Dale End Rd. to the north, Lund Rd. to the north-west and Shortsha Beck to the south-east. The soils are of a clay stagnohumic gley type with a peaty/humose surface with shale often at less than 50cm (Carroll and Bendelow, 1981).

Several experimental field plots were used on this moor (see fig. 11) including the mature stand on the Beck side of the moor (Lowna mature stand -**LMS**) which was also the major collection site for soil blocks used in greenhouse experiments. Little vegetation other than a uniform stand of tall bracken is present though small amounts of *Camplylopus introflexus*, *Polytrichum piliferum*, *Vaccinium myrtillus* and *Festuca ovina* are present. Litter layers are deep at 10-20cm. At the interface of this stand with *Calluna* (Lowna Lund Beck site - **LLB**) the *Calluna* is

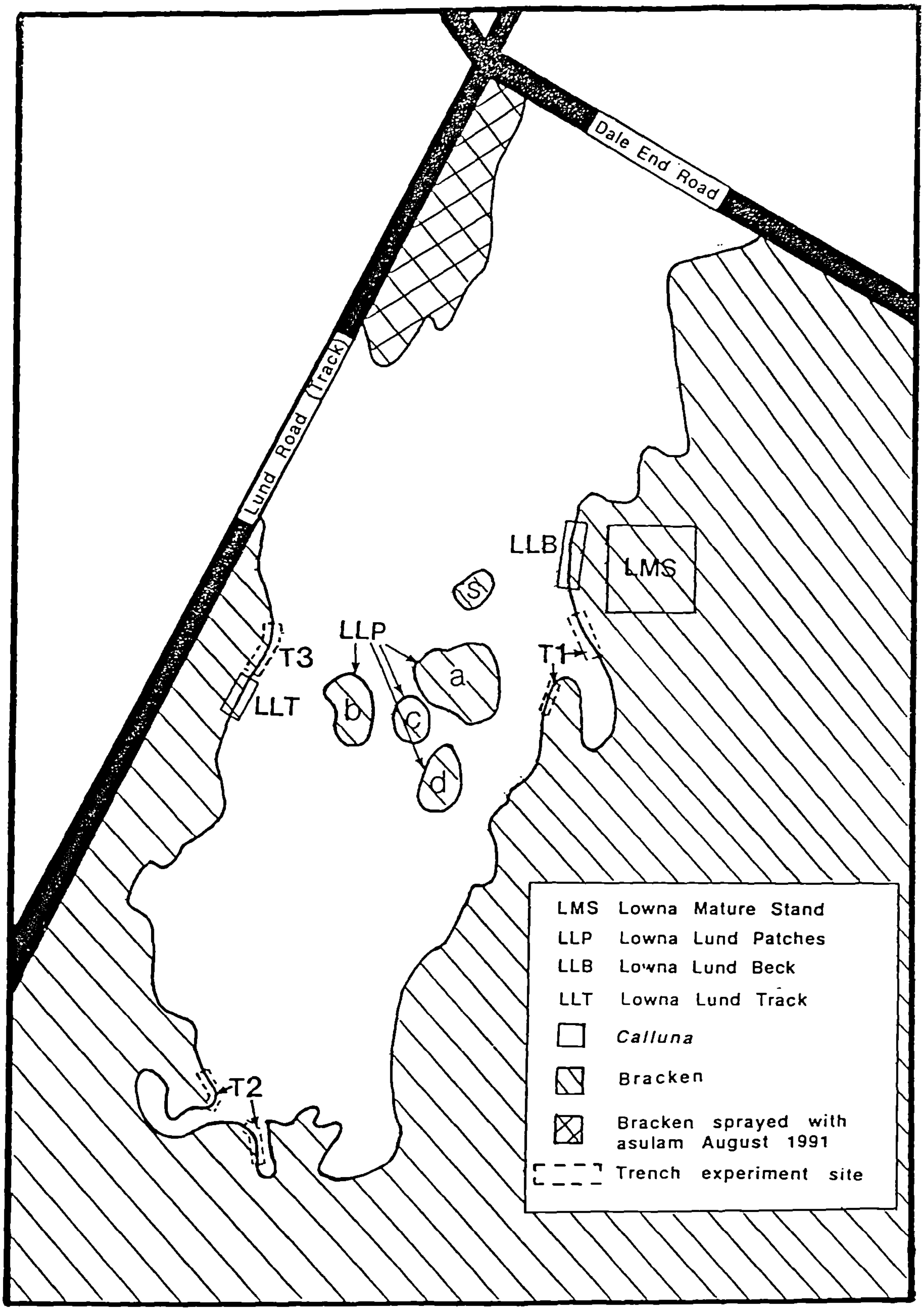


Fig. 11 Sketch map showing the location of experimental sites on Lowna Lund.

Fig. 12 **Overview of Lowna Lund taken from the east.** Showing the Beck mature stand and edge in the foreground, patches and track edge in the background. (15.8.92).

mature (reaching heights of around 25cm) and the bracken is not advancing at any great rate. No obvious change in its position is observed when comparing aerial photographs. Species other than bracken and *Calluna* are again rare at this site with only very small amounts of moss (*Campylopus introflexus*) and lichen present.

At the centre of this moor are 5 isolated circular patches of bracken of varying diameter between which are completely surrounded by *Calluna* (Lowna Lund patches -**LLP**). These patches are almost certainly clonal, having originated from a single sporeling and are therefore of particular interest since they allow both the application of different experimental treatments to a single patch with a uniform genotype and the application of the same treatment to different patches which are very likely to be genetically different. These patches have been present on Lowna Lund for more than 20 years and have remained separate. Image analysis of aerial photographs also confirms that the margins of these patches have not advanced to any significant extent during the past 20 years. Other species present in very small amounts include *Campylopus introflexus* and *Carex nigra* at the patch margins and *Campylopus introflexus* and *Vaccinium myrtillus* at the centre of the patches.

A further experimental plot is found on the western side of Lowna Lund closest to the track called Lund Road (Lowna Lund track-LLT). Here the edge of a mature bracken stand is advancing out of a ditch into an area of mature *Calluna*. In comparison with the beck margin and the margins of the patches there is little litter cover on this plot and the fronds present are short and sparse. The soil in this plot is more sandy than that found on the rest of Lowna Lund and is of a brown earth type over sandstone (Carroll and Bendelow, 1981).

In 1992 plots on the southern bracken-*Calluna* interface were used (Lowna Lund south-LLS). Here a mature bracken stand is advancing slowly into mature *Calluna*. Vegetation other than bracken and *Calluna* found at sites LLT and LLS were as described for LLP and again present only very occasionally.

3.2.3 Harland Moor

Harland is found about 2km north-west of Hutton-le-hole (Grid ref. SE9168) and is again part of the Farndale Estate. The sites used are to the east of Mill Lane on a gently sloping, south-facing piece of moorland which varies in altitude from 140-170m. The soils are of a clay stagnohumic gley type over shales which are very close to the surface forming a very rocky moor (Carroll and Bendelow, 1981).

A large area of *Calluna* was burnt on Harland Moor in the autumn of 1989. Much of the heather burnt was very close to bracken stands and it is very likely that some of the area burnt was covered in the mixture of bracken and *Calluna* which is present over large areas of unburnt moorland on Harland. In much of the burnt area an almost pure stand of bracken was present in the summer of 1990.

3.2.4 Spaunton Knowl

ADAS have fenced off an area of moorland containing a bracken-*Calluna* margin of approximately 100m in length where bracken is known to be advancing into short (approx. 10cm) *Calluna* at Spaunton Knowl. This site is on the Spaunton Estate situated about 1.25km to the north-east of Hutton-le-hole south of the road between Hutton-le-hole and Rosedale near to Loskey Bridge (Grid ref. SE7191). The fenced-off area is a west-facing slope (of altitude 150-190m) with soils of a clay stagnohumic gley type (Carroll and Bendelow, 1981). ADAS are using this site to compare the effects of control treatments on the advance of bracken but the secure nature of this site made it ideal for use in experiments involving radiotracers.

3.2.5 Goathland Mature Stand (GMS)

Data relating to the growth of a mature bracken stand was also collected from a site situated to the south of the road to Goathland from the A169 (Grid ref. SE994843) about 1.75km from Goathland village. The site is at an altitude of 120m and has clay stagnohumic gley-type soils (Carroll and Bendelow, 1981) with deep bracken litter layers (10-20cm). Vegetation other than bracken was almost completely absent except for small cushions of *Campylopus introflexus.*

3.2.6 Goathland Two Howes Rigg (GTHR)

A series of experimental strips were used in the 1991 season along a bracken-*Calluna* margin of about 100m in length at Two Howes Rigg which is situated close to the Goathland Mature Site (Grid ref. SE9983 / SE9984). Mature bracken covers a steep slope (known as Moss Dike) and is advancing into *Calluna* on the plateaux at the top of this slope (at an altitude of 240-250m). Again the soils are of a clay stagnohumic gley type with a peaty/humose surface (Carroll and Bendelow, 1981). Bracken litter is present at the margin to a depth of 5-10cm. Again vegetation other than bracken and Calluna was very rare and almost exclusively mosses (*Campylopus introflexus* and *Polytrichum piliferum*).

3.2.7 Goathland Hunt House Road (GHH)

This site involves another front of bracken invading *Calluna* moorland on which a number of experimental strips were used in 1991. The front is to the East of Hunt House Road about 1.25km to the south-west of Goathland village (Grid ref. SE9982). Again bracken dominates the vegetation on a steep, rocky slope and is advancing into *Calluna* on the plateaux at the top of the slope (at altitude 220m).

The experimental strips on this site stretched along the bracken-*Calluna* margin over a distance of over 500m during which there is considerable variation in the height of the *Calluna* present. Once more soils are of a clay stagnohumic gley-type over shales (Carroll and Bendelow, 1981). The only vegetation present other than bracken and *Calluna* was *Campylopus introflexus.*

4. THE MORPHOLOGY OF BRACKEN AT ITS INTERFACE WITH *CALLUNA*

4.1 INTRODUCTION

Throughout the course of this study data on morphology were recorded with the aim of collecting information as to how an advancing bracken can be identified and how its morphology differs from that of a non-advancing margin or a mature stand away from a margin. The successful identification of advancing bracken fronts would then allow them to be prioritised in control programmes.

The information collected will also allow an assessment of the size of reserves of carbohydrate and rhizome buds available to the bracken plant. These reserves are particularly important in the process of recovery following attempted control treatments and must be heavily depleted if suceessful control is to take place. Only then will the ability of a bracken front to encroach into areas of other vegetation significantly impaired. Differences in sizes of reserves identified in each part of of plant, e.g. pioneering rhizome versus mature rhizome, might allow the identification of parts which may be particularly vulnerable to control attempts.

Whilst the morphology of lowland bracken at its interface with *Calluna* has been studied in depth by Watt (1940; 1945a, b; 1970) there is little comparative work on bracken growing in upland areas. The morphology of bracken has been the subject of some debate in the past (Watt, 1940; Dasanayake, 1960; Webster and Steeves, 1958) which again has largely centred on information collected on lowland sites but is of importance in estimating the potential of bracken to replace fronds removed in cutting treatments or to recover following herbicide treatment.

Data on frond number; frond characteristics including height, height of first pinnae; frond emergence dates and rate of development have been collected alongside data on the mass, shoot type and bud number, position and activity state of the rhizome.

4.2 METHODS

Experimental strips as described in 3.1.4 were used for the collection of morphological data at the bracken-*Calluna* interface. Data on untreated bracken were collected from a varying number of strips on many bracken margins and 1m^2

quadrats within mature bracken stands shown in table 1 overleaf. Quadrats within mature bracken stands were sampled in exactly the same way as those comprising the experimental strips.

Data collected throughout each season is plotted against 'days after 1st May'. Equivalent dates are given in Appendix 2 at the back of this thesis.

Table 1. Numbers of experimental strips at the margins of bracken stands and 1m^2 quadrats within mature bracken stands used for data collection.

Year of data collection	Site	No. of strips or 1m^2 quadrats per treatment	Total number of strips or 1m^2 quadrats sampled
1990	LLB	4	12
	LLT	4	12
	LMS	6/12	36
1991	LLB	10	10
	LLP	6/8	26
	GTHR	4/6/9	24
	GHH	8/12	44
	LMS	5	20
	GMS	5	20

4.2.1 Frond number and emergence rates

Frond numbers were counted at intervals throughout the growing season of 1990 and 1991. During the 1990 season frond numbers in each of the five 1m^2 quadrats comprising a strip were recorded at approximately monthly intervals. For the 1991 season it was decided that more frequent counts on a quarter (0.25m^2) of each quadrat would allow more strips to be sampled and improve the quality of the data obtained. In 1991 therefore counts were made initially at approximately fortnightly intervals but became less frequent as the number of fronds emerging slowed towards the end of the summer.

4.2.2 Frond maturity

During the summer of 1990 newly emerged fronds were coded with a differently coloured ring of wire placed around the rachis on each occasion that frond numbers were recorded. This allowed the identification of fronds emerged in each period between data recordings (approximately one month). The growth and senescence rates of each months new fronds could then be followed.

This colour-coding was discontinued in 1991 when an estimate of frond age was obtained instead by recording the number of fully unfurled pinnae present on each frond. Data relating to the change in the number of fronds present, rather than the numbers of new fronds emerging, are therefore presented for both the 1990 and 1991. These data do not take into account the death of fronds included in the previous data sets. Additionally information on the number of new fronds emerging throughout the season is presented for 1990.

4.2.3 Frond height and first pinnae height

Frond heights were measured at the same time as fronds were counted during both seasons. Measurements were taken from ground-level (i.e. the bottom of any loose litter layer present) to the tip of each frond. The height of unfurled croziers were measured from the ground to the tallest point of the hook. First pinnae heights were measured from the ground to the junction of the lowest pinna and the rachis during the 1990 season only.

4.2.4 Collection of rhizome samples and separation into rhizome types

Rhizome data were collected from the top left quarter of both each 1m^2 quadrat comprising the experimental strips at bracken-*Calluna* interfaces and each 1m^2 quadrat in a dense bracken stand. The samples were collected at the end of the 1991 season during the period September to December. During 1990 samples were also taken at intervals throughout the summer allowing observation of any changes in fresh weight and rhizome bud activity as the season progressed.

The whole of the top-soil containing all the rhizome present within the sample area was removed as a single block, placed in a large plastic bag and transported back to the university where it was stored until the rhizome could be removed from the block. After the rhizome was removed from the soil block it was washed with a high pressure water hose and separated into 3 types as described below:

a) Long shoots - identified basically as described by Watt (1940) as the main carbohydrate storing rhizome, found at greater soil depths and with longer internodes (30-40cm) than short shoots. However, unlike the long shoots described by Watt these shoots were found to support occasional fronds.

b) Transitional shoots - these shoots are similar to those described by Webster and Steeves (1958) in that they form fronds and have both internodal lengths and rhizome diameter intermediate between those of long and short shoots.

c) Short shoots - as described by Watt (1940) as showing short internodal length (0.5-2.0cm) and the usual production of a single frond primordium immediately behind the apex in each season.

These processes and the subsequent recording of rhizome weights and bud details took place within a maximum of 10 days after the block was removed from the moor.

4.2.5 Rhizome fresh weight

The fresh weights of each rhizome type was measured for each sample block using a Mettler 360 top-pan balance. Weighing was carried out immediately after the rhizome had been sorted in order to minimise its weight loss due to drying. Any excess water remaining after washing the rhizome was removed by shaking.

4.2.6 Rhizome bud numbers, positions and activity

The details of rhizome buds or frond primordia were recorded separately for each rhizome type in each sample block. The positions of rhizome buds were found to fall largely into 4 categories (see fig. 4 and Appendix 3):

a) at the apex of the rhizome segment either as the terminal bud or as a frond primordium just behind it;

b) in the axis of two rhizome shoots;

c) adaxial to an old frond base;

d) in the position of a previous years apical frond bud which has remained dormant for some years after initiation.

Numbers of rhizome buds falling into each category were recorded together with their activity state as defined by Lowday *et al.* (1983), " a bud was considered active if it was light coloured and swollen, in contrast to dormant buds which were smaller and covered with a dark brown protective scale."

4.3 RESULTS

4.3.1 Frond number and emergence rates

The number of fronds present changes throughout the growing season as new fronds emerge, whilst others are damaged or become senescent. Fig. 13 shows a general decline in the number of fronds present at bracken-*Calluna* margins as distance from the stand increases. However on some sites (**LLT** and **LLP** 1991, fig. 13 c and f respectively) there are consistently higher frond numbers found in quadrat B than in quadrat A of experimental strips (fig. 10, p56). The rate at which this decline takes place also varies from site to site. At sites where the margin is not thought to be rapidly advancing, e.g. **LLB**, few outlying fronds are expected and a sharp decline in frond numbers between quadrats B and C was indeed observed at this site (fig. 13 b, f) Likewise the margins of the slowly enlarging patches (**LLP**, fig. 13f) show a sharp decline between quadrats C and D. At other sites, where bracken is encroaching more rapidly, the decline is less steep the notable exception being **GHH** (fig. 13d) where there is a steep decline between quadrats B and C).

Frond numbers in a mature bracken stand (**LMS**, fig. 13a) peak at lower levels (mean of 29m^{-2}) than those which are found in quadrat A just behind the interface with mean frond numbers peaking at a range between 34m^{-2} (**LLT** and **LLB** (1990), fig. 13 c, b) and 51.3m^{-2} (**LLP** 1991, fig. 13f). The bracken margin at **LLB** which is advancing only very slowly has low peak frond numbers in both the 1990 and 1991 seasons (fig. 13 b, g) and seems to be behaving similarly to the mature stand.

The time at which the majority of fronds emerge varies between sites. However both absolute numbers of fronds present and the percentage of the seasons fronds which have emerged by the end of May, are greater in quadrat A of experimental strips at the margins of bracken stands than they are in the mature bracken stand (**LMS**), which has 15 fronds m^{-2} at 31st May 1990, as shown in table 2 overleaf. Again the exceptions to this rule are **LLP** and **LLB** which are advancing slowly. The figure for **GHH** is however very low at 38% but this may be explained by the exposed nature of this site.

Table 2. Mean frond numbers m^{-2} and percentage of total frond number for the season in quadrat A of experimental strips at the margin. Figures are taken from figs. 13 and 14 at 31 May.

Year	Site	Frond number m^{-2}	Percentage of season's fronds
1990	LMS	15	53
	LLB	19	20
	LLT	29	91
1991	GHH	23	38
	GTHR	35	70
	LLP	8	56
	LLB	15	60

The bracken margins at the higher and more exposed sites GHH and GTHR (fig. 14 d, e) both suffer a decline in the number of fronds present in the first week of June due to a late frost. This effect is not long-lived with frond numbers recovering to match those of other sites by mid-July.

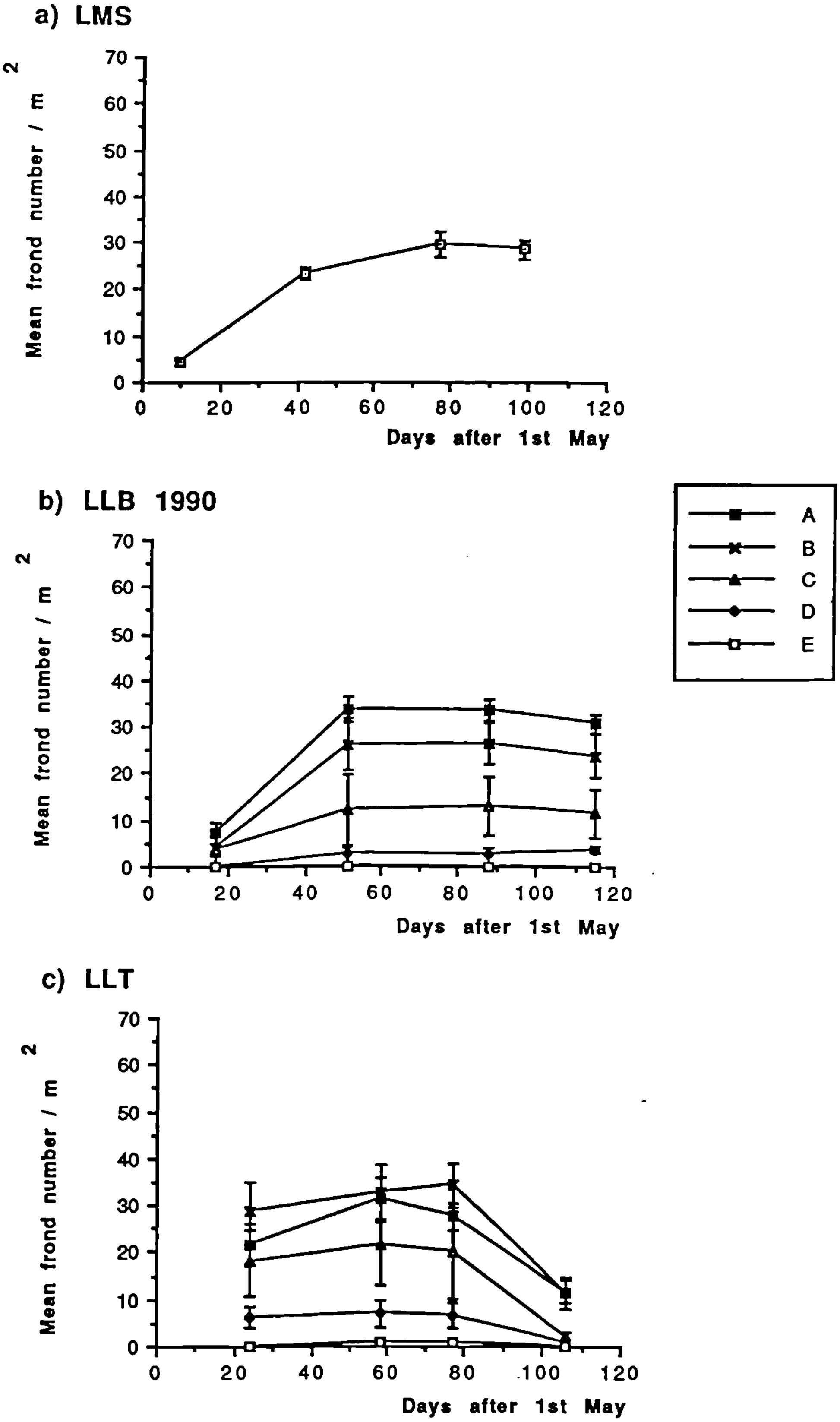


Fig. 13 Mean number of fronds found throughout the 1990 season. The letters A-E represent on graphs a and b represent position in experimental field strip (see 3.1.4). The number of m^2 quadrats sampled is as follows: **LLB (1990)** n=4, **LLT** n=4 **LMS** n=5, **GHH** n=12, **GTHR** n=7, **LLP** n=6 and **LLB (1991)** n=10. Error bars are the standard error of the mean. Continued overleaf.

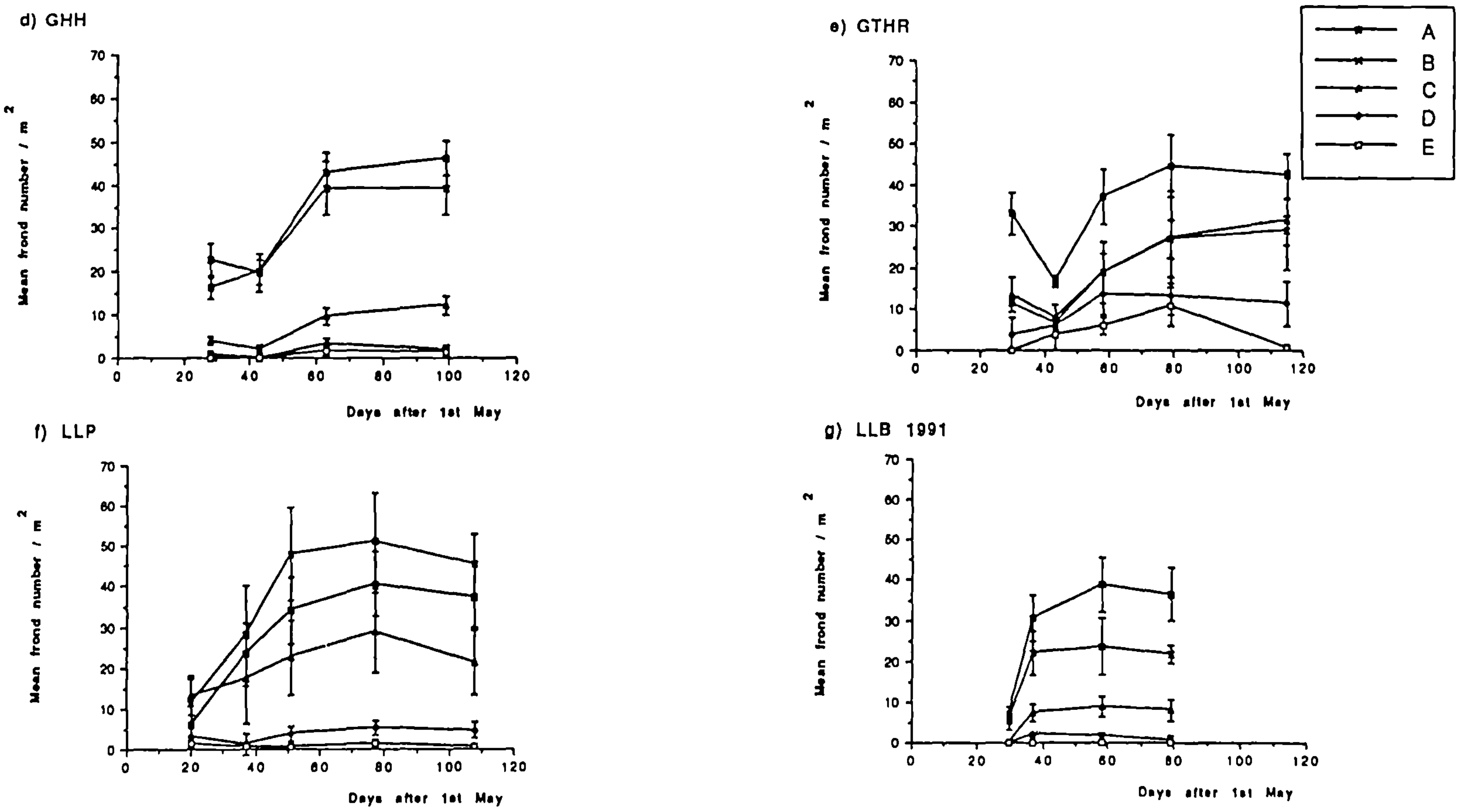


Fig. 13 cont. Mean number of fronds found throughout the 1991 season.

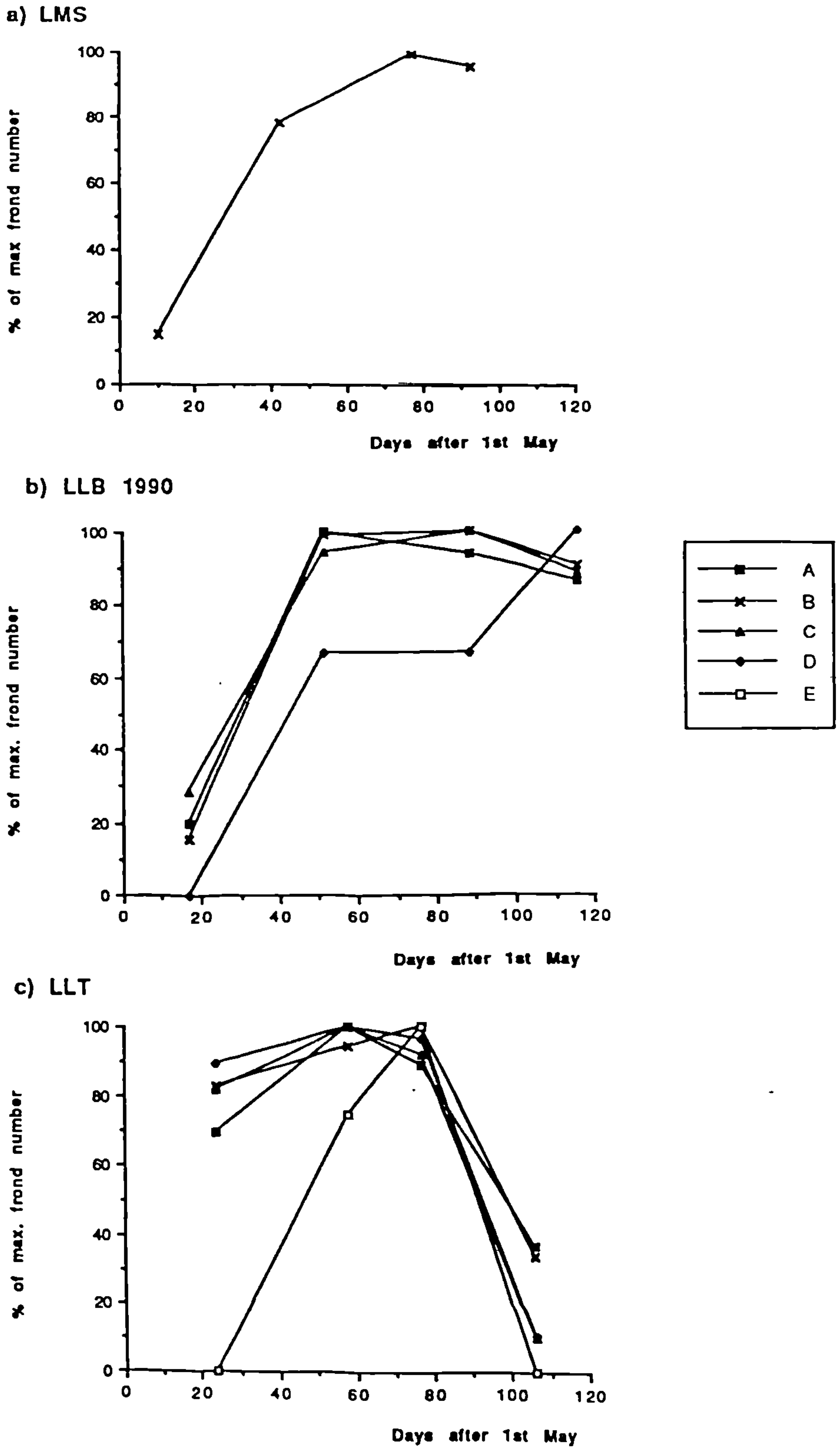


Fig. 14 Change in frond number throughout the 1990 season expressed as a percentage of total frond emergence for the season. The letters A-E on graphs a and b represent position in experimental strip (see 3.1.4). The numbers of m^2 quadrats sampled in each bar are as follows: LLB (1990) n=4, LLT n=4 LMS n=5, GHH n=12, GTHR n=7, LLP n=6 and LLB (1991) n=10. Error bars are the standard error of the mean. Continued overleaf.

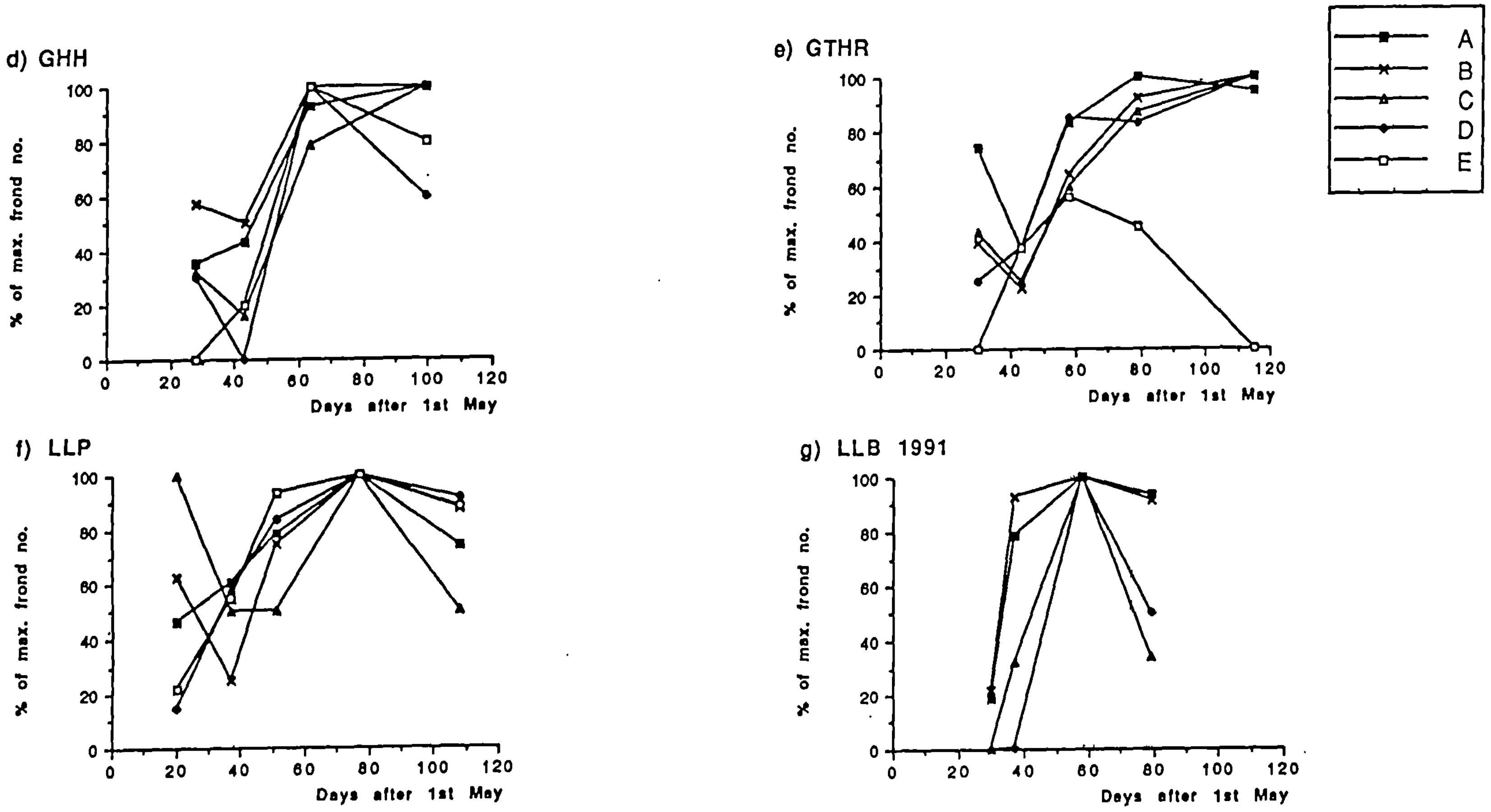


Fig. 14 cont. Change in frond number throughout the 1991 season expressed as a percentage of total frond emergence for the season.

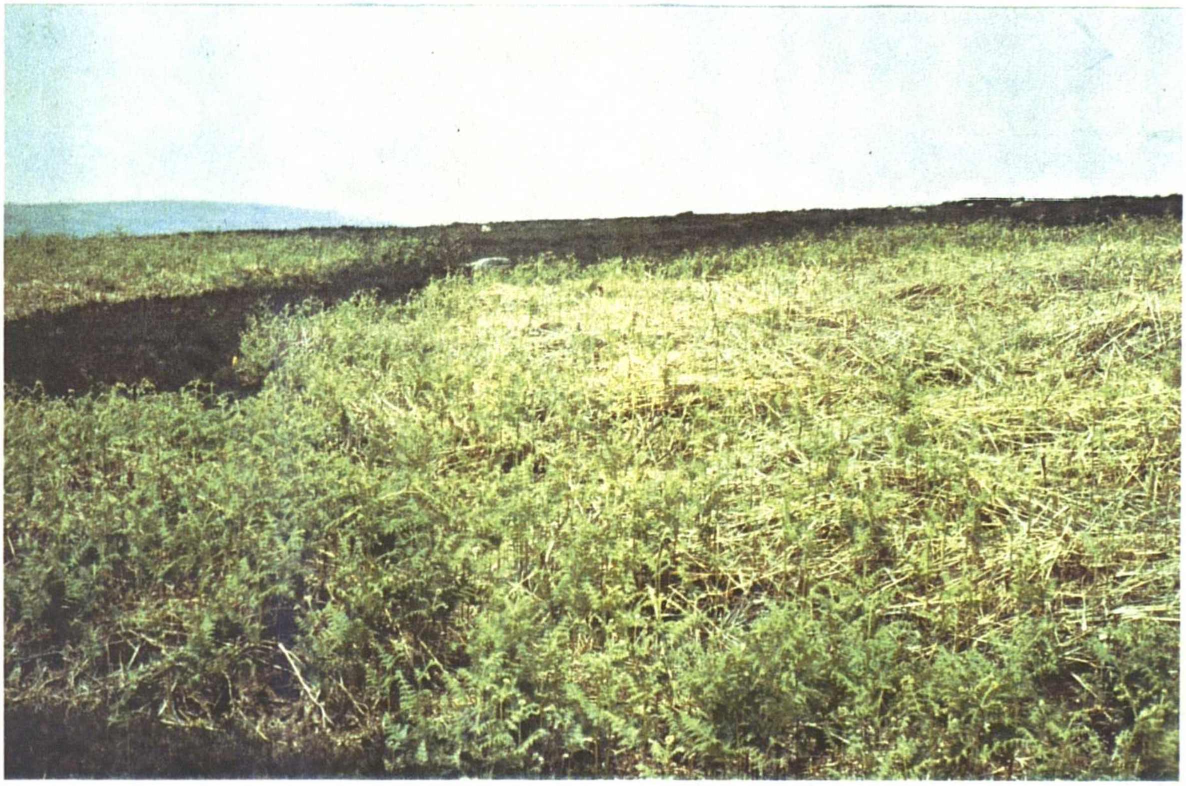


Fig. 15 Lowna Lund Patch A showing stand margins emerging earlier in the spring than the remainder of the stand. (31.5.90).

4.3.2 Frond maturity

New fronds continue to emerge throughout the summer on all sites with new fronds still appearing well into August. However, the majority of fronds emerge before the end of June (fig. 16). The number of new fronds which are produced decline as the season progresses beyond this point. Again fig. 16 shows peak production of fronds in 1990 occuring earlier at the more rapidly advancing site (**LLT**) (fig. 16c) than at the more slowly advancing site (**LLB**) (fig. 16b) or in a mature stand (**LMS**) (fig 16a).

1991 data on the number of juvenile fronds present (fig. 17) again show the presence of a few juvenile fronds present late in the season especially on site **GTHR** (fig. 17b) where many fronds were killed early in the season by frost. Whilst the number of fronds present at the end of the season on this site shows no decline in comparison with other stands as a result of frost damage (fig. 13) these fronds have been unable to reach a similar stage of maturity, as defined by number of pinnae unfurled, as fronds present on other margins. The number of juvenile fronds present peak in late June / early July.

A common feature of the emergence of bracken stands is that the margins (i.e. quadrats A-C) emerge before fronds further back into the stand (fig 15). The outermost fronds in quadrats D and E are not however usually among the first to emerge.

The number of fronds present begins to decline after the middle of July as fronds become scenescent. This decline is most obvious on site **LLT** (fig. 13c) during the 1990 season when conditions towards the end of the summer were very dry. Outlying fronds on this advancing front suffered the effects of drought sooner than did the remainder of the stand. The use of colour coded tags showing the period of emergence for bracken fronds indicated that it was the fronds which emerged earliest which were also the first to become scenescent.

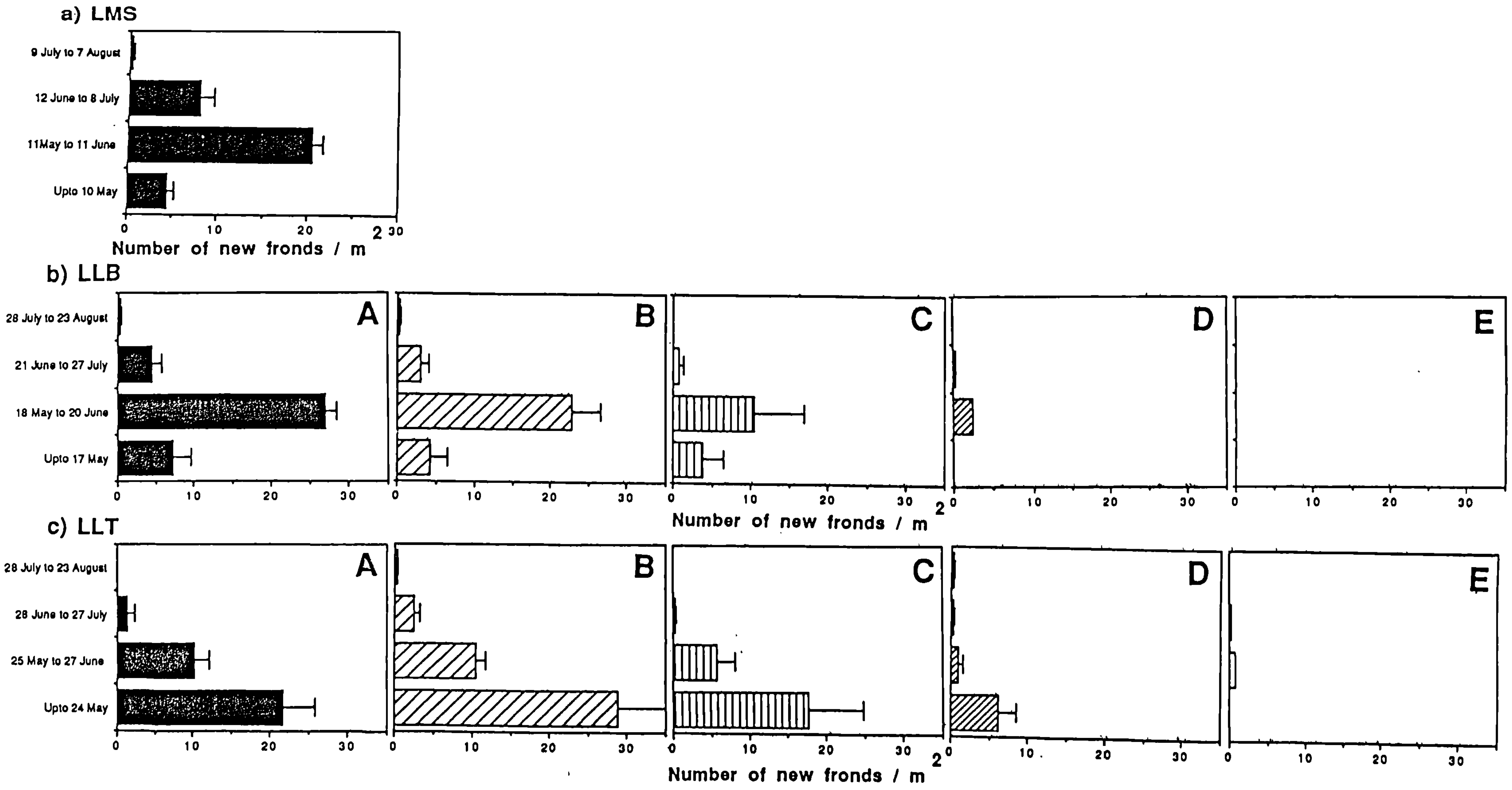


Fig. 16 The number of new fronds present at each data collection for the 1990 season. The letters A-E For figures relating to a) LLB and c) LLT represent position in experimental strip (see 3.1.4). The numbers of m^2 quadrats sampled in each bar are as follows: LLB n=4, LLT n=4 and LMS n=5. Error bars are the standard error of the mean.

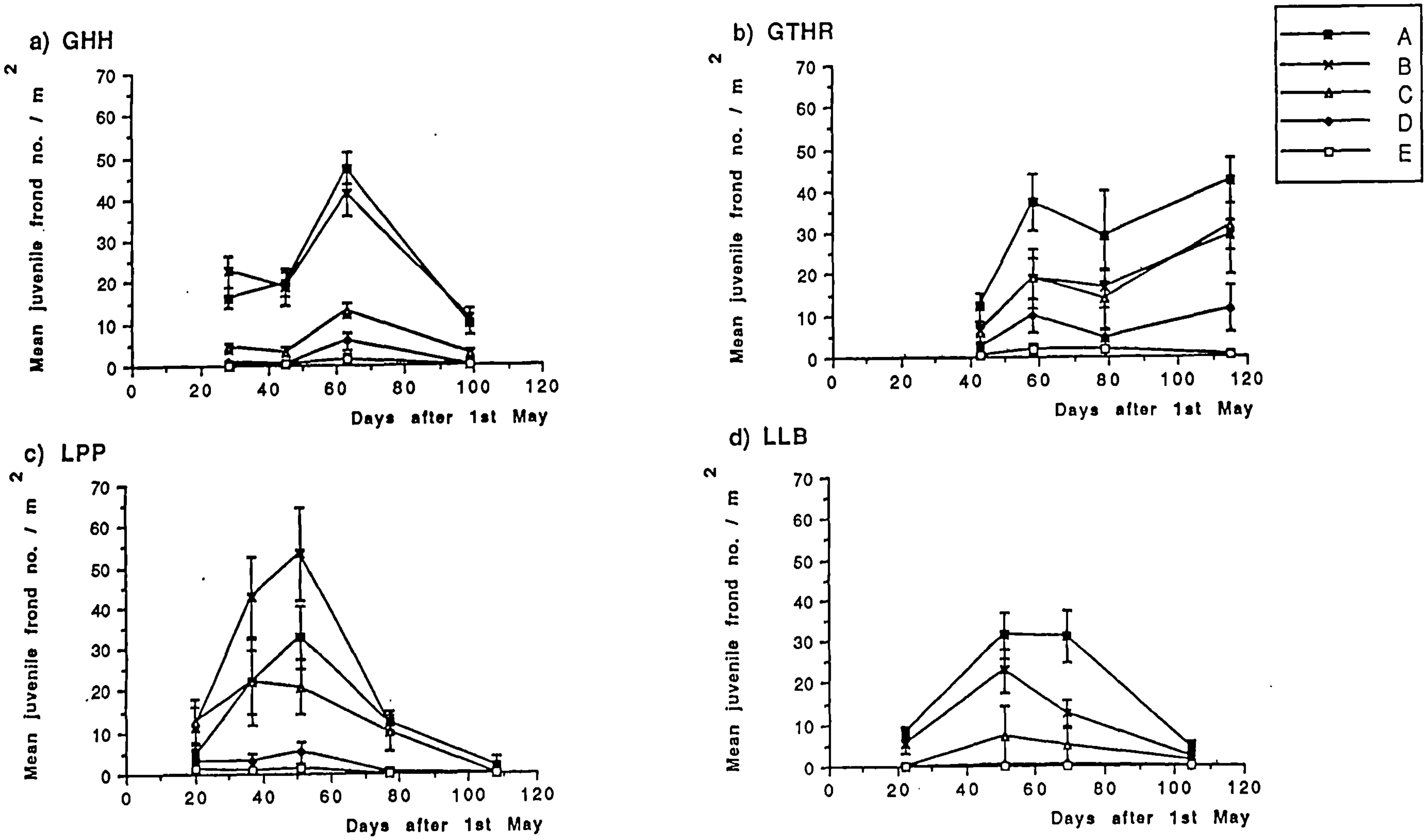


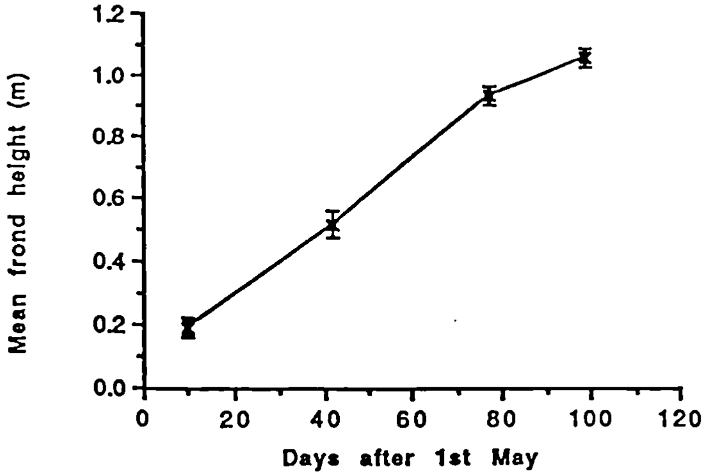
Fig. 17 Mean number of juvenile fronds (i.e. fronds with fewer than 3 pinnae fully unfurled) present throughout the 1991 season. The letters A-E represent position in experimental strip (see 3.1.4). The numbers of 0.25m^2 quadrats sampled in each bar are as follows: GHH n=12, GTHR n=7, LLP n=6 and LLB n=10. Error bars are the standard error of the mean.

4.3.3 Frond height and first pinnae height

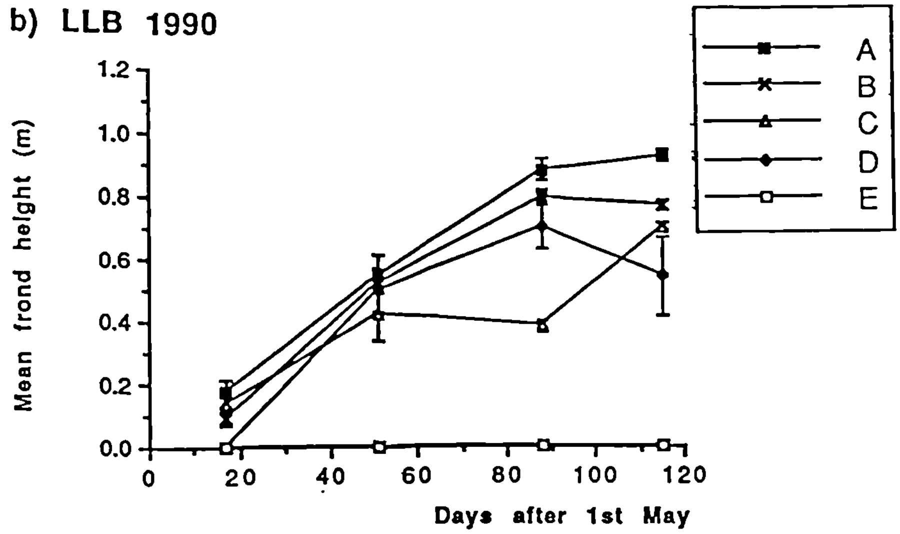
Within a mature bracken stand (LMS) frond heights were observed to increase throughout the summer in an approximately linear fashion before growth stops around the end of July, whilst the increase in frond height at the margins seems to slow slightly earlier (fig. 18). Mean maximum frond heights at all the margins even in quadrat A (GHH 0.59m and GTHR 0.65m, fig. 18 d, e) do not reach those found in the mature stand (LMS 1.06m, fig. 18a) and decline with increasing distance from the stand. Maximum frond heights at the slowly advancing margins (LLB (1991) 0.89m and LLP 0.91m fig. 18 b, f) are again intermediate between those found in the mature stand (LMS) and those found at the advancing margins GHH and GTHR (fig. 18 d, e). The heights of fronds within the equivalent quadrat of experimental strips on each site decline gently from quadrat A to quadrat E (fig. 18).

After the emergence of fronds the bracken crozier grows until the first pinnae unfurl, the length of the stipe between the ground and the first pinnae does not increase to any great after this point (fig. 19). The height at which the first pinnae unfurl varies in a similar way to the height of the frond itself being greater in the mature stand (LMS) than at the stand margins and shorter at the rapidly advancing margin LLT than at the more stationary margin LLB (fig. 19).

a) LMS



b) LLB 1990



c) LLT

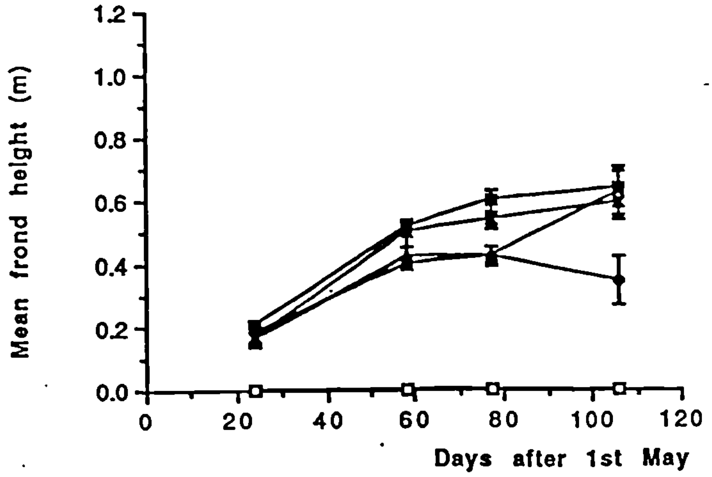


Fig. 18 Change in mean frond height for each m^2 sample quadrat during the 1990 season. The letters A-E represent on graphs b and c represent position in experimental field strip (see 3.1.4). The number of m^2 quadrats sampled is as follows: **LLB (1990)** n=4, **LLT** n=4 **LMS** n=5, **GHH** n=12, **GTHR** n=7, **LLP** n=6 and **LLB (1991)** n=10. Error bars are the standard error of the mean. Continued overleaf.

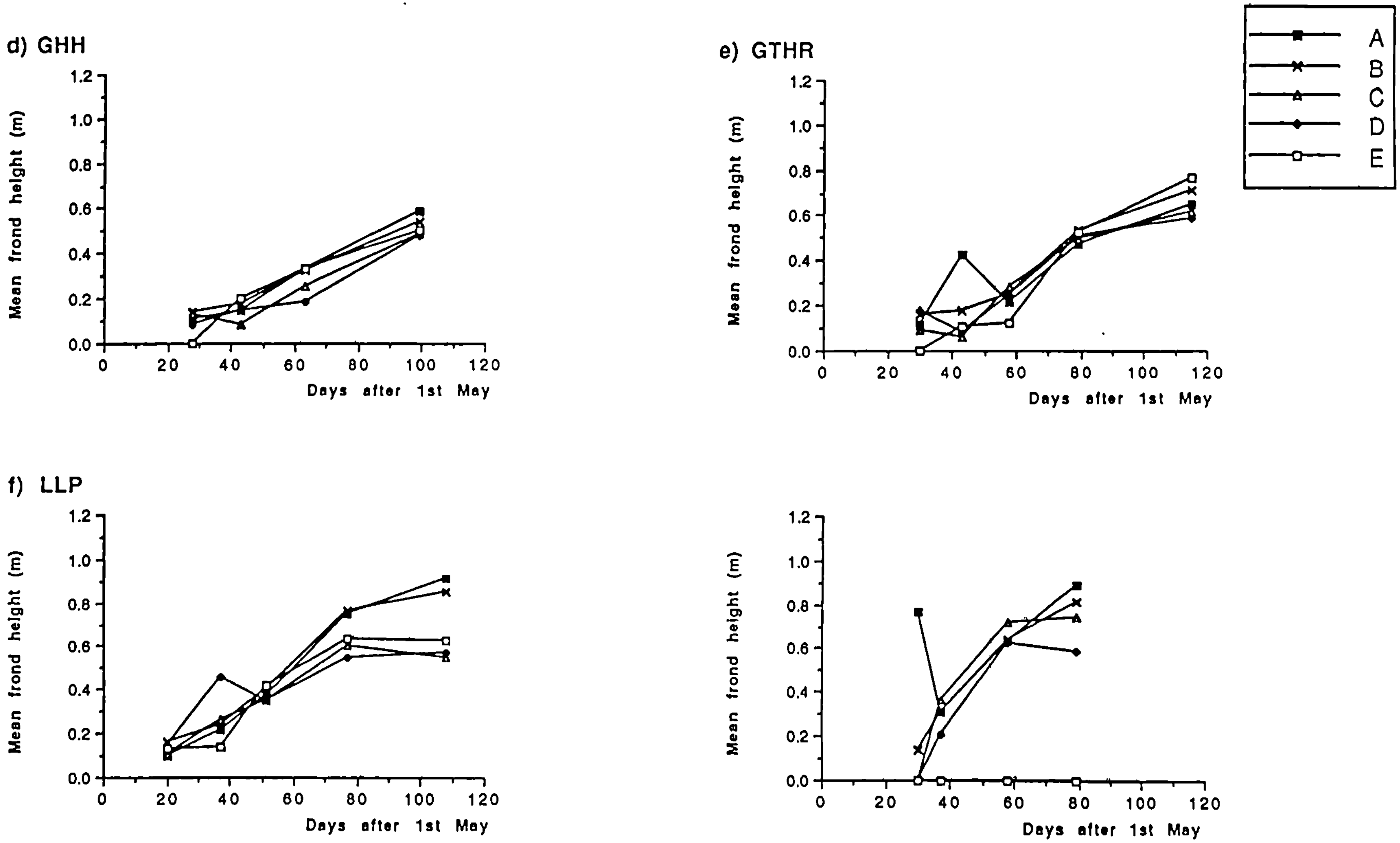


Fig. 18 cont. Change in mean frond height for each 0.25m^2 sample quadrat during the 1991 season.

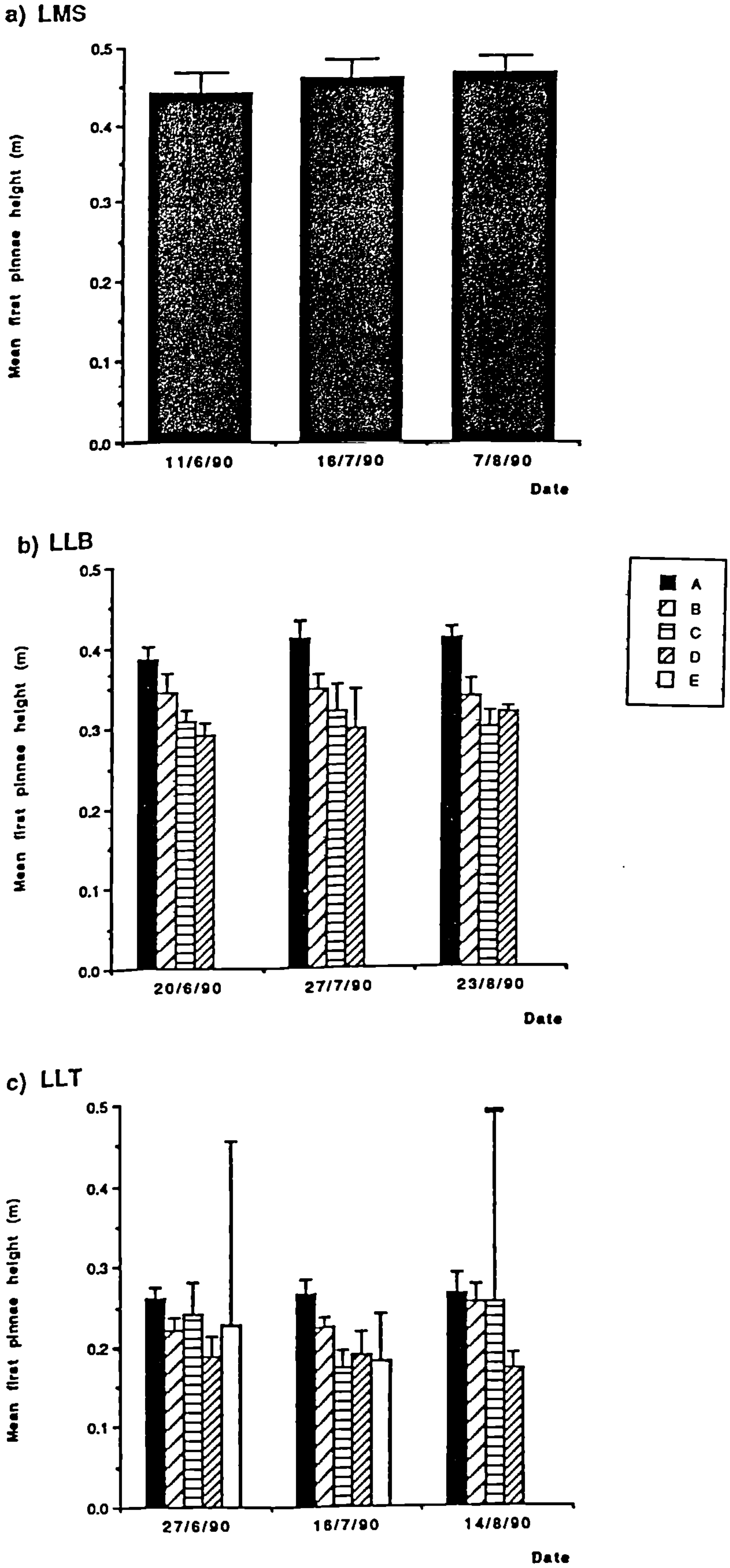


Fig. 19 Mean height for each m^2 sample quadrat of lowest pinnae for fronds growing on Lowna Lund during 1990. The letters A-E represent on graphs b and c represent position in experimental field strip (see 3.1.4). The number of m^2 quadrats sampled is as follows: LLB n=4, LLT n=4 and LMS n=5. Error bars are the standard error of the mean.

4.3.4 Rhizome fresh weight

The rhizome of the bracken plant form a dense mat of high biomass which is often difficult to disentangle in order to study individual rhizome segments. As is expected for the carbohydrate storage organ of a deciduous plant fresh weights of rhizome were observed to follow a cyclical pattern in a mature bracken stand (**LMS**) declining during the early summer months to reach a minimum around the middle of July, a period corresponding to that of frond production, before climbing again to reach a maximum at the time of frond senescence (fig. 20a). Fig. 20b shows that this cycle takes place in rhizome of all shoot types though long shoots making up 65% of the fresh weight of the rhizome in this stand (with transitional shoots 5% and short shoots 30%) obviously show the greatest fluctuations in weight. The cyclic seasonal change in rhizome weight also takes place at the stand margins but is most easily observed in the quadrats closest to the stand (fig. 21).

The mean fresh weight of rhizome present in the experimental strips at the margins of bracken stands decreases with increasing distance from the stand (figure 22). The rate at which this decrease takes place varies between the sites observed but is more steep in sites **LLP** and **LLB** (fig 23 c, d) which are not thought to be rapidly advancing margins than on sites **GHH** and **GTHR** (fig 23 a, b) which are advancing margins. Very little rhizome is found at the margins more than 3m away from the area in which bracken is the dominant vegetation. Rhizomes do not appear to extend for distances of more than 1m beyond the outermost emerged frond.

This decline takes place in all types of rhizome but the proportions of each type of shoot do change on approaching the margin. It is hardly surprising that the large amounts of short shoot characterised by its zig-zag pattern resulting from annual frond formation have not had time to develop at the outermost margins. Instead fronds are more borne more frequently on transitional-type rhizome than is the case further into the stand. There is a greater proportion of the most rapidly elongating long shoots present (e.g. for quadrat A on **GTHR** (fig. 23b) the rhizome is composed of 80% long shoots, 10% transitional shoots and only 10% short shoots). Once again the proportions of each rhizome type on site **LLB** (fig. 23d) are closer to those observed in the main stand (**LMS**) (fig. 20b) than on more rapidly advancing margins **GTHR** (fig. 23b). At **GHH** and **LLP** (fig. 23 a, c) these proportions are intermediate between the proportions seen in **LMS** and those in **GTHR**.

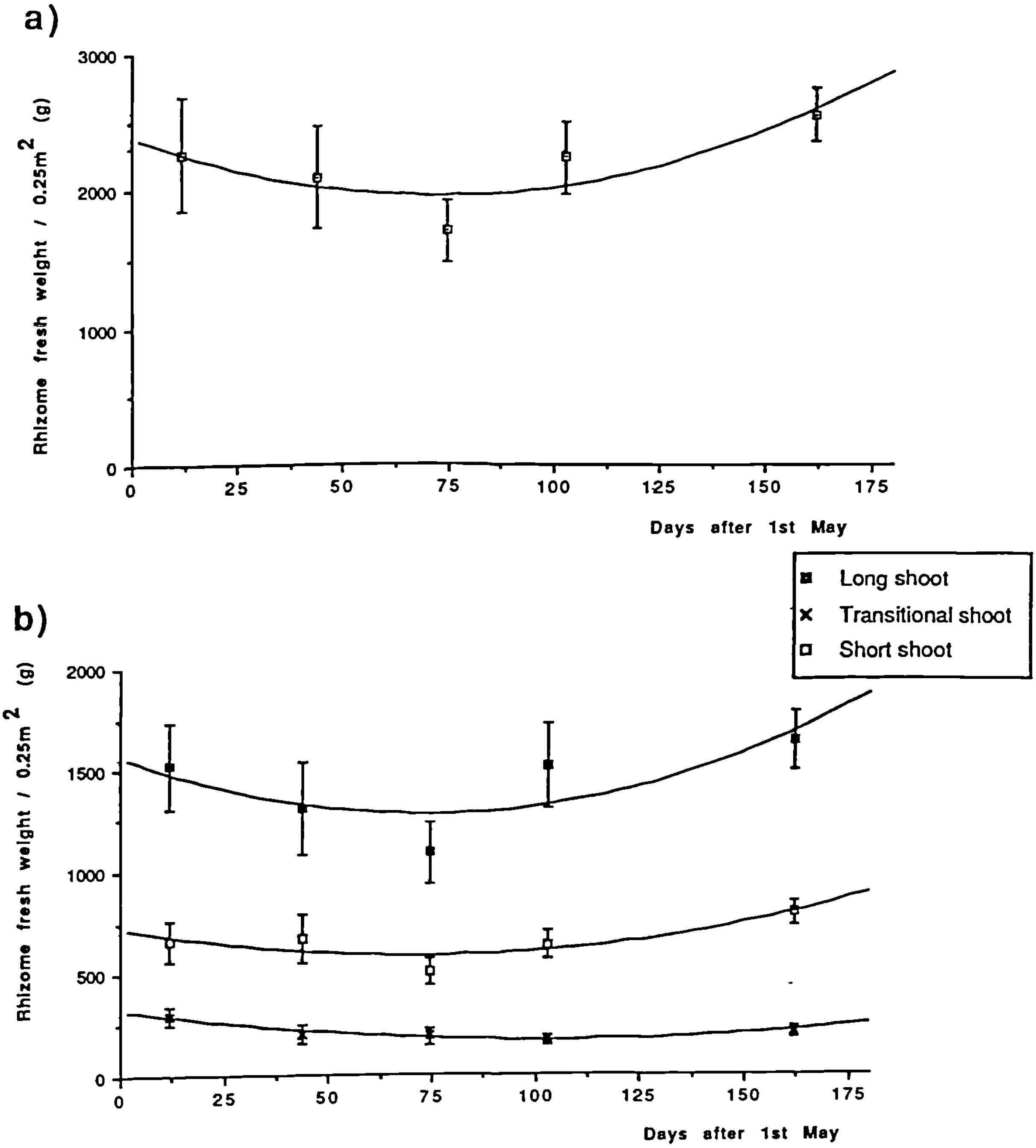


Fig. 20 Change in rhizome fresh weight in a mature bracken stand (LMS) during the 1990 season. Means for five 0.25m^2 sample quadrats are shown. Error bars are the standard error of the mean.

a) Total rhizome $y = 2305.6 - 11.203x + 8.012e^{-2}x^2$ $r^2 = 0.705$

b) Rhizome separated into constituent shoot types.

Long shoots $y = 1510.3 - 7.762x + 5.365e^{-2}x^2$ $r^2 = 0.593$

Transitional shoots $y = 274.2 - 2.834x + 1.395e^{-2}x^2$ $r^2 = 0.940$

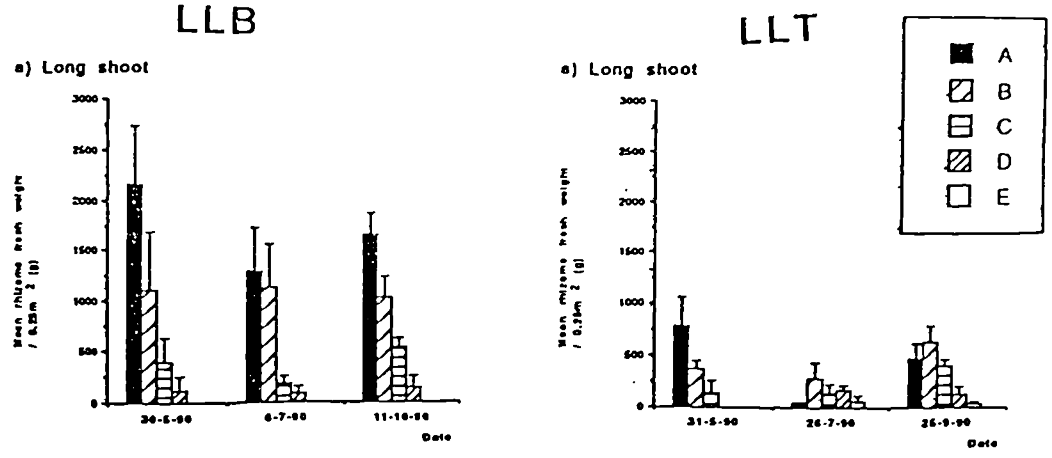
Short shoots $y = 672.6 - 3.794x + 2.682e^{-2}x^2$ $r^2 = 0.732$

LLB

LLT

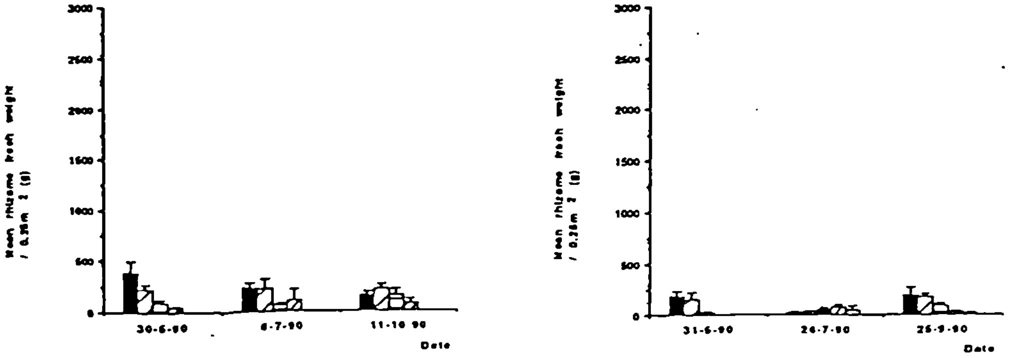
a) Long shoot

a) Long shoot



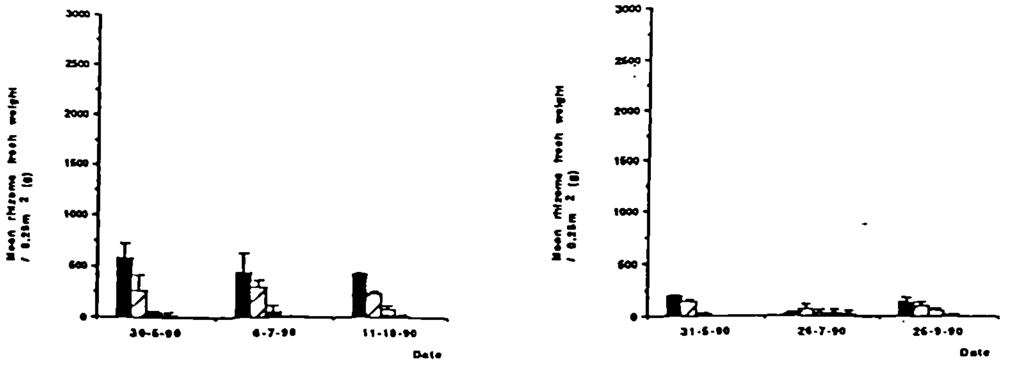
b) Transitional shoot

b) Transitional shoot



c) Short shoot

c) Short shoot



d) All rhizome

d) All rhizome

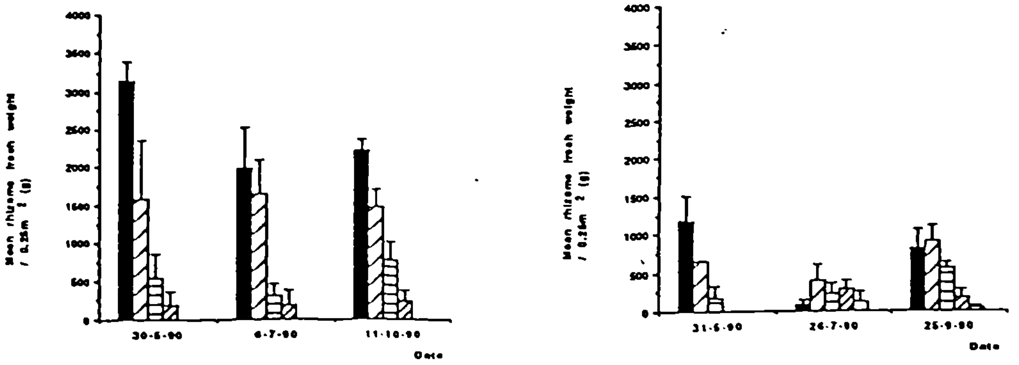


Fig. 21 Mean fresh weight per 0.25m^2 sample quadrat of rhizome for sites LLT and LLB during 1990. Rhizome weights are given for each rhizome type (Graphs a-c) and all rhizome (graph d). The numbers of 0.25m^2 quadrats sampled in each bar are LLB n=4 and LLT n=4 . Error bars are the standard error of the mean

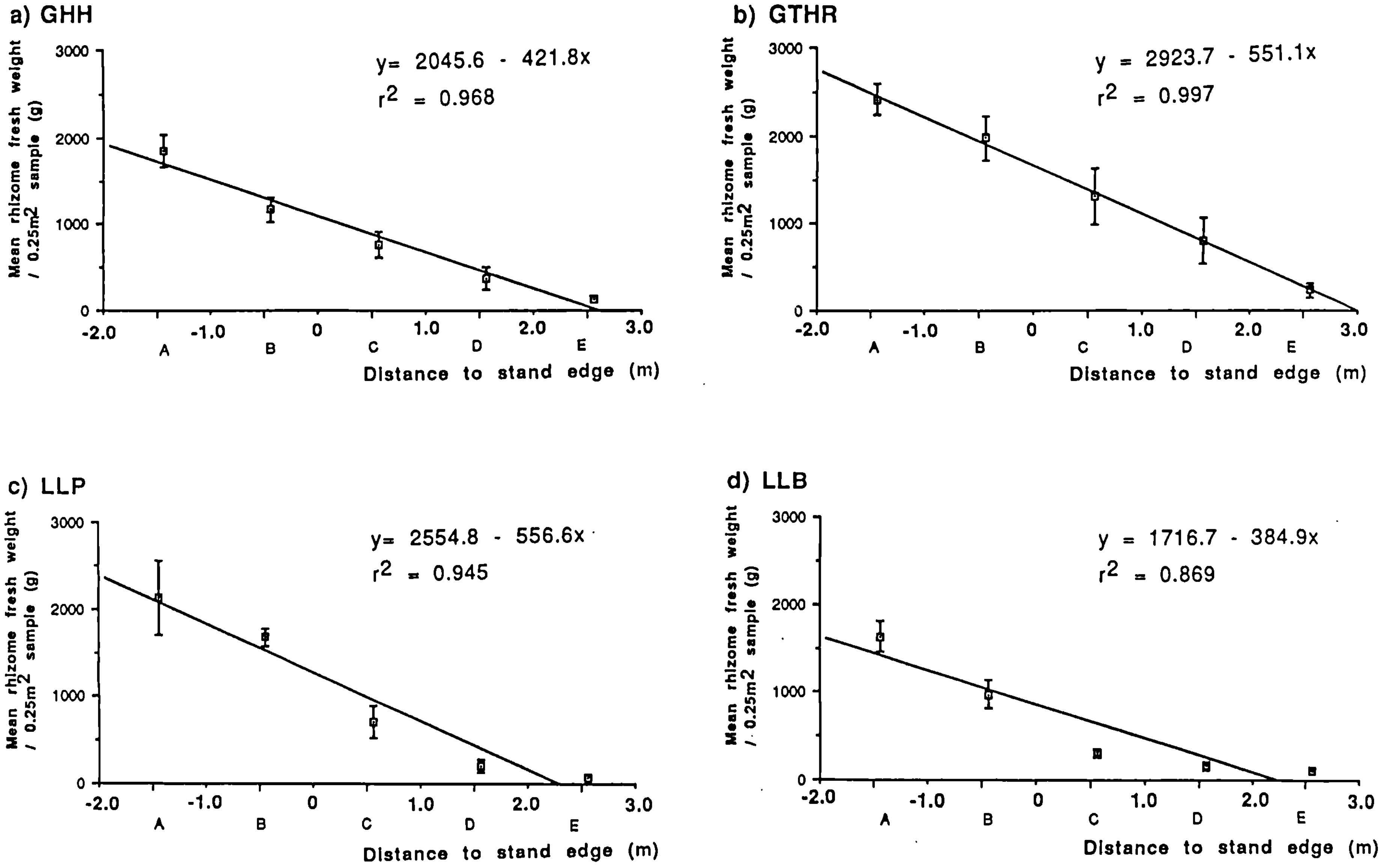


Fig. 22 Mean fresh weight per 0.25m^2 sample quadrat of rhizome for all sites in 1991. The letters A-E represent position in experimental field strip (see 3.1.4). The number of 0.25m^2 quadrats sampled is as follows: GHH n=12, GTHR n=7, LLP n=6 and LLB n=10. Error bars are the standard error of the mean.

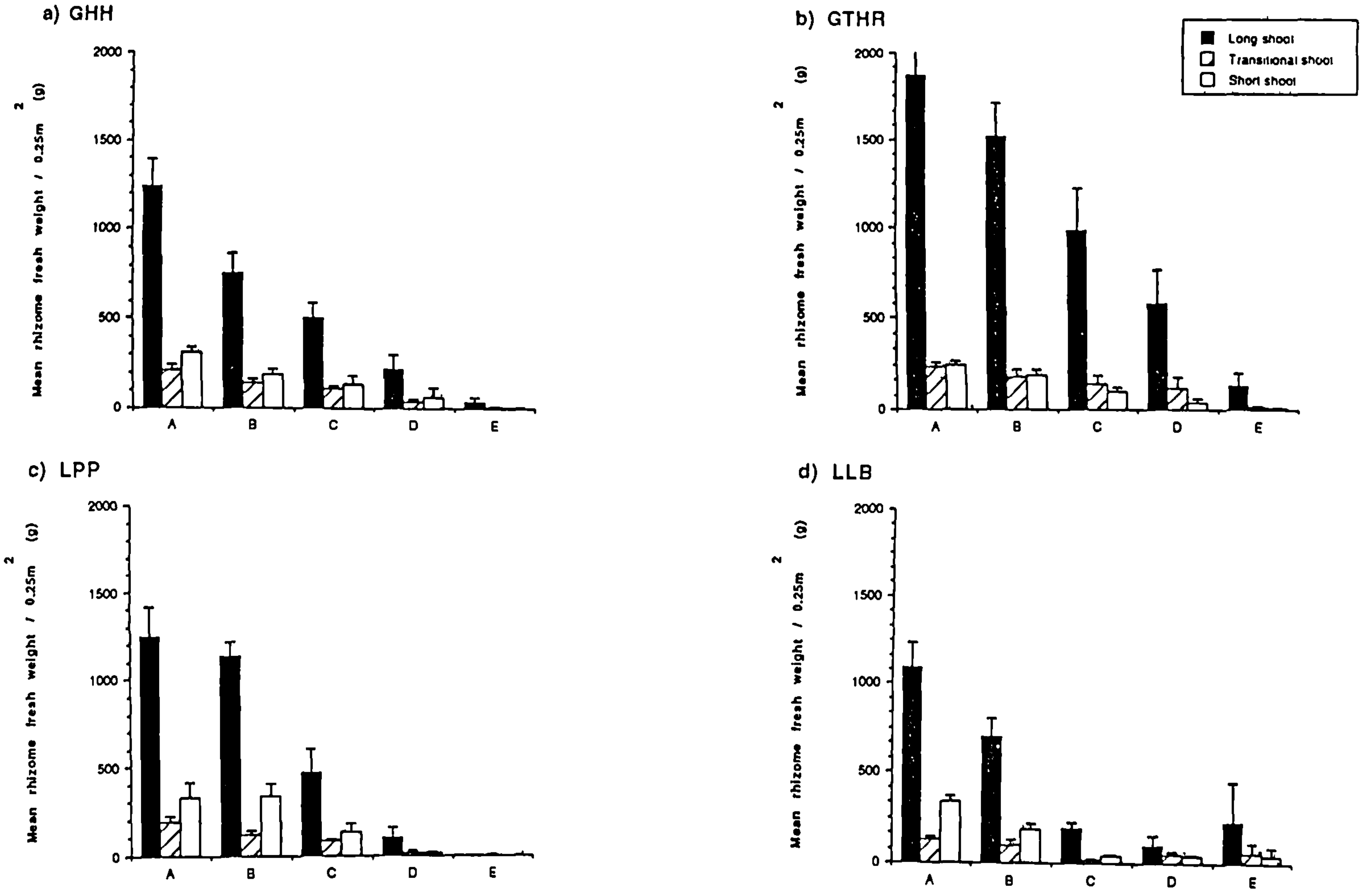


Fig. 23 Mean fresh weight per 0.25m^2 sample quadrat of each rhizome shoot type for all sites in 1991. The letters A-E represent position in experimental field strip (see 3.1.4). The number of 0.25m^2 quadrats sampled is as follows: GHH n=12, GTHR n=7, LLP n=6 and LLB n=10. Error bars are the standard error of the mean.

4.3.5 Rhizome bud numbers, position and state of activity

The decrease in the number of buds present in each quadrat in the experimental strips as the distance from the stand increases (fig. 25 Part 1) is largely a function of the mass of rhizome present in each quadrat. Hence the rate of decline in the numbers of buds present at each site closely reflects the rate of decline in rhizome fresh weight (fig. 23). The rates of decline in bud number at **LLP** and **LLB** (fig. 25 Part 1 c, d) are therefore rapid in relation to those seen at **GHH** and **GTHR** (fig. 25 Part 1 a, b). The higher mean number of fronds present in quadrat A over quadrat B at site **LLP** (fig. 13 f) is accompanied by higher numbers of rhizome buds (fig 25 Part 1c). There is some evidence to suggest that rhizome bud number follows similar trend to that of the fresh weight of rhizome present in the same stand with a small decline in the number of buds present in the early summer as new fronds are formed before new fronds are formed in the late summer (fig. 24).

The number of dormant buds present in the mature stand greatly outnumber active buds with 86.7% of the mean 670 buds m^{-2} present on 4th October, 1990 being in a dormant state. Fig. 25 (Part 1) shows that dormant buds also greatly outnumber active buds at the stand margins though at most of the sites observed the proportion of buds which are active is greater than that found in the mature stand. These proportions do not, however, appear to reflect the rate of advance of the bracken front on which they are found. Percentages of rhizome buds in quadrat A of experimental strips at bracken stand margins which are in an active state (September 1991 data) are given in table 3 below and shown in fig. 25 part 2:

Table 3. Percentages of buds on each rhizome shoot type which are active (in quadrat A of experimental strips).

Site	Long	Transitional	Short	All rhizome
GHH	40.5	11.5	18.5	18.5
GTHR	53.2	20.1	31.4	31.5
LLP	51.1	14.4	26.3	25.4
LLB	44.1	19.3	16.8	21.7

It is interesting to note that a higher proportion of buds on long shoots (the vast majority of which are at the apex) are active in comparison to buds on transitional and short shoots. A change in the composition of rhizome shoot type at the margin, relative to the mature stand, may therefore give rise to a change in the proportion of rhizome buds which are active.

The relative proportions of dormant and active buds is seen in fig. 24 not to vary greatly in the mature stand as the growing season progresses and active buds which develop into fronds are replaced as the next season's frond primordia are formed. Fig. 25 (Part 2) also shows an increase in the proportion of buds which are active in the experimental strips as the distance from the stand increases occuring at all of the margins examined in 1991. The slopes of regression curves fitted to fig. 25 (Part 2) do not, however, differ significantly from zero when t-tests are performed (GHH T=2.11, P=0.23; GTHR T=2.08, P=0.23; LLP T=3.08, P=0.13; LLB T=2.71, P=0.11). This lack of statistical significance probably results from the small number of samples taken at each site.

The majority of active buds present on the rhizome (80% of those counted throughout the season) of the mature stand (**LMS**) are present as terminal buds or frond primordia at the apices of rhizome shoots (fig. 26). Buds are also found in positions adaxial to the frond bases, in the axis of rhizome branches and as buds which once initiated in the usual position of the next seasons frond primordia have remained dormant for several years. Larger proportions of the buds found in these positions are dormant than is the case for buds at the apex. However, large numbers of dormant buds are also present at the apices as many, approximately half, of the apices fail to produce a frond in any given season. The terminal bud at the apex, responsible for rhizome extension, also remains dormant on many rhizome shoots.

The positions of fronds at the bracken stand margins which were observed were similar to those in the mature stand and do not seem to vary between quadrats in experimental strips as distance from the stand increases (fig. 27).

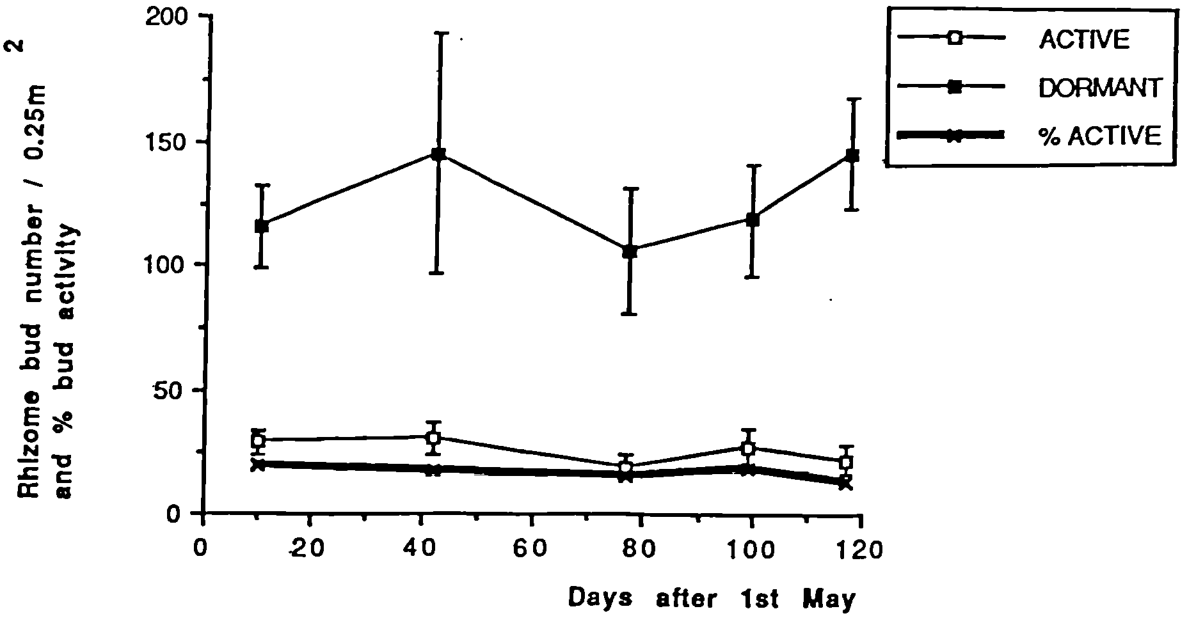


Fig. 24 Change in the mean number of active and dormant rhizome buds present per $0.25m^2$ sample quadrat in a mature bracken stand (LMS) during the 1990 season. Means for five $0.25m^2$ sample quadrats are shown. Error bars are the standard error of the mean.

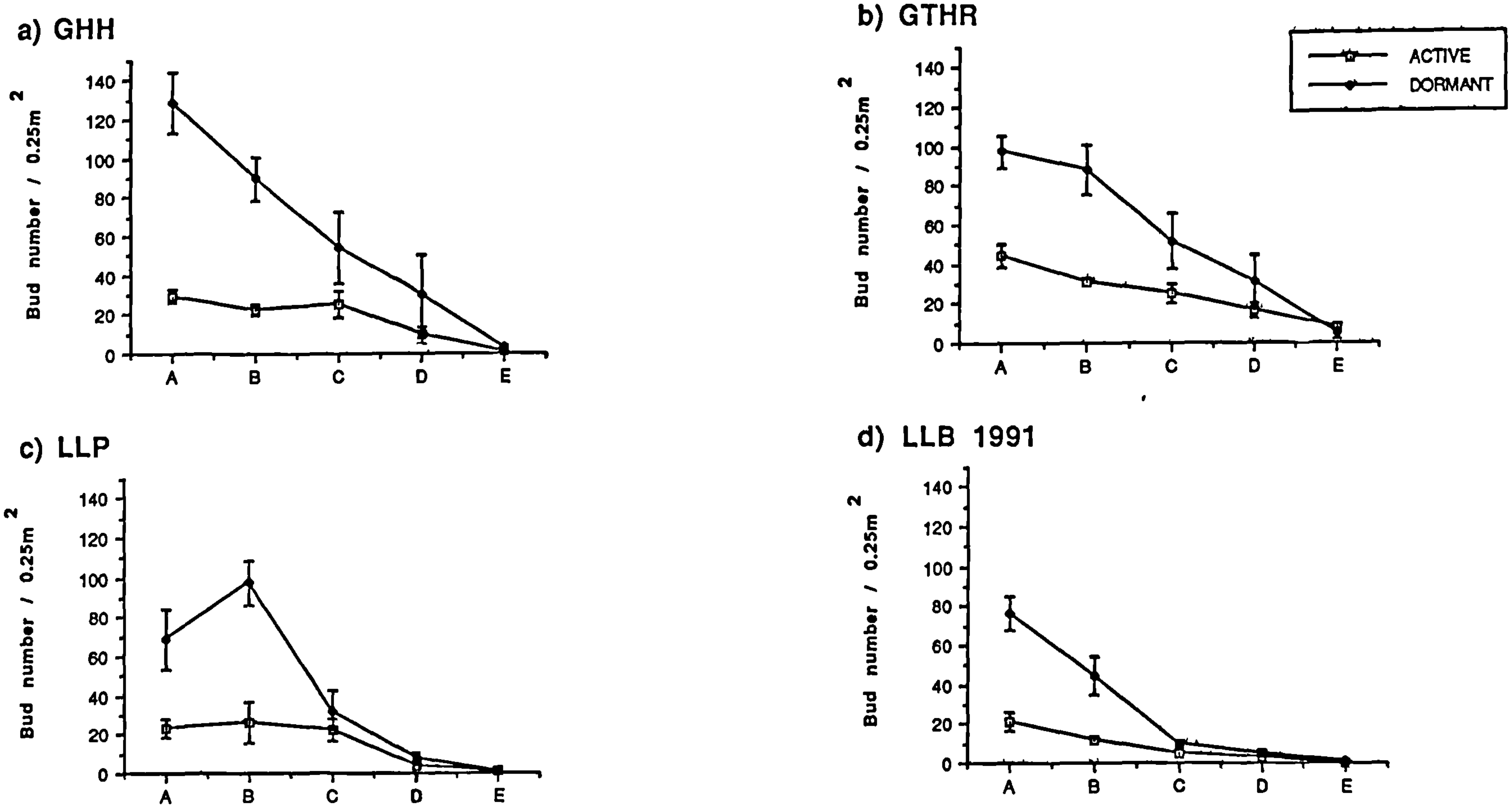


Fig. 25 Part 1. Mean numbers of active and dormant rhizome buds per 0.25m^2 sample quadrat at the margin of a bracken stand in 1991. The letters A-E represent position in experimental field strip (see 3.1.4). The number of 0.25m^2 quadrats sampled is as follows: GHH n=12, GTHR n=7, LLP n=6 and LLB n=10. Error bars are the standard error of the mean.

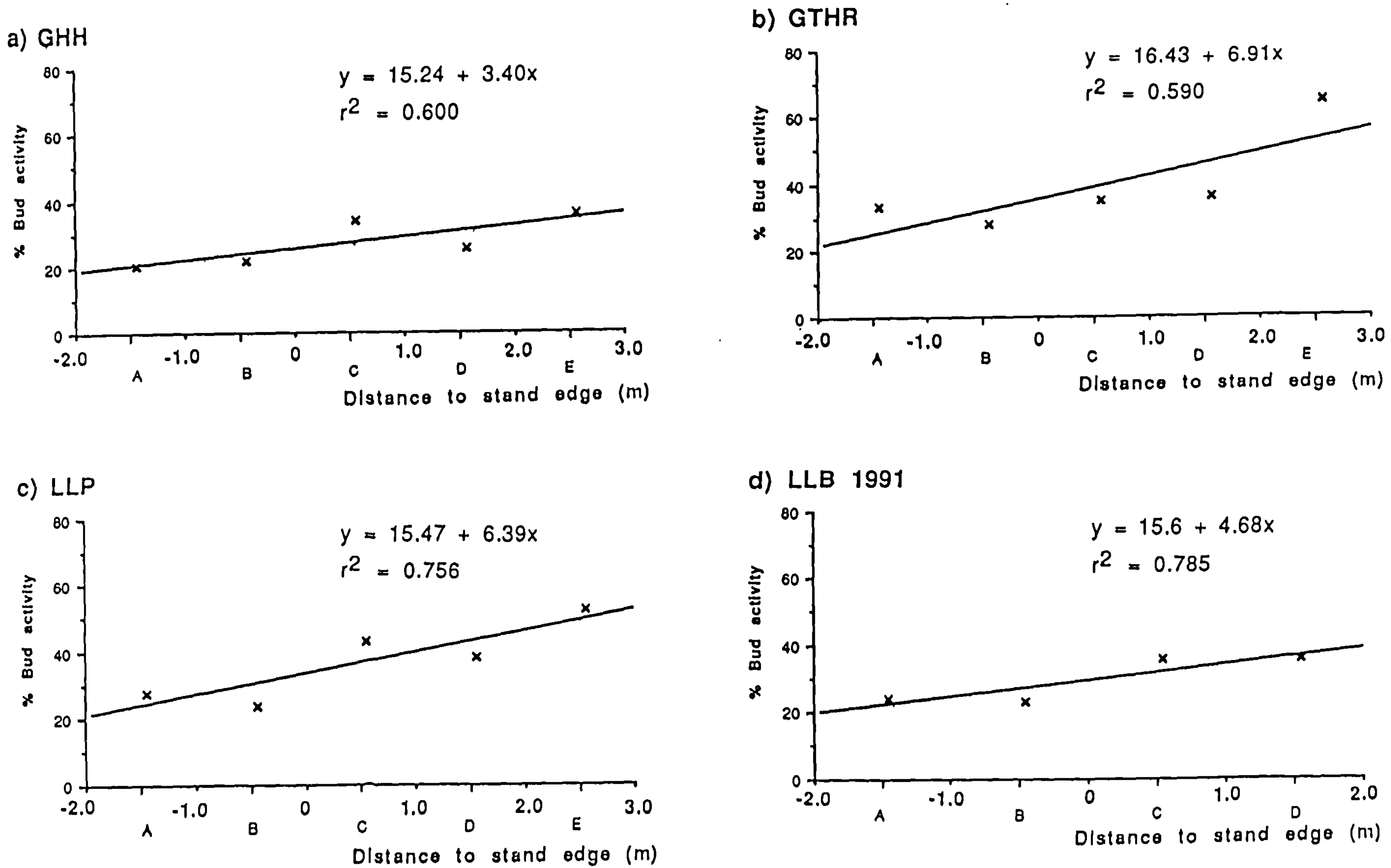
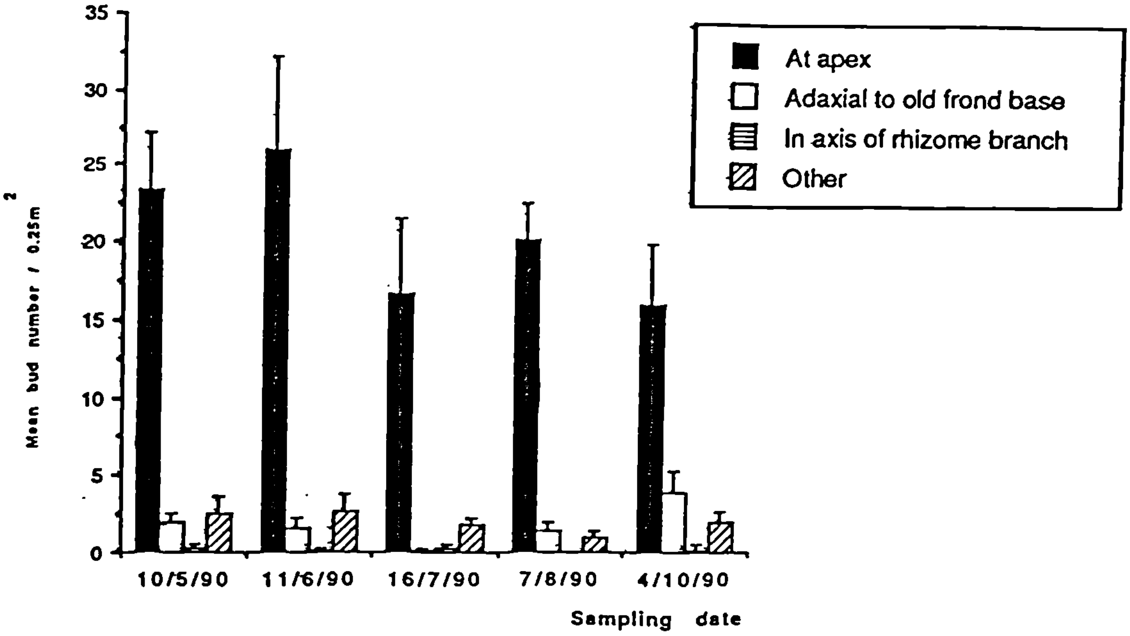


Fig. 25 Part 2. **Percentages of buds in an active state at the margin of bracken stands in 1991.** The letters A-E represent position in experimental field strip (see 3.1.4). The number of 0.25m^2 quadrats sampled is as follows: **GHH** n=12, **GTHR** n=7, **LLP** n=6 and **LLB** n=10. The slopes of the regression curves do not differ significantly from zero when t-tests are performed (**GHH** P=0.23, **GTHR** P=0.23, **LLP** P=0.13, **LLB** P=0.11).

a) Active rhizome buds



b) Dormant rhizome buds

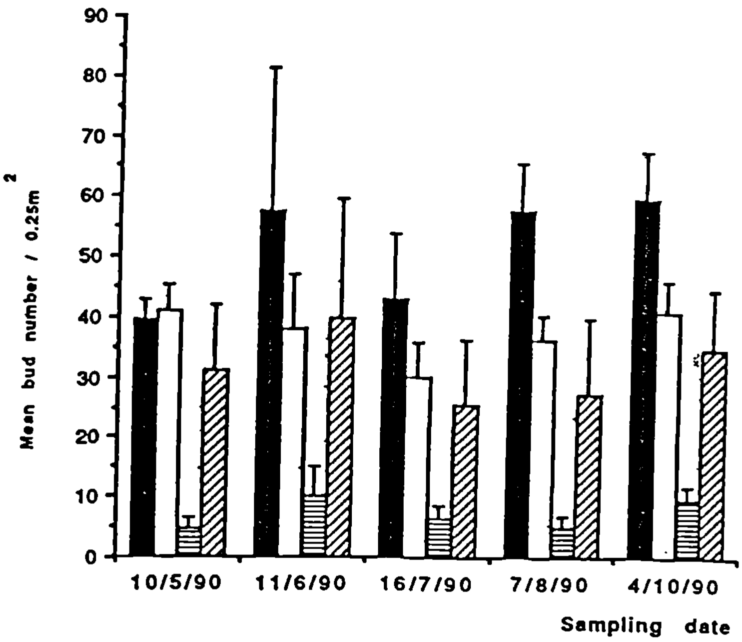


Fig. 26 The positions of a) active and b) dormant buds on the rhizome of bracken in a mature stand (LMS). Means for five 0.25m^2 sample quadrats are shown. Error bars are the standard error of the mean.

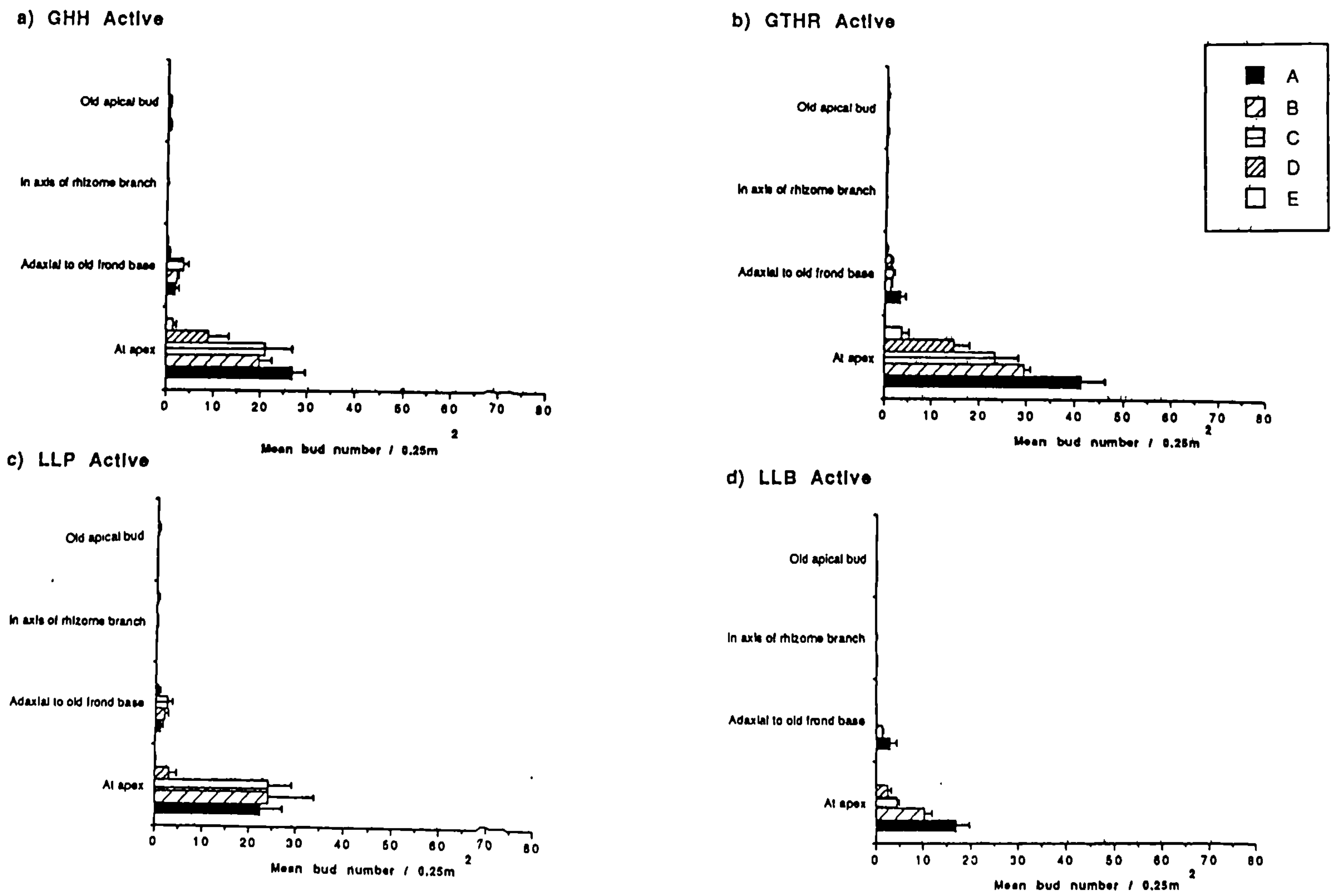


Fig. 27 a) The positions of active buds on the rhizome of bracken at its margins. The data are means for n $0.25m^2$ sample quadrats where n for each site are as follows: GHH n=12, GTHR n=7, LLP n=6 and LLB n=10. Error bars are the standard error of the mean.

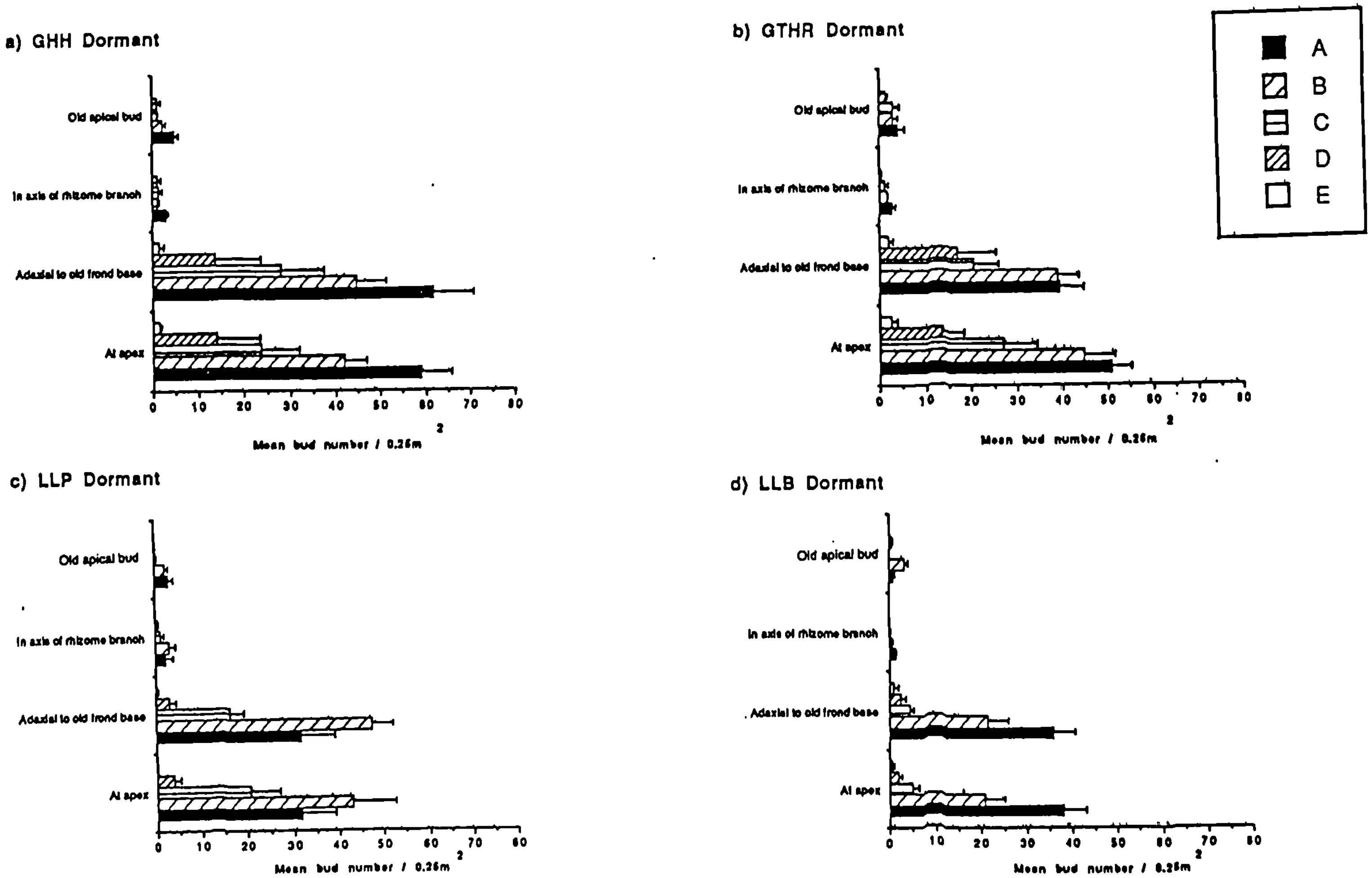


Fig. 27 b) The positions of dormant buds on the rhizome of bracken at its margins. The data are means for n $0.25m^2$ sample quadrats where n for each site are as follows: GHH n=12, GTHR n=7, LLP n=6 and LLB n=10. Error bars are the standard error of the mean.

4.4 DISCUSSION

A number of morphological characteristics which differ at the margin of a bracken stand from bracken further into the stand have been identified. These characteristics include the presence of greater number and height of fronds close to the interface with *Calluna* (i.e. in quadrat A) than are seen in the mature stand. Frond numbers on all of the sites investigated showed a great deal of variation between quadrats sampled at equivalent positions at the margin or within the bracken stand (fig. 13). Data based solely on counting frond numbers is therefore likely to give a poor estimate of the productive potential of bracken rhizome, especially as is the case in this study, when sampling plots are small. The emphasis in the following chapters has therefore been placed on the total activity of the rhizome including both frond and active rhizome bud production which has not been reported so often in the literature to date.

The presence of larger numbers of fronds close to the interface with *Calluna* gives rise to an increase in the number of penetration points available to foliar-applied herbicides. This provides potential for improved distribution of herbicide throughout the rhizome system of marginal bracken relative to bracken in the mature stand.

Shorter frond heights (fig. 18), together with shorter heights of first pinnae (fig. 19), are also observed close to the margins especially for outlying fronds. This difference in height does not seem to be explained solely by differences in depth of litter layers at the margin and in the mature stand. There is some evidence to suggest that frond height is pre-determined before or shortly after emergence since first pinnae heights closely reflect those of the mature frond and do not change greatly during the growing season after the time when the first pinnae unfurl. Frond height is also related to the diameter of the rhizome from which the frond emerges (Watt, 1940). Frond bearing rhizome at the margins are of smaller mean diameter and produce shorter fronds than the rhizome in the mature stand.

Fronds at the margins of bracken stands have also been shown to emerge earlier than those in the mature standard this difference seems to occur even in stands where litter layers in the mature stand are thin. Early emergence of the fronds at the stand margin increases their vulnerability to frost damage as is demonstrated in the data collected on sites GHH and GTHR in the 1991 season (fig. 13 d, e). This damage may be particularly severe at advancing margins where little protection is afforded to the developing croziers from litter. Following early frond emergence maximum frond heights are also reached earlier in the summer at the margins than in the mature stand indicating that fronds at the margin have reached maturity perhaps a few weeks before fronds in the mature stand (fig. 18). This difference would be of importance to the optimal timing of herbicide application if attempting to control bracken at the stand margins alone.

New fronds continue to emerge throughout the season (well into August) by which time those fronds which emerged first are beginning to become senescent (fig. 16). The average maturity of fronds at site **GTHR**, where the emergence of fronds was delayed by a late frost, (as defined by the number of pinnae unfurled) does not reach that at other sites which have not been affected by frost (fig. 17). Fronds at stand margins, particularly the advancing margin **LLT**, were also observed to be the first in the stands to become senescent in the late summer of 1990 when there was a period of drought (fig. 13c). It is perhaps most likely that this was due to the poor supply of water to outlying fronds but may be at least in part due to the age of these early emerging fronds. These observations suggest that fronds develop and senesce within a finite life-span at a rate which is largely independent of the stage of the growing season and will continue to emerge so long as temperatures are sufficient to allow them to do so. Bracken may well therefore respond to an increase in temperature resulting from increased global $C0_2$ levels by continuing to produce fronds through an extended growth season to replace fronds dying through "old-age". It is interesting to note that late emerging fronds do not usually develop from the same rhizome branch as the early emerging fronds which are becoming senescent, but from rhizome apices which have not yet produced a frond in the current growing season.

The size of rhizome reserves both in terms of mass (with rhizome mass being dominated by long shoot rhizome with its primary role in carbohydrate storage) and viable buds is undoubtedly one of the most impressive features of the bracken plant. Data collected from the mature bracken stand **LMS** shows a mean rhizome fresh weight throughout the summer of 1990 of 8.53Kg m^{-2}, more than 5 times the fresh weight of the fronds (1.30Kg m^{-2}). This, in combination with reserves of rhizome buds (with a mean number throughout the summer of 1990 for **LMS** of 625 m^{-2}) 85% of which are in a dormant, and therefore metabolically inactive, has frequently enabled bracken stands to recover from control attempts involving either herbicide treatments which kill active buds, or cutting treatments which are designed to drain the plant of carbohydrate reserves.

The amounts of dead rhizome present in the mature bracken stand are likely to have been vastly under-estimated because of difficulties in extracting decaying material from moorland soil. The presence of large amounts of dead rhizome would point towards some degree of cycling taking place within the rhizome as old rhizome is constantly being replaced with new shoots. Within the mature bracken stands it was possible to observe both the death and replacement of rhizome. This process appears to be occuring simultaneously in the same place with neither process dominant. It is unclear whether the regeneration of rhizome is occuring from the same plant or ramet as that which has degenerating rhizome. There is little evidence of a total return to grass or *Calluna*, as described by Watt (1976), within even small areas of land dominated by mature bracken and though some of the margins studied appear not to be encroaching into *Calluna* there was little evidence available, especially within the short time-span of the study, that they were receding.

Active buds present on the rhizome are found mostly at the rhizome apex (80% of all active buds on **LMS**) (fig. 26). However the terminal bud at the apex frequently remains dormant and many, around 50%, of all apices fail to produce a primordia which develops into a frond in any one season. Fronds are rarely produced on these rhizome shoots from buds in positions other than the apex. These dormant buds at shoot apices could possibly be stimulated into activity and growth following damage to the apex or a developing frond on a different rhizome shoot. Such a response might be mediated, for example, through damage to growing fronds weakening the strength of existing nutrient sinks and allowing previously inactive buds to compete more successfully for nutrients and begin growth.

The morphology of bracken rhizome also shows differences between the mature stand and the stand margins with, for example, the relative proportions of each shoot type of rhizome changing as the margin is approached (fig. 23). These proportions have been calculated on the basis fresh weight of rhizome of each shoot type which is perhaps biased towards the bulky long shoots and under-estimate the lengths of transitional and short type rhizome shoots. Perhaps the most interesting data relating to the morphology of rhizome at the stand margins was that relating to the increased proportions of rhizome buds which are active at the plant's edges relative to its centre. This proportion increases further at the margins on outlying rhizome as distance from the stand increases (fig. 25 Part 2). As the proportion of buds which are dormant and relatively unsusceptible to herbicides decreases then the chances of a successful control treatment are improved. Control attempts on rhizome at the stand margins may therefore have an improved probability of success over attempts in the mature stand.

Differences between margins and the mature plant are often most pronounced where the margin is advancing rapidly. Sites **LLB** and **LLP**, where the margins are encroaching only very slowly if at all, often show characteristics, for example frond number and height (figs. 13 and 18) and rhizome weights (figs. 20a, 22 Part 1) which are intermediate between those of a mature stand and a rapidly advancing front. More rapidly advancing margins are also identified by the rate at which frond numbers and rhizome fresh weights decline at the stand edge, both of these characteristics decreasing more sharply at a slowly advancing margin than at a rapidly advancing margin. The manner in which timing of frond emergence varies between sites seems to depend primarily upon degree of exposure of the site but may also be influenced by the rate at which the margin is advancing.

5. RESOURCE ACQUISITION BY THE STAND MARGIN

5.1 INTRODUCTION

The supply of carbohydrate and mineral nutrients to outlying fronds and pioneering rhizome at the margins of the bracken plant has been investigated. In doing this it was hoped that the extent to which bracken at the margins of the plant is dependent upon the rest of the plant for resources might be determined. Information relating to the extent of dependence of pioneering rhizome on the stand is of importance in the context of bracken control since it is pertinent to the question of the optimal size of swathe to be sprayed with herbicides by tractor or cut when attempting to control bracken at its stand perimeter, and to the size of resources available to these treated areas for subsequent recovery.

Bracken at the margins could gather the resources of water, mineral nutrients and carbohydrates required for growth in two ways. Firstly locally, at the margins from root or foliar uptake minerals and water and photosynthesis of outlying fronds. Secondly via translocation of resources through the rhizome from more mature parts of the plant. Outlying rhizome itself is capable of absorbing minerals and water (Tyson and Sheffield *pers comm.*) and does have thin roots. It would therefore seem likely that pioneering rhizome is at least partially self-sufficient in supplying its water and mineral requirements. At first glance however it seems improbable that the few fronds presence on outlying rhizome are able to meet the photosynthetic requirements of the rhizome to grow and produce further fronds and therefore likely that translocation of carbohydrates from further back into the stand is taking place.

In an initial experiment all transport of water and nutrients between marginal fronds and the remainder of the stand was simply destroyed by the digging of a shallow trench which severed all rhizome connections. The effects on isolated outlying fronds were measured following this treatment. In later experiments, radiotracers (^{32}P-labelled orthophosphate and ^{14}C-labelled sucrose) were fed to bracken rhizomes and the extent to which they were transported both towards and away from the rhizome apices observed. The relative concentrations of both nitrogen and phosphate present in outlying fronds and fronds further into the stand have also been determined at a number of margins. This analysis provides information as to whether the growth of bracken at the margins could be limited by supply of nutrients from the remainder of the plant.

5.2 THE EFFECTS OF ISOLATION ON THE GROWTH OF OUTLYING FRONDS

5.2.1 Methods

The transport of nutrients and water towards and away from the margins of 3 separate advancing bracken stands on Lowna Lund (see fig. 11, p58) were prevented by the digging of trenches (of approximately 20cm in depth and 10cm in width) which severed all rhizome connections. The trenches ran parallel to the interface for a distance of 2m. In the first part of the experiment carried out at sites T1, T2 and T3 the trenches were dug on 10 March at 3 distances into the bracken stand as shown in fig. 28. and described overleaf:

a) along the interface between bracken and *Calluna* dominated vegetation (0 m)
b) along a line 0.3 m further into the bracken stand than the interface between bracken and *Calluna* dominated vegetation (0.3m)
c) along a line 1.0m further into the bracken stand than the interface between bracken and *Calluna* dominated vegetation (1.0m).

In addition, control plots again of 2m in length were used in which no trench was dug. Lateral transport of resources through rhizome entering from the sides of experimental plots was prevented where the trenches were dug 0.3m or 1.0m into the stand by continuing to dig perpendicular from the trench to a point beyond the edge of the bracken stand (see fig. 28). Treatments a) (Om) and c) (1.0m) were replicated 3 times at site T3. Treatment b) (0.3m) and the no trench control plots were included in the second part of the experiment described below and therefore replicated twice at T1 and twice at T2.

In the second part of the experiment carried out on sites T1 and T2 a random block design with 2 replicate blocks at each site was used with each block incorporating 4 treatments with trenches dug as before:

a) control plot with no trench
b) a trench dug on 10 March, 1992 0.3m into the bracken stand
c) a trench dug on 12 April, 1992 0.3m into the bracken stand
d) a trench dug on 10 May, 1992 0.3m into the bracken stand

For both parts of the experiment the height and number of fronds present in a strip beginning at the interface between bracken and *Calluna* (Om) and extending outwards away from the bracken stand were recorded twice during the summer on

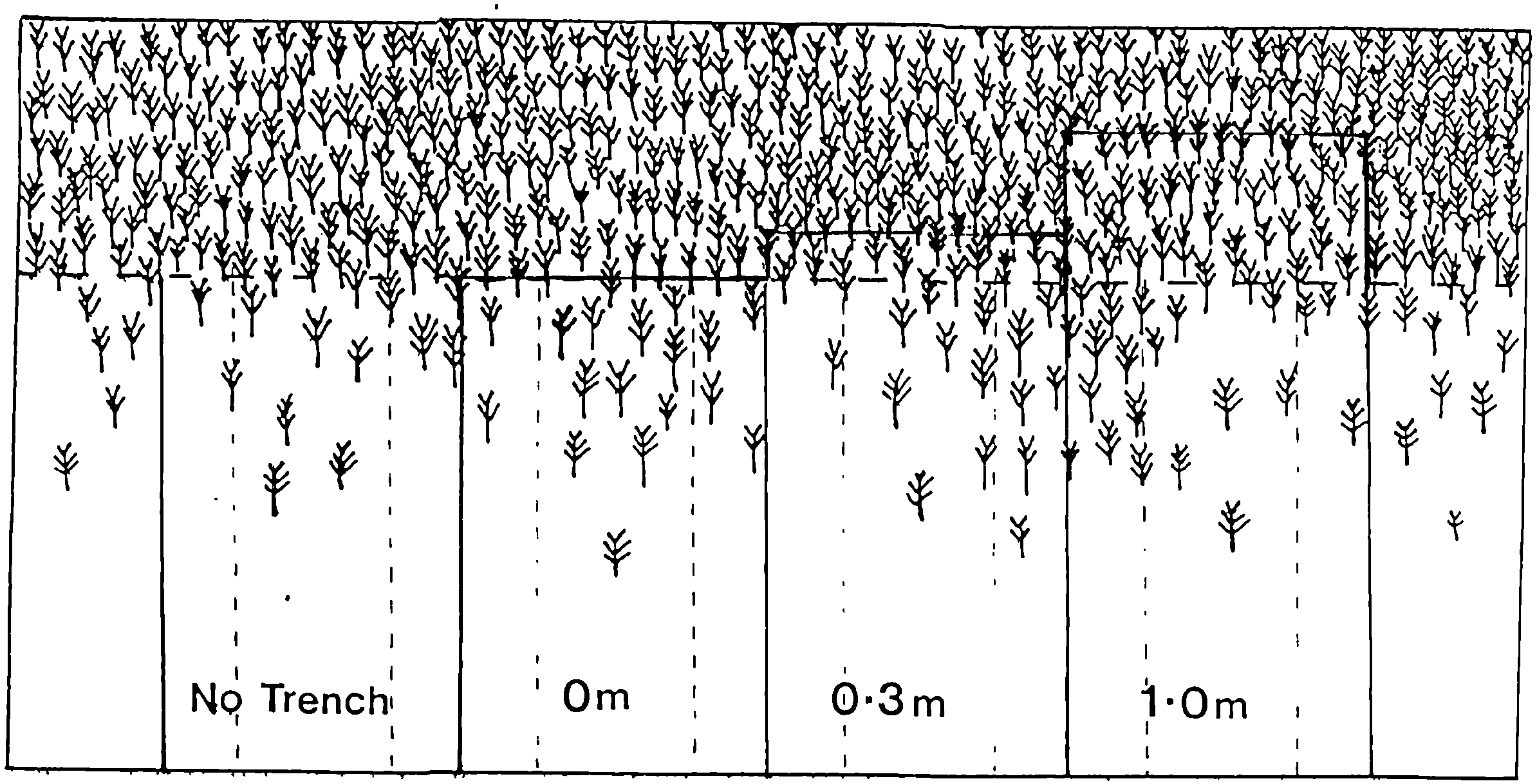


Fig. 28 Diagram of an experimental block used in the investigation of the effects of isolation on the growth of outlying fronds (Part 1). The interface at which bracken ceases to be the dominant vegetation is marked by the horizontal broken line. Vertical broken lines show the positions of strips from which data were collected. The line marked in red shows the position of trenches.

20 June and 23 July. These strips were made up of 1m^2 quadrats in the middle 1m of each 2m experimental plot (see fig. 28).

5.2.2 Results

The digging of trenches isolating outlying rhizome at the margins of a bracken stand does not appear to greatly impair the ability of the outlying rhizome to produce fronds or to stunt the growth of these fronds. In the first part of the experiment involving the digging of trenches at different distances into the bracken stand from the bracken-*Calluna* margin the site at which the trenches were dug proved highly significant in determining the height and number of fronds produced. It is therefore impossible to make valid comparisons between treatments carried out at T3 (trenches at 0m and 1.0m) and those carried out at T1 and T2 (no trench and trench at 0.3m). However when comparing the treatments within a site there is no evidence to suggest that frond production or heights are any greater where 1m of rhizome remains attached to, and able to transport nutrients and water to, outlying rhizome relative to those plots where the trench was dug along the interface leaving outlying fronds totally isolated from the area in which bracken is the dominant vegetation. Similarly frond numbers and heights where a trench was dug 0.3m from the interface in the stand show no significant decline over those in plots where no trench was dug (fig. 30).

There is a slight decrease in the frond height relative to those of other treatments in those plots where trenches were dug early in the spring in March or April (fig. 29) but this is statistically insignificant in t-tests. It is possible that the nutritional and / or water requirements for the seasons growth have already been transported from the mature stand prior to the time at which the trenches were dug. However, in the light of the observation that bracken at the outermost margins is rapidly susceptible to drought late in the season this does not seem to be a probable explanation (fig. 31). The data suggest that *the rhizome outlying in the* outermost 2-3 metres of a bracken stand are largely independent of the remainder of the stand for provision of nutrients, both mineral and carbohydrate, and of water.

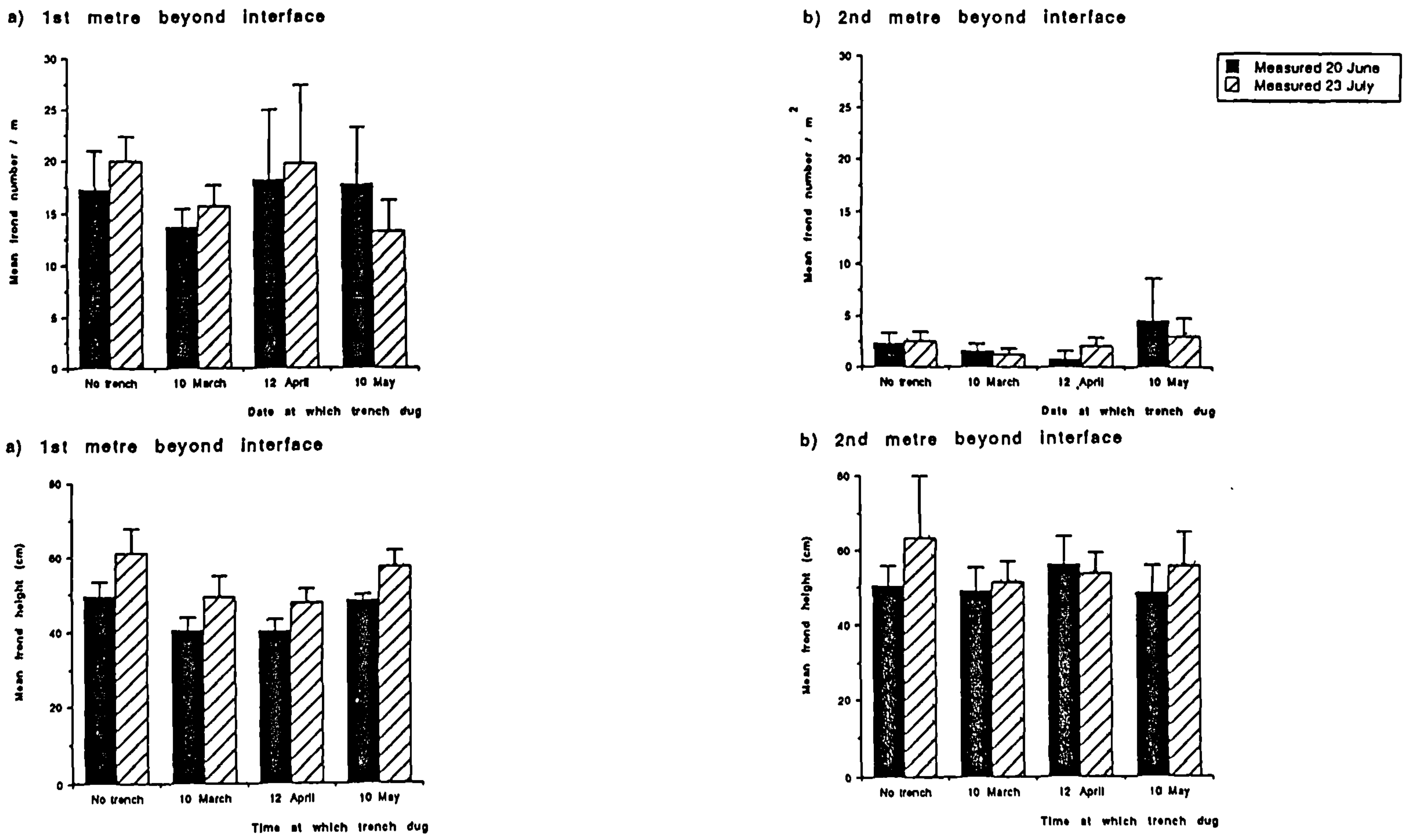


Fig. 29 The effect of the isolation of outlying rhizome at the margin of a bracken stand on frond height and number (Part 1). Trenches were dug at different distances into the bracken stand on 10.3.92. Data were collected on two dates 20.6.92 and 23.7.92. Error bars are the standard error of the mean.

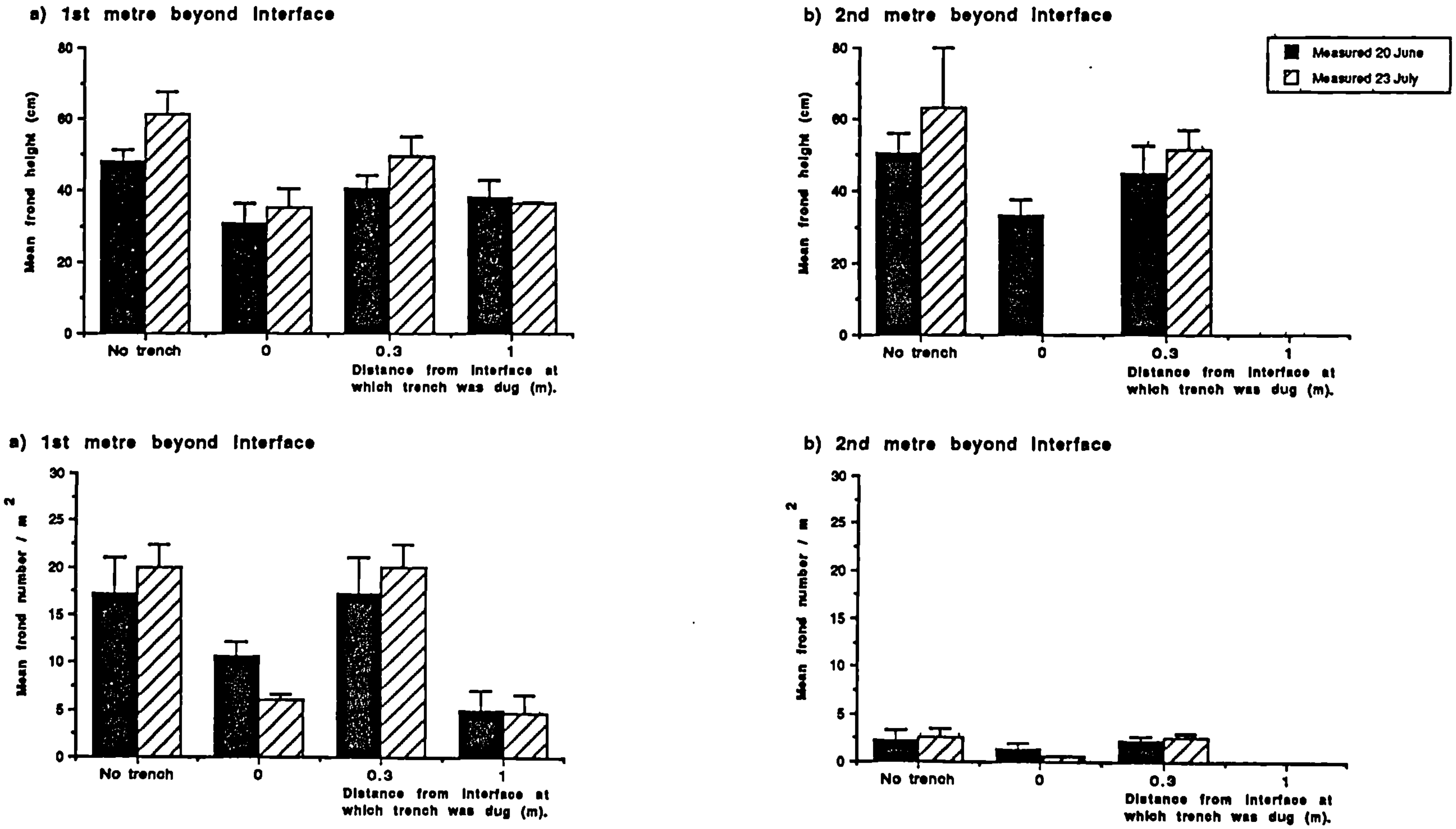


Fig. 30 **The effect of the isolation of outlying rhizome at the margin of a bracken stand on frond height and number (Part 2).** Trenches were dug at different times prior to frond emergence. Data were collected on two dates 20.6.92 and 23.7.92. Error bars are the standard error of the mean.

Fig. 31 Senescence of outlying fronds under drought conditions in late summer at Lowna Lund. (15.8.91).

5.3 ANALYSIS OF THE PHOSPHATE AND TOTAL NITROGEN CONTENT OF FRONDS AND RHIZOME AT THE MARGINS OF A BRACKEN STAND

5.3.1 Introduction

In order to estimate the ability of the outermost edges of the bracken plant to obtain sufficient nutrients to support themselves, either by uptake by outlying rhizome and roots themselves or through transport from further back in the stand, information was collected on the concentrations of nutrients present in outlying fronds for comparison with fronds closer to the main stand at different occasions throughout the growing season.

5.3.2 Methods

5.3.2a Collection and storage of plant material

Both frond and rhizome samples were collected for nutrient analysis from all the experimental sites used at 3 occasions during the 1991 growing season (20th May, 21 June and 26 July). Frond samples were taken from the uppermost 2 pinnae and included both material from the mid-rib of the pinnae and pinnule tissue. Two frond samples were taken at each sampling site one from the outermost fronds at the margin (henceforth referred to as outlying fronds) and a second from a point 1-2m further into the bracken stand than the bracken-*Calluna* interface (a position equivalent quadrat A on the experimental strips see 3.4.1) (henceforth referred to as stand edge fronds). Rhizome samples included rhizome of all living types. These were again collected from a point 1-2m further into the bracken stand than the bracken-*Calluna* interface.

After soil had been removed from the rhizome samples by washing, all the plant material was oven dried for 48 hours at 70-80°C before crushing into small pieces of less than 0.5cm^2 in size. The material was then stored for several months until the analyses took place. Before weighing sub-samples for analysis the material was once again heated to 70°C for 24 hours and allowed to cool in a desiccator.

Table 4 The number of samples each of frond and rhizome material used for nutrient content analysis. Figures represent number of samples taken on 3 separate occasions.

Site	No. samples for total nitrogen analysis	No. samples for phosphate analysis
LMS	3	3
GMS	4	4
LLB	3	3
LLP	3	8
LLT	0	3
GHH	3	7
GTHR	3	3

5.3.2b Analysis of plant total nitrogen

The method used for the analysis of plant total nitrogen was basically that of Bremner (1965) but used a modified indicator solution.

1. Approximately 1g of finely cut plant material (weighed to 4 decimal places) was placed together with 2 copper Kjeldahl tablets, 6 glass beads and 20ml conc. H_2SO_4 A.R. in a 100ml Kjeldahl flask. Blanks containing no plant material were set up in the same way.
2. The flasks were heated gently until frothing ceased and then more strongly until the solution cleared and became pale green in colour (a period of around 6 hours).
3. After cooling, 50ml water was added to each flask and after further cooling the solution filtered through Whatman No. 43 filter paper. Solutions were then made up to 100ml and stored in a refrigerator until nitrogen determination took place.
4. In order to distil off ammonia from the solutions, a 5ml aliquot was placed in the inner chamber of a Markham still, together with 6ml NaOH solution (50%m/v). Steam was passed until 30ml of the distilate was collected in a flask containing 10ml of boric acid indicator. This indicator comprises 5g H_3BO_3A.R. crystals dissolved in warm water, 45ml methyl red solution (0.02% methyl red in 60% ethanol) and 15ml bromocresol green solution (0.1% bromocresol green in 60% ethanol). Approximately 50ml of tap water was added to this mixture before making up to 2000ml.

5. The contents of the flask were titrated against M/100 HCl until a permanent pink end-point was reached. Total nitrogen concentration ($\mu g\ g^{-1}$) is then equal to:

$$\frac{\text{Titre (corrected for blank) ml} \times 140 \times \text{Dilution factor of 20}}{\text{weight of plant material (g)}}$$

5.3.2c Analysis of plant phosphate concentration

Phosphate was analysed by a method adapted from that described by Cresser and Parsons (1979). Plant material was digested in a perchloric-sulphuric acid mixture and phosphate content determined by spectrophoretic assay of the molybdenum blue reaction.

1. Samples of 0.05g-0.2g plant material, a distilled water blank and a series of 4 phosphate blanks made up of sodium dihydrogen orthophosphate ($NaH_2PO_4.2H_2O$ A.R.) at dilutions of $10\mu gl^{-1}$, $30\mu gl^{-1}$, $100\mu gl^{-1}$ and $300\mu gl^{-1}$ were each placed in a phosphate-free flask.
2. 7ml of triple acid reagent comprising a 10:1:1 mixture of nitric : suphuric : percloric acids was added to the flasks and left to digest for a period of approximately 12 hours. This mixture was then heated until the nitric and percloric acids had boiled off. Only the sulphuric acid remained, refluxing in the flasks as oily droplets. At this point the flasks were removed from the heat and cooled.
3. After cooling 20ml water was added to each of the flasks and a 200µl aliquot of the resulting solution diluted in 3800µl water and 1000µl phosphate reagent. This reagent comprises 50ml 2.5M H_2SO_4 15ml ammonium molybdate solution (4% w/v), 5ml potassium antimony tartrate solution ($8x10^{-3}$ M) and, added last, 30ml ascorbic acid solution ($4x10^{-2}$ M).
4. After standing for 10 minutes a blue colour developed which was assayed on a Beckman DU-5 spectrophotometer referenced against the phosphate blanks.

5.3.3 Results

5.3.3a Total nitrogen concentration

Analysis of total nitrogen concentration gave results, shown in fig. 32, of between 9.5-34.7 mgN g^{-1} in frond material and 5.62 - 22.14 mgN g^{-1} in the rhizome. Nitrogen concentration did not change in the same way at all of the sites observed but without exception total nitrogen concentrations are considerably higher in frond tissue than in rhizome tissue. With the exception of site **LLP** (fig. 32d) frond total nitrogen concentration in both outlying and stand edge fronds are high in croziers and young fronds at the end of May and rise further as the fronds mature throughout June. As growth slows and full frond maturity is reached towards the end of July the total nitrogen concentration falls sharply. The concentration of total nitrogen in outlying fronds is slightly lower than that in fronds at the stand edge but change throughout the season in a similar manner. The difference in outlying and stand edge concentrations of total nitrogen are greatest at site **LLP** where the margin is advancing only very slowly.

The concentration of total nitrogen in the rhizome did not change to any great extent throughout the growing season showing only a slight decline as the fronds are developing at most sites. However at **GMS** (fig. 32b) there is even an increase in rhizome total nitrogen concentration in the early summer. Other than at **GMS** there is little evidence that any replenishment in the amount of total nitrogen present in the rhizome has occurred before the end of July.

5.3.3b Phosphate concentration

The concentration of phosphate present in bracken fronds, shown in fig. 33, was found to vary between 5.04 -1.42 mgP g^{-1}. Once again phosphate concentrations were found to be lower in the rhizome than those in the fronds varying from a maximum of 2.67 mgP g^{-1} to 0.36 mgP g^{-1}. Phosphate concentrations do not vary greatly between the sites observed and, as for total nitrogen concentration, differences between sites which do occur do not correspond to differences in the rate at which the front is advancing at each of the sites from which plant material was sampled. Concentrations of phosphate in frond tissue are again high in newly emerged croziers and young fronds and, like total nitrogen concentrations usually rise slightly throughout June before beginning to decline in July. Concentrations of phosphate in fronds at the stand edge are consistently higher than those found in

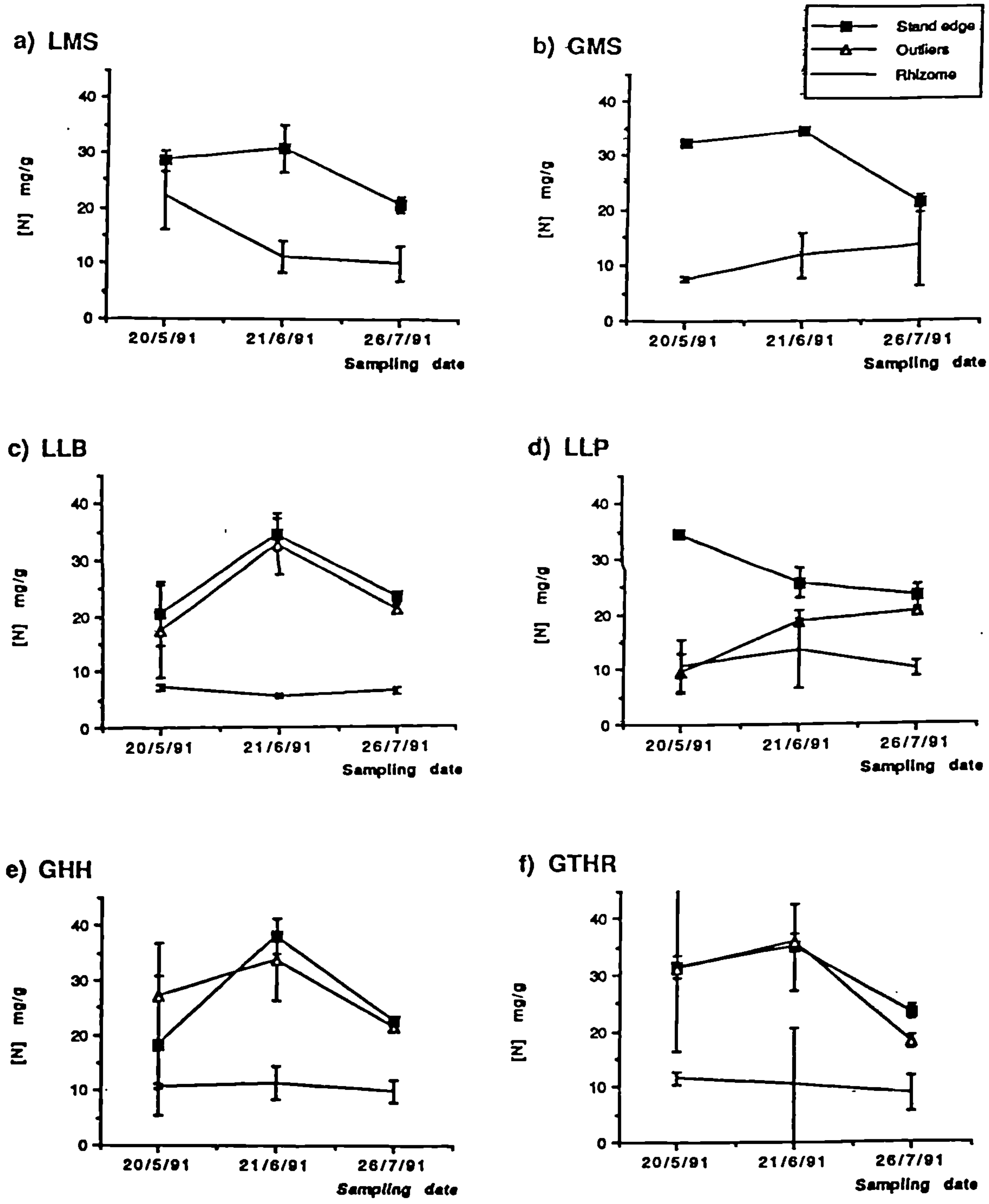


Fig. 32 **The total nitrogen concentrations present in samples of bracken frond and rhizome tissue throughout the 1991 growing season.** Outlying fronds are those outermost at the margin whilst stand edge fronds were taken from a position equivalent to quadrat A in experimental strips. Error bars are the standard error of the mean.

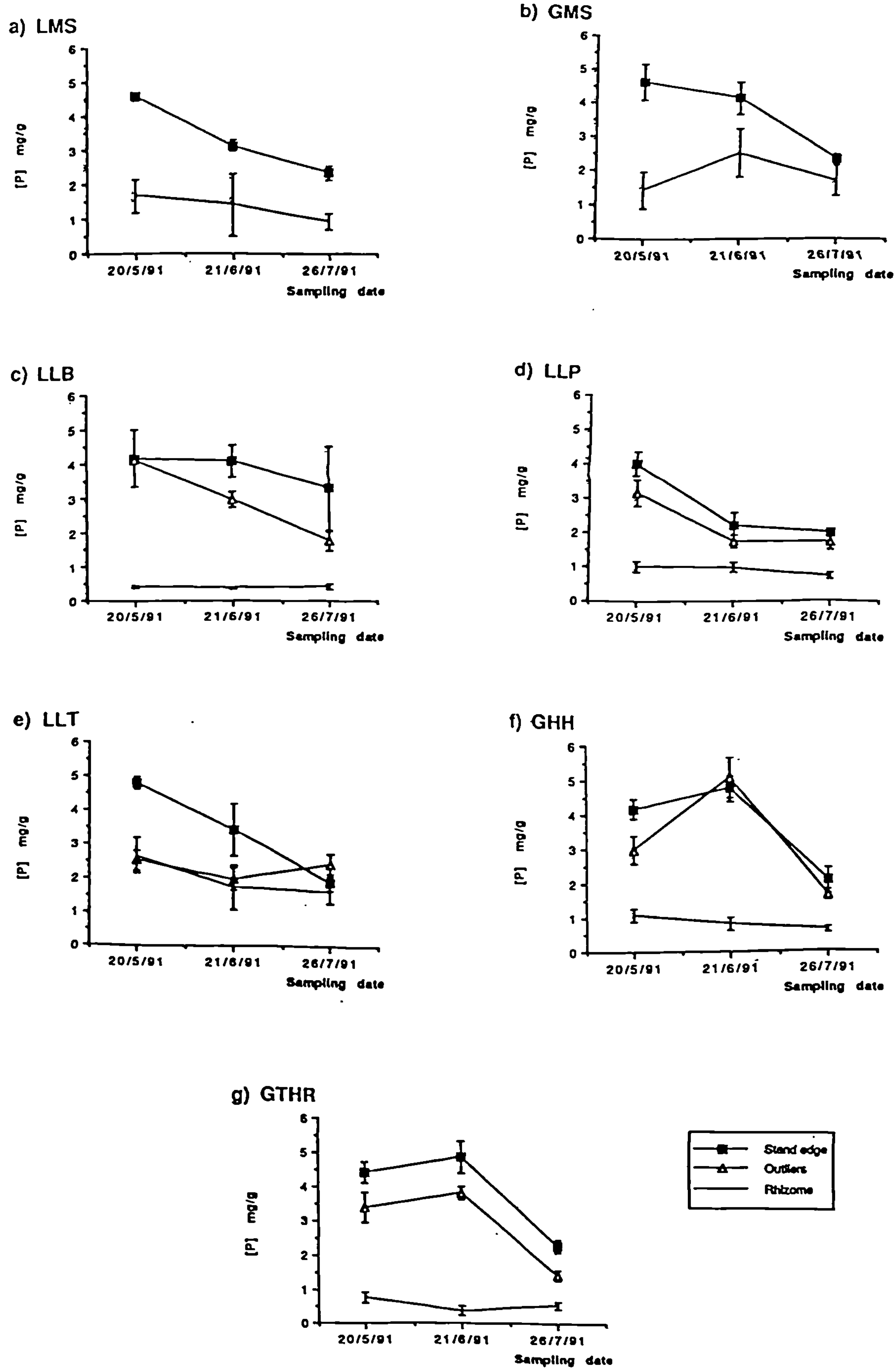


Fig. 33 The phosphate concentrations present in samples of bracken frond and rhizome tissue throughout the 1991 growing season. Outlying fronds are those outermost at the margin whilst stand edge fronds were taken from a position equivalent to quadrat A in experimental strips. Error bars are the standard error of the mean.

outlying fronds even at sites where the margins are not thought to be advancing rapidly.

Rhizome phosphate concentrations are lower than those found in frond material and do not change significantly as fronds emergence and develop through the early summer. Only on site GTHR (fig. 33g) is there any evidence of any recovery in rhizome phosphate concentrations before late July though a later rhizome sample collected on 10 September 1991 on some of the sites does provide evidence that such a recovery has taken place by the end of the summer.

5.3.4 Discussion

The concentrations of nutrients observed in samples taken from sites throughout the North York Moors show patterns similar to those recorded by previous workers. The increase in total nitrogen concentration as fronds mature was also reported by Hunter (1953) to take place during the first 80 days post-emergence before declining as the fronds age further. The absolute total nitrogen and phosphate concentrations (shown in fig. 32 and 33) are similar to those previously reported.

Concentrations of total nitrogen and phosphate within the rhizome both diminish slightly as the fronds develop and there is little evidence that either begin to recover before late July. However the large bulk of rhizome available from which nutrients can be drawn during the development of fronds mean that fluctuations in rhizome concentrations of total nitrogen and phosphate are not great. Concentrations of phosphate in the rhizome do seem to recover in September and there is some evidence that seasonal cycling of nutrients is occuring within the bracken plant. The possibility remains however, that nutrients are being released into the soil when fronds senesce and taken up by the roots and rhizome each spring.

Hendrick (1921) observed variations in total nitrogen concentration occuring between the sites he sampled which were not easily explained, the only apparent differences between the sites being exposure levels. Between site variations in total nitrogen and phosphate levels in these analyses were not large and could easily be explained by differences in soil nutrient concentrations. Hendrick (1921) also supports the idea the bracken total nitrogen concentration is influenced by total nitrogen concentration in the soil and can be increased by the use of fertilisers. This is of relevance to the next chapter in this study because it suggests that there may be scope for the use of fertiliser treatments in influencing the control of rhizome bud dormancy. However, it is variation in nutrient concentrations between stand edge and outlying fronds that are of greatest interest within the context of this chapter.

Phosphate concentrations and on some sites total nitrogen concentrations, in outlying fronds were observed to be lower than those occuring in fronds at the stand edge. This result suggests that neither nutrient uptake by roots and rhizome at the margin (possibly hampered by competition from *Calluna*) nor transport of minerals from the mature stand are sufficient to maintain nutrient levels in outlying fronds at a similar level to those further into the stand. The supply of nutrients to growing points at the apices of pioneering rhizome shoots is a likely limiting factor in the expansion of a bracken margin.

5.4 THE MOVEMENT OF RADIOLABELLED NUTRIENTS THROUGH BRACKEN RHIZOME

5.4.1 Methods

Radiotracer experiments were carried out on isolated rhizome segments in boxes (see 3.1.1, p51 and fig. 6, p52) and at a secure site on the university campus using the model advancing bracken front described in 3.1.3 (p53) and shown in fig. 8 (p55). In these systems the loose peat in which the rhizome is growing allows the excavation of the rhizome, the feeding of radiotracers via the root or injection into the rhizome, and its subsequent reburial without damage to the rhizome itself (though some roots are detached). After a period, during which the tracers are transported along the rhizome, the rhizome can be dug up again and the extent to which the tracers have been transported measured. It was possible to remove intact pieces of rhizome of up to 2m in length from the peat beds.

A similar experiment to follow the movement of ^{32}P-labelled orthophosphate was attempted in the field at Spaunton Knowl (see section 3.2.4) but the removal of intact pieces of rhizome of more than 20-30cm in length from compacted moorland soil in the presence of dense *Calluna* roots proved extremely difficult. It was therefore impossible to excavate rhizome before feeding of the tracer took place without causing substantial damage. The tracer was therefore injected into the soil rather than fed to the roots or injected directly into the rhizome tissue.

In all tracer experiments, the radiolabelled nutrients were fed at points along the rhizome both close to the apex and close to more mature rhizome in an attempt to discover the extent to which and direction in which transport was occuring.

5.4.1a ^{32}P-Orthophosphate

A number of intact roots attached to rhizome segments of approximately 20cm in length were introduced into a vial containing 3-4ml of a solution of ^{32}P - orthophosphate in a pH 7 buffer (containing 0.3 kBq ml^{-1}). The vial was then sealed with parafilm and placed together with the rhizome segments in boxes containing Irish Moss Peat. After a period of 7 days the rhizome was removed, cleaned and 0.5mm thick sections of the rhizome cut. These sections were then placed in scintillant fluid and counted for radioactive emisions on a 1212 Minibeta liquid scintillation counter (LKB Wallac).

The same process was repeated for larger rhizome pieces grown in peat beds. In experiments in the field at Spaunton Knowl access to attached and intact roots proved impossible and 25ml of the ^{32}P-orthophosphate solution was instead injected into small holes along a 15cm line perpendicular to the path of a rhizome branch which was extending out of an advancing bracken margin. This treatment took place on 6 August, 1991, the rhizome was excavated after a period of 10 days and treated in the same way as that described above.

A total of 22 rhizome shoots were fed ^{32}P-orthophosphate solution (8 in boxes, 8 in peat beds and 6 in the field).

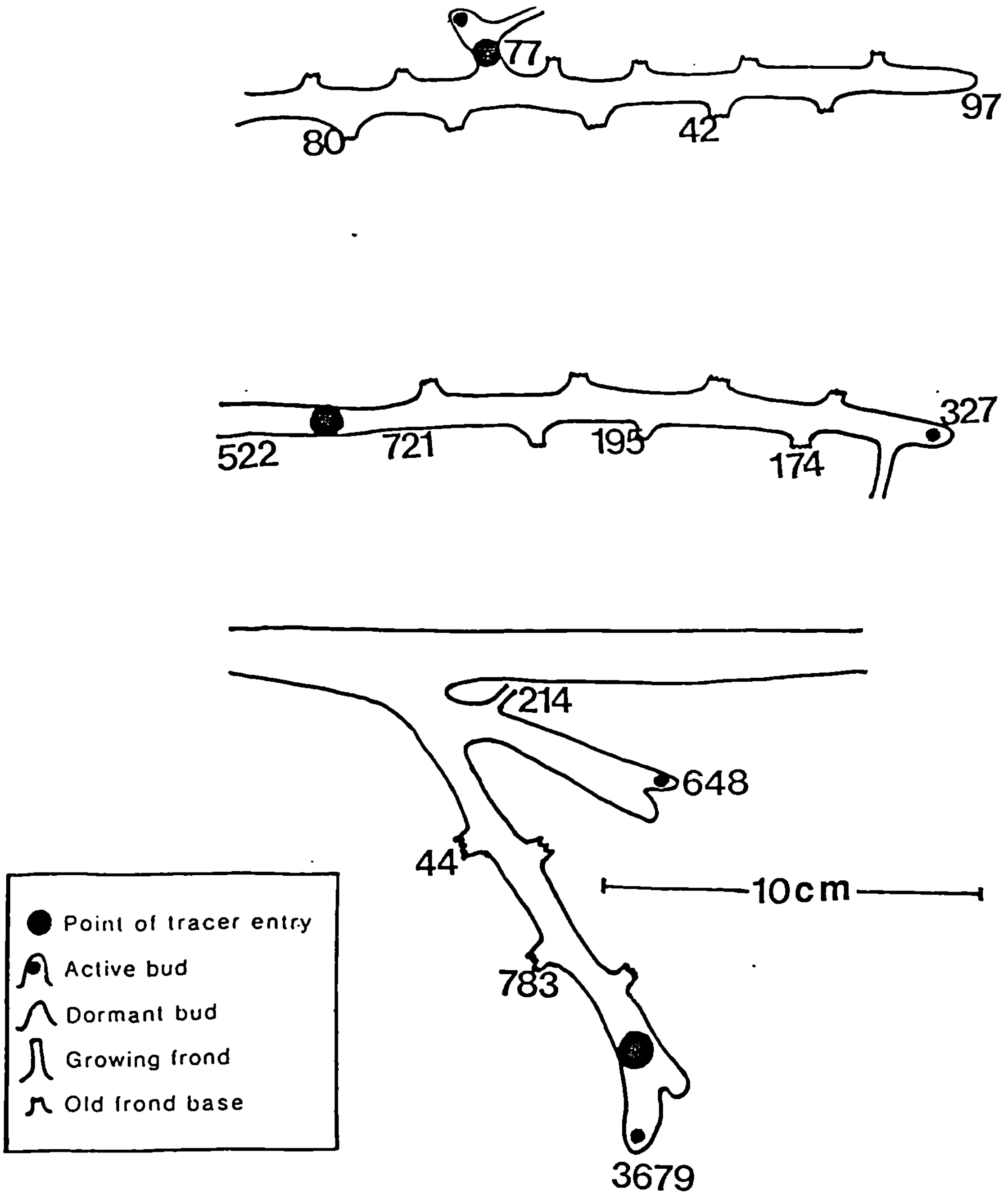
5.4.1b ^{14}C-Sucrose

The movement of ^{14}C-sucrose through bracken rhizome was observed both in isolated rhizome segments and in the model advancing margin in peat beds in much the same way as ^{32}P-orthophosphate. Each of 20 rhizome segments (10 isolated segments in boxes and 10 in the peat beds) was injected with 0.05ml of a solution of ^{14}C-sucrose containing 10kBq ml^{-1} [NEC-100X Sucrose, ^{14}C (U) - NEN®]. After a period of 7 days the rhizome was collected and the movement of the radiotracer observed in the same way as described for ^{32}P-orthophosphate above.

5.4.2 Results and discussion

The results of the scintilation counts are presented simply as counts per minute per gram of rhizome (after correction for background). It would be inappropriate to present the data in any other form since the rhizome tissue counted was contaminated by soil and other impurities causing the efficiency of counting to be variable (though usually better than 80%).

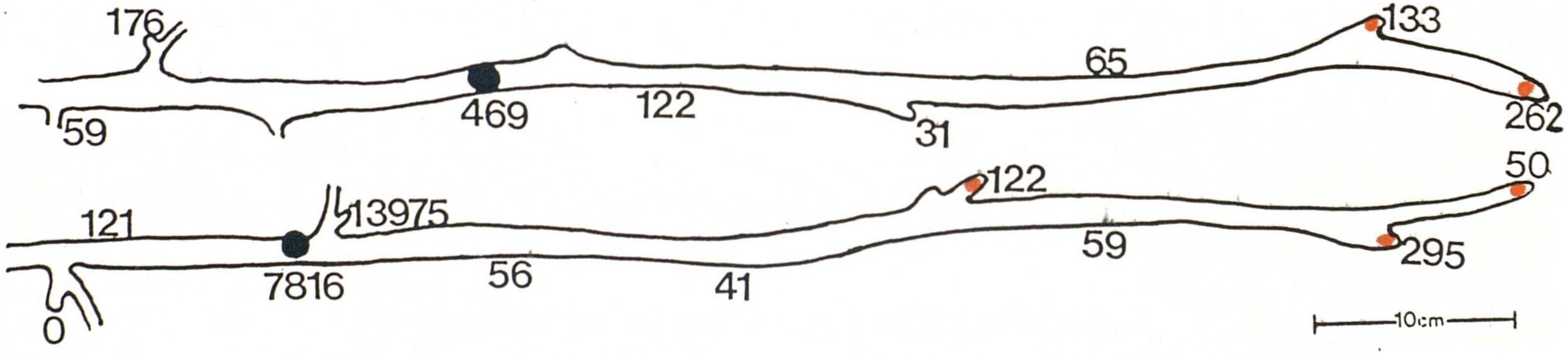
^{32}P-orthophosphate is successfully taken up into bracken rhizome as a result of root feeding in both bracken grown in peat in boxes and in the model advancing front. The radiotracer was also taken up into the rhizome when injected into moorland soil although difficulties in estimating the precise location of the rhizome before these injections took place, and problems in removing intact lengths of rhizome from such soil, meant that it was inefficient to attempt to collect data of this kind under field conditions. ^{14}C-sucrose was also successfully taken up by and transported through the rhizome following its injection directly into rhizome tissue.



a) Isolated rhizome segments

Fig. 34 The typical movement of ^{32}P-orthophosphate through the rhizome of bracken for a) isolated rhizome segments b) rhizome in the model advancing margin (peat beds) and c) bracken at an advancing margin in the field. Figures represent CPM g^{-1} of rhizome tissue.

b) Model advancing margin



c) Advancing margin in the field

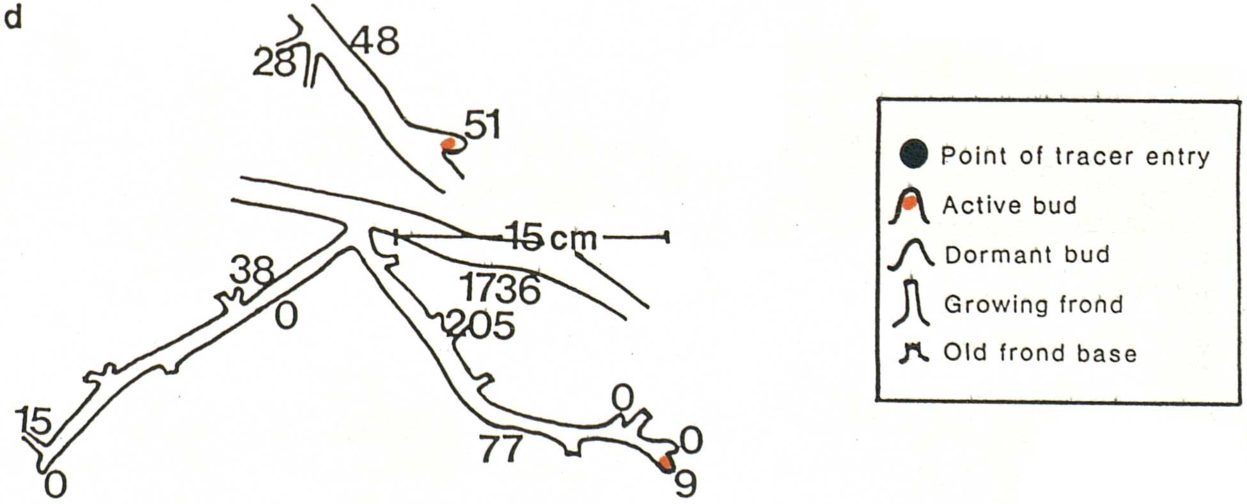
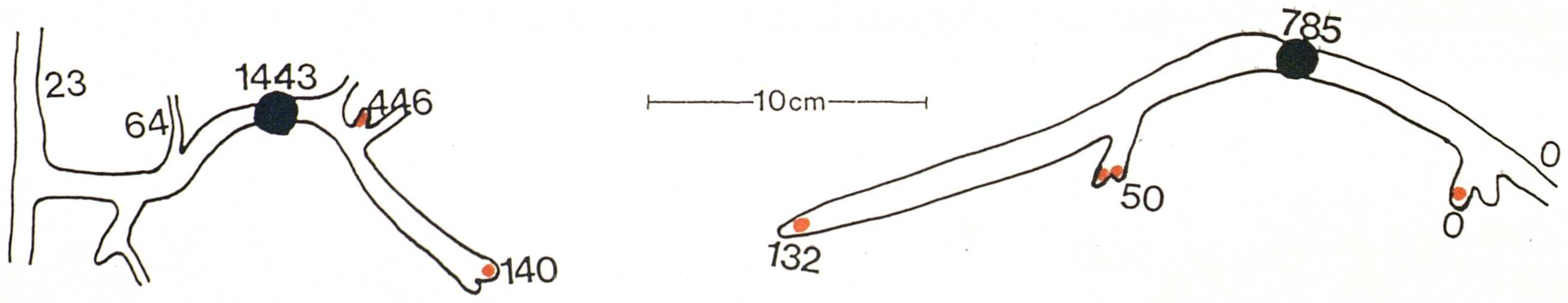


Fig. 34 The typical movement of ^{32}P-orthophosphate through the rhizome of bracken continued. Figures represent CPM g^{-1} of rhizome tissue.

a) Isolated rhizome segments



b) Model advancing margin

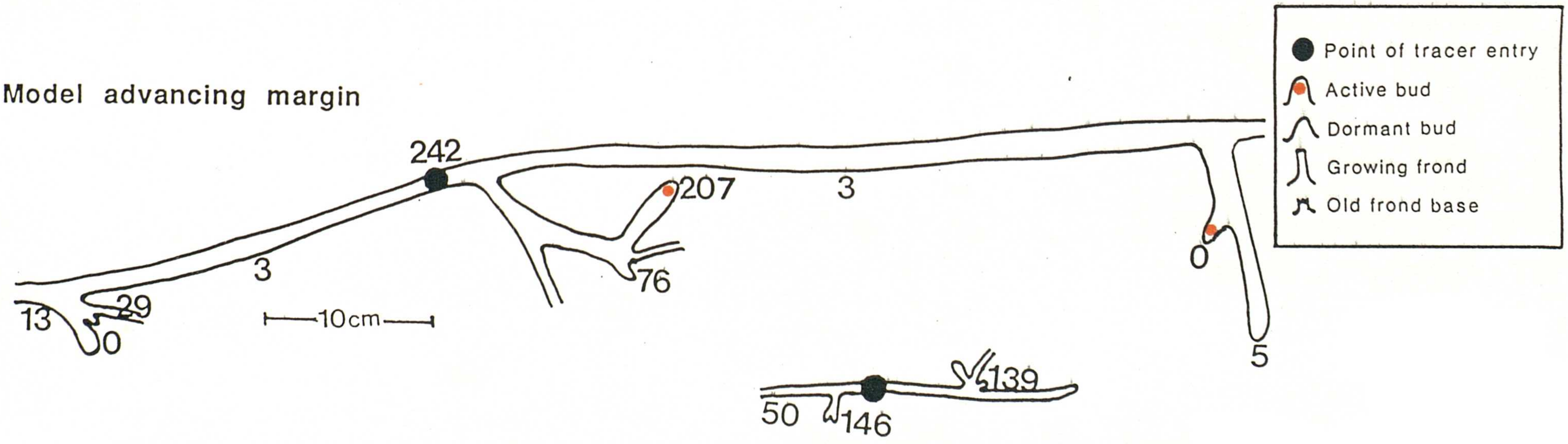


Fig. 35 The typical movement of ^{14}C-sucrose through the rhizome of bracken for a) isolated rhizome segments and b) rhizome in the model advancing margin (peat beds). Figures represent CPM g^{-1} of rhizome tissue.

Neither ^{32}P-orthophosphate nor ^{14}C-sucrose travelled through the rhizome for distances of more than 1m during the course of this experiment. ^{32}P - orthophosphate proved to be the more mobile of the 2 radiotracers with ^{14}C - sucrose being observed to travel no more than 30-40 cm through the rhizome (fig. 34 and 35). Both ^{32}P-orthophosphate and ^{14}C-sucrose were transported in directions both towards and away from the outermost margins of bracken rhizome in the model advancing front and in this system, as well as in boxes and in the field travelled towards metabolic sinks, usually active buds, where the radiolabelled nutrients accumulated. Radioactivity also accumulated around growing fronds and to a lesser extent dormant rhizome buds.

Roots present on marginal rhizome shoots were shown to be capable of the uptake of significant quantities of mineral nutrients and may be responsible as the largest source of mineral nutrients for outlying rhizome at the margin. Additionally trench experiments have provided little evidence for the large-scale provision of carbohydrate nutrition in the form of photosynthates from mature fronds growing away from the outermost margins. Again outlying bracken seems to be largely independent of the remainder of the stand for carbohydrate nutrients and outlying fronds must be responsible for the carbon-fixation which allows rhizome at the margin to continue its slow advance. Further extension of outlying rhizome may therefore occur, perhaps including the development of a further frond close to the shoot apex, late in the season after the carbohydrate resources required have been supplied by earlier emerging fronds.

5.5 DISCUSSION

Although a rather crude experiment which involves a degree of damage and disturbance to the physiology of the bracken margins studied, the isolation of marginal rhizome at the perimeter of bracken stands by the digging of trenches clearly demonstrates that this rhizome is largely independent of the mature bracken stand for its requirements of nutrients, both mineral and carbohydrate, and of water. Frond numbers and their heights were not diminished even when trenches were dug at the interface between bracken and *Calluna*, completely removing the possibility of transport from more mature bracken to outlying fronds, or very early in the spring (March). It is possible, though improbable since no reduction in the growth of outlying fronds was observed at all after trenches had been dug, that sufficient reserves are available to provide for the needs of outlying rhizome for the first season after transport from the remainder of the stand was prevented. Data from these plots will therefore also be collected in the 1993 season.

Evidence from the analysis of the mineral nutrient concentrations of bracken at and close to the margins serves to support the observations of the trench experiment with concentrations of phosphate and total nitrogen in the outermost fronds remaining below those of fronds further back into the stand. The transport of radiolabelled nutrients (both mineral and carbohydrate) whilst occuring in the direction of actively growing rhizome buds, seems to occur only over short distances and is not biased only towards those active buds present at the apices of pioneering rhizome. It is possible however, that given a longer time-period more radiaolabelled nutrients might have accumulated at these points.

The evidence would suggest that the ability of a bracken front to advance is dependent on localised external environmental conditions at the margins such as the availability of mineral nutrients and water, competition from other species or soil O_2 content. Whole plant characteristics, such as maturity, size, genetics or age may have a less dominant effect on the ability of a margin to advance. The lack of large-scale transport of nutrients through the rhizome of bracken also has implications for the attempted control of bracken. These results suggest that translocation of herbicides throughout the rhizome system of bracken may also be limited.

6. CONTROL OF BUD DORMANCY

6.1 INTRODUCTION

The large reserves of carbohydrate nutrients and buds available in the rhizome have made a major contribution to the success of the bracken plant, allowing it to encroach into heather moorland and become a problem in many areas. The presence of metabolically inactive dormant buds on the rhizome have also proved difficult to reach with herbicide treatments and act as a potential source of recovery in subsequent years. The mechanisms controlling the dormancy of these buds is therefore of obvious interest when considering how best to control bracken. A series of experiments have investigated factors which might act to increase the proportion of rhizome buds which are in an active state. Such treatments may prove useful as part of bracken control programmes being used as pre-treatments which act to increase the vulnerability of previously dormant buds before herbicides are applied.

The influence of the dominant growing frond in suppressing the growth of further fronds and buds has been widely demonstrated in previous experiments involving both frond cutting treatments (e.g. O'Brien, 1963; Lowday and Lakhani, 1987) and the excision of the rhizome apex (Daniels, 1985). The application of NPK fertilisers have also been shown to increase both rhizome growth and frond production (Daniels, 1986). It is therefore possible that the application of nutrients enables dormant buds to overcome correlative nutritive inhibition imposed by the dominant apical bud. Competition from other plants, in this study *Calluna* , may limit the availability of resources such as water, nutrients or light to developing frond buds resulting in the suppression of their growth.

Less work has been carried out on other factors which may have a role in determining levels of rhizome bud activity. Plant growth regulators (ethene and gibberellic acid) have been widely used to control the bud dormancy of deciduous plants (Perry and Helmers, 1973) and may be effective in breaking the dormancy of bracken rhizome buds. Sub-lethal doses of some herbicides have also been reported in the past to have a stimulatory effect on the growth of both shoots and roots in several species and also to promote stolon tillering in *Agropyron repens* (Parker, 1976; Wiedman and Arnold, 1972).

All of these factors were therefore investigated in an attempt to find methods of stimulating the rhizome bud activity of bracken. Again experiments were conducted on 3 different systems:

a) on isolated rhizome segments in boxes,
b) in undisturbed blocks of moorland soil
and c) as treatments applied in the field.

6.2 BRACKEN CUTTING AND THE ROLE OF APICAL DOMINANCE

6.2.1 The excision of apical frond primordia

6.2.1a Method

A total of 107 rhizome branches of length varying between 8cm and 25cm with an intact apex at one end were collected from a mature bracken stand on Lowna Lund (LMS) at the end of January 1990. The growing apical frond primordia of 54 of these shoots, chosen at random, were removed with a razor blade. These shoots were labelled and all of the rhizomes planted in boxes of Irish Moss Peat which were placed in a greenhouse. There was no significant difference between the numbers of active or dormant buds present on the rhizome branches from which frond primordia were removed and on those which remained intact before the excisions took place.

6.2.1b Results

The removal of the apical frond primordia resulted in an increase in the number of active buds present per rhizome shoot shown in fig. 36. A mean of 3.17 (±0.27) active buds (including the excised primordia) were produced on those shoots from which the frond primordia had been removed, and the effects of apical dominance released, whereas the mean on those shoots on which the primordia remained intact was 1.83 (±0.17).

Fig. 37 shows the positions at which active rhizome buds are found on those rhizome shoots from which the primordia had been removed and those on which the primordia remained intact. Primordia replacing those which were removed were formed on many rhizome segments with more than one primordium being present at the apex of many shoots. Increased activity at the apex also gives rise to an increase in the number of terminal buds at the apex which are active either due to the activation of terminal buds which had previously been in a dormant state or the development of lateral branches at the apex.

The increase in the number of active buds is not due to the growth of rhizome at the apices alone but also results from the activation of dormant buds in a position adaxial to previous years fronds and from buds which had become dormant after

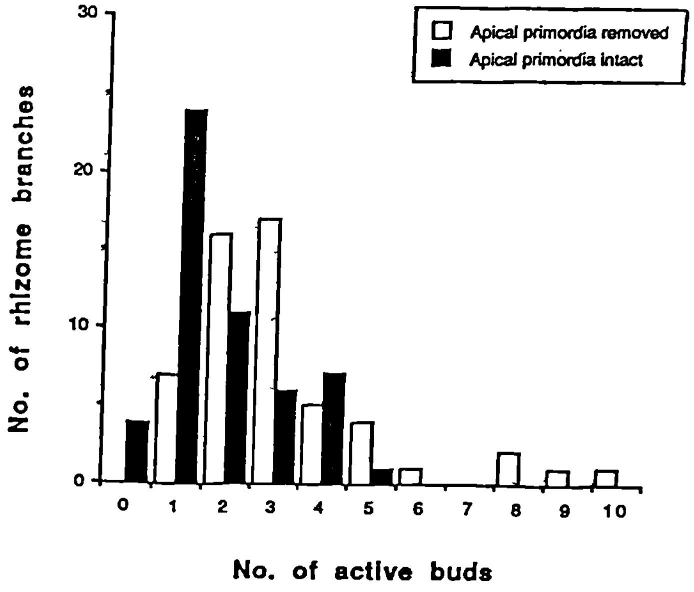


Fig. 36 Increase in the mean number of active buds present per rhizome segment resulting from the excision of the apical frond primordium. The removed primordium is included in the data for the apex removed treatment.

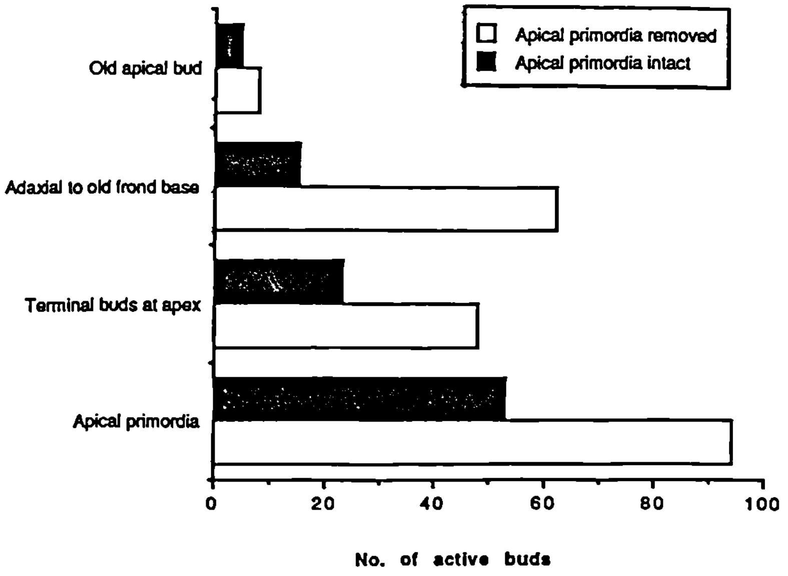


Fig. 37 The positions of active rhizome buds in rhizome apices with and without intact apical primordia. Again the removed primordium is included in the data for the apex removed treatment.

previous initiation in the normal position of frond primordia at the apex. Increases in the number of active buds in these two positions of 413% and 62% respectively over rhizome shoots with intact apical primordia were seen on those shoots from which apical primordia were excised.

The removal of apical dominance by active frond primordia has been observed both to promote new growth at the apex and to activate buds which were already present but in a dormant state.

6.2.2 The effect of a single cutting treatment on bracken grown in moorland soil blocks

6.2.2a Method

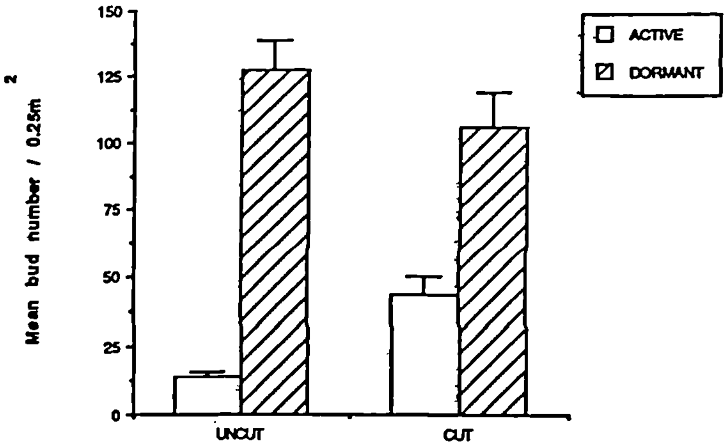
Twenty blocks of 50cm x 50cm in size which included all the rhizome present under that area were collected from patch S on Lowna Lund (see fig. 11, p58) in early May 1990. This area of moorland is dominated by bracken but considerable amounts of *Calluna* are still present and the bracken is growing more sparsely than that in the other Lowna patches (LLP) or in the mature bracken stands (LMS and LLT) on either side of this moor. The blocks were transferred to a greenhouse where they were grown until 20th June 1990 when the fronds were removed from half of the blocks which had been selected at random.

On 2 October, 1990 remaining scenescent fronds were removed from all of the blocks and the rhizome separated from the soil. The rhizome material was then divided into its shoot types, weighed and the number and positions of active and dormant buds recorded as previously described for the collection of morphological data (see 4.2.4 , 4.2.5 and 4.2.6; p64 and 65).

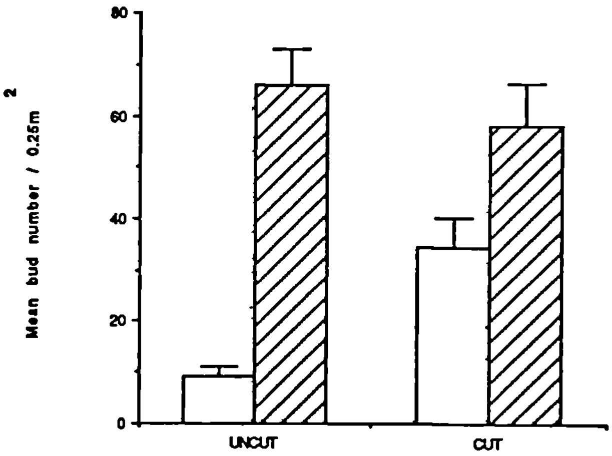
6.2.2b Results

The effects of the removal of fronds from bracken grown from rhizome in moorland soil blocks are similar to those observed in isolated frond segments although the physiology of the rhizome is disturbed to a lesser extent. Fig. 38a shows an increase in the mean number of active buds present on the rhizome of bracken which had received a single cutting treatment over mean active bud numbers on rhizome in uncut control blocks. This difference is statistically significant in a t-

a) Total buds



b) At the apex



c) Adaxial to old frond base

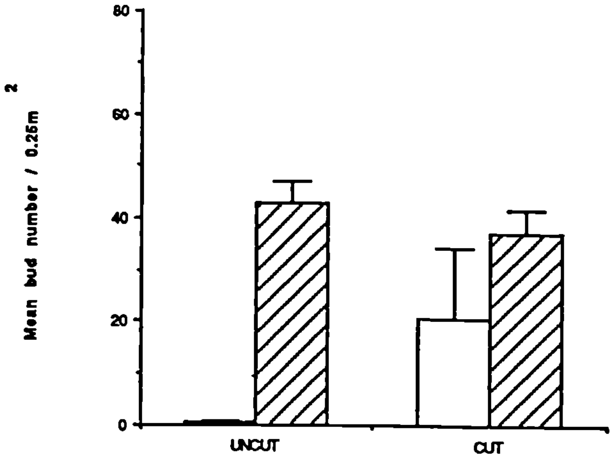


Fig. 38 The influence of a single cutting treatment on bracken grown in blocks of moorland soil; a) the total number of buds present, b) buds present at the rhizome apex and c) buds adaxial to previous fronds. The data presented are means for ten 50cm x 50cm blocks. Error bars are the standard error of the mean.

test with data transformed to $(n+1)^{1/2}$ (P=0.0003). Again both active bud numbers at the rhizome apex (fig. 38b) (P=0.0001) and in a position adaxial to previous years frond bases (fig. 38c) (P=0.0000) are greater on those blocks where the cutting treatment took place. As a result of frond removal the activation of buds which had previously been dormant has occurred in these positions once more, as had the promotion of new growth at the apex.

6.2.3 Cutting treatments in mature bracken stands under field conditions

6.2.3a Method

Since cutting treatments on both isolated rhizome shoots and rhizome grown in moorland soil blocks had resulted in increased bud activity, a field experiment was begun to study the effects of cutting treatments on bracken in undisturbed conditions. Two mature bracken stands were selected one at the centre of patch **A** on Lowna Lund (see fig. 11) and the second at Goathland (GMS) (see 3.2.5).

At both sites an experiment using a 4 x 4 latin square design was set up with experimental plots of size 1m^2 separated by 1m guard strips. The treatments were as follows:

a) uncut control
b) cut in late June
c) cut in late July
d) cut in late June and in late July

Fronds were removed at ground level and their numbers, height, unfurled pinnae number and fresh weight recorded. At the end of the growing season in early September any remaining fronds were harvested and their details recorded. The total rhizome material from the centre 50cm x 50cm area of each quadrat was collected, washed, divided into its rhizome types, weighed and the number and positions of active and dormant buds recorded.

6.2.3b Results

The effects of cutting on rhizome activity were not demonstrated as clearly in the field when bracken in a mature stand was cut as when individual frond primordia were excised, or fronds grown from rhizome from moorland soil blocks were cut in the greenhouse. This experiment was carried out on small 1m^2 plots over a period of a single growing season and suggests that successive cutting treatments are required in order to stimulate rhizome activity. Depletion of rhizome supplies of carbohydrates and buds did not taken place as a result of one or two cuts in a single season.

An early (end of June) cutting treatment on the mature stand at the centre of Lowna Lund patch A did however produce an increase in the total number of fronds produced in the season (fig. 39a). Frond numbers resulting from a single early cut are significantly greater than those in uncut plots in transformed $((n+1)^{1/2})$ t-tests ($P=0.028$). However, no such response was apparent when bracken was cut in both late June and late July ($P=0.19$) and little stimulation in frond production was produced by a later cut at the end of July. Total seasonal frond production at **GMS** (fig. 39b) does not increase greatly above uncut levels following either of the single cutting treatments. But there appears to be some increase in frond number in the plots where bracken is cut twice ($P=0.11$).

Active rhizome bud numbers did not increase above uncut levels in those plots where cutting treatments took place and on the Lowna site actually declined (fig. 39a). The percentage of buds were in an active state also either declined or remained approximately the same. There was also little evidence of any depletion in rhizome mass resulting from the cutting treatments over this short period.

On rhizome branches where fronds growing at the apex have been removed during cutting treatments the development of replacement fronds, either at the apex or from previously dormant buds elsewhere on the shoot, is not often apparent. It seems likely therefore that the replacement of fronds following frost or cutting treatments might occur largely on shoots other than that carrying the damaged frond.

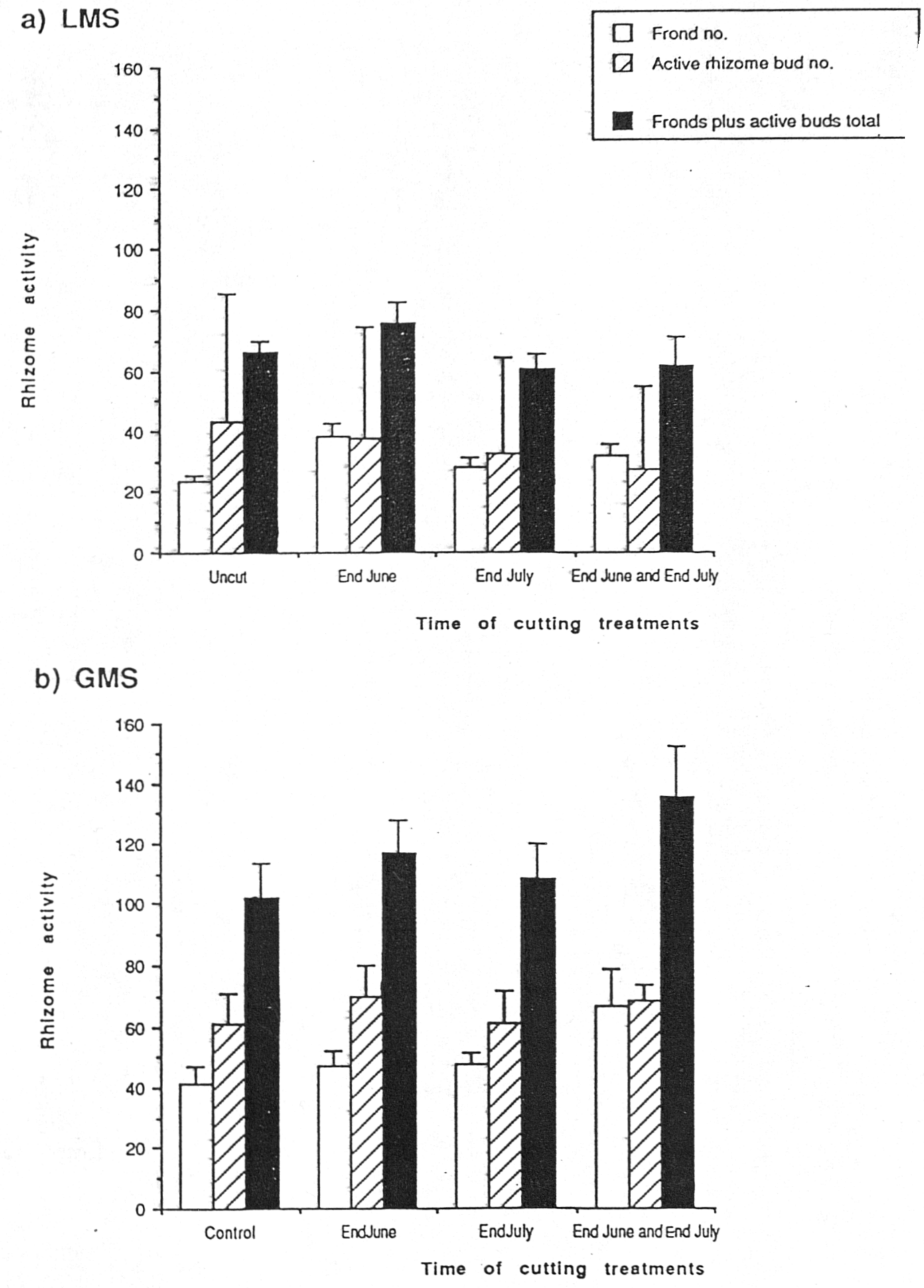


Fig. 39 The effects of cutting treatments on bracken in a mature stand growing in the field. Each bar represents the mean for four 50cm x 50cm replicate sample blocks. Error bars are the standard error of the mean.

6.2.4 Discussion

The pronounced stimulation of rhizome bud activity observed following the excision of apical frond primordia or cutting of fronds grown from rhizome in moorland soil blocks was not reproduced as clearly under field conditions. Reasons for this difference are uncertain but may involve the small size ($1m^2$) of treatment plots used in the field and their lack of isolation from the surrounding bracken stand. The effects of frond removal on rhizome which is able to import mineral nutrients, photosynthates and possibly factors which promote bud dormancy, from neighbouring rhizome may therefore be less obvious than effects on more isolated rhizome.

It is possible that the removal of a growing frond or apical primordia promotes the growth of new fronds on other rhizome branches. Where rhizome is not isolated from shoots carrying intact growing fronds the effects of removing fronds within a small area would be to merely reduce the number of growing fronds influencing the rhizome. The effects of removing only a proportion of fronds to which a rhizome branch is attached would therefore be expected to produce a diluted stimulation of rhizome activity and new frond production. Such a situation might occur if, for example, growing frond were acting as a strong sink for nutrients and preventing the growth of dormant buds and further growth at the rhizome apex due to nutrient starvation. The effects of removing the growing fronds would be lessened if intact growing fronds remained on an attached rhizome branch in close proximity. This explanation may also account for the greatest stimulation of rhizome bud activity occuring following cutting treatments which take place early in the summer (mid-June to late July) (Williams and Foley, 1976) when fronds are growing and represent a large metabolic sink.

Cutting treatments over a large area, especially where such treatments are repeated (Santon, 1990) provide an excellent method of depleting rhizome mass and promoting rhizome activity both at the apex and from buds which have been previously dormant. Cutting would undoubtedly prove useful as a stimulatory pre-treatment prior to the application of herbicides as described by Lowday and Lakhani (1987) and Kirkwood *et al.* (1982).

6.3 THE USE OF NUTRIENT FERTILISERS IN THE STIMULATION OF RHIZOME ACTIVITY

6.3.1 Treatment of isolated rhizome segments with a general NPK fertiliser

6.3.1a Method

Rhizome material collected from Skipwith Common on 15th March 1990 (Grid ref. SE380665) was planted in a series of 6 boxes each containing Irish Moss Peat and subsequently grown in a greenhouse. Each box (of size 30cm x 60cm) contained 5 segments each of long and short shoot rhizome all of which were 25cm in length. The rhizome segments did not necessarily include an apex and were allocated between the boxes at random. Rhizome details including the numbers, positions and activity states of the buds present were recorded for each segment of rhizome at the time of planting.

12g of 'Phostrogen' (Phostrogen Ltd.) NPK (10:10:27) fertiliser was applied in 2g doses at 10 day intervals (at a concentration of 1g l^{-1}) to 3 of the boxes which were chosen at random. The remaining 3 boxes were treated only with tap water. After 2 months the number and heights of the emerged fronds were recorded together with the numbers, positions and activity states of the rhizome buds.

6.3.1b Results and discussion

The physiological disturbance of isolating rhizome segments and their subsequent growth in loose peat serves to release apical dominance and promote bud activity even before the effects of nutrients are observed. However, fig. 40 clearly shows the presence of a greater number of active rhizome buds and emerged fronds in boxes to which nutrients were applied over control boxes. These results are statistically significant when compared in t-tests for $(n+1)^{1/2}$ at P=0.023 and P=0.083 respectively. In addition to promoting growth at the apex and the formation of greater numbers of frond primordia there is evidence of enhanced levels of release of existing dormant buds. 56.9% of dormant buds present at the commencement of the experiment became active during its course, whilst this percentage was 28.9% in controls. The application of nutrients also resulted in the growth of plants which were larger and healthier than control plants.

This experiment, although a preliminary one, does suggest a role for mineral nutrients in the release from dormancy and promoted growth of rhizome buds which is worthy of further investigation.

6.3.2 The response of bracken grown in moorland soil blocks to nitrate, phosphate and potassium fertilisers

6.3.2a Method

50cm x 50cm blocks of moorland soil containing all of the rhizome present under that area were collected from a mature bracken stand on Lowna Lund (LMS) on 14 November, 1990. The blocks were placed in plastic bags and chilled at 4°C in a cold room for 2 months to imitate a period of winter chilling. After this time the blocks were transferred to a glasshouse and on 15 January, 1991 the first treatments were applied in a randomised block design. Treatments, each applied to 5 replicate blocks, were as follows:

a) Untreated control

b) 6 doses at 2 week intervals of 1 litre NH_3NO_4 solution at a concentration of 0.2g l^{-1}. Equivalent to a total dose of 48 Kg N ha^{-1}.

c) 6 doses at 2 week intervals of 1 litre KCl solution at a concentration of 0.1g l^{-1}. Equivalent to a total dose of 24 Kg K ha^{-1}.

d) 6 doses at 2 week intervals of 1 litre Na_2HPO_4 solution at a concentration of 0.1g l^{-1}. Equivalent to a total dose of 24 Kg P ha^{-1}.

The blocks were harvested on 15 April, 1991 at which point fresh weight of fronds and rhizome, frond numbers and heights and rhizome bud numbers, positions and activity were recorded. The concentration of phosphate in both frond and rhizome tissue was also analysed.

6.3.2b Results

The application of nitrogen and phosphate fertilisers resulted in a increase in the number of fronds produced and the number of active buds present on the rhizome over the numbers in untreated control blocks (fig. 41 a, c). When analysed

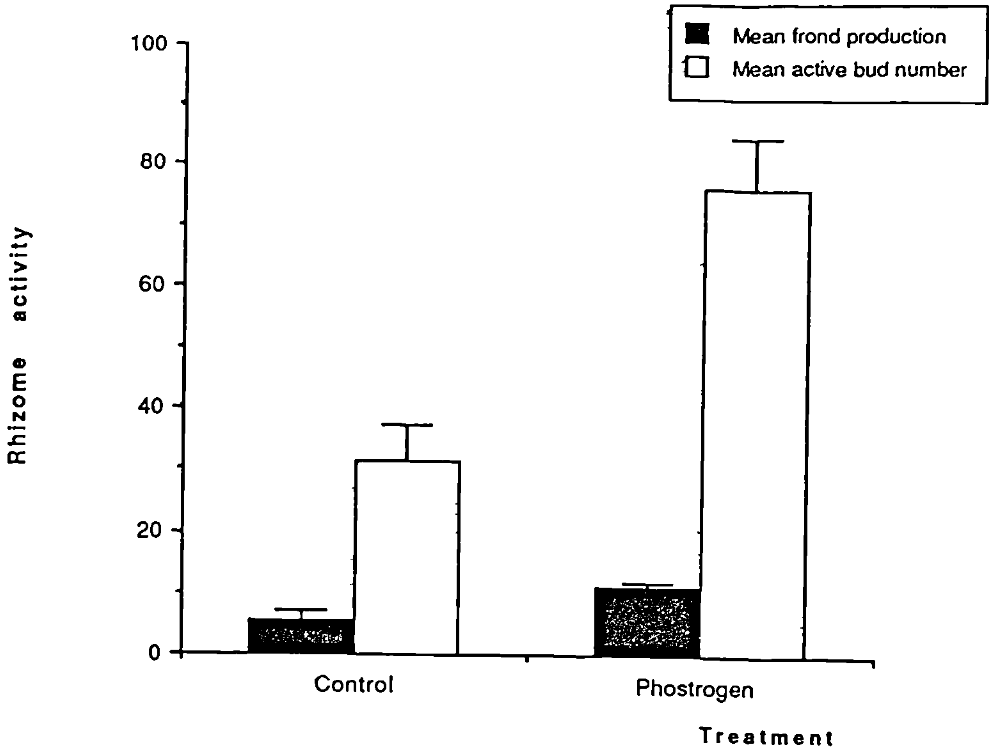


Fig. 40 The effects of the application of a general purpose NPK fertiliser ('Phostrogen') on frond production and rhizome active bud number. Each block represents the mean of 3 replicate boxes (each containing 10 rhizome segments) for each treatment and controls. Error bars are the standard error of the mean.

data transformed to $(n+1)^{1/2}$ was compared using a t-test for nitrogen and phosphate treated blocks in comparison with untreated blocks values of $P=0.057$ and $P=0.06$ respectively are produced. The application of potassium fertiliser produced no change in the number of fronds or active buds produced over the numbers seen in untreated control blocks.

Application of all the mineral nutrients produced very little change in frond height (fig. 41b) with, if anything, a slight (though statistically insignificant) reduction from the frond height seen in control blocks resulting from the application of phosphate and potassium. The increase in mean fresh weight of frond per block over controls observed following the application of nitrogen fertilisers (fig. 41d) therefore resulted largely from an increase in the number of fronds produced rather than a change in the size of the fronds. The application of phosphate resulted in smaller mean fresh weights of fronds per block than those observed in control blocks indicating that though slightly more fronds were produced they were stunted in height.

Again there is evidence that rhizome activity is promoted both from new growth at the rhizome apex and the activation of dormant buds. The percentages of rhizome buds which were in an active state increased following nutrient treatment as shown in table 5 below:

Table 5. Effects of fertilisers applied to bracken grown in blocks of moorland soil on percentages of rhizome buds which are active.

Treatment	All rhizome buds	Rhizome buds at the apex
Untreated	33.2	50.5
Nitrogen	47.6	64.7
Phosphate	49.8	68.3
Potassium	40.6	53.2

The application of phosphate fertilisers also produced an increase in the phosphate concentration of both frond and rhizome tissues (fig. 42).

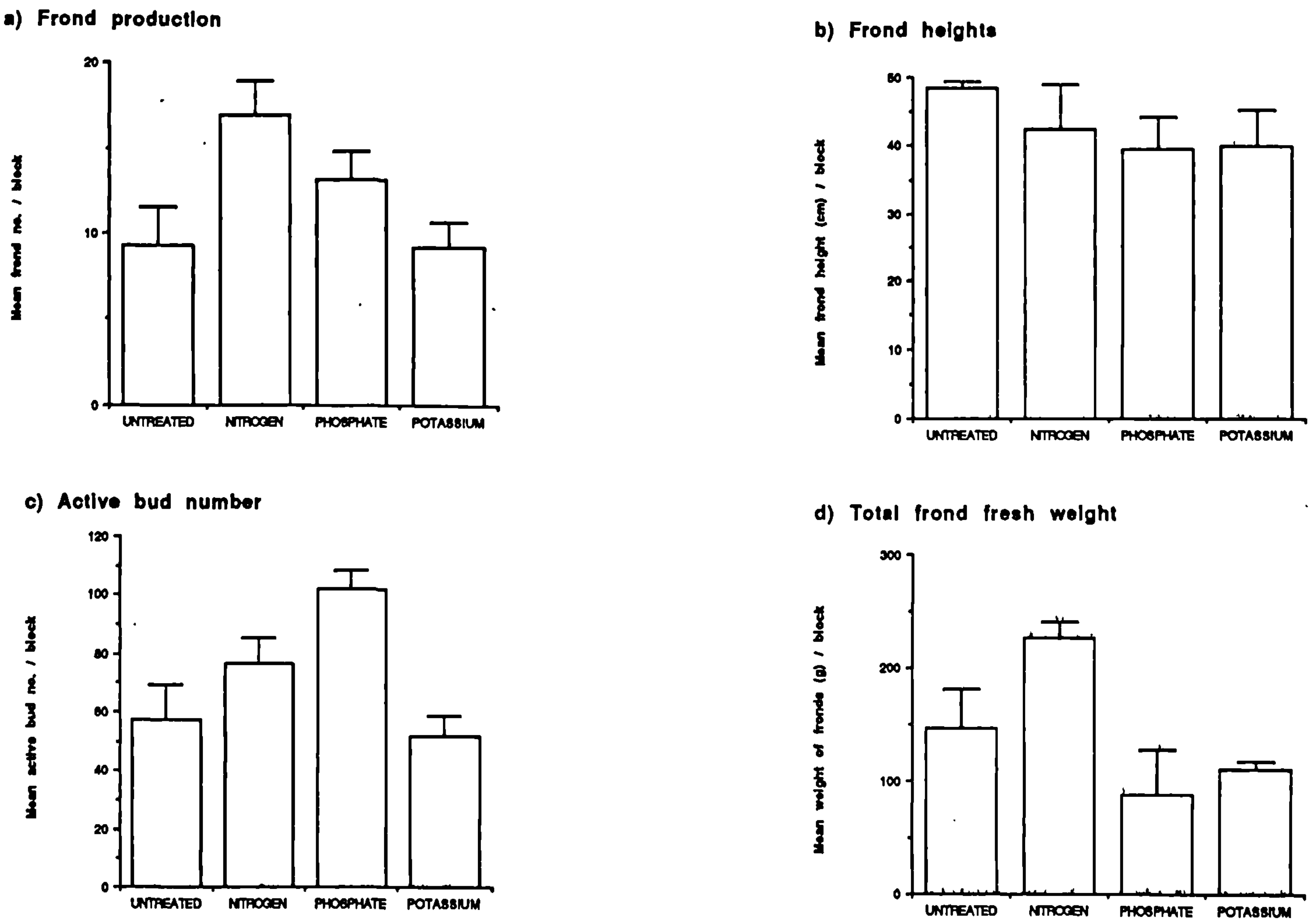


Fig. 41 The effect of application of fertiliser treatments to rhizome contained in blocks of moorland soil, on bracken growth and rhizome activity. The data presented are means for 5 replicate blocks per treatment. Error bars are the standard error of the mean.

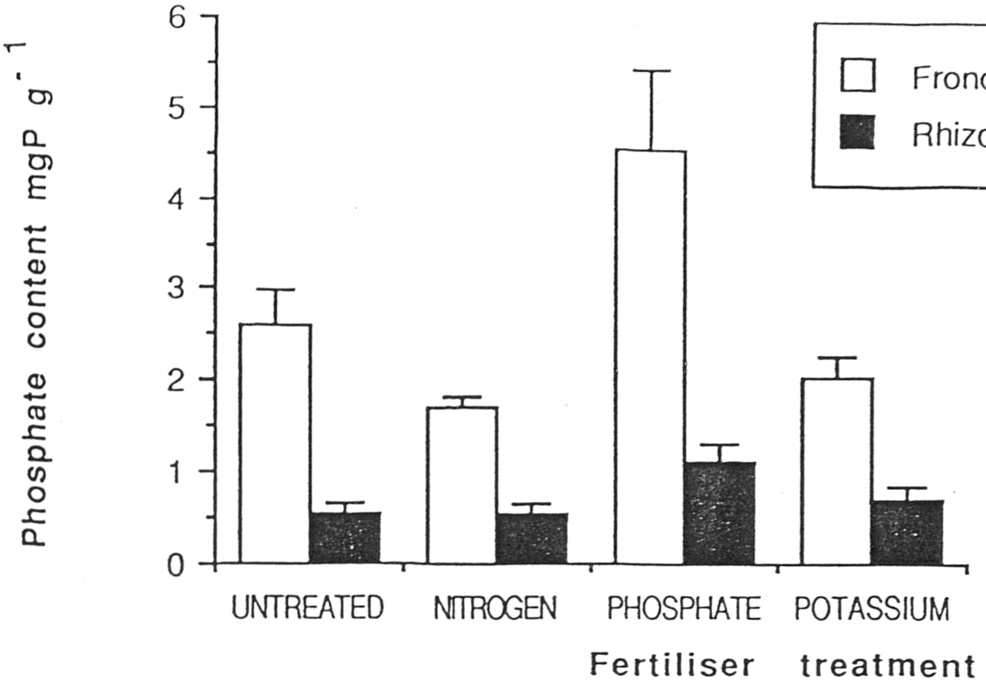


Fig. 42 The phosphate content of frond and rhizome tissue taken from bracken grown in a glasshouse from rhizome in moorland soil blocks. Bars represent means for 5 replicate 0.25 m^2 blocks for each treatment. Error bars are the standard error of the mean.

Again any response to potassium fertiliser was less apparent and although the mean phosphate concentration in rhizome was enhanced above control levels there was actually a decrease in the phosphate concentration of frond tissue. The most obvious improvement in phosphate concentrations was seen in rhizome tissue as a result of phosphate treatment. This increase produced a result of P=0.054 when phosphate treated rhizome was compared with untreated blocks in a t-test.

6.3.3 The response of bracken margins to fertiliser treatments in the field

6.3.3a Method

Fertiliser treatments were applied to experimental strips (as described in 3.1.4.) at the margins of 2 bracken stands **GHH** (12 strips per treatment) and **LLP** (6 strips per treatment). The treatments were applied at the beginning of May 1991 and were as follows:

a) Untreated control

b) A 1:1 mixture of NO_3^- and NH_4^+ (as $NaNO_3$ and $(NH_4)_2SO_4$) applied at a rate of 28g m^{-2}. Equivalent to a dose of 50Kg ha^{-1}.

c) K_2SO_4 applied at a rate of 11g m^{-2}. Equivalent to a dose of 50Kg ha^{-1}.

d) Superphosphate applied at a rate of 11.5g m^{-2}. Equivalent to a dose of 50Kg ha^{-1}.

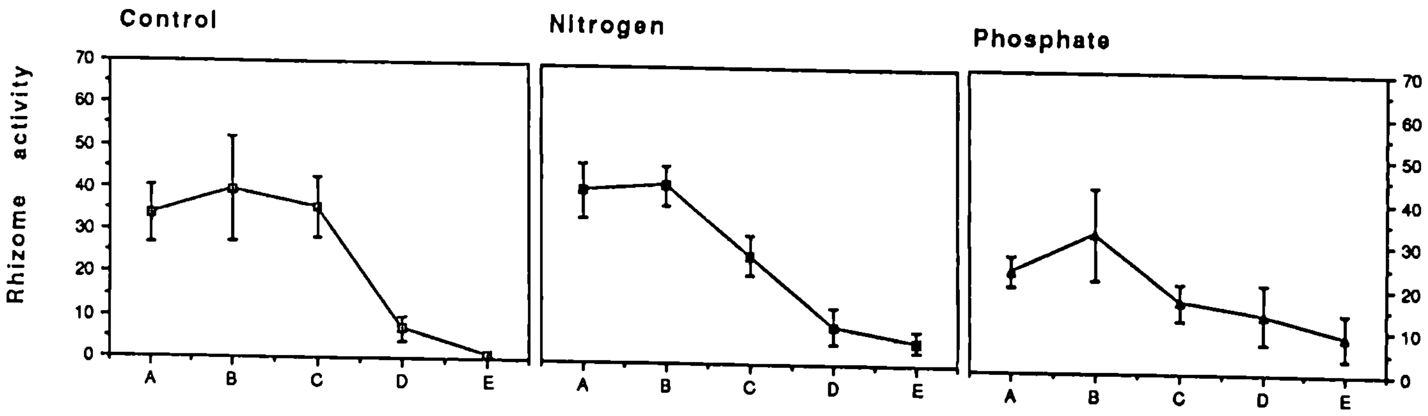
Frond numbers, heights and unfurled pinnae number were recorded at fortnightly intervals throughout the growing season. Rhizome data was collected from 50cm x 50cm blocks at the end of the season and again fresh weights and rhizome bud numbers, positions and activity recorded for each rhizome type.

6.3.3b Results

Increases in rhizome activity (as defined by the sum of fronds produced and active buds present on the rhizome) observed in the field were less obvious than those observed under more standardised conditions, e.g. without the effects of competition from *Calluna* at different stages of maturity which are excluded from rhizome grown in boxes or in soil blocks.

On site **LLP** (fig. 43a) where bracken is advancing only very slowly, there is little evidence of stimulation of rhizome activity above levels seen in control strips for any of the minerals applied with the possible exception of the outermost rhizome (quadrats D and E of experimental strips) where nitrogen and phosphate do seem to produce a small increase in activity. Elsewhere in the strips however (quadrats A and C) less rhizome activity is actually observed in strips treated with phosphate than in controls.

a) LLP



b) GHH

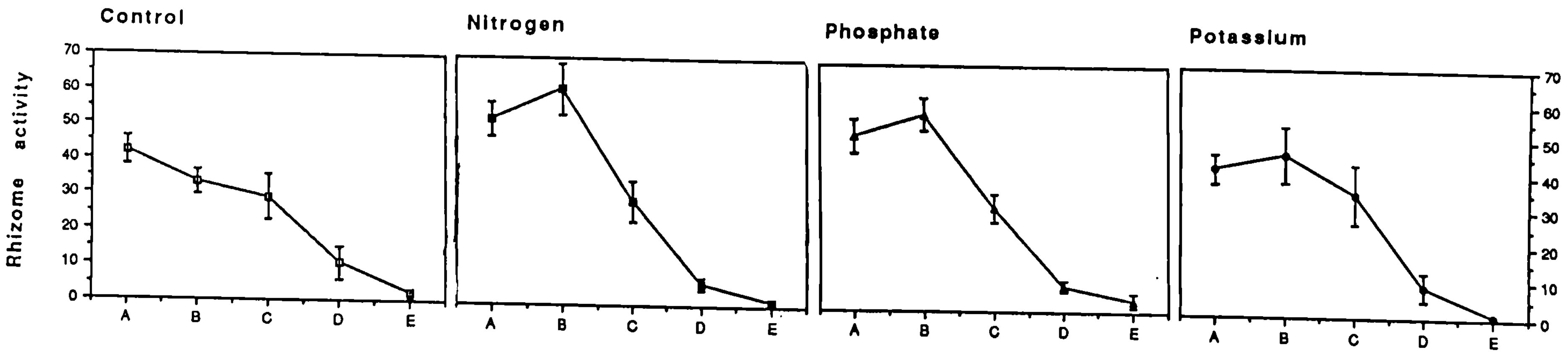


Fig. 43 **The effects of fertilisers on the activity of bracken rhizome in experimental strips.** See 6.3.3a for application rates. The data presented as rhizome activity is made up of the sum of active bud number and frond production for the 1991 season. The letters A-E represent quadrats within experimental strips (see 3.1.4). Each point is the mean of 0.25m^2 samples taken from a) 6 and b) 12 experimental strips. Error bars are the standard error of the mean.

On site GHH (fig. 43b) there is more evidence of the stimulation of rhizome bud activity following the application of fertilisers. A statistically significant increase is found in t-tests when both frond numbers ($P=0.011$ for nitrogen and $P=0.026$ for phosphate) and active bud numbers ($P=0.003$ for nitrogen and $P=0.008$ for phosphate)(transformed to $(n+1)^{1/2}$) are compared between quadrat B of experimental strips treated with nitrogen or phosphate and control strips. There is also a small amount of evidence of potassium increasing rhizome activity in this quadrat. In quadrat A rhizome activity is also slightly increased over levels seen in control strips in strips treated with nitrogen and phosphate though this difference is not statistically significant in t-tests. Frond production also occurs in greater numbers than is seen in control strips in quadrats C and D in strips which were treated with phosphate. Again this is statistically significant in t-tests with $P=0.01$ and $P=0.02$ respectively.

Further away from the bracken stand frond numbers and the numbers of rhizome buds present are obviously smaller and stimulation of enhanced rhizome activity resulting from the application of mineral fertilisers is not obvious.

6.3.4 Discussion

Several workers (Daniels, 1986; Leakey *et al.*, 1978; McIntyre, 1964;1965) have pointed out the importance of mineral nutrients in the control of apical dominance in rhizomatous plants.

The application of fertilisers to isolated rhizome segments grown in loose peat provided a clear indication that mineral nutrient availability has an influence in controlling the dormancy of rhizome buds and could be of use in stimulating the activity of these buds. This system however, is highly invasive and in itself causes promotion of rhizome bud activity even before nutrient treatments are applied. Application rates of fertilisers used on isolated rhizome segments were those recommended by the manufacturer of the general purpose fertiliser used and were not dissimilar to rates used in subsequent experiments.

The use of moorland soil blocks provided a less intrusive system than the use of isolated rhizome segments with the number of rhizome buds produced by control blocks being close to those observed in a mature bracken stand in the field. The rates of nutrients applied to these blocks and to experimental strips in the field are equivalent to low agricultural doses. It was hoped to achieve an observable effect of nutrients on bracken rhizome activity without the use of nutrient doses which are unrealistic for agricultural use.

Data from the experiment using bracken grown from rhizome in moorland soil blocks, although showing variation between replicates in each treatment, does show some increase in rhizome activity resulting from the application of nutrients. This is especially the case where nitrogen and phosphate fertilisers were used. Analysis of frond and rhizome material for phosphate concentration also provided evidence that there is scope for increasing the phosphate concentration of bracken tissue through application of nutrients. With these data in mind it was decided to embark upon an experiment, involving more replicates for each treatment, to investigate the effects of nutrient fertilisers on rhizome activity under field conditions.

Increases over control levels in rhizome activity were again observed in the field at site GHH following nutrient applications. These increases were less obvious than those observed under more standardised conditions in the experiments using isolated rhizome segments or bracken grown from rhizome in moorland soil blocks. This is in part due to the increased number of differences in conditions between replicates, e.g. competition with *Calluna* whose stage of maturity differed between replicate strips given the same treatment. The fertiliser treatments were applied early in the spring in an attempt to maximise any stimulation effect on the developing frond primordia. As a result of this some of the fertiliser was almost certainly lost through leaching as the summer progressed and a second nutrient application later in the season may have produced further stimulation of rhizome activity. A relatively large number of small experimental strips were used in the field in an attempt to achieve a representative mean estimate of rhizome activity for each treatment within the time available for data collection.

The data suggests a role for mineral nutrients in the stimulation of rhizome bud activity in bracken rhizome which can be produced under field conditions at the margins of bracken stands, at least under some conditions. The greater response of the advancing margin GHH, over the less mobile margins at LLP, may indicate that rhizome buds at GHH had a greater capacity to become activated by nutrient treatment and show that nutrient treatments alone are not always sufficient to stimulate enhanced rhizome activity.

6.4 SUB-LETHAL HERBICIDE DOSES AND RHIZOME ACTIVITY

6.4.1 The effects of low doses of bracken control herbicides on bracken grown in soil blocks

6.4.1a Method

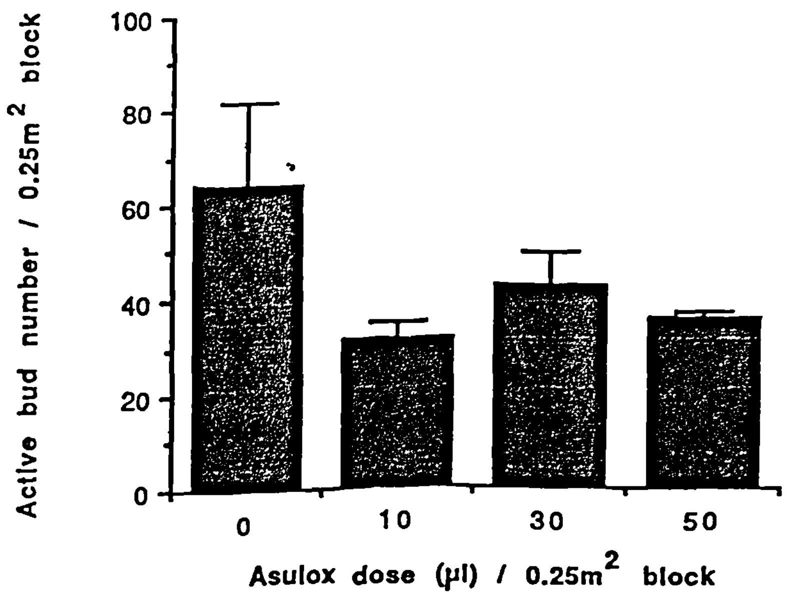
50cm x 50cm soil blocks were collected from a mature bracken stand on Lowna Lund (LMS) (see 3.4.1) on 9 April, 1991 and 9 May, 1991. These blocks were transferred to a greenhouse where they were grown until fronds had emerged and unfurled fully. At this point herbicide treatments, each in 75ml water, were sprayed onto both upper and lower frond surfaces. Glyphosate in the form of "Tumbleweed" (Fisons, 14.3% a.i.) was applied to those blocks collected on 9 April, 1991 and asulam as "Asulox" (Embetec Crop Protection, 40% a.i.) applied a few weeks later to those blocks collected on 9 May, 1991. Herbicide doses applied to each of 5 replicate blocks were as follows:

Table 6. Herbicide doses applied to bracken grown in $0.25m^2$ soil blocks.

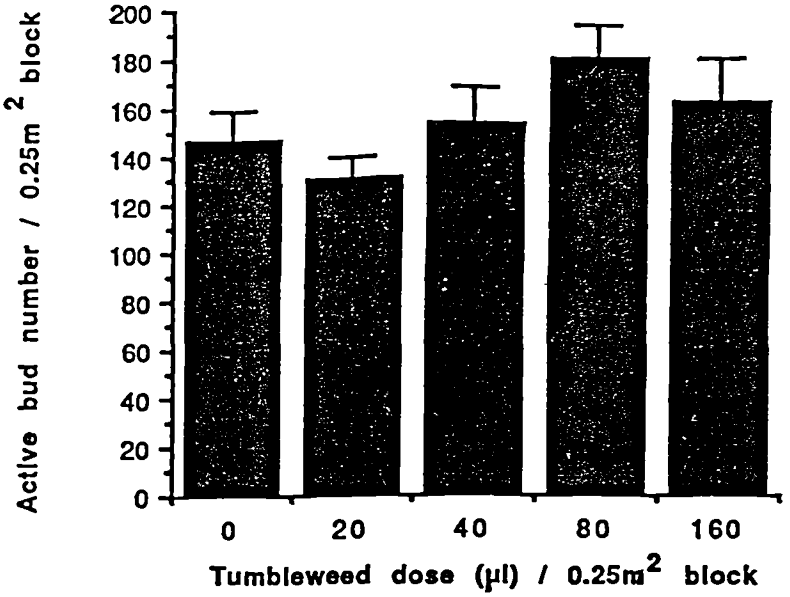
Tumbleweed (μl)	Glyphosate (mg)	Glyphosate (kg ha^{-1})
0	0	0
20	2.86	0.11
40	5.72	0.23
80	11.44	0.46
160	22.88	0.92

Asulox (μl)	Asulam (mg)	Asulam (kg ha^{-1})
0	0	0
10	4	0.16
30	12	0.48
50	20	0.8

The blocks were harvested on 19 August, 1991 (glyphosate treated) and 9 September, 1991 (asulam treated) at which point fresh weight of fronds and rhizome, frond numbers and heights and rhizome bud numbers, positions and activity were recorded.



a) Asulam



b) Glyphosate

Fig. 44 The effects of low doses of bracken control herbicides a) 'asulox' (a.i. asulam, 40%) and b) 'tumbleweed' (a.i. glyphosate, 14.3%) on rhizome active bud number. Data presented are means for a) 4 and b) 5 0.25m^2 blocks. Error bars are the standard error of the mean.

6.4.1b Results

The results of the application of low doses of asulam and glyphosate to bracken grown from rhizome in soil blocks are presented in the form of active bud numbers in fig. 44. The applications of even low doses of asulam produced a reduction in the mean number of active buds per block found on the rhizome. Doses of 80 µl/block tumbleweed does appear to have had a small stimulatory effect on rhizome bud activity but t-tests (data transformed to $(n+1)^{1/2}$) produce insignificant results for both responses. There was no difference in the number of fronds produced on untreated blocks and blocks treated with either herbicide at any of the doses applied.

Differences between untreated rhizome activity levels in blocks in each part of this experiment may be explained by the slightly different site of collection within **LMS** or the different timing of collection. Variation between replicate blocks in this experiment make it difficult to draw firm conclusions but it seems possible that at the higher doses of glyphosate investigated a stimulatory effect on bracken rhizome may be being produced which is worthy of further investigation in the field.

6.4.2 The effects of low doses of bracken control herbicides on bracken in the field

6.4.2a Method

Low application rates of asulam and glyphosate were hand-sprayed onto both frond surfaces of mature bracken on 25 July, 1991. The bracken sprayed was in the experimental strips on site **GTHR** and bracken growing in 4 strips for each herbicide was compared with that in 6 control strips at the end of September, 1991. Numbers of active and dormant buds present, and their positions on the rhizome were counted in 50cm x 50cm blocks removed from each quadrat comprising each of the strips (see 3.1.4).

Doses of herbicide applied were 350 µl m^{-2} 'Tumbleweed' (Fisons, 14.3% glyphosate a.i.), equivalent to 0.5 kg ha^{-1} glyphosate and, 120 µl m^{-2} 'asulox' (Embetec Crop Protection, 40% asulam a.i.), equivalent to 0.48 kg ha^{-1} ha asulam. Each herbicide application was diluted in 75ml m^{-2} water.

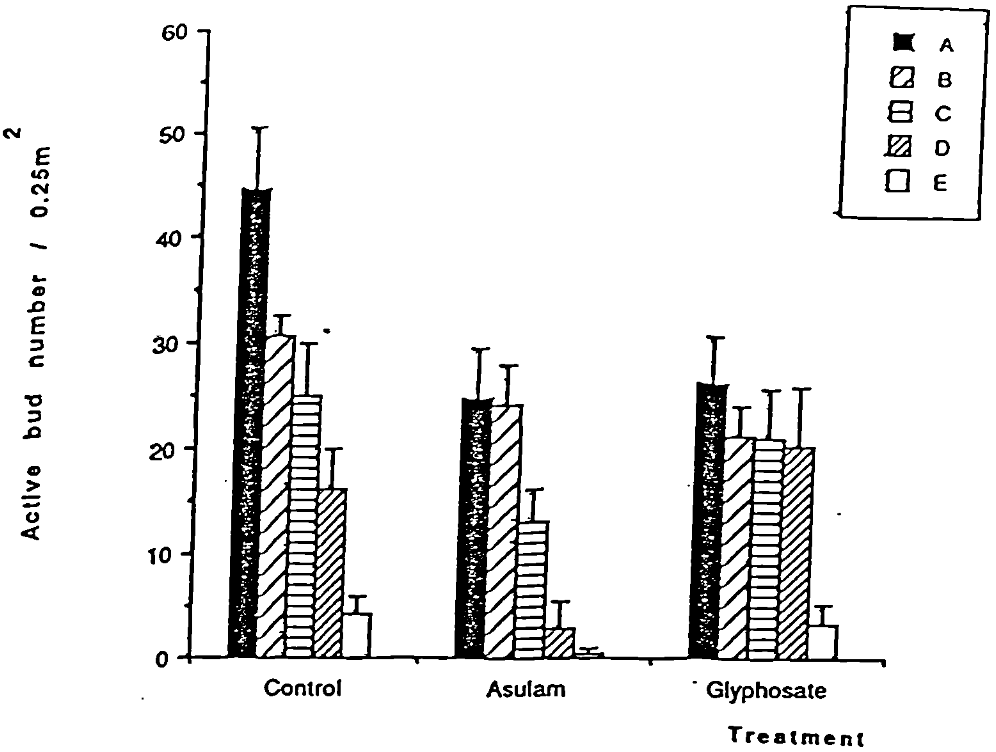


Fig. 45 The effects of low doses of bracken control herbicides, asulam (at 0.48Kgha^{-1}) and glyphosate (at 0.5Kgha^{-1}) applied in the field, on rhizome active bud number. Data presented are the means of n experimental strips where control n=6, asulam n=4 and glyphosate n=4. Error bars are the standard error of the mean.

6.4.2b Results

The data shown in fig. 45 shows the reduction in rhizome active bud number resulting from treatment with even very low doses of bracken control herbicides. The application of 0.48 kg ha^{-1} asulam, a rate well below the recommended dose for bracken control of 4.4 kg ha^{-1}(Veerasekaran *et al.*, 1978), reduced mean numbers of active buds present on the rhizome in all 5 quadrats comprising the experimental strips. Glyphosate at 0.5 kg ha^{-1} also reduced mean numbers of active buds present on the rhizome in all quadrats except quadrat D. Again this is a significantly lower dose than the more than 2 kg ha^{-1} recommended for bracken control (Williams and Foley, 1975).

6.4.3 Discussion

The application of low doses of asulam reduced rhizome active bud numbers in both bracken grown from rhizome in moorland soil blocks and bracken in the field. These experiments produced no evidence to suggest that, even at very low doses, this herbicide has any stimulatory effect on rhizome activity. Asulam is used in over 90% of bracken control programmes involving herbicides and it is reassuring to observe that applications of low doses, perhaps resulting from a helicopter emptying its tanks at the end of a spraying operation, have no stimulatory effect on bracken growth.

Whilst producing no stimulatory effect on rhizome bud activity in the field low doses of glyphosate (0.5 kg ha^{-1}) did appear to have a small stimulatory effect in experiments using bracken grown in a glasshouse from rhizome in moorland soil blocks. This response although small, may be worthy of further investigation.

6.5 THE INFLUENCE OF COMPETITION FROM *CALLUNA* ON RHIZOME ACTIVITY

6.5.1 Introduction

The regular burning of *Calluna* is practised in order to achieve a mosaic of heather of different ages and has often been partially blamed for the encroachment of bracken into areas previously dominated by *Calluna*. This is especially the case in areas where burning is infrequent and the burning of old *Calluna* plants at high temperatures result in poor short-term recovery of *Calluna*. The problem is worsened if a break of mature *Calluna* is not left at the time of burning to hold an advancing bracken front in check. Such is the situation shown in figs. 46 and 47 (next page), the *Calluna* on Harland moor has been burnt into *an established area of* bracken. The result of this burn was almost complete domination by bracken of a large area previously covered by *Calluna* in the following season.

6.5.2 Comparison of rhizome activity in an area of mixed bracken-*Calluna* vegetation with an area from which *Calluna* foliage was removed by burning

6.5.2a Method

The vegetation of much of Harland moor (see 3.4.3) is dominated by a mixture of *Calluna* and bracken which appear to be in equilibrium. In the autumn of 1989 some of this mixture was burnt such that *Calluna* foliage was removed whilst bracken rhizome remained undamaged. The effects of the removal of competition by mature *Calluna* plants (and a possible nutrient flush resulting from the burning) on the activity of bracken rhizome was observed by sampling the rhizome from ten 30cm x 30cm quadrats of moorland which had been burnt and 10 identical quadrats from an adjacent area of moorland which had not been burnt. The quadrats were selected at random. Rhizome weights, types and bud number, position and activity were recorded.

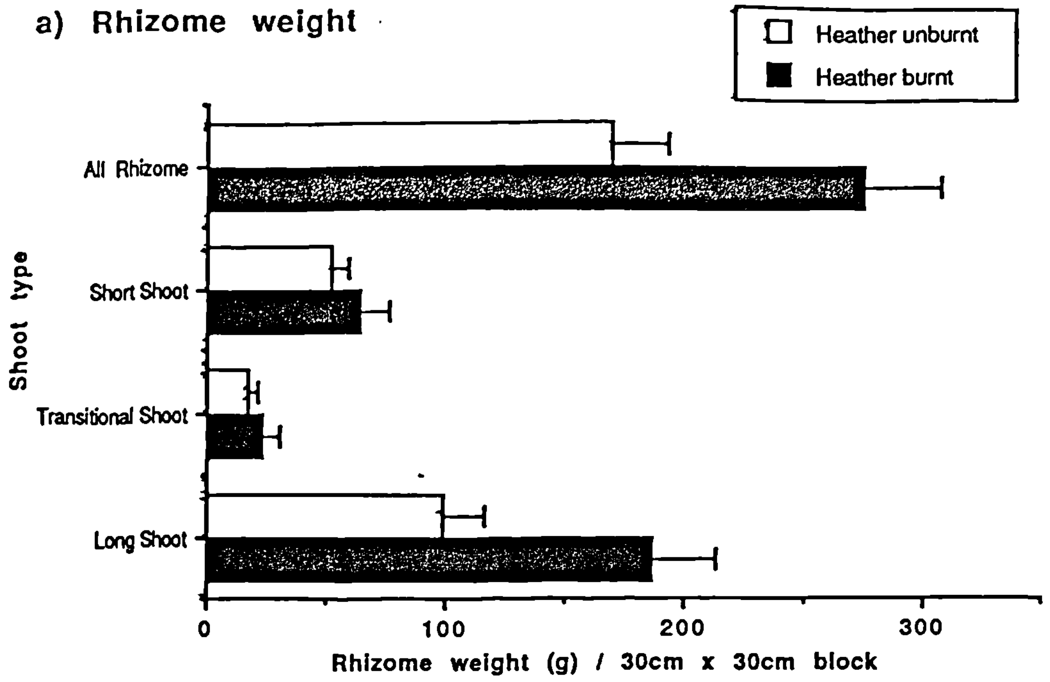
6.5.2b Results

Both bracken mean rhizome weights (0.68 Kg m^{-2} ($\pm$0.096 Kg m^{-2})) and mean active bud numbers (55 ($\pm$14.7)) are considerably lower in the bracken-*Calluna*

Fig. 46 Harland moor showing an area where *Calluna* has been burnt into a bracken stand in the autumn of 1989. A mixture of mature *Calluna* and bracken is seen in the background. (1.2.90).

Fig. 47 The rapid encroachment of bracken in Summer 1990 into an area previously dominated by mature *Calluna*. (15.8.91).

a) Rhizome weight



b) Active bud number

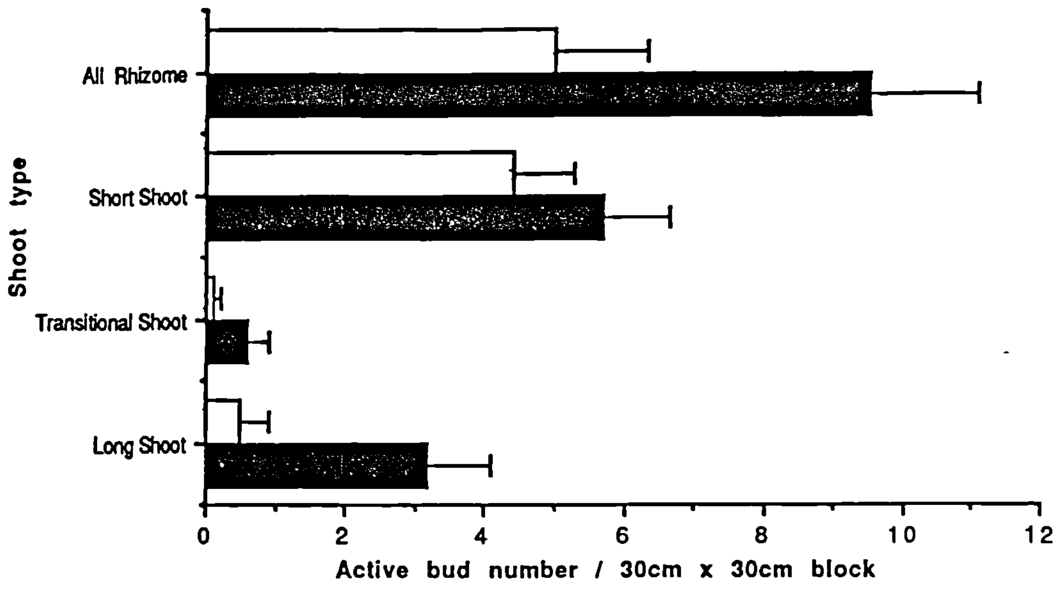


Fig. 48 Changes in rhizome a) fresh weight and b) active bud number resulting from the removal of *Calluna* from a bracken-*Calluna* mixture by burning. Data presented are means for rhizome from ten 30cm x 30cm sample areas. Error bars are the standard error of the mean.

mixture found on Harland Moor than in the almost monoculture mature bracken stand (**LMS**). On Lowna the mean rhizome weight at 10th May 1990, also taken for a time before frond emergence, was 5.9 Kg m^{-2} (±0.85 Kg m^{-2}). Mean active bud numbers present at this time were 116 (±18.6). The rhizome types which were present in the two stands did not vary greatly. Proportions of long, transitional and short shoots were 65%, 5%, 30% respectively in the mature stand at **LMS** and 59%, 10%, 31% respectively in the bracken-*Calluna* mixture on Harland moor. The only change occuring in these ratios is a shift from long shoots to transitional shoots in the mixture, a feature which is typical of bracken margins.

The result of the removal of *Calluna* by burning is a rapid increase in the weight of rhizome present in those areas where *Calluna* was burnt over those areas in which *Calluna* remains in the mixture with bracken (fig. 48a). The increase is statistically significant in a t-test (P=0.029). This increase occurs in all rhizome types but the greatest increase is in the rapidly elongating long shoots. The proportion of total rhizome made up of long shoots therefore increases from 59% where *Calluna* remains in the mixture with bracken, to 68% where the *Calluna* is burnt.

The increase in rhizome weight present as a result of *Calluna* burning is accompanied by an increase in the number of active rhizome buds present. This increase, shown in fig. 48b, occurs largely on the long shoots and is probably largely explained by the increase in rhizome of that type. Again the increase is statistically significant in a t-test (P=0.023).

6.5.3 Removal of Calluna by cutting at the interface with a bracken stand

6.5.3a Method

All *Calluna* visible above the ground was removed from a number of experimental strips (see 3.1.4) with a strimmer at 2 bracken fronts - **GTHR** (9 strips) and **LLP** (8 strips). These strips were compared with control strips on the same margin, 6 strips on **GTHR** and 7 strips on **LLP**. Cutting took place in early April before the emergence of the first bracken croziers so that the seasons bracken fronds were not damaged by the treatment. The *Calluna* which was cut was removed from the site by raking.

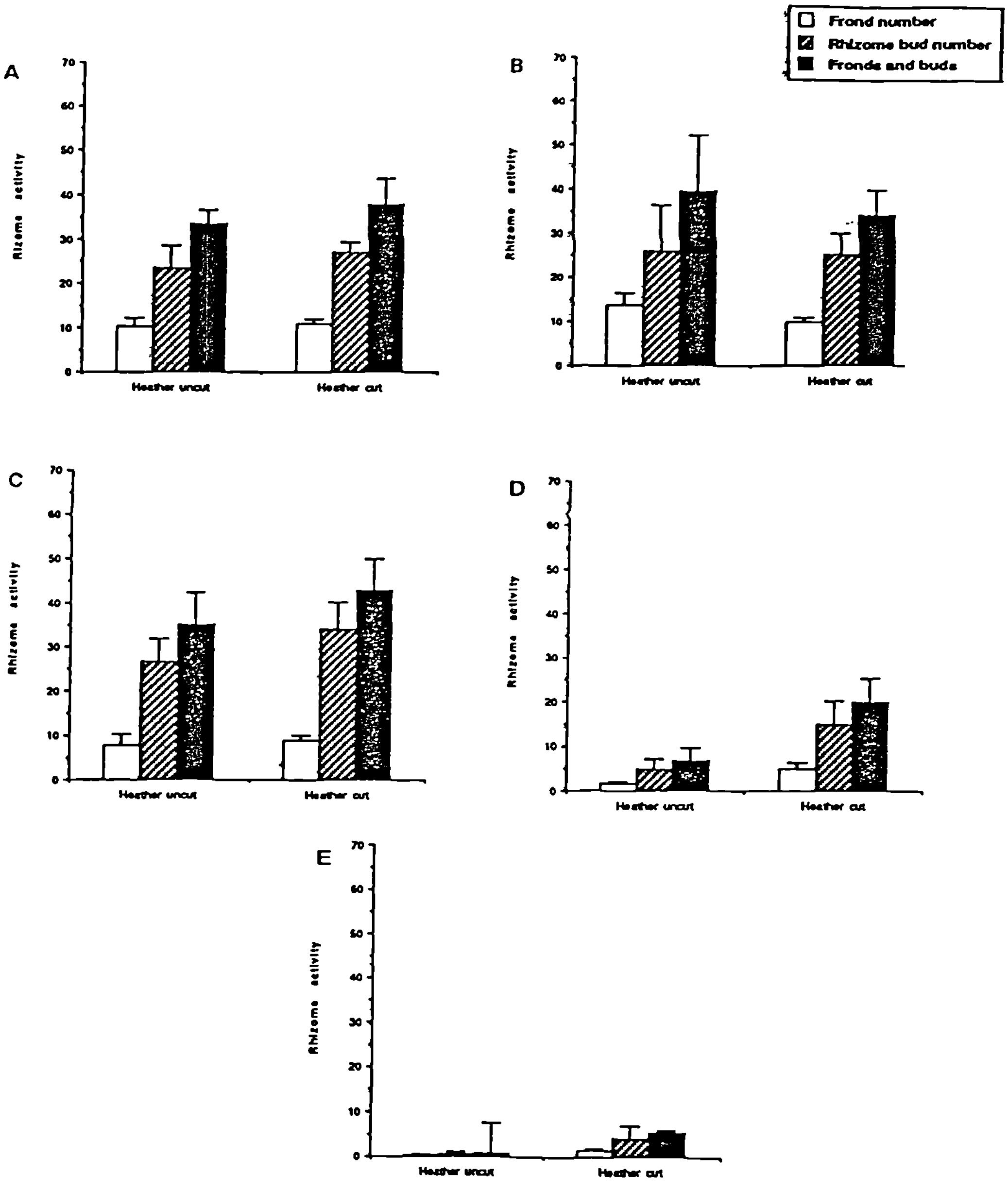


Fig. 49 The effect of removal of *Calluna* by cutting from experimental strips at bracken margins a) LLP and b) GTHR (shown overleaf) on bracken rhizome activity. The data presented are the means for a) 8 and b) 9 treated strips, and a) 6 and b) 7 control strips. Error bars are the standard error of the mean.

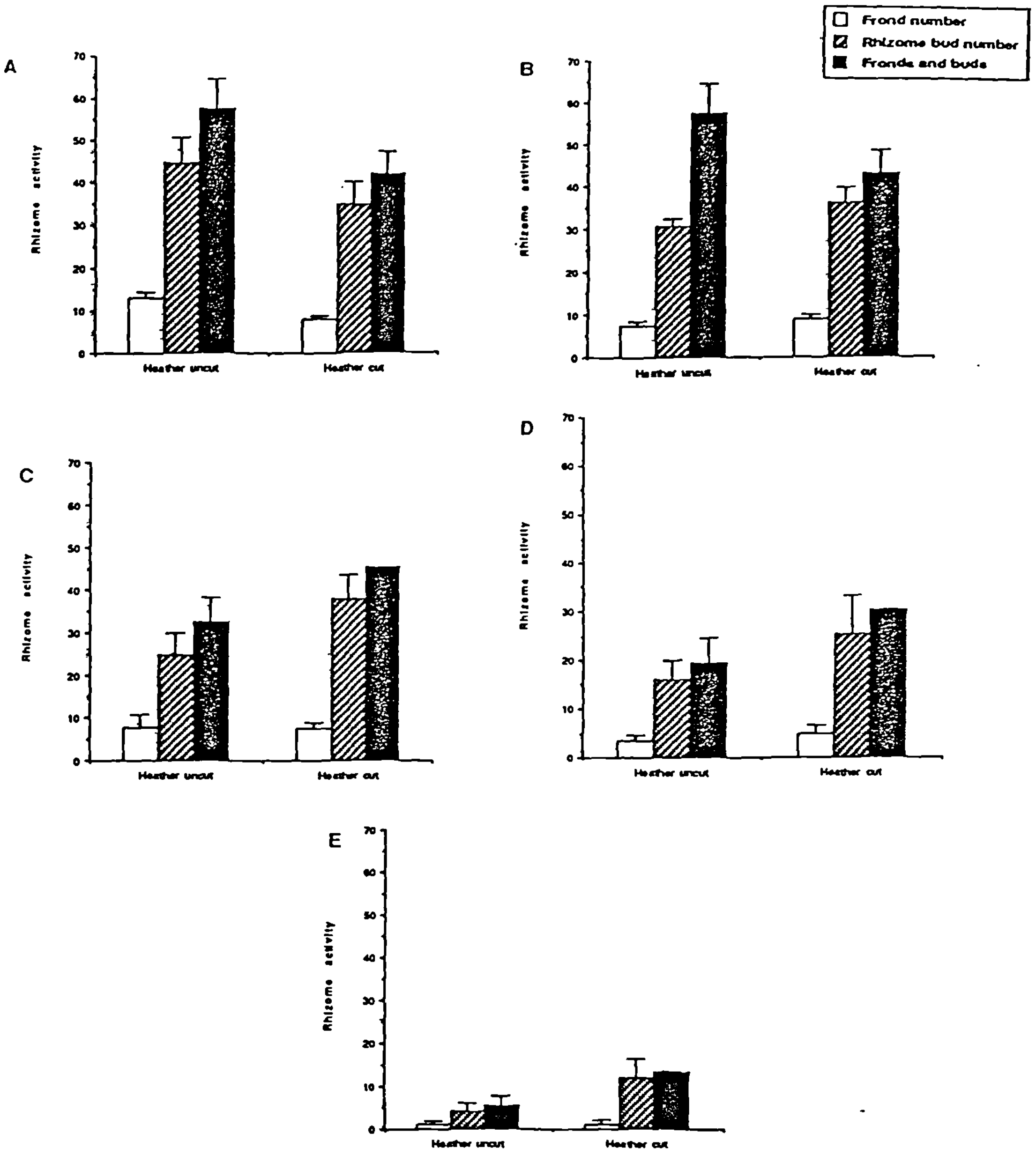


Fig. 49 cont. The effect of removal of *Calluna* by cutting from experimental strips at bracken margins b) GTHR.

Frond numbers, heights and unfurled pinnae number were recorded at fortnightly intervals throughout the growing season. Rhizome data was collected from 50cm x 50cm blocks at the end of the season and again fresh weights and rhizome bud numbers, positions and activity recorded for each rhizome type.

6.5.3b Results

Within the short course of the experiment (just one seasons growth) there is little evidence that the removal of small areas of *Calluna* by cutting in this way has promoted the advance of pioneering rhizome over that in control strips. Neither frond numbers nor active bud numbers significantly increased in all of the quadrats in the experimental strips on **GTHR**, or in quadrats A-C on **LLP**. Only in the outermost quadrats on **LLP** was there a statistically significant increase in frond numbers found in transformed $((n+1)^{1/2})$ t-tests ($P=0.039$ in quadrat D) and the total of frond and active bud numbers ($P=0.059$ in quadrat D).

6.5.4 Discussion

The most significant increases, both of total rhizome present and number of active buds on the rhizome, resulting from the removal of *Calluna* occur on Harland Moor where bracken was already well-established but did not become dominant until *Calluna* was removed. The removal of *Calluna* by burning, rather than cutting, may also give rise to release of a flush of mineral nutrients which can be rapidly exploited by the bracken which is already present (Allen *et al.*, 1969).

It is not surprising that the visible effects of removal of *Calluna* by cutting are seen most clearly on the outermost pioneering rhizome in quadrats D and E of the experimental strips on **LLP**. Here the *Calluna* which was removed is more mature and larger than that on **GTHR**. The effects of *Calluna* removal cannot be expected to be as great in quadrats A and B of experimental strips where bracken is the dominant vegetation. Bracken was not able to exploit the removal of *Calluna* by cutting in the same way as the removal of *Calluna* by burning on Harland Moor was exploited within a very short time period. This difference might be explained by the absence of the rapid release of nutrients following cutting. The results of these experiments indicate that sufficient time may be available for the recovery of *Calluna* following cutting close to an advancing bracken margin before bracken encroaches and becomes dominant in areas previously occupied by *Calluna*. However, where high-temperature burns take place because of the burning of old

Calluna plants, nutrients are released in the burning and bracken is able to encroach rapidly to exploit resources made available. This is especially the case where bracken is already present in a mixture with *Calluna*.

6.6 THE ROLE OF PLANT GROWTH REGULATORS IN THE CONTROL OF RHIZOME ACTIVITY

6.6.1 Introduction

The role of plant growth regulators in the control of bud dormancy is poorly understood. However ethene has been used for many years to break the bud dormancy of fruit trees and gibberellins have also been applied to break the bud dormancy of deciduous plants (Perry and Helmers, 1973). Work on the role of hormones in controlling the bud dormancy of plant storage organs has mainly involved the potato (*Solanum tuberosum*) with both ethene (Pratt and Goeschl, 1969; Rappaport *et al.*, 1965) and gibberellins (Poapst *et al.*, 1968) being found to break dormancy and stimulate sprouting in the potato tuber. A preliminary experiment was therefore set up to investigate the possible effects of these hormones on the dormancy of buds in the rhizome of bracken.

6.6.2 Treatment of isolated rhizome segments with gibberellic acid (GA_3) and Ethrel 'E'

6.6.2a Method

5 segments each of long and short shoot rhizome of 25cm in length were planted in a series of boxes containing Irish Moss Peat and left to grow in a glasshouse. Rhizome segments were allocated between the boxes in a random manner and did not necessarily include an apex. The rhizome was collected from Skipwith Common on 15th March,1990. 3 replicate boxes were used for each treatment which were applied as follows:

a) untreated control
b) the cut ends of the rhizome segments were dipped into GA_3 powder
c) one cut end of each rhizome segment was soaked in a solution of Ethrel 'E', an ethene releasing compound for 1 hour.

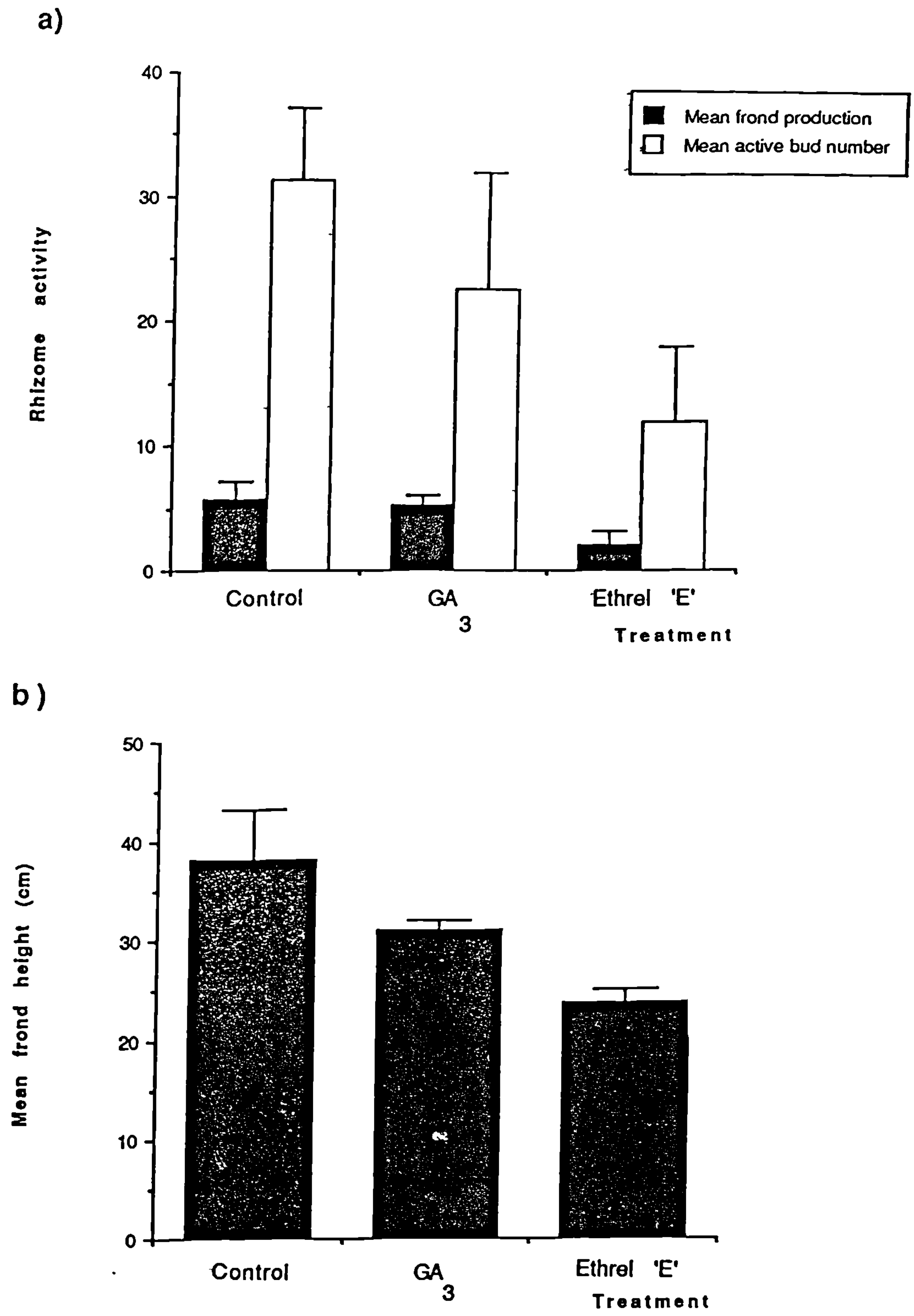


Fig. 50 The effects of gibberellic acid and ethene (as released by ethrel 'E') on a) rhizome activity and b) frond heights of isolated rhizome segments. Each block represents the mean of 3 replicate boxes (each containing 10 rhizome segments) for each treatment and controls. Error bars are the standard error of the mean.

6.6.2b Results and discussion

The treatment of isolated rhizome segments with plant growth regulators resulted in the reductions from untreated levels in frond production, rhizome bud activity and mean frond height shown in fig. 50. The experiment provides no evidence for the stimulation of rhizome by either of the compounds used. Treatment with these compounds resulted in the formation of stunted fronds which, particularly following treatment with Ethrel 'E', often became necrotic and died before reaching maturity. Following discussion with other research workers (Kirkwood pers comm.) who had experienced similar results and, due to difficulties in administering these treatments in large scale experiments particularly in the field, it was decided to dismiss plant growth regulators as agents in the stimulation of bracken rhizome activity.

6.7 RHIZOME ACTIVITY IN THE RECOVERY FROM HERBICIDE TREATMENT

6.7.1 Introduction

Successful treatment with asulam achieves great reductions in frond number of more than 95% in the season after spraying. However regrowth occurs unless respraying and follow-up treatments take place giving full frond density after about 5 years (Veerasekaran *et al.*, 1978). This recovery may come in part from the invasion of bracken from areas adjacent to the treated area but in larger sprayed areas growth arises from rhizome buds which have survived the herbicide. A large number of dormant buds are present on the rhizome, which may remain in a metabolically inactive state for many years after their initiation before being stimulated into activity (Daniels 1981). Several authors (Veerasekaran *et al.*, 1978; Lowday, 1987) have suggested that recovery is initiated by buds found on the long storage rhizome shoots.

Isolated fronds growing on three areas of moorland which had recently been treated with asulam were dug out and their positions on the rhizome observed.

6.7.2 Site descriptions

1. Spaunton roadside (Grid ref. SE710 908)

A track of approximately 10m in width around the edge of the bracken stand was tractor sprayed with asulam in the late summer of 1989. Good control has been achieved with less than 1 frond m^{-2} present at the time the observations were made in August 1992. Other vegetation was sparse with mosses predominating. Bracken litter was very shallow (fig. 51).

2. Lowna Lund (Grid ref. SE693919)

The area of bracken at the NE edge of Lowna Lund close to the meeting of Lund Road and Dale End Road was sprayed by helicopter with asulam in August 1991. The level of control achieved was poor with 1-2 fronds m^{-2} present. Again other vegetation was sparse with some *Calluna* present but litter layers were deeper (5-10cm) than on the Spaunton roadside site.

3. Spaunton Rosedale Road (Grid ref. SE696909)

At this site bracken control by the aerial spraying of asulam had been carried out prior to 1989, bracken litter was not present and a good recovery of grass species has been achieved. Very few fronds were present (approximately 1 every 5-10m^2) (fig. 52).

Fig 51. Recovery from herbicides Site 1 - Spaunton Roadside. (15.8.91).

Fig. 52. Recovery from herbicides Site 3 - Spaunton Rosedale Road. (15.8.91).

6.7.3 Observations and discussion

At all the sites live rhizome which appeared undamaged by herbicide treatment was present. At sites 1 and 2 the rhizome on which fronds were found was similar to the pioneering rhizome found at stand margins in that more than one growing bud was present at the apex and there was little evidence of many years of frond production on alternate sides of short shoots. At site 3 where the best control has been achieved and the greatest period of time has past since treatment the rhizome giving rise to fronds has a juvenile appearance having a softer, lighter brown covering than has normally been observed in mature rhizome. Much of the rhizome present at this site was dead though some rhizome which appeared to be severely necrotic still bore fronds.

At all sites the fronds did not, as has been suggested previously, originate from dormant buds occuring deep in the soil on storage rhizome. Most of the fronds excavated were found growing from close to the apex of a rhizome shoot (31/36 (86%) at site 1; 29/40 (73%) at site 2; 11/15 (73%) at site 3). At many of these apices (45% at site 1; 31% at site 2; 36% at site 3) more than one frond primordia were present beyond the frond. The majority of the remaining fronds were found on short shoots originating from buds which had become dormant after initiation (6% at site 1; 27% at site 2; 13% at site 3) or from previously dormant buds at the axis of lateral shoots (8% at site 1; 12% at site 2). None of the fronds observed originated from dormant adaxial buds at old frond bases.

Information on the timing of recovery of bracken rhizome following herbicide treatment, and the manner in which this recovery takes place, is of importance to bracken control programmes in determining the best strategy for follow-up treatments after herbicide spraying.

6.8 DISCUSSION

The experiments in this chapter show that several of the factors investigated to have had a stimulatory effect on the activity of bracken rhizome. It is interesting that the isolation of small segments of rhizome (of 20-30cm in length) provokes greater formation of active rhizome buds even before the application of further treatments. Whilst isolation of these shoots obviously disrupts the physiology of the rhizome in many ways, this result would tend to suggest that there is a factor, not related to dominance by the apex, which is coming from the basal end of the rhizome shoot and supporting the dormancy of lateral buds and prevention of further growth of the terminal bud at the apex. Leakey and Chancellor (1975) also reported the importance of "parental" factors in maintaining apical dominance in *A. repens* and were unable to substitute plant growth regulators NAA (napthaleneacetic acid) and BAP (6-benzylamino purine) for the apex in preventing the growth of lateral buds in rhizome segments which had been isolated from the remainder of the plant.

Difficulties in achieving the translocation of herbicides throughout the extensive rhizome system of bracken have often been cited as one of the major problems experienced in controlling bracken by herbicide spraying (Veerasekaran *et al.*, 1978). Metabolically inactive dormant rhizome buds, in particular, have proved difficult to reach with asulam and have acted as sources of recovery and re-invasion by bracken following herbicide control.

The stimulation of bud development and subsequent bud reserve depletion following cutting treatments have been well documented (Williams and Foley, 1976; Lowday, 1984a) and cutting has also been recommended in the past as a pre-treatment prior to asulam spraying used to deplete dry matter, increase frond number and the proportion of rhizome buds which are active and to reduce height to a uniform level beneficial to herbicide uptake (Lowday and Lakhani, 1987). The results presented here suggest that phosphate and nitrogen fertilisers might be used in a similar manner to cutting pre-treatments for the stimulation of rhizome activity prior to herbicide spraying. Such a treatment would be prohibitively expensive in the control of bracken over large areas of moorland but would be more useful where bracken on smaller areas of perhaps more valuable land is to be controlled. Nutrient application would have the added advantage of promoting the subsequent recovery of other vegetation. Nutrients were shown to stimulate rhizome activity both at the apex, exhausting carbohydrate reserves in the formation of new fronds and creating additional sinks which may improve herbicide distribution through the rhizome, and also in buds which had been previously dormant elsewhere on the rhizome.

The promising effects of low doses of glyphosate in stimulating rhizome activity produced in bracken grown under glass from rhizome in moorland soil blocks was not reproduced under field conditions. Treatment of large areas with such a non-selective herbicide would undoubtedly give rise to problems of damage to non-target species (Mitchell, 1977) and would only be possible in areas accessible to machinery.

The importance of not burning *Calluna* close to mature bracken stands, and especially into areas where bracken is already present, must be stressed. Where bracken-*Calluna* mixtures are present it may become necessary to burn *Calluna* in the building phase before allowing it to reach a degenerate phase at which point bracken may well become the dominant vegetation. In this case burning will result in rapid stimulation of bracken rhizome activity. It is important to control bracken by herbicide spraying within a short period of time after *Calluna* burning otherwise bracken will rapidly become dominant. Transient flushes of nutrients resulting from the burning of *Calluna* may well act to stimulate bracken bud activity and frond development, producing a similar effect to the pre-treatment of bracken with fertilisers prior to herbicide spraying.

On the sites observed within the North York Moors where bracken control with asulam had recently taken place rhizome recovery was occuring predominately at the apices of short, frond-bearing shoots rather than from dominant buds on deep storage rhizome. It is not clear whether these apices had been dormant at the time of herbicide treatment. There was also some evidence of recovery from buds in the axis of lateral rhizome branches and in the positions of frond primordia which had become dormant shortly after their initiation. The majority of buds in these positions on undisturbed rhizome are in a dormant state. Much of the rhizome from which recovery was beginning appeared to have been damaged by the herbicide in a manner similar to that reported by Lowday (1987). Most severe damage is localised to frond primordia and terminal buds whilst much of the remainder of the rhizome network survives, if not in a totally healthy state. Treatment of bracken by asulam may, in the long term, actually rejuvenate the bracken stand since much of the regrowth seems to be coming from the younger short shoots rather than shoots which have been producing fronds for many years.

7. GENERAL DISCUSSION

The treatment of bracken with the herbicide asulam can, at least initially, result in excellent control with reductions in frond number of more than 95% in the season following control (Veerasekaran *et al.*, 1978). The total and permanent eradication of bracken, even in localised areas, by aerial spraying of asulam is however difficult, if not impossible. Success of the control treatment is dependent upon achieving an even cover of the bracken stand, usually by spraying from a helicopter. Spray misses can often occur in the field when, perhaps due to wind or navigation problems, the herbicide has not reached the bracken fronds in sufficient doses. Unless good follow-up programmes are carried out after the initial spraying, this poorly controlled bracken then acts as a source of rapid re-invasion into areas which have been adequately controlled. Even where asulam has been applied in the correct dose, much of the rhizome may survive in a damaged state. This rhizome is then able to produce fronds from surviving buds, usually at the apices of rhizome branches, which may have been dormant at the time of herbicide treatment. This growth may occur several seasons after control has taken place and herbicides may, in the long-term, actually re-juvenate the rhizome by acting as a chemical pruning agent removing older rhizome and allowing regrowth from younger shoots. After good bracken control has been achieved, either by chemical, mechanical or biological means, there remains the problem of removal of litter and the re-establishment of alternative vegetation.

The information collected during the course of this project supports the use of herbicides to control bracken at its margins by tractor spraying of small perimeter belts wherever this is physically possible. Advancing fronts, characterised by a gentle decline in frond and first pinnae height, frond number and in rhizome biomass, should be prioritised in order to prevent further bracken encroachment. Such a technique may be especially useful when finances available for control do not extend to aerial spraying of large areas of bracken.

Morphological data has shown the presence of greater numbers of fronds just behind the interface with *Calluna* than are seen in a mature bracken stand. This increase in frond number provides an increase in the number of penetration points available to the herbicide. The proportions of rhizome buds which are in a active state are also higher at the stand margins relative to mature bracken. This may increase rhizome susceptibility to herbicide treatment at the margins where fewer buds are metabolically inactive and able to survive herbicide treatment in a dormant state.

Deep litter layers and allelopathic chemicals produced by bracken which hamper its replacement by more favoured plant species, have not accumulated to the same extent at stand margins relative to the remainder of the stand. Sources of propagation of other plant species either by seed or vegetative growth are in close proximity to the cleared area. Regeneration of vegetation still present under sparse bracken at the stand margins will often occur.

Work carried out on transport of resources to the margins of a bracken stand has indicated that, at least in the short term, little transfer of water, mineral nutrients or carbohydrate nutrients takes place from the mature bracken stand to outlying rhizome. Where bracken is controlled at its margins therefore, it is unlikely that recovery could be supported by provision of resources from untreated bracken close by. There is a requirement for the rapid establishment of alternative vegetation and the continued spraying of the perimeter of the bracken stand in order to prevent re-invasion and to force back the bracken stand further with each successive treatment.

The use of cutting treatments prior to asulam spraying have been demonstrated in the past to improve control efficiency by the use of two complementary control methods (Lowday and Lakhani, 1987). Cutting pre-treatments result in better control and slower bracken recovery by depleting rhizome carbohydrate and bud reserves (Lowday, 1984a), by increasing the number of fronds which are available as take-up points for the herbicide and also by stimulating the activity of dormant rhizome buds through the removal of the dominant growing frond.

Several workers (Daniels, 1986; Leakey *et al.*, 1978; McIntyre, 1964;1965) have pointed out the importance of mineral nutrients in the control of apical dominance in rhizomatous plants. Stimulation of rhizome bud activity was observed in isolated rhizome segments and in bracken grown from rhizome in moorland soil blocks. These stimulatory effects were not as clearly observed in the field but this is not surprising when the very short period of time over which the experiment was carried out, and the large size of the bracken system which the experiment attempted to disturb, are considered. What is perhaps more surprising is that on one of the experimental sites (GHH) a stimulatory effect on rhizome bud activity was detected. Bracken may also be responding to deposition of nitrogen as a result of atmospheric pollution resulting in the stimulation of rhizome activity. The use of fertiliser treatments in the field as stimulatory pre-treatments, working in a similar manner to cutting treatments, may be possible where the land is relatively valuable and where more favoured vegetation is able to quickly invade the cleared area and take advantage of the applied nutrients. Again such a situation may arise at the margins of a bracken plant. The importance of forward planning concerned not only with the question of how bracken is best controlled but also how alternative vegetation is to be re-established quickly is of vital importance to any control programme.

It is unlikely that a single or several biological control agents could eradicate bracken from a given area. If such agents were to be released at some time in the future the need for bracken control involving herbicide treatments would not be removed. It is possible that biological agents may again improve the success of herbicide treatments by depleting rhizome resources of dry matter and buds in a similar way to cutting treatments.

Upland sheep farming within the U.K. is an economically marginal industry which is in decline. As this decline occurs, interest in the control of bracken as an agricultural weed of moorland pastures is expected to fall, leading to a decrease in labour and cash available for bracken control programmes. Similarly, the number of workers employed as gamekeepers in the grouse shooting industry within the North York Moors has also declined in recent decades. Labour inputs into the regular burning of mature *Calluna* stands have fallen leading to the burning of over-mature *Calluna* and its subsequent slow recovery. Both the sheep and grouse industries continue to lose valuable income because of the encroachment of bracken (Lawton, 1990) but without outside help are presently not in an economic position to be able to embark upon widespread control programmes.

Help in sharing the financial costs of bracken control programmes has been available to landowners from the North York Moors National Park Department and from MAFF. Whilst support to the sheep and grouse shooting industries are important to both MAFF and the National Park department, perhaps the most important objective of the national park in supporting bracken control programmes is the conservation of the heather moorland habitat.

Increasing concerns about the risks posed by the presence of bracken to human health either from ingestion of bracken spores or contaminated dairy products are presenting a new reason to prevent the further encroachment of bracken. In a period when both upland sheep farming and grouse shooting are in decline it is perhaps more realistic to look upon bracken domination of upland vegetation as an ecological and medical problem rather than a mostly agricultural problem. As such it is necessary to find additional sources of funding, both for bracken control and for research into improving control methods, from sources concerned primarily with conservation (including existing support from the National Park Department) and human health.

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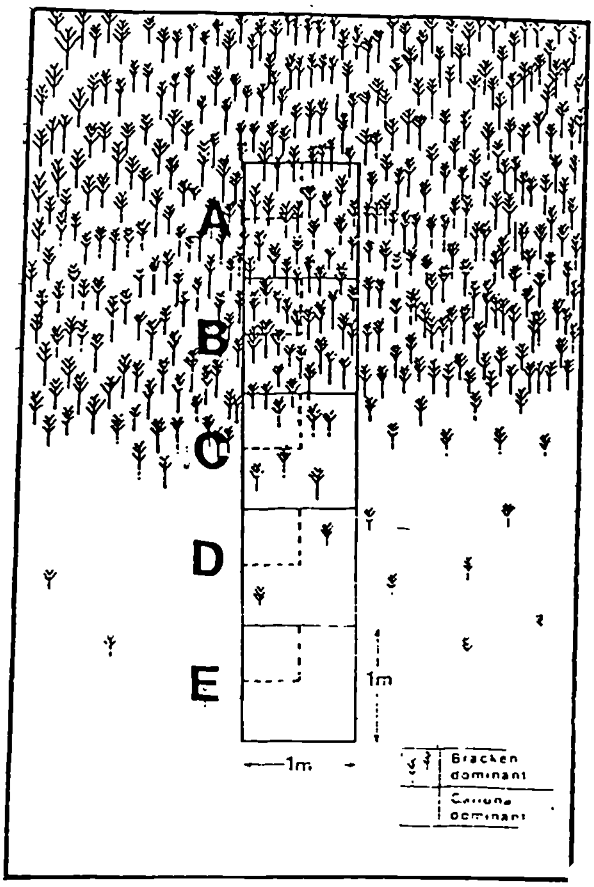
Appendix 1 Experimental sites and their encroachment rates

Lowna mature stand	LMS	Mature stand
Goathland mature stand	GMS	Mature stand
Lowna lund beck	LLB	Non-advancing bracken margin
Lowna lund patches	LLP	Non-advancing bracken margin
Lowna lund track	LLT	Advancing bracken margin
Goathland Hunt House	GHH	Advancing bracken margin
Goathland Two Howes Rigg	GTHR	Advancing bracken margin

Appendix 2 Days after 1st May and equivalent dates

Days after 1st May	Date
1	1 May
20	20 May
32	1 June
40	9 June
60	30 June
53	1 July
80	18 July
95	1 Aug
100	6 Aug
120	26 Aug
126	1 Sept

Appendix 4 Sketch diagram of experimental strip showing positions of quadrat



Appendix 3 Generalised diagram of rhizome bud positions