BRACKEN (*Pteridium aquilinum* (L.) Kuhn) STAND CHARACTERISATION ON THE NORTH YORK MOORS: *A STUDY OF THE RHIZOME AND FROND SYSTEM WITH REGARD TO A LARGE SCALE CONTROL PROGRAMME*

by

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Abstract

Large-scale rhizome sampling on the North York Moors together with an assessment of published bracken sampling protocols concluded that small-scale sampling of the rhizome system is inadequate to describe upland bracken stands accurately. It is also concluded that the frond cannot be used as an indicator of the rhizome system before or after treatment to achieve bracken control. An improved sampling strategy is proposed which increases the reliability of data collected and the validity of any conclusions drawn form such data.

The structure of bracken rhizome systems, from separate stands on the North York Moors, were found to be distinct from one another and demonstrated intrinsic variation which could affect a differential response to control. The most important components of the rhizome system, when considering chemical control using asulam are: the number of buds likely to remain viable afterwards; the rhizome biomass which may effect herbicide dilution; and the origin of frond production which may affect herbicide distribution.

The effect of asulam was to cause severe localised damage to buds and apices detectable one year after treatment but the rhizome dry weight remained unaffected. In one instance asulam appeared to have a stimulatory effect on bracken by breaking bud dormancy, this was related to the characteristics of the stand before treatment. It is recommended that the use of asulam is restricted to pioneer or building stands which have a high number of active buds in relation to dormant buds, and a low rhizome dry weight. Crushing bracken once a year effected a temporary reduction in rhizome dry weight, and an increase in frond number (which could improve asulam absorption). A combination of crushing and asulam reduced both bud number and rhizome dry weight and was thus the most successful treatment studied for reduction of bracken vigour. In particular, stands adjacent to valued plant communities should be targeted for control. It is suggested that bilberry could be used as a buffer zone between heather and invading bracken.

The use of large-scale bracken control programmes in upland regions was questioned due to the apparent ineffectiveness of asulam on the rhizome system, and the difficulty of implementing a programme of successful follow-up and after-care management. A broad classification of upland bracken, based on the rhizome, was recognised, and general models of selective bracken control suggested, by evaluation of the rhizome system with regard to the number of dormant and active buds, and the rhizome dry weight.

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Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

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Relevant scientific seminars and conferences were regularly attended at which work was often presented and papers prepared for publication.

Signed.....S. Holloway.............

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Courses and conferences attended.

Staff Development Research Seminars attended at Seale-Hayne Faculty of Agriculture, Food & Land Use, University of Plymouth. 1991-1994.

International Bracken Group Autumn Meeting. North York Moors National Park, Helmsley, North Yorkshire. September 1992.

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Chapter 1. Introduction.

1.1 The spread of bracken in the U.K.

Bracken [*Pteridium aquilinum* (L.) Kuhn] is an internationally widespread cosmopolitan species that is spreading in the U.K. Due to agricultural, environmental, economic and social changes *Pteridium aquilinum* has become a problematic weed for a number of ecological, amenity and health reasons. There are currently chemical and mechanical methods of control available with the possibility of biological control in the future. Nevertheless, no method of control has proven to be completely effective in eliminating bracken from large areas.

In the U.K., pre 3500 BC, bracken was common but rarely dominant in woods, being suppressed by the low light availability found under a dense canopy of mixed oak forest (Smith 1986). When clearance of woodland began in the Neolithic, bracken was able to colonise the exposed ground and out-compete other ground flora (Rymer 1976). Further deforestation throughout the Bronze Age, medieval period and this century increased the dominance of bracken (Taylor 1986) to the point where it has now come into direct confrontation with local fauna and flora and the rural community.

In the U.K. bracken now occurs across a wide range of habitats from woodland and open moor to coastal heath, commons, field margins and roadside verges (Hopkins 1990). The large pool of potential colonising bracken has proved to be a problem when certain changes in agricultural practices take place. Woodland clearance and land that is set aside, abandoned or poorly managed provides ideal areas for bracken to expand further.

In the U.K. the total extent and encroachment rates of bracken that have been recorded vary, accuracy being hindered by extrapolation from local studies, low density (summer) bracken, bracken growing under woodland and the use of remote sensing techniques which suffer from inaccuracies in slope cover estimation. Estimates on bracken cover in Great Britain range from 2880 km^2 (Bunce, Barr & Whittaker 1981) to 6361 km^2 (Taylor 1986) representing 1.3% - 2.8% of the total land area, respectively. However, it has been postulated that the increase in cover recorded merely represents long-term regrowth from depleted rhizomes from the large areas of bracken controlled before 1960 (Marrs, Pakeman & Lowday 1993).

Between 1972 and 1986 an increase of 30% was recorded in the number of swards in which bracken was present in a study of upland farms in seven areas of Wales, the Pennines and Shropshire (Hopkins, Wainwright, Murray, Bowling & Webb 1988). Encroachment has also been recorded for several other upland areas including the North York Moors (Brown 1986), Wales (Taylor 1986) and Scotland (Miller, Morrice & Whitworth 1990). Estmates of the current spread of bracken are placed between 1 - 3% a year on a local, regional and national scale (Taylor 1986; Hopkins *et al* 1988; Miller *et al* 1990).

However, a study of Less Favoured Area hill farms in Northern Britain and Wales, and an area of the Lleyn Penninsula showed a local decrease in bracken infestation (Buse 1989; Lawton & Varvarigos 1989). An overall decrease of 19.2 km^2 of the total bracken infested land has been suggested for the National Parks (Countryside Commission 1991). However, these decreases are artifacts of the survey methods and are due in large part to the timing and the definition of 'bracken cover' of the survey. Decreases in bracken infestation are attributable to bracken control schemes, local agricultural practises and a shift to commercial forestry.

1.2 The taxonomy and morphology of bracken.

1.2.1 Taxonomy.

The bracken fern, *Pteridium aquilinum*, belongs to the broad grouping of Pteridophyta (vascular cryptogams) which include the most ancient of the land plants i.e. ferns, clubmosses, horsetails and quillworts (Page 1976). The ferns and fern allies are comprised of over 15,000 species and have evolved over a period of 300 million years (Page 1986). A species of fern similar to *Pteridium aquilinum* has been recorded from the late Jurassic period 55 million years ago (Zhen & Zhang 1983) and bracken is now considered to have the widest natural range of any vascular plant in the world (Jermy, Arnold, Farrell & Perring 1978).

In the U.K. there are three taxa of the genus *Pteridium aquilinum*, the most common *Pteridium aquilinum* (Kuhn) subspecies *aquilinum* var. *aquilinum* comprising 95% of the total population of bracken. This species was defined as a distinct genus in 1879 after Kuhn in v.d. Decken, Reisen in Ost-Africa. A full account of the history of taxonomy was compiled by Tryon (1941). The taxa has the widest ecological amplitude, is vegetatively vigorous and capable of reproduction and colonisation on a massive scale. These attributes make *Pteridium aquilinum* (Kuhn) subspecies *aquilinum* var *aquilinum* a serious threat to agriculture, conservation, recreation, game and forestry (through propagation difficulties).

The other two taxa given the rank of subspecies are *Pteridium aquilinum* subsp. *latiusculum* (Desv.) C.N.Page and *Pteridium aquilinum* subsp. *atlanticum* (Page 1989, 1990). The subspecies *latiusculum* is native of Scottish *Pinus sylvestris* pinewood, is more resilient to frost damage than subsp. *aquilinum* and is able to tolerate a shorter growing season. In contrast the taxa *Pteridium aquilinum* subsp. *atlanticum* is a low altitude grass turf species found within the milder oceanic climes of the Western Scotland Atlantic fringe.

This project focuses on *Pteridium aquilinum* (Kuhn) subspecies *aquilinum* var. *aquilinum*. This species will be referred to as bracken. If other sub-species are being discussed this will be indicated by giving the full Latin nomenclature.

1.2.2 The structure of the mature plant.

The major morphological features of bracken are illustrated in Fig. 1 and Thomson (1990). In the northern hemisphere fronds appear during April and May, mature during June/July and senesce in September/October. The leaves are solitary, 2 to 3 pinnate, stout and the fronds can reach a standing crop weight of 1200 gm^{-2} (Watt 1976).

The litter produced by the fronds is resistant to decay (Frankland 1976) and can reach depths in excess of 80 cm and dry weights of 3000 gm^{-2} (Watt 1976). These figures will however depend on exposure and direct and indirect interference by man. The rhizome is responsible for frond production, lateral extension of the plant and acts as a storage organ for carbohydrate. There are two major forms of rhizome, i) bifurcating long shoots and ii) short shoots (Fig. 1).

i) Long shoots occur deep in the soil (10-30cm) and are primarily for carbohydrate storage and lateral spread (up to 2.1 m/year recorded in invading stands (Fletcher & Kirkwood 1979)).

ii) The short shoots bear over 80% of frond-producing buds (Lee, Cooke & Bines 1986). Growth is perpendicular up to 2.5 - 10.0 cm below the surface where the shoot then grows parallel to the soil surface. The overall growth of the short shoot is slow; one frond produced per year at 0.5 - 2.0 cm intervals (Daniels 1981). The first bud of a short shoot is normally dormant and can remain viable for up to 12 years. At the base of each frond a basal bud may remain dormant which is capable of producing either lateral branches or a new frond

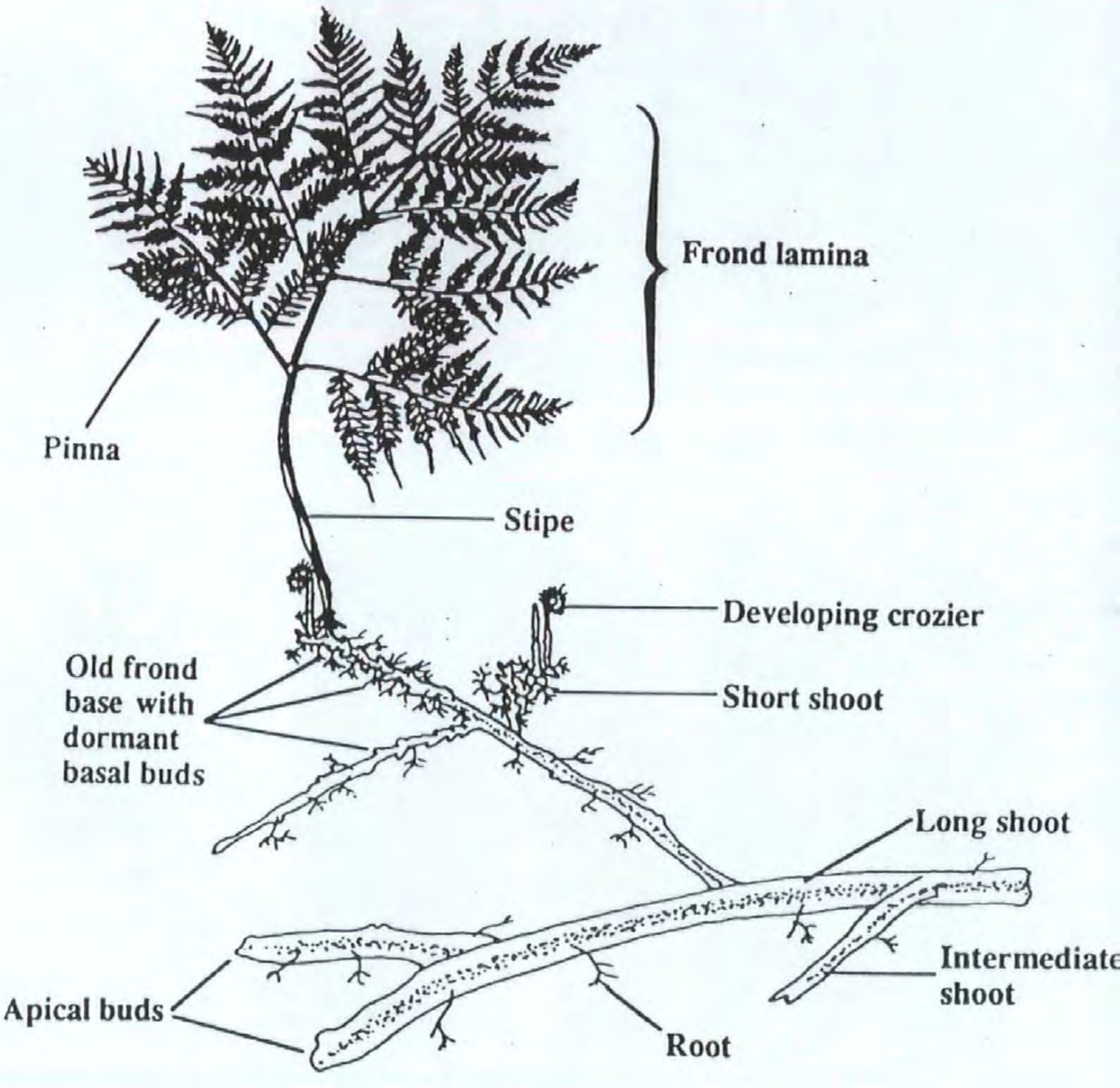


Figure 1. The major morphological features of bracken. Adapted from Thomson (1990) and Daniels (1981).

if damage takes place (Daniels 1981; Watt 1976).

There is also a third category of shoot, the intermediate shoot, which demonstrates characteristics of both the short and long shoots by its ability to store carbohydrate and to produce large numbers of frond-producing buds. The distribution of each rhizome category will depend on local soil conditions (Watt 1940) eg depth, porosity, shear strength, organic matter content, drainage. Roots growing from the rhizome tend to be brittle and arise in acropetal succession close behind the shoot tip (Webster & Steaves 1958). They are especially prevalent on the short shoots and younger long shoots.

1.2.3 The life cycle of bracken.

The lifecycle of bracken begins with the release of millions of spores from the mature sporangium on the adult sporophyte. A number of conditions must be met for successful spore germination including high nutrient status, high pH and the right weather. Bracken spores will not germinate under established stands due to unsuitable soil conditions, the deep litter layer and competition from the adult sporophyte.

Land ideal for sporal colonisation is often associated with land management and interference such as agriculture, forestry and road construction (Dyer 1990). Spore germination has been especially linked to firing of the land which releases high levels of nutrients (Watt 1976) resulting in a marked increase in pH and an increase in soil moisture and temperature (Oinonen 1967).

Once fertilisation has taken place the sporeling develops a simple bipennate leaf and rhizome. If the sporeling survives over winter, the rhizome system increases in extent and mass and frond production increases. The adult sporophyte becomes fertile 3 to 4 years later (Thomson 1990).

The established bracken sporophyte consists of an extensive underground rhizome network with the capability to colonise large areas vegetatively. Watt (1947) recognised a five-stage cycle of growth in bracken stands at Lakenheath Warren. The work of Watt concentrated on the pattern of growth of bracken with regard to community structure. Five phases of development were recognised by Watt (1945, 1947); i) grass heath (no bracken), ii) pioneer iii) building, iv) mature and v) degenerate (although this final stage may be difficult to identify). Growth was related to soil depth, frost occurrence (Watt 1950,1964), litter accumulation (Watt 1969), aeration (1979) and competition from heather (Watt 1955). Both the rhizome and frond were studied in detail (Watt 1940, 1945).

At the pioneer stage, bracken will invade other communities such as grass heath or Calluna moor due to lateral competition of the rhizomes. Fronds tend to be generally short in height and the rhizomes parallel and few in number. The height and density of the fronds and the rhizome density gradually increases during the building stage to maturity. After maturity a degenerate phase may be reached which is characterised by rhizome fragmentation. This phase then gives way to the hinterland.

The rhizome network can be extremely large with a total diameter of 390 m being recorded (Sheffield, Wolf & Haufler 1989). An individual bracken clone can survive for up to 1000 years (Oinonen 1967) with individual rhizomes surviving for approximately 35-75 years (Watt 1940). Any one bracken stand may also consist of singular or multiple clones (Wolf, Sheffield & Haufler 1990). Although sexual reproduction in bracken had been considered rare (Conway 1953; Oinonen 1967; Page 1976) it has now been realised through electrophresis that it may be more frequent than first assumed, adding to the genetic variation of bracken populations (Wolf, Haufler & Sheffield 1988). If variation is present within a bracken stand there may also be present genes conveying resistance against chemical or biological control. This may go towards explaining the rapid regrowth observed within some treated stands and not others.

1.2.4 The annual growth cycle of bracken.

The growth cycle of bracken consists of distinct biomass movements between the frond and rhizome system over time (Williams & Foley 1976). During the winter period bracken survives via the underground rhizome system. Due to minimal respiration loss, biomass levels rarely fall below 50% of the total rhizome dry weight (excluding loss from frost damage). As soil temperatures increase during the spring, the rhizome carbohydrate reserves are utilised for frond production and expansion (Ader 1990).

The photosynthate produced by the young fronds is utilised for further growth and expansion until full frond growth is achieved around late July. Once frond growth has ceased the source/sink locations shift with translocation of photosynthate to the rhizome replacing the carbohydrate reserves which were depleted during the spring (Watt 1976). The carbohydrate reserves reach a maximum during senescence, resulting in the production of new rhizome tissue.

1.2.5 The extent of bracken growth.

Bracken has overcome environmental constraints enabling colonisation over a wide range of climatic and edaphic conditions (Page 1979). Through cytological and morphological evidence it has been suggested that bracken originated in the moist tropics and subtropics along rainforest margins, where a number of ferns (eg *Hypolepis* and some *Pteridium*) of similar life-form exist today. Bracken evolved the ability to invade adjacent areas of poor soils exposed to the sun and susceptible to frequent seasonal firing (Page 1990). Bracken, unlike similar genera such as *Hyolepis* and *Paesia*, spread to temperate regions facilitated by the long distances covered by spores (subspecies *aquilinum* occurs on the Hawaiian Islands, Page 1976) which can rapidly colonise newly exposed ground such as volcanic ash (Yoshioka 1974; Wolf *et al* 1988).

Bracken is now one of the world's most widespread cosmopolitan species and is absent only from the Arctic Circle, Antarctica, tropical mountains above 3000 m, temperate mountains above 600 - 1000 m, areas of calcareous soils and in intensely farmed regions such as the Fens, England.

Bracken is limited by frost incidence which determines both the latitudinal and altitudinal extent of growth (Watt 1976; Smith 1986; Ader 1990) and the length of the growing season of the fronds. Due to the rhizome requiring a high aeration status, bracken is also intolerant of high soil moisture conditions as found in marshes, bogs, heavy clay soils and other waterlogged areas (Poel 1951). Rhizomes may nevertheless be found under seasonally damp areas or under previously dry land which is now waterlogged (Poel 1961; Watt 1979). Bracken is tolerant of drought due to low cuticular transpiration and stomatal response minimising water loss during periods of high evaporation (Tinklin & Bowling 1969).

Vigorous growth of bracken may be observed on leached brown earths with a mull or moder humus and little vegetative competition. The low nutrient status of the soil is overcome by the recycling of nutrients within the plant. At the end of the summer most nutrients located within the fronds are translocated back into the rhizome system. Nutrients contained within the litter layer and substrate are absorbed by the roots and mycorrhizae of the rhizome (Chen & Lindley 1981).

1.2.6 The competitive strategies of bracken.

Bracken is a highly competitive fern due to a number of strategies detrimental to the establishment and growth of less competitive species (Page 1986).

i) Bracken has a low palatability to livestock and wild fauna. In areas where bracken is invading into grass or heather sward, the browsing of fronds is uncommon (except in dry weather). This imposes pressure upon the remaining palatable species through preferential grazing. Bracken also demonstrates anti-predation strategies using biochemical weaponry against invertebrates (Cooper-Driver, Finch, Swain & Bernays 1977; Cooper-Driver 1985). The gametophyte and juvenile sporophyte was found by Hadfield & Dyer (1988) to contain hydrogen cyanide which may deter small herbivores, and may protect against fungal attack.

ii) Allelopathic compounds released from the fronds and as leachates from the litter layer may effectively suppress colonisation from competing species (Frankland 1976; Gliessman 1976; Gliessman & Muller 1972; Rice 1974). Allelopathy seems to be most prevalent in the early summer from the young fronds, and in the autumn, when compounds are released during decomposition of the fronds (Dolling 1994). This can hamper any follow-up management unless the suppressing litter is removed.

iii) The ability of bracken prothalli to colonise sites which have been fired has long been recognised (Fritsch 1927; van Leeuwen 1936; Lousely 1947). Sporelings are lime-loving (calcicole) and base-tolerant indicating adaptation to burned areas (Page 1984). This differs from the adult plant which is lime-hating (Calcifuge). Bracken already established adjacent to a fired area may also out-compete other vegetation by rapidly colonising via its underground rhizome system. This method of colonisation was recorded on Wheeldale moor, OS785982, on the North York Moors by A Wilson (1985), (Plate 1 and 2), and frequently occurs where heather has been burnt adjacent to bracken. The firing of vegetation such as *Calluna vulgaris* near bracken stands can result in the rapid colonisation by bracken of the newly exposed ground, mainly through the rhizome system which out-competes the slow growth of the heather, and in some cases from sporelings (Fletcher & Kirkwood 1979; Page 1982b).

iv) Bracken has a high reproductive capacity and propagule mobility from the release of millions of spores from each frond (Oinonen 1967; Page 1979). However, spore colonisation seems to be rare because germination is restricted to sterile, fired sites (Oinonen 1967). If establishment does occur through spore colonisation, the development of the plant can be rapid (Melville 1965).

Plate 1 Bracken colonising a severely burnt area on Wheeldale Moor, 1985 (Photo: A Wilson).

Plate 2 A rhizome short shoot advancing into the burnt area on the soil surface, Wheeldale Moor, 1985 (Photo: A Wilson).

v) Bracken demonstrates a pronounced vegetative longevity. To develop from the spore to the fertile adult sporophyte takes 3 to 4 years (Conway 1949; Page 1976; Thomson 1990). The underground rhizome system may survive for up to 35 - 75 years (Watt 1940). Individual plants may be centuries old (Oinonen 1967). Related to this is the size of a bracken plant. Sheffield *et al* (1989) noted that the diameter of an individual plant may be less than 30 m but could be up to 390 m. Portions of fragmented rhizome also have the ability to form new plants (Watt 1976). The large size and fragmentation of some bracken plants may therefore create problems for control.

vi) Wide climatic and edaphic tolerance (Conway 1949; Page 1976, 1979, 1982; Watt 1976). Bracken is mainly restricted by frost incidence (Ader 1990; Smith 1986; Watt 1976) and high soil moisture (Poel 1951). The increasing infestation of areas of high elevation on moorland suggests that bracken may be becoming more frost-tolerant or that climatic warming is occurring. The increased drainage of land which has been carried out within the last century has also increased the potential area for bracken colonisation. This problem may be increased through current set aside policies within C.A.P.

vii) Bracken, with over 300 million years of evolution, is relatively resistant to any naturally occurring disease through the development of disease-resisant mechanisms. The gametophyte is also protected against potentially harmful fungal pathogens (Hutchinson 1976).

viii) Bracken, being cytologically and genetically polymorphic, demonstrates extensive field variability. This is an attribute which is shared with other Pteridophytes in both temperate and tropical climates (Page 1979, 1982). Polymorphy manifests itself in the considerable field variability and in certain biochemical traits, and may be reflected in differences in biochemistry and physiology (Hadfield & Dyer 1988; Jones & Sheffield 1988; Wolf *et al* 1988; Jurabel, Sheffield & Moore 1989). Polymorphisms have been found in both nuclear and chloroplast DNA, although these are not taxa specific (Wolf, Sheffield & Thomson *in press*). Several distinct genotypes within natural populations of bracken at 7 different localities have been found, using electrophoresis and isozyme analysis of pinnule extracts (Sheffield *et al* 1989).

ix) Extra-floral nectaries, first described by Darwin (1877), located on the axils of expanding pinnae and pinnules, attracts, amongst others, the aggressive wood ant *Formica lugubris* (Lawton, MacGarvin & Heads 1986). The ants protect the fern from harmful pests and browsers, ie slugs and snails, during the early stages of frond development (Lawton 1976; Page 1982b).

1.3 The advantages and disadvantages of the bracken habitat.

The negative effects of bracken infestation have been well documented (Barber 1986; Brown 1991a, 1991b; Page 1986; Pakeman & Marrs 1991, 1992). Although having a variety of uses in the past, including as animal bedding, for producing potash, thatching material, a dye, and for packing soft fruit and fish (bracken acts as a preservative due to its cyanide content), the negative aspects of bracken now outweigh any present day potential uses (composting; biofuel) of this problematic weed.

Bracken is known to be carcinogenic to livestock and humans (Evans & Mason 1965; Evans 1976; Evans, Prorok, Cole, Al-Salmani, Al-Samarrai, Patel & Smith 1982; Hirono 1993). Ingestation by livestock can cause tumours and acute poisoning (Parker & McCrea 1965; Evans 1976; Jarrett, McNeil, Grimshaw, Selman & McIntyre 1978). These symptoms are prevalent in Wales, Scotland and the south-west of England due to the grazing of upland areas infested with bracken. Of concern in upland regions is the occurrence of progressive retinal degeneration, or bright blindness of sheep (McCrea & Head 1978, 1981; Hirono, Ito, Yagyu, Haga, Wakamatsu, Kishikawa, Wishikawa, Yamada, Ojika & Kigoshi 1993).

There are also carcinogen-related dangers related to human ingestion of bracken fronds which occurs in Japan and Brazil (Hirono 1993; Marliere *et al in press*). The bracken carcinogen, Ptaquiloside, has also been found in the milk of cattle feeding on bracken which has implications for human health (Evans, Widdop, Jones, Barber, Leach, Jones & Mainwaring-Burton 1971; Evans, Jones & Mainwaring-Burton 1972; Villalobos-Salazar, Meneses & Salas 1989; Hopkins 1990; Alonso-Amelot 1993). There is also increasing concern about the possibility of health risks from bracken spores in the air and in water supplies (Evans 1987; Trotter 1990; Lacey & McCartney 1994).

The incidence of bracken-related syndromes in livestock increases veterinary bills, so placing further economic pressure on a system of farming which has become increasingly difficult to maintain. Further difficulties are caused by the shepherding problems associated within areas consisting of a dense and tall bracken cover, and the loss of grazing quality and quantity which effectively reduces the stocking capacity of the land.

This problem also effects the number of grouse which are produced on moorland areas. The red grouse (*Lagopus lagopus*) feeds and nests mainly within heather. As bracken invades into heather swards there is an associated loss of habitat (for nesting and food) for the grouse.

Bracken affects livestock, grouse and humans indirectly by providing an ideal habitat for the sheep tick *Ixodes ricinus* (Brown 1993; Sheaves & Brown *in press*). Tick-related diseases include tick pyaemia, tick-borne fever, louping ill (Duncan, Reid, Moss, Phillips & Watson 1978; Hudson & Watson 1985; Hudson 1987) and Lyme disease (Mathewson 1993; Brown *in press*; Sheaves & Brown *in press*).

In an ecological sense, communities of bracken have a simplified flora and fauna. Dense shading and other competitive strategies (see section 1.2.6) ensure that few plant species can survive. There are few invertebrates present on bracken (Brown 1986) and therefore little food available for some species of mammal and bird. Invasion of bracken into heather communities is consequently detrimental to nationally important species such as the Dartford Warbler (*Sylvia undata*) and Merlin (*Falco columbarius*) (Bibby 1978, 1986). Shading also discourages vole and reptile activity.

The advantages of bracken are few. It is considered an attractive landscape feature, especially during senescence, and can act to control public access to more valuable sites (Brown 1991a, 1991b). However, it may be argued that a large monoculture of bracken merely simplifies the landscape and tends to concentrate people onto non-infested moor, so increasing trampling pressure and land degradation.

Bracken has some conservation value as an important habitat for some birds (STOG 1988) such as nightjars (*Caprimulgus europaeus*) (Gribble 1983; Burgess & Evans 1989), the willow warbler (*Phylloscopus trochilus*) and whinchats (*Saxicola rubetra*) (R. Brown *pers. comm*). Bracken also provides shelter for mammals eg the bank vole (*Clethrionomys glareolus*) and red deer (*Cervus elaphus*). Important species of butterfly have been linked to bracken, particulary the High Brown Fritillary (*Argynnis adippe*) (Warren & Oates *in press*). There are also 11 bracken specific species of invertebrate (Lawton 1986).

Rare species of groundflora are found under bracken eg chickweed wintergreen (*Trientalis europea*) and dwarf cornel (*Cornus suecica*) on the North York Moors (S Rees *pers. comm*). These species largely remain dormant underneath bracken, emerging after control treatments have taken place (Brown *pers. comm*). However, the author has observed chickweed wintergreeen growing successfully underneath dense bracken cover on the North York Moors (Plate 3). Although having little commercial usage the potential of bracken as a mulch or composting medium has also been investigated (Pitman *in press*).

Plate 3 Chickweed wintergreen growing under bracken on Rosedale Bank Top, June 1994.

1.4 Methods for the control of bracken

The encroachment of bracken has long been a problem for land managers. Descriptions of bracken control can be found as far back as the early 18th Century when infested grounds were ploughed up and dunged in order to return the land to a state suitable for grazing.

> 'I have seen the roots of it (bracken) in some grounds, eight foot deep. The best cure is often mowing of it while in grass. If you plow it up, plentiful dunging of it, and ashes are very good, but the certainest cure for it is urine'
>
> (Mortimer 1708).

During this period cutting and cultivation were already established as effective means of reducing bracken cover. More recently, chemical methods of control have been utilized, in particular the aerial application of the herbicide asulam. Both mechanical and chemical means of bracken control are, however rarely successful in completely eradicating the bracken problem from any given area. A solution may be found in the use of biological control agents although the release of alien invertebrates into the U.K. is controversial. Mycoherbicides are also proving to be potential bracken control agents and may play a significant role in future control programmes, particularly in areas of conservation interest.

1.4.1 The chemical control of bracken.

The aerial application of a herbicide has proved to be the only viable method to control large-scale bracken infestation on inaccessible hill land where mechanical means of control are impossible. There are three herbicides approved for the control of bracken; dicamba, glyphosate and asulam. Neither dicamba nor glyphosate are cleared for aerial application and have a restricted use due to their poor selectivity in relation to non-target species and because of their relatively short-term persistence (Embetec 1990).

The herbicide presently applied to control bracken is asulam, marketed in the UK as Asulox by Rhône Poulenc Agriculture (ADAS 1988). Asulam provides a 95% control for *Senecio jacobaea*, *Senecio vulgaris*, *Hypochaeris radicata*, *Rumex obtusifolius*, *Cirsium vulgare*, *Holcus lanatus and Pteridium aquilinum* (Harper, Burr & Colvert 1974). Asulam is approved for aerial application having passed field trials for usage on heathland SSSI's (Fitzgerald 1985) and is innocuous against birds, mammals, crustacea, fish and micro-organisms (May & Baker 1974; Gallo, Guardigli & McGinnis 1975; Ingham & Gallo 1975; Monsanto 1977; Heywood 1982).

The use of asulam accounted for 98% of the total herbicide applied by air in 1990 in the U.K. with 5 292 ha sprayed in total (Marrs, Frost, Plant & Lunnis 1992). Nevertheless, concern has been expressed over the danger of asulam drifting into areas containing sensitive and rare fern and bryophyte communities (Horrill, Thomson & Dale 1977; Williams 1980). The implementation of suitable buffer zones around areas of conservation interest will minimise the damage incurred. For example, the North Peak Environmentally Sensitive Area has been recommended to use 250 m buffer zones when spraying with asulam (Marrs *et al* 1992). There are also the problems of large-scale landscape changes which are unsightly, hydrological changes resulting in increased run-off and soil erosion from slopes, regeneration of bracken within a relatively short period of 3 - 4 years and high costs *c*.£120 ha^{-1} (Pakeman & Marrs 1992). It has also been postulated that eradication of bracken would be long-term (45 years) if using asulam on a six-year cycle of spraying (Marrs, Pakeman & Lowday 1993). Nevertheless many of the advantages of using asulam, particularly its use over large areas via aerial spraying, are considered currently to outweigh the disadvantages in many circumstances.

Unlike many other weed species, bracken has considerable ability to dilute herbicide concentrations because of the substantial biomass of the fronds and rhizome system relative to the surface area. Asulam has the ability to overcome these problems by being site-selective and highly active. Asulam (Fig. 2) is made from the sodium salt, asulam [methyl(4-aminophenylsulphonyl)carbamate] which is phloem absorbed and translocated with the basipetal flow of assimilates to the buds and apices of the rhizome (Veerasekaran Kirkwood & Fletcher 1976, 1977a, b, 1978; Lowday 1984a).

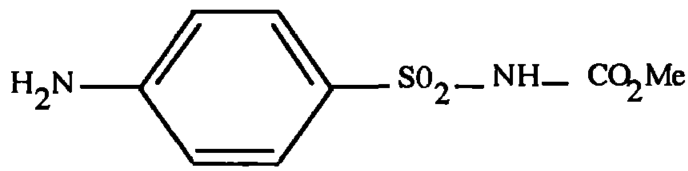


Fig. 2. The formula for asulam [methyl(4-aminophenylsulphonyl)carbamate].

Asulam operates by shortening the chromosomes during mitosis which in turn inhibits protein synthesis leading to plant tissue growth of the meristem being halted. This generally means that cell division is disrupted and further growth of the active buds and rhizome apices is halted. The synthesis of RNA (ribonucleic acid), which plays an important role in the synthesis, of protein, is inhibited after 14 days by 40%. Protein levels are reduced by 18% along with a decrease in the respiratory metabolic rate (Veerasekaran *et al* 1976; Kirkwood, Veerasekaran & Fletcher 1982).

Buds which have absorbed sufficient levels of asulam gradually blacken in the outer cortical tissues, eventually disrupting the cortex and the stellar tissues (those tissues immediately inside the endodermis and outside the primary vascular tissues). The outer cortical cells become distorted and lignify (Veerasekaran *et al* 1976). Finally, fissures develop in the cortex and the buds rot due to microbial attack of the exposed tissues.

Due to the large biomass levels of the rhizome system, some remote buds on long shoots may receive a sublethal concentration of asulam and will remain capable of frond production (Lowday 1986; Soper 1986). Those buds which are dormant and not active 'sinks' will also not accumulate lethal levels of the herbicide. This may result in a degree of control which is less than the desired 95-99% kill (Lowday 1984a).

In order to increase the success of herbicidal control, cutting of the bracken may be carried out 10 weeks before. This stimulates some dormant buds to become active viable buds and thus raises the absorption rate of the herbicide. Cutting will also decrease rhizome biomass thus decreasing carbohydrate levels.

The levels of asulam translocated to the 'sinks' is directly correlated with the total amount absorbed which in turn is influenced by frond development, 'sink' activity, temperature, humidity, the surface of application and surfactant use (Veerasekaran *et al* 1977a), cuticle waxiness and herbicide formulation (Kirkwood & Archibald 1986).

The recommended rate of asulam use is 4.4 kg to 4.5 kg per hectare (Ball & McCavish 1980; Sparke 1985; Lowday 1986; Rhône-Poulenc 1992). Rates below this level do not give satisfactory long-term control (Veerasekaran *et al* 1978). The asulam is applied during mid-July to late August when the frond has just fully unfurled with 3 pairs of extended pinnae (Watson 1982). During this period the bracken frond has the maximum area for herbicidal input before the leaf cuticle hardens against chemical absorption (Heywood 1982; Page 1984).

	^{14}C distribution (% of applied dose)			
Frond age (days)	25	46	65	120
uptake	32.2	26.6	17.2	9.2
acropetal	6.0	5.0	1.2	0.1
	(18.5)*	(18.8)	(7.0)	(1.1)
basipetal	2.8	3.9	3.6	2.2
	(8.7)	(14.7)	(20.1)	(24.0)
rhizome/buds	1.8	3.0	3.0	2.0
	(5.6)	(11.3)	(17.4)	(21.7)

* % of absorbed dose

Table 1. The translocation of [^{14}C] asulam in relation to frond age and the percentage of absorbed dose in the rhizome and buds. (Kirkwood *et al*, 1982).

The optimum application window has been calculated by Kirkwood *et al* (1982). Application of [^{14}C] asulam was found to be most beneficial when the fronds are between 65 and 120 days old from first emergence when the translocation of assimilates is mainly basipetal to the rhizome and not acropetal to the young pinnae system (Table 1). The exact timing of application for optimum efficacy will ultimately depend on the local environmental conditions.

The asulam is highly soluble and rainfall will quickly remove the chemical from the bracken fronds, thus a dry weather period of up to 12 hours before and after spraying, is recommended for successful absorption (Heywood 1982). If the correct timing of application is achieved control on heavy bracken cover (75 fronds m^{-2}) should result in a 98 to 99% kill of fronds (≤1 frond m^{-2}), (Bostock 1980; Lowday 1986; Veerasekaran *et al* 1978).

The addition of a surfactant enhances the penetration of asulam eg 0.1% Agral 70 (Holroyd & Parker 1970), 1% ethyln CP (Veerasekaran *et al* 1978).

1.4.1.1 The mode of application of asulam.

The success rate of control by asulam will depend upon the mode of application which must be tailored to suit the terrain and area of bracken to be sprayed. In hill regions the use of tractor mounted booms is often impossible due to the unsuitable terrain. The substantial stem damage that is caused by tractors also decreases the absorption and translocation of the herbicide (Robinson 1986). However, where suitable, carpet or felt wipers may be used to good effect (Young 1994). The reason for this is that wipers apply the asulam on the lower (abaxial) surface of the frond which is capable of greater uptake than the higher (adaxial) surface (Kirkwood *et al* 1982).

The application of asulam with hand sprayers, eg Micro Ulva+, is a viable solution where small scale control programmes are to be implemented. However, knapsack sprayers are bulky and require an on-site water supply (ADAS 1988). The use of ultra low volume sprayers, which atomise the concentrated herbicide or micron ultra-spinning discs, are more practical although handspraying is fatiguing and the prolonged exposure to bracken a possible health risk from tick infestation and spores.

The most effective method of control on large uneven hill areas such as the North York Moors is the aerial application of asulam by helicopter. Helicopter-mounted spray booms give a thorough cover of asulam on steep slopes, are highly manoeuverable, quick over large areas and require little intervention from the landowner (Davies, 1986). The main problems to be overcome are air vortices caused by the rotors, droplet evaporation and spray deposition which depend on the droplet size and the height of the spray run (Heywood 1982) and spray drift (Joyce 1985; Shire & Bennett 1985; M.A.F.F. 1989).

The recommended droplet size is 200 u, which can be applied using 'raindrop' nozzles at a height of 6 m (depending on the local weather conditions). This size of droplet both decreases environmental contamination and reduces vortice effects. As the height of application increases, however, the problems of missed strips, spray overlap and slope error also increase (Robinson 1986). This can have a serious environmental impact if the spray drifts into areas such as wet flushes where plant species are considered sensitive to asulam spray (Williams, 1980).

1.4.2 The mechanical control of bracken.

The four main forms of mechanical control available to land managers are burning, cultivation, crushing and cutting. Burning is of limited use due to encouragement of bracken spread via the underground rhizome system and from sporal regeneration (Oinonen 1967; Watt 1976). It can, however, remove the dense litter layer so exposing young croziers and buds to frost damage.

The cultivation of bracken stands is effective but topographically restricted to flat non-stony soils. There are also problems for archaeological features, ground nesting birds and rare flora. The cultivation of bracken infested land has limited usage on the North York Moors where infestation frequently occurs on steep sided in-bye land and on rocky, uneven moor. Also the moorland soil profiles and associated flora and fauna must not be damaged.

Where cultivation is unsuitable for ecological or archaeological reasons, crushing is often a viable alternative. This involves the use of tractor mounted, deep ribbed bracken crushers such as the Cuthbertson (ADAS 1988). It is recommended that crushing is carried out twice per year for three years thus causing a net drain on rhizome carbohydrate reserves and a decrease in total dry matter (Embetec 1990; Pakeman & Marrs 1991). The use of tractor mounted rollers, however, is impractical and even dangerous on steep moorland sides.

The cutting of fronds is the most popular form of mechanical control. It is carried out on a variety of scales from hand-weeding of small areas (Biggin 1982; Stanton 1990) to large scale control programmes utilising tractor-pulled cutting implements (Fitzgerald, Martin & Auld 1985). The frequent cutting of smaller areas is more successful in reducing bracken vigour than cutting larger areas infrequently (Watson 1982).

In order to maximise the depletion of dry matter from the system the timing of crushing or cutting is critical. The dry mass of the rhizome is lowest between mid-June and late July during which the fronds are developing at the expense of the rhizome system (Williams & Foley 1976; Lowday 1986; ADAS 1988). After this period frond development depends more upon current photosynthesis with rhizome reserves beginning to be replaced by the basipetal flow of assimilates.

An early July, crush or cut would cause the premature transfer of the fronds to the litter thus halting carbohydrate replenishment by basipetal translocation of assimilates (Williams & Foley, 1976). It is rare that total eradication is achieved although on some smaller areas this may be possible (Stanton, 1990). Cutting twice a year over a 10 year period has been found to reduce short shoots to 2-4% and long shoots to 8-11% of untreated levels on Cavenham Heath, Breckland (Marrs *et al* 1992). It has been postulated by Marrs *et al* (1993) that control would have to be long-term. It would take between 19 and 21 years to eradicate bracken when cutting once or twice a year. It is often the case, however, that bracken stands will rapidly recover once the treatment has ceased (Lowday & Marrs, 1992).

1.4.3 The biological control of bracken.

Classical biocontrol involves the use of an introduced species to control an alien pest or weed. Previous usage of alien invertebrates to control some native weeds has failed in Britain. The chrysomelid beetle *Haltica carduonum*, for example, did not succeed in controlling the creeping thistle *Cirsium arvense* (Baker, Blackman & Claridge 1972). Nevertheless, successful control has been achieved elsewhere in the world with over 86 weeds in 20 countries being controlled by biological agents (Julien 1982; Lawton 1986). Doubt is expressed, however, by those who stand to benefit most from biocontrol such as hill farmers (Lawton 1989) as well as conservation bodies concerned over the irreversible nature of biocontrol agents.

In Britain, bracken does not have any effective enemies (Braid 1947). In total, 27 species of insect exploit the fronds but most of these are rare relative to the biomass of the plant material available (Lawton 1982). After intensive laboratory screening, the South African noctuid moth *Conservula cinisigna* and the pyralid moth of the *Panotima sp nr. angularis* were found to be suitable as possible biocontrol agents (Lawton 1989). The caterpillars of both species attack the frond, *Conservula* damages the rachis whilst *Panotima* defoliates and attacks the vascular system thus debilitating the movement of carbohydrate to the rhizome (Lawton, 1988). The final release of these biocontrol agents has, however, not been permitted (Fowler 1993).

Fungal pathogens are also possible agents for bracken control e.g. *Asochyta pteridis* and *Phoma aquilina* which cause curl tip, *Ceratobasidium anceps* causing pinnule blight and

Cryptomyce pteridis, the causal agent of leaf curl and tar spot (McElwee & Burge 1990). The fungal pathogen most damaging to bracken in the U.K. is *Ascochyta pteridis* which has been found in many localities (Angus 1958, Burge & irvine 1985). It can cause considerable damage to the frond, reducing vigour and density (Womack & Burge 1993). The main problem has been a suitable means of getting the fungal pathogens into the bracken frond. However, Burge & Womack (1994) have developed two stable invert emulsions which have a sufficiently low viscosity to be applied by conventional spray apparatus. The fungal spores are suspended in water droplets which have an oil covering ie Marcol 52 at 43.5% w/w and contain the emulsifying agent Arlacel 780. The emulsions have a sufficient water retaining capacity to facilitate fungal spore germination and mycelial growth. The spores are also protected from adverse environmental conditions and are able to overcome host resistance factors.

Alternatives to the use of exotic insects or fungal pathogens do exist eg tree planting in order to reduce the bracken stand to a non-aggressive woodland state via shading (Biggin 1982). If deciduous woodland is planted rather than coniferous plantation it can provide a niche for a wide variety of flora and fauna increasing species diversity within a given area (Pakeman & Marrs 1991). The National Parks would support suitable planting of native species in certain areas, however, opposition comes from moorland owners and keepers who regard woodland as a loss of open habitat for grouse and as an area of potential predator habitat.

1.5 The problems associated with the after-management of bracken controlled areas.

The success of any bracken control programme will ultimately depend on suitable land management taking place after treatment. Clearly, bracken-infested areas with little or no underlying flora and a deep litter layer will have to undergo intensive management in order to produce vegetation that is suitable for grazing and/or grouse production (Pakeman & Marrs 1992b).

The vegetation which follows bracken control is rarely comprised of the communities which were present before bracken infestation. Vegetation development will depend upon a variety of factors including the groundflora present under the bracken canopy, the seed bank, seed rain, litter depth, climatic conditions, grazing pressure and management (Pakeman & Marrs 1992).

Those areas with an abundant flora have greater potential for recovery and full revegetation. This is especially important for slower growing species such as *Calluna vulgaris* if a return to grouse moor is required. However the levels of sheep grazing would have to be controlled in order to allow recovery. Overgrazing by sheep has been recognised as a causal factor in the loss of heather moorland in the Peak District (Anderson & Yalden 1981), Lake District (Marsden 1989) and on Exmoor (Miller, Miles & Heal 1984). If bracken is controlled sheep tend to congregate on the open areas and so there is little development of vegetation (ADAS 1985). A reduction of over-grazing of heather has been found to result in its rapid recovery (Heasson 1977). Therefore consideration is needed of the livestock carrying capacity of land which is undergoing a bracken control programme.

Invasion of other weed species eg foxglove (*Digitalis purpurea*), nettles (*Urtica dioica*), sheeps sorrel (*Rumex acetosella*) and grasses such as wavy hair grass (*Deschampsia flexuosa*) and creeping soft grass (*Holcus mollis*) is a problem that is often encountered (Cadbury 1976). A particular obstacle to after-management on the North York Moors is the invasive bryophyte *Campylopus introflexus* (Equihua & Usher 1988, 1993; Equihua 1991; Zamora 1991; Marrs & Pakeman 1992). This moss prefers a Calluna habitat on moor areas but can also be found beneath the bracken frond canopy. The tendency of *Campylopus introflexus* to fragment creates an unstable surface for the germination and establishment of vascular species and can lead to soil erosion on sloping land, particularly if heavy grazing occurs. This problem is particularly apparent on the Spaunton Estate at Hutton-le-Hole (Plate 4). The result is one inhibitory monoculture (bracken) being exchanged for one which is just as problematic.

Plate 4 Campylopus introflexus infestation in 1994 at Hutton-le-Hole following bracken spraying in 1984.

Ideally, implementation of a large-scale control programme will include selecting those areas which can be easily returned to a condition useful for agriculture or grouse production. The control of areas of bracken, which will prove difficult or costly to follow-up and which will result in stark expanses of unsightly litter which has no landscape value, should be avoided. Therefore, there is a need to classify areas of bracken on their suitability for control. This has already been considered by the Peak District National Park which has produced a code of practice for bracken control (Peak District National Park 1992). Bracken is classified according to land quality, terrain, accessibility, conservation, landscape and amenity value. From this classification can be drawn the decision to either preserve, adapt or convert bracken infested areas (Taylor 1993).

1.6 An evaluation of bracken sampling techniques.

1.6.1 Introduction.

There are difficulties associated with the examination of any plant species which demonstrates variable forms and can multiply vegetatively, ie through rhizome fragmentation (Moore & Chapman 1986). Whereas greenhouse and laboratory experiments are important by significantly reducing uncontrolled variation, bracken population biology must be a primarily field based subject. Therefore, the sampling strategy of the research must be tailored to fit the experimental aims. For example, a study on the genetic behaviour of individual bracken plants or the translocation of herbicide may be achieved through laboratory experimentation. However, population biology and the reaction of stands to control measures must be examined in the field.

Field research on bracken can be problematical. The performance of an individual bracken plant will display temporal changes, ie seasonal changes, related to phenology of growth, differences in the stage of life cycle and cyclic changes, ie bracken occupying different patches of the same habitat, may display different population properties (Watt 1947a, b; Moore & Chapman 1986).

1.6.2 Potted and micro-plot sampling to determine bracken morphology and the effects of control treatments.

1.6.2.1 The use of potted samples.

The use of potted bracken samples is practical when studying the effects of herbicide treatments on a small scale ie studies of the absorption and translocation of [^{14}C]-asulam (ie 'source-sink' functional criteria) using potted examples of small fragments of rhizome (Veerasekaran *et al* 1976; Kirkwood *et al* 1982; Lowday 1984a; Soper 1986; Kirkwood 1990). Potted bracken is also useful in studying the potential of new herbicides such as tribenuron-methyl on bracken (West & Butler 1991).

It would be unwise, however, to base conclusions about bracken morphology and susceptibility to control measures on results gained from single plants in potted experiments. This is because bracken is polymorphic for almost all characteristics and will respond readily to differences in the local environment. Therefore, genetic variation and the biomass of bracken in the field must be taken into account when considering conclusions from experiments using potted bracken.

The mode of application must also be considered. Within small-scale experiments the application of asulam can be precisely controlled. In the field, however, most large-scale control programmes using asulam are achieved by the use of aerial spraying which may be less effective due to problems such as air vortices, slope inaccuracies and weather conditions (Davies 1986). Consequently, the total kill of rhizome and buds due to the application of asulam recorded by Holroyd & Parker (1970) using 25 cm diameter potted samples would rarely occur in the field and give an exaggerated indication of control success.

1.6.2.2 The use of micro-plots.

The study of single plants in micro-plots is applicable when examining the growth potential, development and morphology of individual bracken plants (Lawrie, West & Truman 1992). Although similar to potted experiments, bracken fragments grown within micro-plots have a larger area within which to expand and develop. Micro-plots often consist of a well drained, sandy-clay loam soil with peat (4:1), at pH 5, and contain no other species; therefore growth conditions are at an optimum, although restricted by the size of the plot. Micro-plots eliminate encroachment and interference from neighbouring bracken rhizomes by an impenetrable barrier such as concrete.

Bracken grown within micro-plots is useful for examining the potential growth and development of a given fragment of rhizome. However, the conditions under which the bracken is grown do not reflect field conditions. Therefore, any conclusions must be considered carefully if comparisons to bracken growing in the field are to be made. A 20 cm long fragment of rhizome grown in a 1.42 m x 27 m by 30 cm deep micro-plot has been shown to have a considerable potential growth rate of 26 m per year (Lawrie *et al* 1992). This rate of growth may, however, be exaggerated due to the conditions under which the bracken is cultivated. In the field bracken has to cope with soil and drainage stress, competitiion from other vegetation, climatic limitations, and interference from livestock and human activities.

Single plant experiments avoid the problems of variation within and between clones which are encountered in natural communities of bracken (Sheffield *et al* 1989). Specific genotypes can be studied with regard to morphology and the response to control treatments (West 1992).

Nevertheless, conclusions achieved through the use of potted bracken and micro-plots cannot accurately predict the reaction of bracken to control in the field. The bracken is grown under unnatural conditions and is restricted in radial growth by the size of the plot. Radial growth may also be encouraged by the removal of apical buds (Lawrie *et al* 1992). Control treatments are often applied to the bracken within the first or second year of planting (West 1992). At this stage of development the bracken is considered juvenile with an underdeveloped and restricted rhizome system. Therefore, the large biomass levels of rhizome and the high number of buds which are encountered under field conditions are not accounted for and will therefore effect any conclusions drawn.

1.6.3 Field sampling to deterermine bracken morphology and the effects of control treatments.

1.6.3.1 The use of field sampling to determine bracken morphology.

Research on the morphology of bracken in the field has been concentrated on two areas of the U.K. Watt, between 1937 and 1979, published a series of papers examining the growth characteristics of both the frond and rhizome system within a population of bracken located at Lakenheath Warren, Cambridgeshire.

The experimental design for the sampling of the rhizome utilised 14 pits per area of size between 61.0 cm^{-2} and 30.5 cm^{-2} (Watt 1940, 1947). Frond sampling was carried out using quadrats 30.5 cm^{-2} (Watt 1945) and 3.1 m^{-2} (Watt 1947). Plot size varied between 3 m x 0.6 m and 7.6 m x 0.6 m (Watt 1964). Much of the work carried out by Watt, however, did not utilise plots but described general areas within bracken populations (Watt 1940, 1945, 1947, 1950, 1955). The inconsistencies in sampling undermine the validity of the conclusions and render comparisons with results from other studies difficult.

Although Watt gave a comprehensive view of bracken growth and development, sampling was carried out only at Lakenheath Warren. The data give a base line from which extrapolation to other areas of the U.K., particularly upland bracken communities, may not be feasible due to variability within and between bracken populations.

Bracken morphology in the field has also been studied in Western Scotland with regard to under-storey vegetation composition (Williams 1977) and the seasonal variation in rhizome carbohydrate content (Williams & Foley 1976). Both studies used 25 m^{-2} plots, vegetation samples taken from 20 x 10 m^{-2} quadrats and rhizome samples from 3 x 4 m^{-2} pits. The large sampling size of both the vegetation and rhizome make repetition of the study impractical. If bracken is highly variable over a given area then the use of a small number of large pits to sample rhizomes may reduce the spatial variability that may have been found using a larger number of smaller samples. Inference to general bracken stand morphology may therefore prove to be invalid due to the sampling strategy.

1.6.3.2 The use of field sampling to determine the response of bracken to control methods.

The response of bracken to control measures in the field needs to be predicted. This requires both a large-scale approach to sampling and a detailed examination of the rhizome system. Most sampling procedures, whether on small scale micro-plots or larger field trials, consider the response of bracken to control treatments with regard to frond appearance and development. Examination on the effect of control treatments on the rhizome system tends to be either secondary or not considered (Holroyd & Parker 1970; Veerasekaran *et al* 1978; Ball & McCavish 1980; Williams 1980; ADAS 1982, 1985; Biggin 1982; Lowday & Marrs 1983, 1992; Horsnail 1986; Lowday 1986; Soper 1986; Marrs, Pakeman & Lowday 1993).

The importance of the rhizome in the control of bracken has been recognised for a long time, Hendrick (1918) states;

> "The problem of control (of bracken) hinges round the large underground rhizomes weighing up to 50 tons per acre"

The lack of rhizome sampling after asulam application is surprising as the rhizome is the site within which the herbicide acts. The frond is responsible for only the absorption and translocation of the asulam. Although the number of fronds in the year following application indicates the effect of asulam on the rhizome buds, the degree of damage cannot be assessed without a comprehensive examination of the rhizome system.

Pit size is important in assessment of the rhizome. Most researchers in the U.K. use a pit size of 50 cm x 50 cm (Lowday, Marrs & Nevison 1983; Lowday 1984a; Lowday 1986; Lowday & Lakhani 1987; Marrs *et al* 1993; Pakeman & Marrs 1994) although 1 m x 1m pits have also been utilised (Veerasekaran *et al* 1978). However, the reasons for the use of these pit sizes are not discussed. A pit of this area cannot be readily replicated without a large amount of labour and therefore only a low number of samples, usually one per plot, have been taken.

The examination of the rhizome within one or two pits per plot (Veerasekaran *et al* 1978; Lowday *et al* 1983; Lowday 1984a; Lowday 1986; Lowday & Lakhani 1987; Marrs *et al* 1993; Pakeman & Marrs 1994) cannot indicate overall control success if the original morphology of the bracken population was highly variable. The effect of asulam on the rhizome may also vary due to assimilation differences and this must be taken into account when evaluating control success and in predicting the likely dynamics of the rhizome system.

There is also the problem that most large-scale research on control in the U.K. to date has concentrated on Breckland heath bracken, particularly at Weeting Heath and Cavenham Heath (Veerasekaran *et al* 1978; Lowday *et al* 1983; Lowday 1984; Lowday 1986; Lowday & Lakhani 1987; Lowday & Marrs 1992; Marrs *et al* 1993). The problems are similar to those associated with the work of Watt on bracken morphology. Because of the considerable variability of bracken, results gained on control success from one geographical area or location may not be applicable to other areas.

1.6.4 Conclusions on bracken sampling techniques.

In theory, variation in frond morphology within and among clones cannot be assessed without the excavation of whole plants or complete stands (Hellum 1968). In practice, this is not feasible due to the labour involved and the destructive nature of sampling. Results may still be misleading as individual clones have been found to fragment, in response to disturbance, which can cause the extent of genetic individuals to be underestimated and the number of individuals to be overestimated (Sheffield *et al* 1989).

The sampling strategy will depend on the intended application of the results. Small-scale trials using potted bracken are useful when examining the translocation of herbicides within a simplified frond and rhizome system and the degree to which a single plant may be affected by control measures. Description of the morphology of a single bracken plant is also possible using small scale trials. However such trials cannot account for the field variability found within natural populations of bracken.

Field trials allow the examination of morphology and response to control measures within a given area of bracken. Conclusions gained from field research are more applicable to the 'real world' situation than those from laboratory controlled environments. Nevertheless, sampling of both the rhizome and frond system must be on a sufficient scale to account for field variability.

1.7 The North York Moors National Park bracken control programme.

The North York Moors National Park (Fig. 3) includes the largest single tract of heather dominated moorland in England (500 km^2). The moor consists of an isolated upland block underlain by rocks of the Jurassic system (Fig. 4) and rises sharply to over 402 m above surrounding plains (Carroll & Bendelow 1981). The vegetation mainly consists of dry upland heath dominated by heather (*Calluna vulgaris*) which is managed for sheep and grouse forage. The most common subdominant plants are bilberry (*Vaccinium myrtillus*) on the steeper slopes and cross-leaved heath (*Erica tetralix*) in the wetter areas. Bracken covers most of the surrounding slopes, even the more exposed north and east facing banks, and competes with the heather by encroachment onto the moor (Plate 5). There are also 5 000 ha of blanket and valley peats with associated wet moorland and bog communities. The moors have a wide range of land usage including grouse moor, permanent grass for sheep through longstanding common rights, coniferous forestry and where conditions are more favourable, arable cropping. The moor is also valuable for communities of upland birds and for its diverse flora and fauna and is a major attraction to tourists (North York Moors National Park 1991; Brown 1986, 1991c).

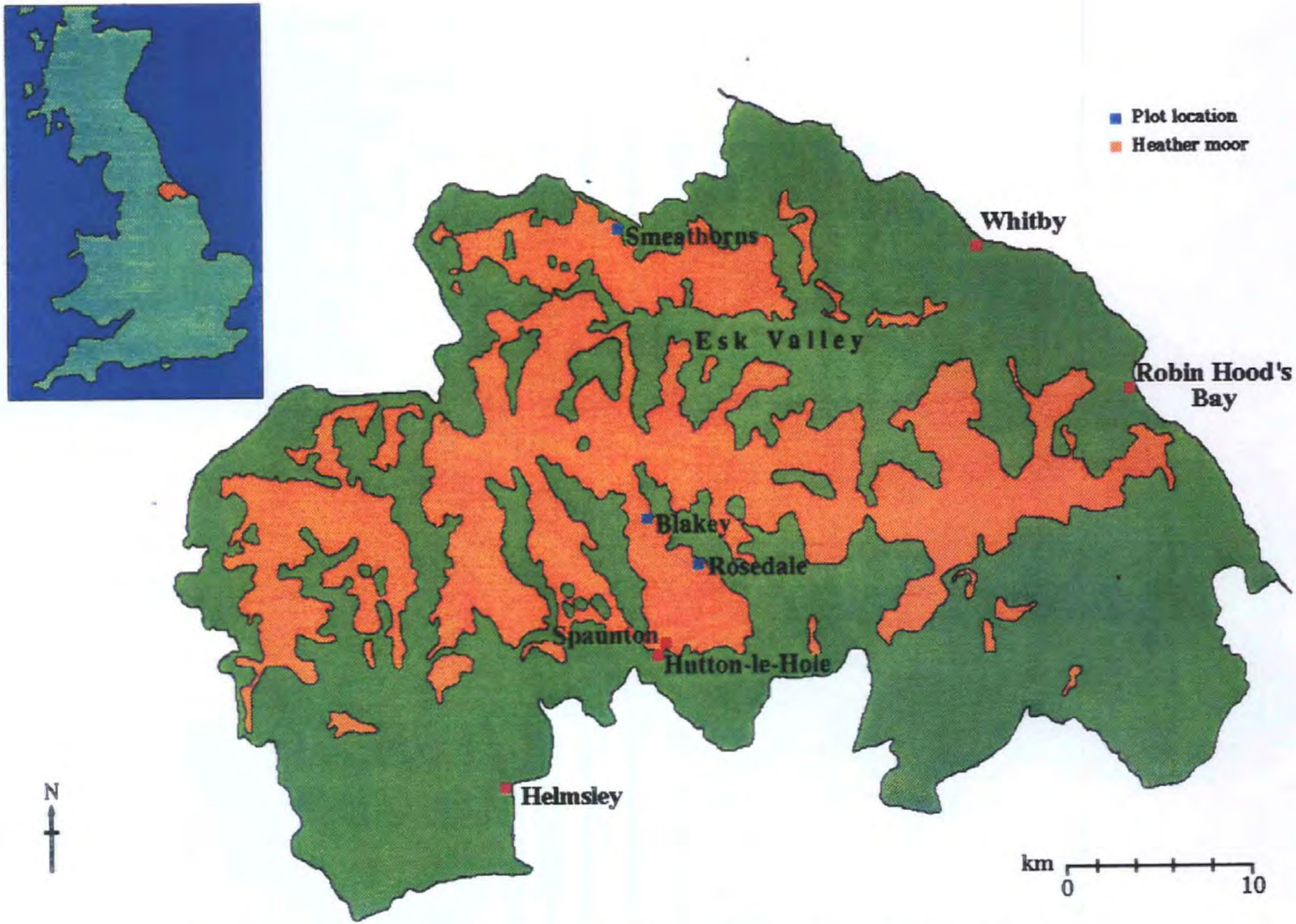


Figure 3. The North York Moors National Park.

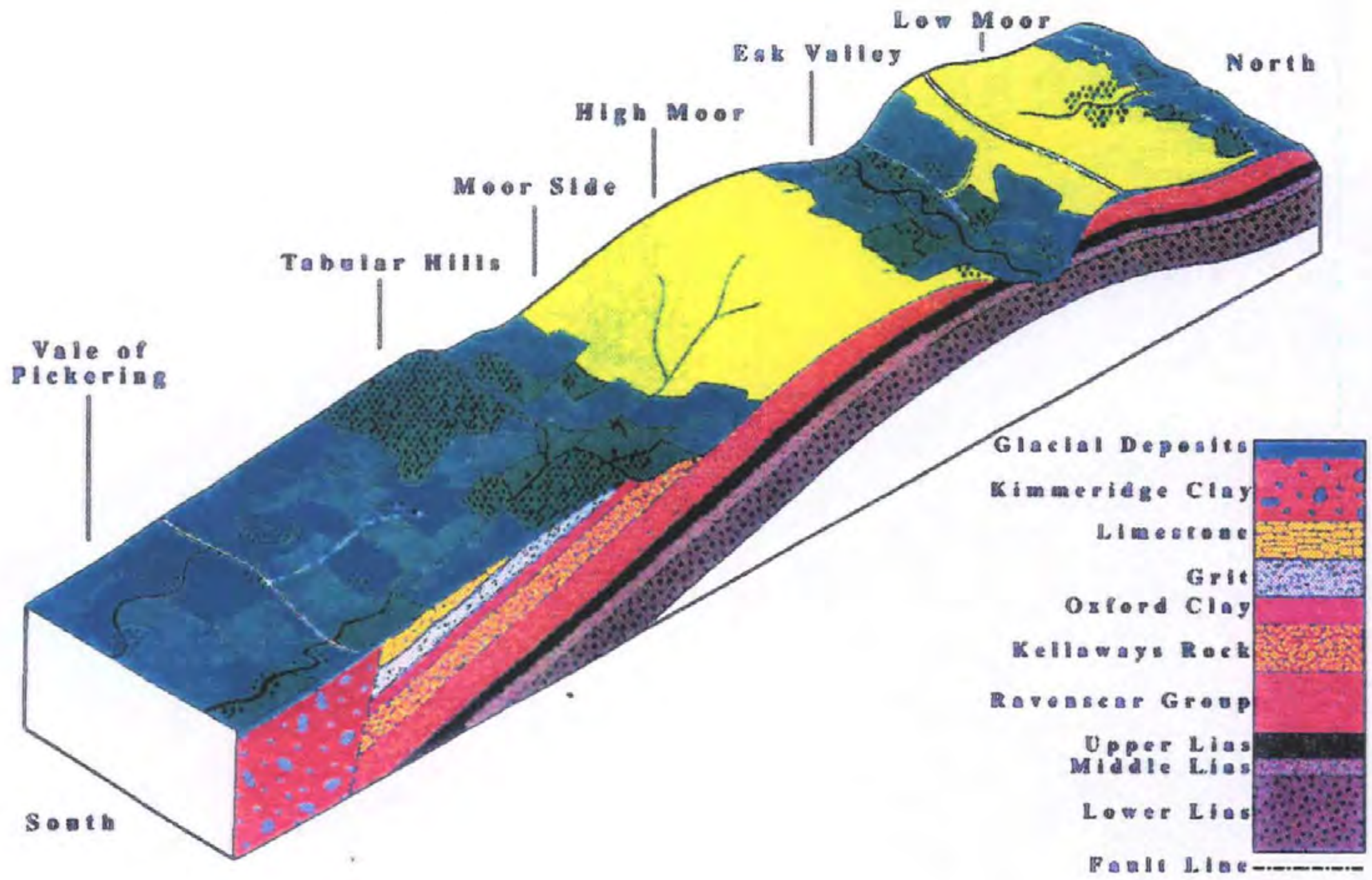


Figure 4 The geology of the North York Moors - cross section (North York Moors National Park 1990).

The North York Moors National Park has experienced changes in land management coupled with changing environmental factors, eg climatic warming, which have resulted in the increased spread of bracken onto the moorland. In 1988 approximately 140 km^2, or 28% of the total moor area was encroached by bracken (North York Moors National Park 1991). The increase in bracken has threatened agriculture, forestry, game and conservation resulting in effects detrimental to the local economy. In response, the National Park Committee launched an integrated 5 year bracken control programme in order to reduce the bracken area to less than 10% by the year 2000 (Embetec 1990; Brown 1991b). The programme proposed that of the 12 000 ha of well established bracken some 7 300 ha were suitable for primary control. Between 1988 and 1993, 6 490 ha were controlled using aerial sprayed asulam with grant aid from M.A.F.F. and the North York Moors National Park Authority (Rees *pers. comm.*). A further 222 ha were controlled in 1993 without grant aid.

Plate 5 Encroachment of bracken from the valley sides on to thre heather moorland on the Spaunton Estate, June 1994.

Despite the high level of control that has been applied to the moorland, bracken still persists in many previously treated areas. Although differences in spray results between regions can be partly attributed to the variability of weather conditions, the local environment, ineffective spraying and the spray dilution, the reoccurrence of fronds in some stands and not in others cannot be wholly explained. An understanding of the poor spray results is hampered by the lack of monitoring that has been carried out over the 5 years of the control programme. There is a need to examine frond and rhizome relationships in individual stands of bracken and, if possible, to classify stands according to the structure of the rhizome system and to the degree of response to control measures. This would contribute towards explaining the differential response of bracken to control and the variable rates of recovery that occur. Such an examination forms the focus for this thesis.

Chapter 2 Thesis aims and structure.

2.1 Introduction.

This study is concerned with investigating the control of bracken (*Pteridium aquilinum* (l.) Kuhn), with special regard to rhizome morphology, in the North York Moors National Park. For the reasons listed in the literature review, bracken is on balance regarded as detrimental to the economy and ecology of the moors. There has been growing concern over the advancement of bracken into heather-dominated communities on the North York Moors, as well as on to other upland areas of the U.K. Recent trends in agricultural policies such as set-aside and the possibility of global warming could extend the area into which bracken can colonise, particularly in upland areas.

It is therefore not surprising to find that the control of bracken has been a major topic for debate for many years. Various chemical, mechanical and biological solutions have been put forward but many have proved to be ineffective, or detrimental to un-targeted species of flora. Despite the wealth of research that has been carried out there is currently only one method for the large-scale control of bracken in upland regions which is the use of asulam herbicide.

It has been observed by previous researchers that asulam will give a good frond kill in the year after spraying but that regrowth is expected after 3 to 4 years, unless a programme of after care management is initiated. The present study investigated whether the use of asulam, on the scale applied on the North York Moors, could be considered practical in an area where there was limited possibility of after-management taking place, other than through the use of repeated follow-up spraying. This was achieved by the examination of bracken stands on different locations of the moor, before and after spraying had taken place. Although frond data was collected, the primary purpose of the study was in the examination of the morphology and the effect of treatment on the rhizome system in the field.

Furthermore, previous research on bracken control has concentrated on the amount of frond 'kill' rather than any detailed study on rhizome susceptibility. The present study questions the use of frond data, examines the relationship of the frond to rhizome morphology and evaluates the subsequent effects of control treatments. The study of the rhizome also called into question previous sampling methodologies which have been based on the taking of a small number of samples.

The North York Moors National Park was chosen as the site of study for a number of reasons. Firstly, each moorland estate is privately managed by gamekeepers and landowners who liaise with National Park staff. There were consequently comprehensive management maps available for most of the moorland which identified areas of bracken infestation and sites of previous and future bracken control. Secondly, the implementation of the bracken control programme gave an ideal situation within which to monitor on a large-scale the effect that treatments are having on field bracken. Thirdly, the geography of the region made it possible to examine the effects of treatment on bracken growing within different parts of the moor and to examine the possibility of establishing consistent bracken, environment and treatment response indicators.

The study is of potential economic value in an applicable area of upland management and is of scientific value for the opportunity it presents to clarify the nature of bracken in an upland region and the effects of control treatments in the field.

2.2 Aims and objectives.

The aims and objectives of the study were;

1. To quantify the success of the North York Moors National Park bracken control programme.

2. To classify separate bracken plots in relation to rhizome morphology in order to predict the success of control treatments. The information gained was to be used to formulate management strategies for improved practical bracken control.

3. To examine the relationship, if any, between frond and rhizome morphology, and to compare the effect of control treatments on both constituents.

4. To make a critical appraisal of previous rhizome sampling methodology.

The following broad hypothesis were formulated;

1. Bracken growing on different geographical locations will demonstrate differences in

rhizome morphology which will have consequences for control measures.

2. The use of the frond response alone will not accurately demonstrate the effectiveness of bracken control.

3. Previous studies on the rhizome in other locations are not applicable to the field situation on the North York Moors.

2.3 Thesis structure

The present study is based on an initial gathering of rhizome and frond data in 1992, before any bracken control treatments had taken place. Evaluation of the results is used to elucidate; i) if differences in morphology can be discerned between bracken growing in plots on different locations of the North York Moors; ii) the effect any differences may have on subsequent control treatments and iii) the suitability of the sampling methodology in describing bracken rhizome morphology. The second data set, gathered in 1993 after treatments had taken place, is used to monitor changes and to test hypotheses on the effects that the treatments have had on bracken within plots, and the differences in control success observed between plots, after one year. The conclusions are used to formulate practical bracken management guidelines for the North York Moors and for other upland areas of the U.K.

3.1 Plot information.

3.1.1 Plot location

To classify bracken stand morphology and relate it to the effectiveness of bracken control, large sampling plots were utilised covering a range of control methods and site locations. The study was conducted on eight plots (Table 2) at three locations across the North York Moors (Fig. 3): (i) the Spaunton Estate high moor at Blakey Ridge and Rosedale Bank Top; (ii) Spaunton Estate moor side at Blakey and Rosedale; and (iii) the Skelton & Brotton Estate low moor at Smeathorns. Both estates encompass land on the low moor, moor side and high moor which is mainly used for game shooting. On Blakey and Rosedale the main problem was the infestation of bracken on the moorland sides which was encroaching onto the heather moor. On Smeathorns bracken invasion into heather was occurring from an old field system which had been abandoned. There was a bracken control programme on both estates using asulam, and on Smeathorns bracken control included crushing.

Plot	Moor type	Treatment	Aspect	Slope	Elevation (m)	Grid Ref.
Rosedale 1	High moor	Control	86 NE	7	295	SE 722949
Blakey 1	"	Asulam	76 NE	13	360	SE 685990
Rosedale 2	Moor side	Control	54 NE	23	260	SE 722953
Blakey 2	"	Asulam	76 NE	17	335	SE 688984
Smeathorns 1	Low moor	Cut	68 NE	12	197	NZ 676133
Smeathorns 2	"	Cut/Asulam	82 NE	10	193	NZ 676135
Smeathorns 3	"	Asulam	82 NE	7	202	NZ675135
Smeathorns 4	"	Control	68 NE	4	190	NZ676137

Table 2. The treatments, locations and local geography of the study plots.

Plot locations were chosen according to certain criteria:

1. The bracken stands were suitable for the implementation of control methods, especially crushing, and/ were within the North York Moors spray programme for 1992.
2. The stands had experienced no previous bracken control management. This was ascertained through discussions with gamekeepers and the study of estate maps, which included information on any control programme. Further information was obtained from the National Park.
3. Plots were within established bracken stands and not within degenerate bracken (Watt 1947a, 1947b).
4. The stand was large enough to encompass the large plot size (> 100 m x 50 m) including suitable buffer zones.
5. Plots were far enough apart to be unaffected by spray drift (>30 m).
6. The permission and help from landowners and gamekeepers. No field experiment on the North York Moors would have been possible without the consent of the landowners, and the help from gamekeepers in selecting suitable plots and in the implementation of control measures.
7. The plots were placed in areas where interference with nesting grouse, and other moorland birds, would be kept to a minimum. Consultation with National Park staff identified areas which were sensitive and so could not be used, ie archaeological monuments and sites valued for their species diversity and/or conservation interest.
8. The practicality of sampling rhizomes from remote stands or stands on steep valley sides. Due to the geography of the region, and the intended sampling size, plots had to be easily accessible.

All plots were northeast-facing and ranged in elevation from 193 m to 360 m (Table 2). The level of stock grazing varied between the plots according to the density and height of bracken fronds and the availability of understorey vegetation. It was postulated that all plots, if successfully cleared of bracken cover, had the potential to be restored to grouse moor and/or rough pasture. This potential was nevertheless dependent on a number of factors including stock pressure, continuing bracken control, the invasion of other weed species and bryophytes and the implementation of a suitable aftercare strategy including heather regeneration.

3.1.2 Plot size

Plot size was selected to ensure that the bracken sampled was consistent with the scale of the North York Moors control programme and that adjacent bracken stands did not interfere with the sampling. Each sampling plot measured 100 m x 50 m which included a 5 m buffer zone (Fig. 5). The 5 m buffer zone ensured that each plot was not influenced by adjacent bracken or damaged by excessive trampling around the sides of the sampling area. The plots were more than 30 m apart. This distance has been demonstrated to eliminate the effects of asulam spray drift (Marrs *et al* 1992).

Replication of the plots was considered impractical in this research project due to the potentially high variability of bracken stand morphology and the intensive sampling required. To replicate sites within treatments, smaller plots would have to be utilised and the practical relevance to the field situation would decrease due to the heterogeneous nature of the bracken plant. Essentially, the larger plots were treated as matrix samples which has its origins within the heterogenous bracken stand representing the North York Moors.

Each plot was separated into two 40m x 40m subplots, one being utilised for bracken and the other for understorey vegetation sampling. The separation was necessary due to the destructive nature of the rhizome sampling which in turn would have had an adverse affect on associated vegetation species. None of the plots had been previously treated for bracken control.

3.1.3 Geology and soil description

The plots on both the high moor and the moor side were located to the south of the Esk Valley. The high moor plots were situated on the upper slopes of the heather moor which overlies the Ravenscar group of sandstones. The moorside plots were situated on the deeply incised valley sides which consist of older erodible Upper Lias shales and Middle Lias sandstone and ironstone. This latter deposit has been exploited as a source of iron with particularly large mining works in evidence at Rosedale (Carroll & Bendelow 1981).

The plot pedology is classified according to Carroll & Bendelow (1981) and Avery (1973). The soils on both the high moor and moorside consist of the Newtondale series of pelosolic brown rankers. This type of non-calcareous soil is typical of moderate to steep sloping valley sides and escarpments. Where soil can accumulate, stagnohumic gley soils may

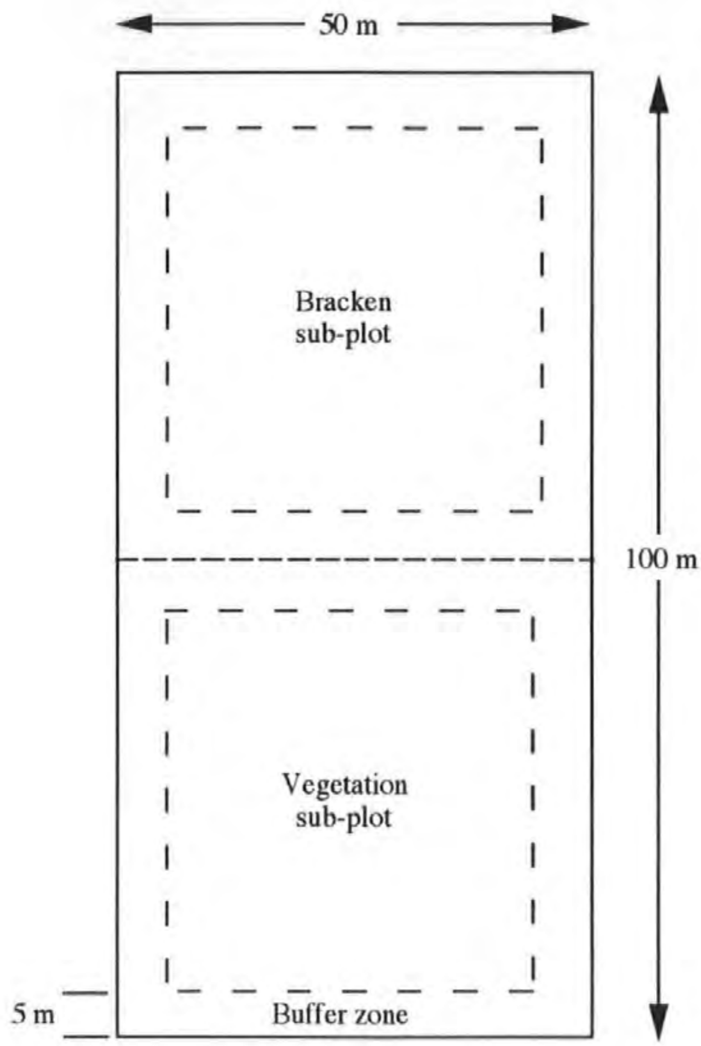


Figure 5 Plan of the plot design for bracken and vegetation sampling.

develop. This was evident at Blakey 2 where the local relief and a spring line forms a depression in the moorside so decreasing slope angle. Apart from Blakey 2 the soils were characteristically bouldery with numerous protrusions from the soil surface.

The plots on the low moor were located to the north of the Esk Valley on the Middle Oolite Group of Kellaways sandstone and Oxford Clay. Smeathorn plots 1, 2 and 3 consisted of a well drained humus-ironpan stagnopodzol of the Maw series. Smeathorns 4 consisted of a pelo-stagnogley clayey soil of the Crewe series. The gentle to moderately undulating geography of the region and the lack of prominent boulders meant that the use of mechanical methods of bracken control was possible at Smeathorns.

A descriptive study of the soil depth, vertical rhizome growth, litter depth and shear strength within the profile was undertaken on all plots (Figs. 6 and 7). Twenty randomly located pits were dug down to the less penetrable mineral horizons which commonly consisted of yellow sandstone. The soil and litter depth was recorded along with the maximum depth of rhizome growth. Before excavation the shear strength of the soil profile was recorded using a shear vane (this provided an *in-situ* test on the torque required to turn blades inserted into the soil at various depths). Measurements were taken at 10 cm intervals to the depth of 50 cm.

Mean soil depth (cm) was found to range between [27.30 (±2.29)] and [50.00 (±1.63)] (Fig. 6). Anomalies occured due to the greater soil depth found on the moor side at Blakey 2 and on the low moor at Smeathorns 3. The deeper soil at Blakey 2 was explained by the local geography of the immediate area which formed a small basin where deposits could accumulate. The depth of soil at Smeathorns 3 was less readily explained by the accumulation of deposits as the local geography did not represent a receiving site. It was concluded that the continued accretion of heather and bracken litter had allowed the build up of a deeper soil in this area and that erosion had been limited by the low angle of slope (7^o).

A comparison of soil depth to the vertical growth of rhizome was undertaken (Figs. 6 and 7). Rhizome depth on the plots was found to be related to soil depth [$r^2 = 0.906$ ($P<0.01$)]. Rhizome growth was mostly restricted to the top 30 cm of soil with only a few long shoots penetrating into the deeper layers. The rhizomes on Blakey 2 and Smeathorns 2 and 3 extended deeper into the soil because of the increased depth of the organic horizons. The mineral horizons continued vertically beyond the extent of rhizome growth. All plots exhibited an increase in shear strength with depth of soil (Figs. 8a and 8h). However, the profiles at Rosedale showed a decrease in shear strength after 30 and 40 cm (Fig. 8a). This was attributed to the disturbed nature of the soil at Rosedale, due to mining, and to the presence of

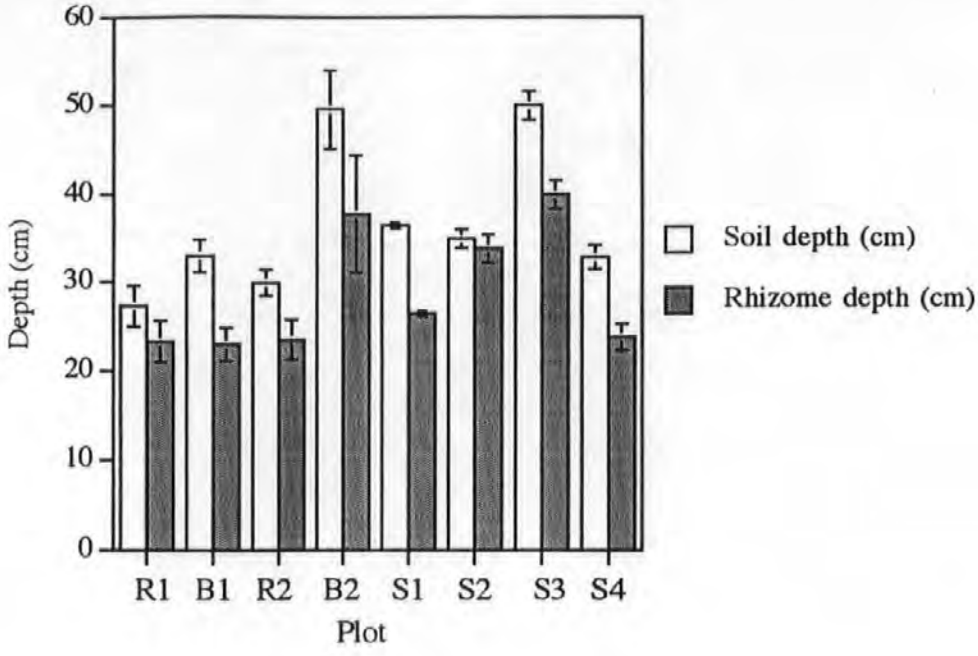


Figure 6 The mean soil depth and the maximum mean depth of rhizome penetration.

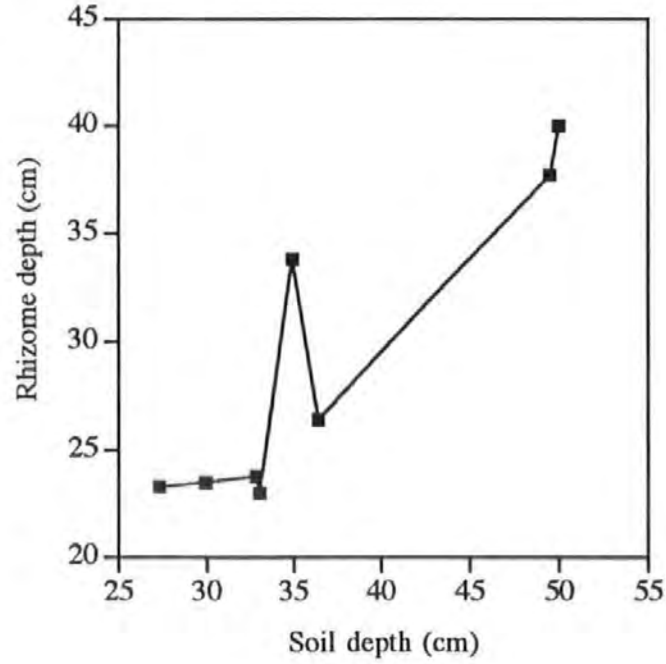


Figure 7 The mean rhizome depth plotted against soil depth

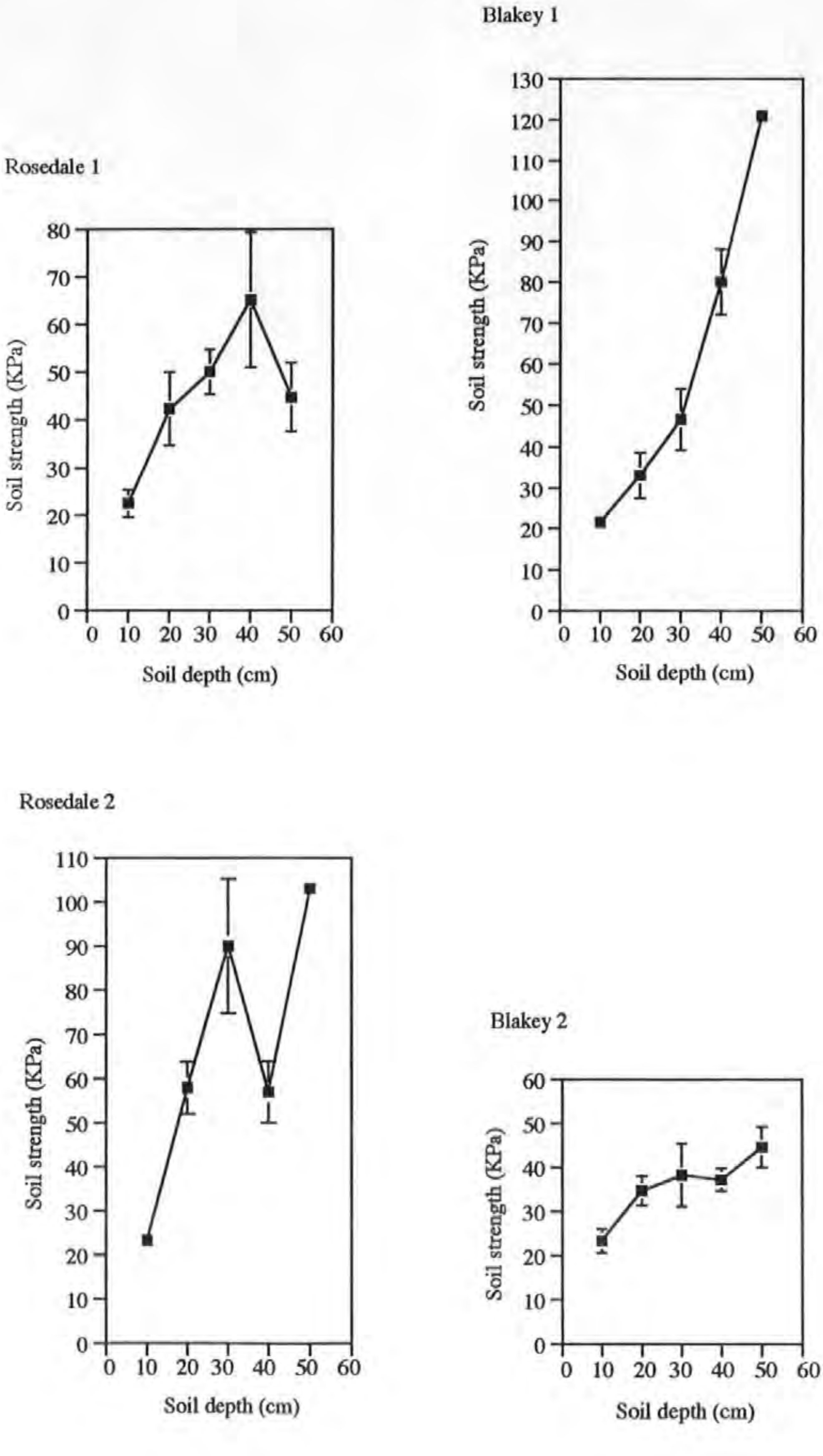


Figure 8a Mean soil shear strength (KPa) in relation to soil depth (cm) on the high moor and moor side.

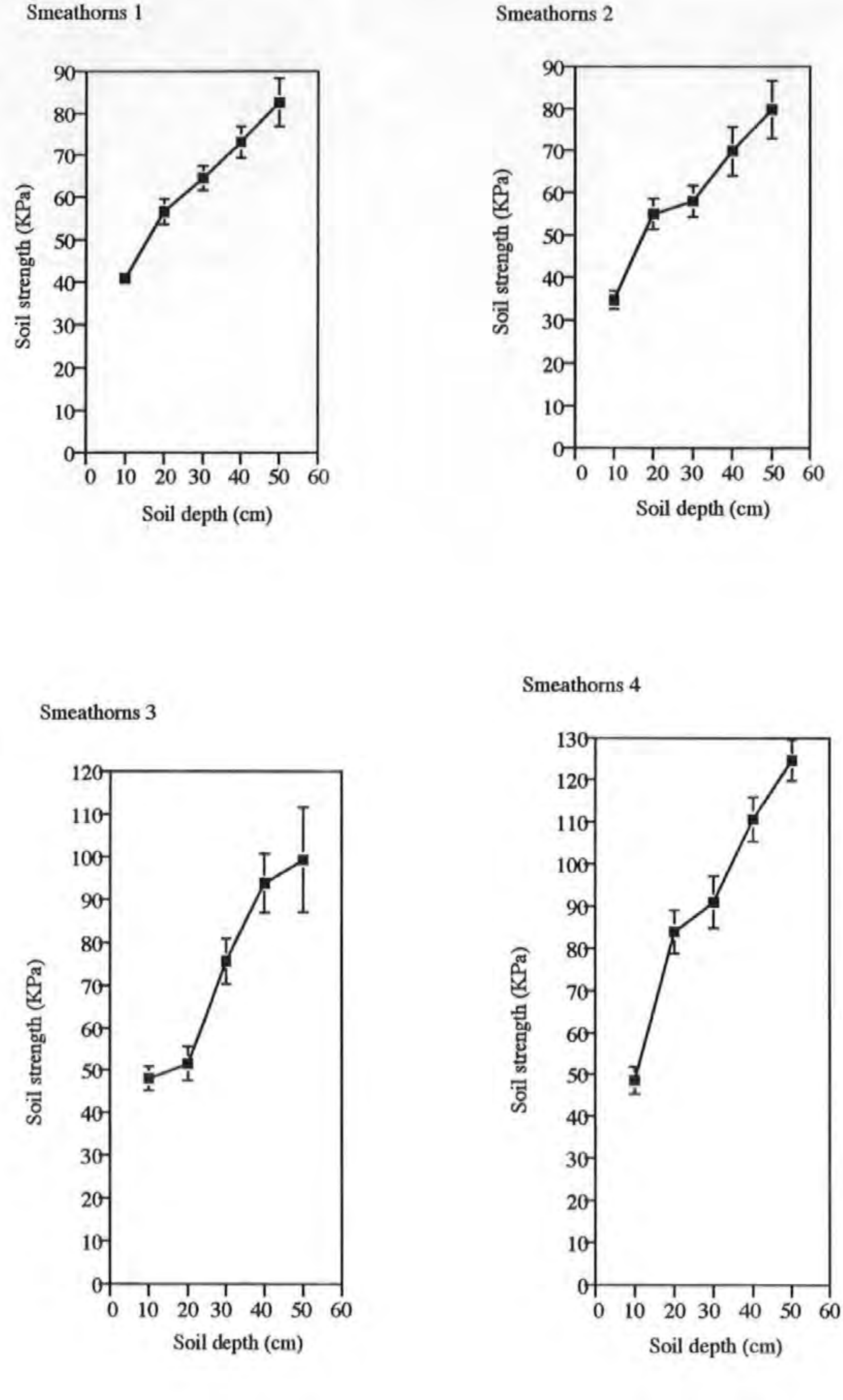


Figure 8b Mean soil shear strength (KPa) in relation to soil depth (cm) on the low moor.

an irregular iron pan which was observed during excavation. The iron pan may restrict soil drainage on the plot and also rhizome penetration into the lower soil horizons. In all plots some rhizomes were observed to grow down to, but not into, the less penetrable and less nutrient-rich mineral horizons. The mean and maximum penetrability of the rhizome was found to vary considerably between plots (Table 3). Rhizomes were found to tolerate shear strengths up to 90.87 (±6.16) kPa at Smeathorns 4.

It has been previously found that although rhizome penetrability is not adversely affected by denser soils, root growth will decline (Watt 1979). Therefore, rhizomes will tend to be restricted to soils of a lower shear strength. It is concluded that, although bracken rhizomes have the penetrability to grow into the deeper mineral layers, growth was restricted by root intolerance to an increase in shear strength. Where rhizome growth was apparent at great depth it was presumed that this represented fluctuations in the vertical arrangement of the soil. Also, the rhizome was found to spread into areas of reduced shear strength, ie old root channels and cracks in the mineral horizons.

Plot	x depth of rhizome (cm)	Max. depth of rhizome growth	Mean shear strength (kPa) *
Rosedale 1	23.30 (±2.30)	35.0	65.20 (±14.20)
Blakey 1	23.00 (±1.87)	29.0	46.60 (±7.30)
Rosedale 2	23.50 (±2.22)	35.0	57.00 (±7.00)
Blakey 2	37.70 (±6.68)	68.0	44.64 (±4.59)
Smeathorn 1	26.40 (±0.51)	28.0	64.50 (±2.83)
Smeathorn 2	33.80 (±1.62)	42.0	69.81 (±5.87)
Smeathorn 3	40.00 (±1.63)	45.0	99.30 (±12.30)
Smeathorn 4	23.80 (±1.50)	30.0	90.87 (±6.16)

* shear strength is given to the nearest 10 cm of maximum rhizome growth

Table 3 The mean and maximum depth (cm) recorded for rhizome growth in relation to soil shear strength.

3.1.4 Litter depth and percentage cover.

Mean litter depth (cm) was found to be highly variable between plots, [3.60 (±0.31)] to [10.10 (±0.53)] (Fig. 9). The accumulation of litter reflected both frond production and local rates of decomposition. The litter on the high moor was approximately 1 cm deeper than that found on the moorside at Blakey and on the low moor. This may have been due to lower seasonal temperatures on the high moor which would have caused a decrease in decomposition rates. An anomaly was the deep litter on the moorside at Rosedale [10.10 (± 0.53)]. The reason for this substantial accretion of litter, which made up approximately a third of the total soil profile, may have been due to vigorous frond growth in the preceding years. Accumulation may have also occurred due to the local relief, which consisting of a series of small gulleys and rises, may have reduced loss due to erosional factors.

The percentage cover of litter, using thirty 50 cm x 50 cm quadrats per plot, was high on all plots apart from Rosedale 1 (Fig. 10). No discernible relationship was ascertained between litter cover and litter depth, ie a high percentage cover of litter did not necessarily mean that there was a deep litter layer. The litter cover on the Rosedale 1 plot was found to be low but the litter depth was similar to Blakey 1.

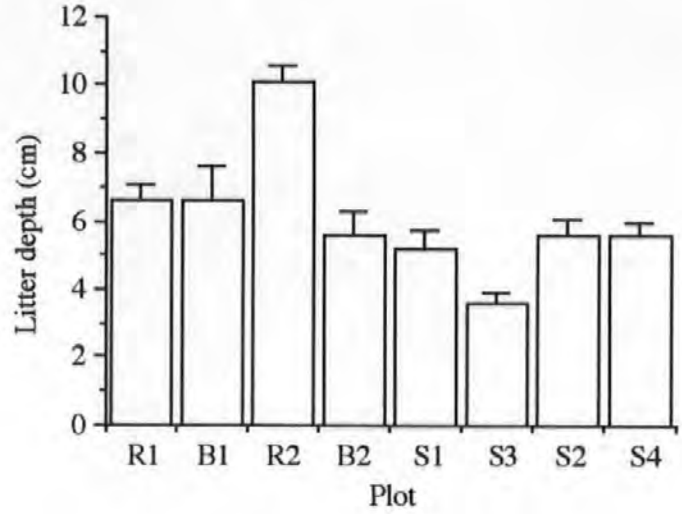


Figure 9 Mean litter depth

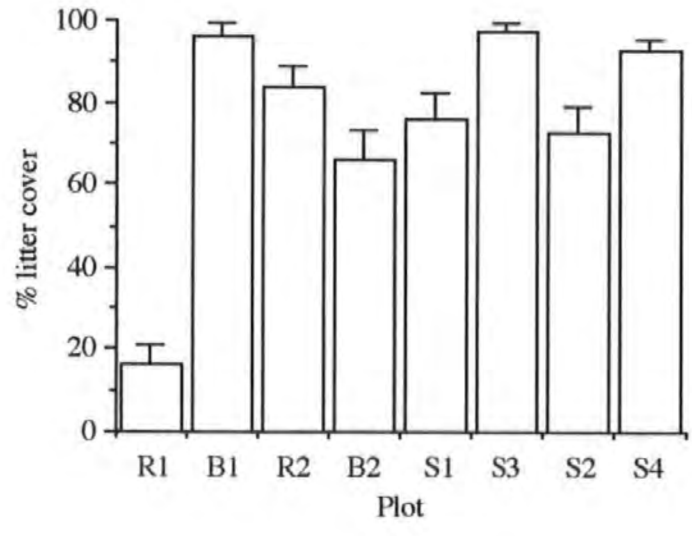


Figure 10 Percentage cover of litter within each plot

3.1.5 Vegetation monitoring

3.1.5.1 Vegetation sampling strategy

Each bracken plot included a sub-plot of 40 m x 40 m for the sampling of vegetation based on Goldsmith, Harrison & Morton (1986) and Greig-Smith (1983). Vegetation samples were taken in June 1992 using 30 50 cm x 50 cm quadrats (Goldsmith *et al* 1986). To ensure randomness, ie that each sample had an equal chance of being sampled, quadrats were located within plots using paired random numbers at distances along two axes.

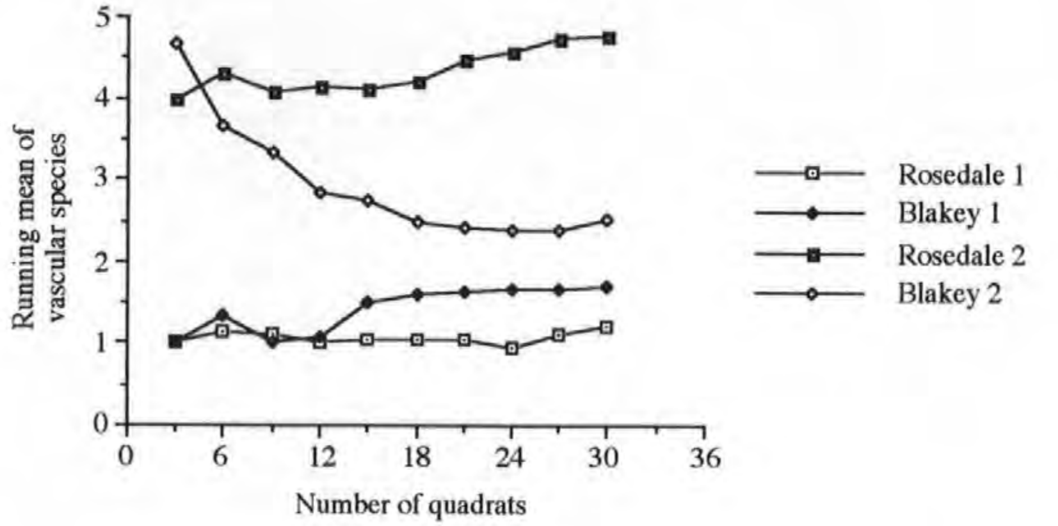
Each quadrat was subdivided into 100 smaller quadrats in order to make the recording of species presence more accurate, and to give an overall percentage of species (Archibald 1949). Species were considered present if aerial shoots were discernible or if the plant was actually rooted within the quadrat (Greig-Smith 1983). This non-destructive method of sampling had the advantage of repeatability over time and caused minimal damage to the vegetation. The number of quadrats sampled was based on the work of Goldsmith *et al* (1986).

By plotting the number of quadrats against the running mean number of vascular species, the minimum sample number required was chosen at the point where the number of species became consistent (Figs. 11a and 11b). At this point further sampling would have produced very few, if any, new species within the sampling area. The mean number of vascular groundflora species associated with bracken changes little between 24 and 30 quadrats.

3.1.5.2 Vegetation description

The high moor plots and Smeathorns 2 had between approximately 1 and 1.5 species per quadrat, consistently. Sampling beyond 18 quadrats produced few if any new species. The other low moor plots also showed a consistent number of species per quadrat after approximately 18 quadrats, but with a higher number, between 2 and 2.5, of species. The moorside plots showed greater variation in the running mean of species and only show consistency after 24-30 quadrats. This is because of the dynamic nature of the moor side, which comprises of more vegetation communities and ecotones than the heather moor. Taking into consideration the running means, that most statistical tests require a minimum of 30 samples, and the time available, 30 samples was considered sufficient for this study.

11a



11b

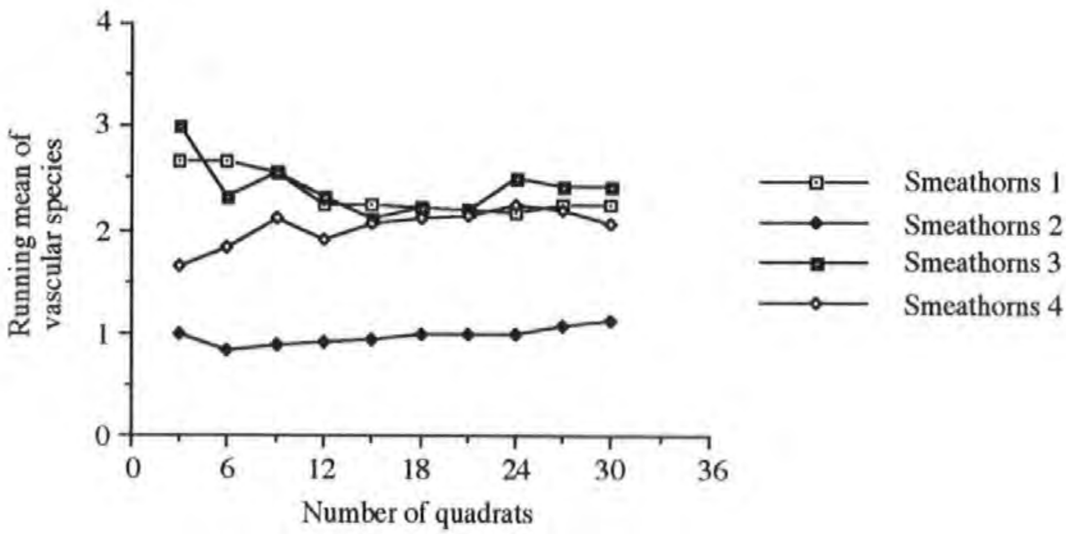


Figure 11a, b The running mean number of vascular species plotted against the number of quadrats. After Goldsmith, Harrison & Morton 1986

The validity of the vegetation sampling was investigated by 'walking' each plot to estimate the total number of species present. This was achieved by walking the plot along 1 m strips and noting the different species present. The total number of species was compared to the number of species recorded using the vegetation sampling strategy.

The vegetation data was analysed using two-way indicator species analysis (TWINSPAN) (Hill 1979). A copy of the table can be found in Appendix I. The moorland vegetation data was taken down to the third level comprising of 8 vegetation communities. All communities were dominated by bracken.

The high moor plots were dissimilar from one another in their under-storey vegetation communities and related species diversity. The quadrats within Blakey 1 represented vegetation communities comprising fewer species-rich quadrats than Rosedale 1 and included quadrats similar to those within Rosedale 2 and the Smeathorn plots. The major vegetation communities representing Blakey 1 were dominated by a dense mat of *Vaccinium myrtillus* and *Trientalis europea* with a scattering of *Festuca rubra* and the bryophyte *Hypnum jutlandicum.* The third Blakey 1 community had no dominant under-storey species and only one occurrence of *Vaccinium myrtillus.*

The quadrats from Rosedale 1 mostly comprised of an understorey dominated by *Vaccinium myrtillus* at levels of 100% cover. However, the growth of bilbery was observed to be less dense than at Blakey 1. Growing among the bilberry were a high number of vascular sub-species including *Festuca rubra, Festuca ovina, Galium saxatile, Anthoxanthum odoratum* and *Luzula campestris* and a scattering of bryophytes including *Hypnum jutlandicum, Polytrichum commune* and *Campylopus introflexus.*

The reason for the differences in species composition between the high moor plots may be explained by the degree of bracken litter accumulation. Although mean litter depth was not significantly different between the high moor plots, the percentage cover of litter was dissimilar. The proportion of litter cover at Blakey 1 was high [96.33 (±2.93)] compared to that at Rosedale 1 [16.43 (±4.21)]. The low level of litter cover at Rosedale 1 permitted other vascular species to germinate and colonise beneath the bracken canopy.

There was less distinction found between the two moorside plots as regards vegetation community composition. Both plots had quadrats representing communities dominated by *Oxalis acetosella, Vaccinium myrtillus* and *Campylopus introflexus* with varying levels of *Galium saxatile, Anthoxanthum odoratum,* and *Polytrichum commune.* Rosedale 2 also contained a high number of quadrats dominated by *Vaccinium myrtillus* with *Festuca rubra* and a scattering of *Trientalis europea* and *Campylopus introflexus.*

The under-storey vegetation of the lowland plots was principally dominated by the *Vaccinium myrtillus*, *Festuca rubra* and *Pteridium aquilinum* communities. Smeathorns 2 and 4 were also dominated by a community comprising principally of *Festuca rubra*, *Festuca ovina*, *Galium saxatile* and *Anthoxanthum odoratum*. The under-storey vegetation of Smeathorns 2 also contained species indicative of damper conditions, ie *Juncus effusus* and *Polytrichum commune*, due to the presence of a small spring line.

Vegetation analysis of the sample plots using TWINSPAN showed that the species diversity of flora under bracken was low regardless of the plot location. Most under-storey communities, regardless of location, were comprised of a mix of *Vaccinium myrtillus* and *Festuca rubra* with few associated species. Where more species were apparent there was a smaller percentage cover of bracken litter.

3.1.6 Plot treatments

Three treatments have been investigated: (i) the use of asulam herbicide; (ii) crushing; and (iii) a combination of crushing followed with the application of asulam.

Asulam was applied by a commercial operator using a Bell 47G3B1 helicopter fitted with a 12 m boom with 72 raindrop nozzles. Asulam was applied as the product Asulox at the recommended rate of 4.4 kg a.i. ha^{-1} in 44 l spray volume (May & Baker 1987) to the plots at Blakey and Smeathorns 3 in late July 1992 as part of the annual North York Moors control programme. The bracken was actively growing with a minimum of three pairs of pinna. No rain fell for at least 24 hrs before and after the application of asulam. Herbicide symptoms were virtually absent in the year of spraying but the following season manifested as reduced frond regrowth.

The treatments consisting of crushing and a combination of crushing and asulam were applied on the lowland moor. Bracken control using crushing was included to monitor any change in rhizome dry weight and the possiblity of dormant bud stimulation. Crushing was carried out using a Cuthbertson bracken crusher in July 1992 on Smeathorns 1 and 2. This was followed by spraying on Smeathorns 2 in late August 1992. Smeathorns was the only practical area for crushing experiments to be set up due to the availability of equipment and the relatively even surface of the land. The other plots available on the North York Moors were considered too steep or rocky for crushing to be a feasible option. Crushing was carried out in

July due to the availability of equipment, the work schedule of the gamekeeper and to reduce disturbance to moorland birds.

To compare the performance of bracken in treated and untreated plots controls were set up on Rosedale and Smeathorns 4, adjacent to the treated areas but distant enough to be unaffected by spray drift. The control plots indicated if changes in stand morphology were occurring on an annual basis without the intervention by man.

3.2 Sampling strategy

3.2.1 The rhizome

Rhizome samples were collected from twenty 30 cm^{-2} randomly positioned pits within each plot in late July 1992 before control treatments were applied. A study has found no difference in the rhizome morphology recorded using pits of size 20 cm x 20 cm and pits 50 cm x 50 cm (B. Sheaves *pers comm*). As the investigation required destructive sampling which would have interfered with the monitoring study, different quadrats were sampled in 1993. The number of samples was increased in 1993 from 20 to 50 per plot, after initial examination of the 1992 rhizome data and the subsequent optimum sample size study (Chapter 4).

Plate 6 Excavation of bracken rhizome on Rosedale 1. June 1994.

Each pit was excavated to the depth of the deepest rhizome, between 30-60 cm (Plate 6). The soil was carefully sifted using a 5 mm mesh sieve in order to remove all bracken rhizomes. The bracken was washed by hand, air dried for 24 hours to remove excess moisture, and classified into 3 shoot types; (i) frond bearing rhizome (short shoots); (ii) storage rhizome (long shoots); and (iii) intermediate shoots (Chapter 1). The number of active, dormant, dead and past buds were counted for all shoots. Buds were considered active if light in colour and slightly swollen, and dormant if smaller with a hard dark-brown covering (Lowday & Marrs 1983). Dead buds were distinguished by removing the tip and examining the inner layer. Buds affected by asulam were distorted due the fissuring and decay of the cortex, exposing the internal tissues to microbial attack (Veerasekaran *et al* 1976). The past buds were those that had previously produced fronds. They were identifiable by the remains of the frond stipe.

Measurements taken of the weight before and after oven drying gave data on the biomass levels of the rhizome system for each sample. The rhizomes were oven dried at a constant 80^{0}C for 24 hours (after 24 hours the rhizomes were weighed every hour to check that all moisture had been removed) and the dry mass recorded (Lowday & Lakhani 1987). The sampling strategy was repeated in July 1993 after treatment had taken place.

3.2.2 The frond

Frond counts were taken from ten random 1 m x 1 m quadrats per plot in late July 1992 and 1993 when the fronds were completely unfurled, and before treatment had taken place. The frond density was recorded and a subsample of 10 fronds per quadrat measured for height, lamina and pinna length. Height of the frond was taken as the length between the tip of the lamina and where the stipe met the rhizome. The lamina, which is the expanded leaf portion of the frond, was measured from where it joined the stipe to the tip of the frond. The pinna length was taken at the first order subdivision of the frond from the stipe to the pinna tip (Thomson 1990). Fronds were weighed in the field using a spring balance and polythene bag to record the biomass.

Chapter 4. An investigation of the sampling strategy required for evaluating rhizome shoot and bud numbers on the North York Moors.

4.1 Introduction

Previously published methods for the sampling of bracken rhizomes were considered inpractical for the accurate description of morphology and/or the success of control treatments (Chapter 1). The sampling of bracken in the North York Moors National Park in 1992 demonstrated the inherent variability of the rhizome system both within plots and between plots (Chapter 5). The sampling programme in 1993 therefore included an intensive examination of the rhizome system within the high moor plots. This was to evaluate i) the 1992 results with regard to the variability found within twenty 30 cm x 30 cm pits, and ii) to ascertain the number of pits of size 30 cm x 30 cm required to increase the accuracy of prediction of the population mean for shoot and bud number.

4.2 Methodology

The sample pit size of 30 cm x 30 cm was retained as this was considered practical for large-scale sampling. No significant difference in unit rhizome dry weight (72 hrs drying at 80^{o}C) had been found between samples taken from 20 cm x 20 cm and 1 m x 1m pits in a comparable study (B Sheaves *pers. comm*). Large pits can be used only once to sample an area as replication is impractical due to the labour involved and the destruction caused.

An empirical approach was used to determine the number of samples required to optimise the precision of the population mean (μ) of bud and shoot numbers on Rosedale 1 and Blakey 1. These plots were chosen in order to compare a control plot with a plot sprayed with asulam which had previously been found to display differences in rhizome characteristics. Rhizome sampling and analysis was achieved using the methodology of chapter 3 with the exception that the number of pits sampled was increased from 20 to 100 within each plot.

Samples were analysed in 10 sample lots and the mean and 95% confidence limits calculated for shoot and bud characteristics, and plotted on running mean graphs. Estimation of the population mean at determined levels of precision, ie short shoot number was not to deviate by more than 3 shoots, was used to ascertain the number of samples required when using a pit size of 30 cm x 30 cm.

4.3 Results

The description of shoot number, if using 10 or less samples, was inaccurate due to the large population mean (μ) and high confidence limits (Figs. 12-14). For example, 10 samples of short shoot from Blakey 1 had a mean of 7.50 shoots and a 95% confidence interval (CI) of 8.46 shoots (Fig. 12). Therefore, there was a 95% probability that μ lay between 3.27 and 11.73 shoots. The short shoots from Rosedale had a mean of 9.00 shoots and a CI of 7.24 shoots. This gave a 95% probability that μ lay between 5.38 and 12.62 shoots. The confidence intervals were considered too large in relation to the mean to accurately define the population characteristics of bracken shoots at Rosedale and Blakey.

The optimum number of samples must be set where the sample mean is considered to satisfactorily represent the population mean. For short shoot numbers the CI did not significantly decrease until between 40 and 50 samples were taken. This number also applied to both long and intermediate shoot number (Figs. 13 and 14). If 50 is taken as the level where the precision of μ is satisfactory then the 95% CI at Rosedale is 2.83 short shoots and at Blakey 2.42 short shoots (Table 4.1 and 4.2). The mean number of short shoots on both plots was lower and the level of accuracy much greater for 50 samples than for 20 samples. The confidence intervals continued to decrease from 50 to 100 samples but the degree of reduction was much smaller than that found between 10 and 50 samples.

An increase in sample number affected the mean number of dormant and active buds in a similar way to shoot number. The use of 10 samples to describe bud numbers or control success was not valid due to the wide confidence limits of the data (Figs. 15 and 16). The population mean and confidence intervals for dormant buds at Blakey 1 were particularly high (Fig. 15). A sample number of 10 at Blakey 1 had a mean of 28.60 buds and a 95% CI of 41.76 (Table 5.1). Therefore there was a 95% probability that μ lay between 7.72 and 49.48 buds. Although the mean number of active buds, 3.50, was lower in comparison to the mean number of dormant buds the 95% confidence limits were still large, 0.86-6.14 buds (Figure 16). The importance of these findings are increased when it is considered that Blakey 1 had been previously sprayed. This is because a low number of samples gives the impression that there were high numbers of unaffected dormant buds remaining (Fig. 15), and that active bud kill had been more successful (Fig. 16).

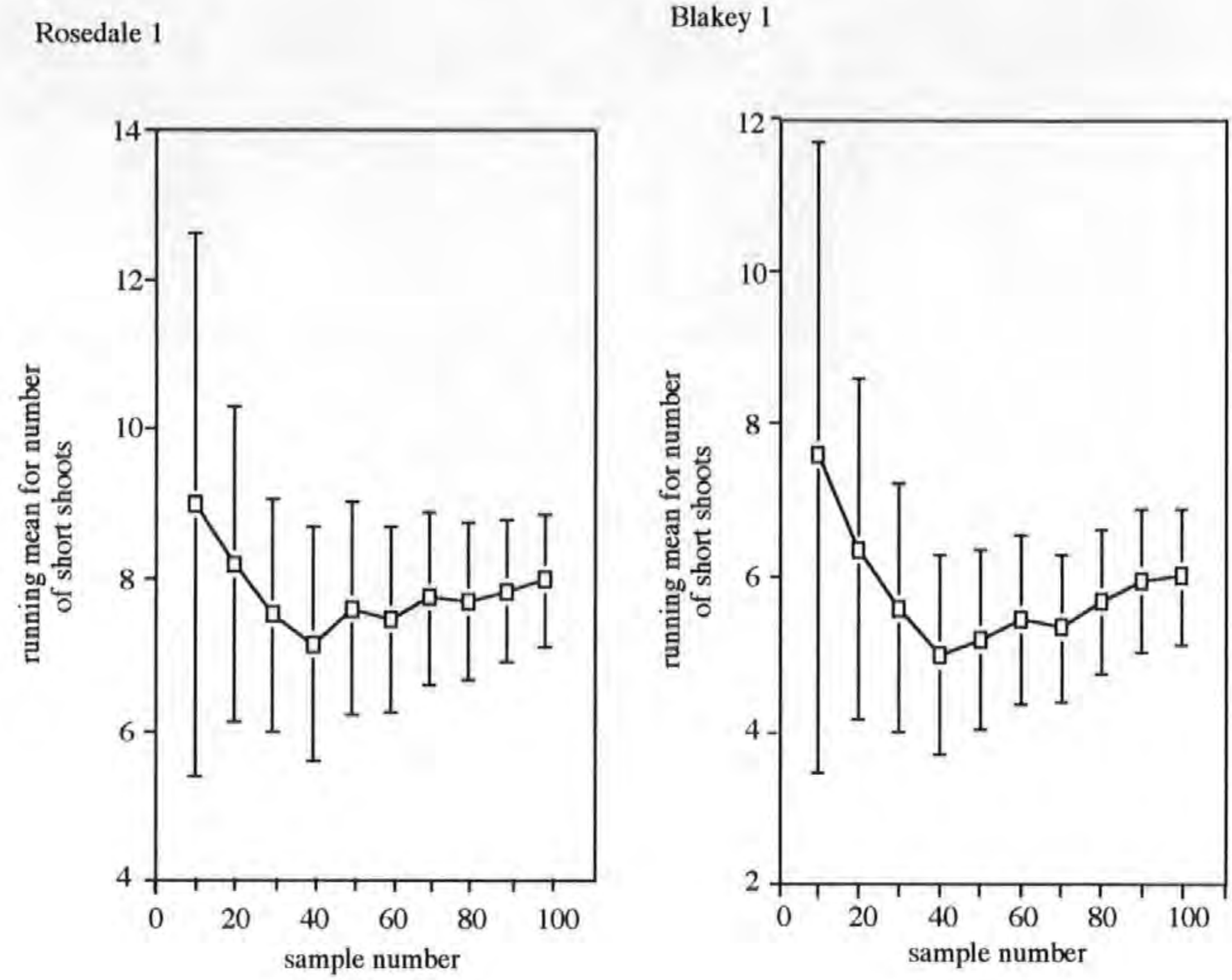


Figure 12 The running mean and 95% confidence interval for short shoot number.

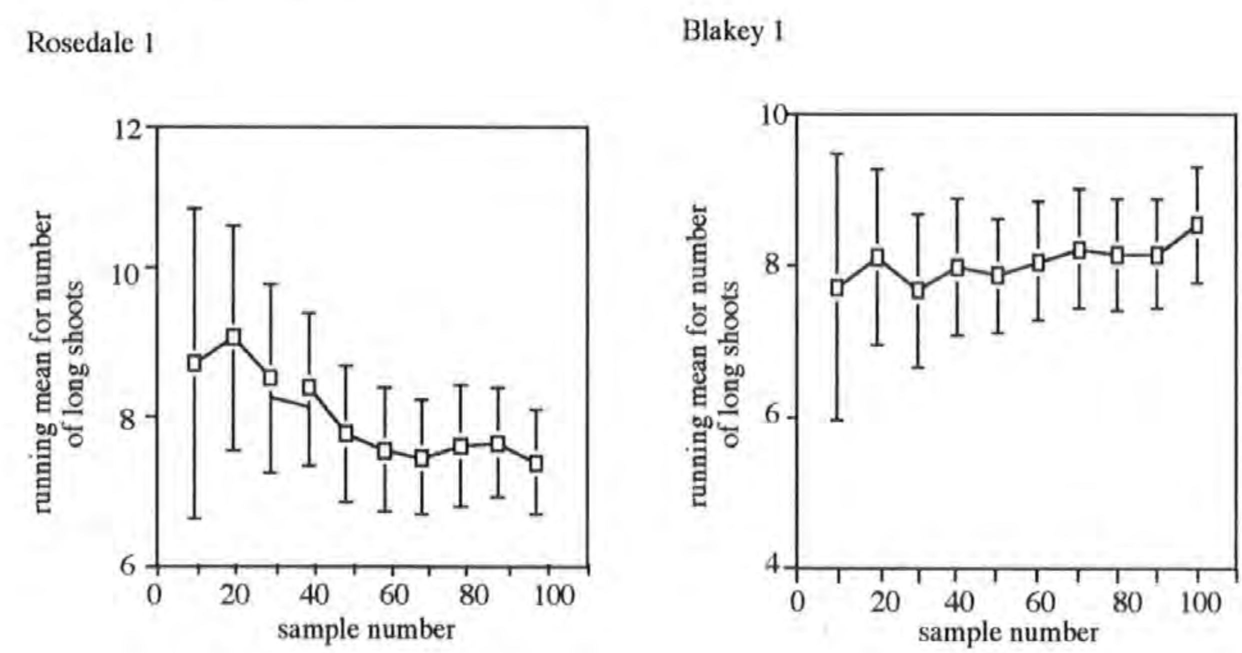
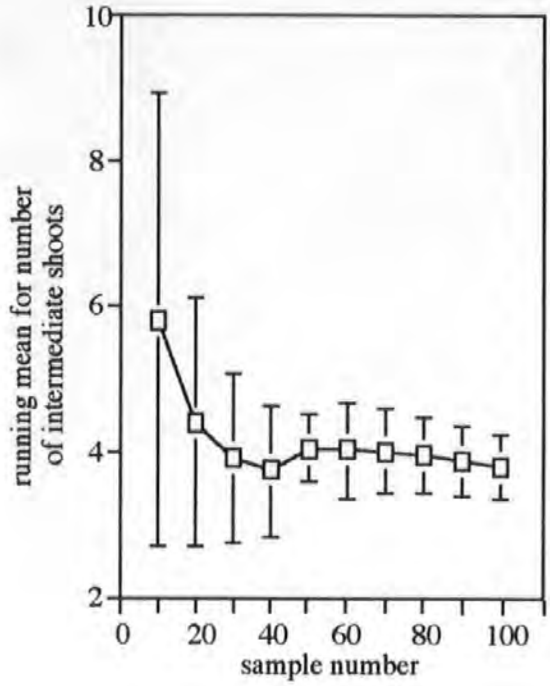


Figure 13 The running mean and 95% confidence interval for long shoot number.

Rosedale 1



Blakey 1

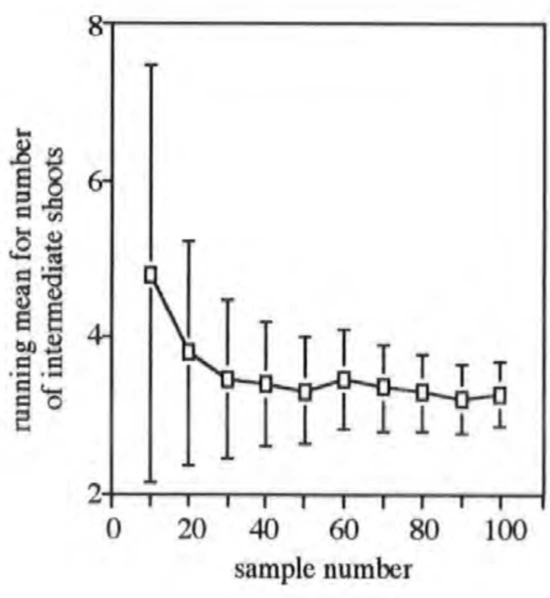


Figure 14 The running mean and 95% confidence interval for intermediate shoot number.

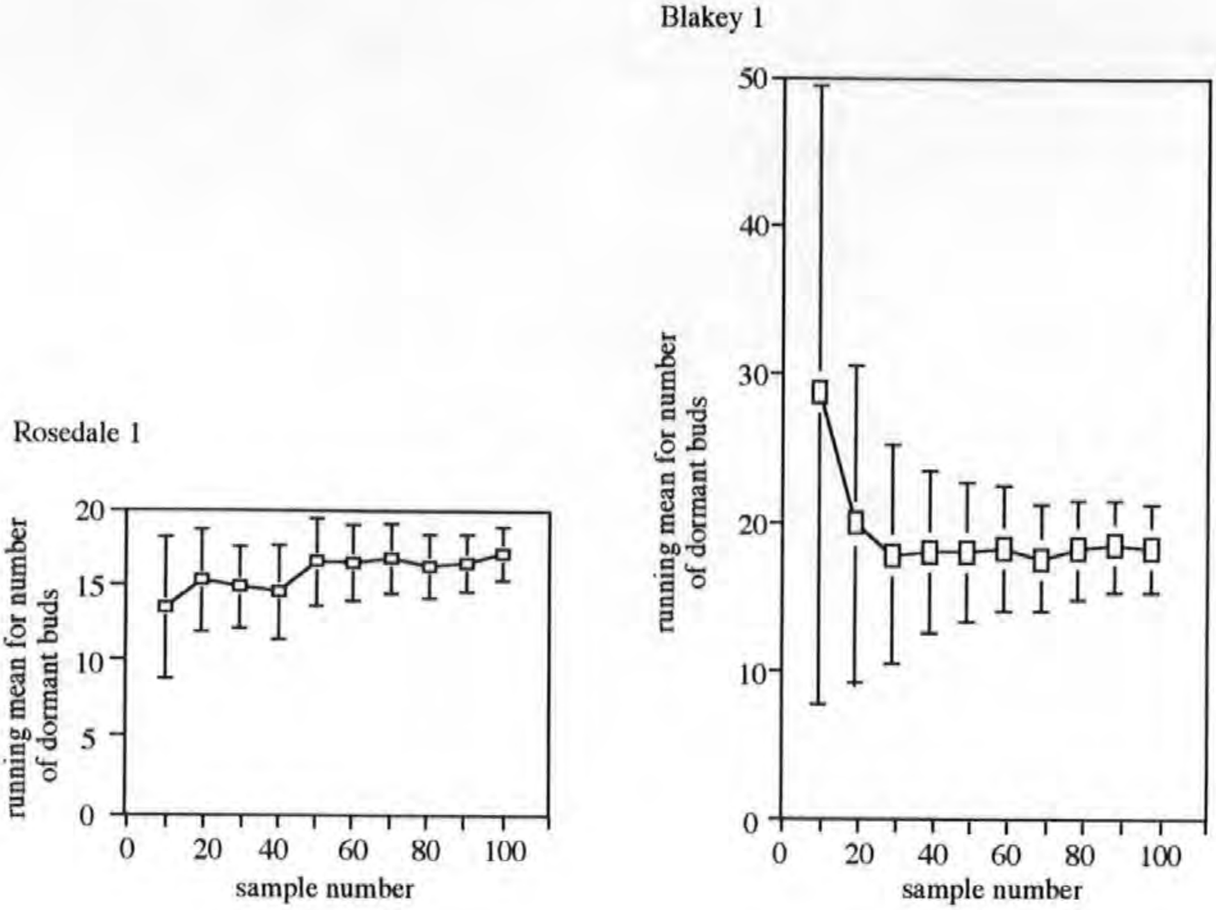


Figure 15 The running mean and 95% confidence interval for dormant bud number.

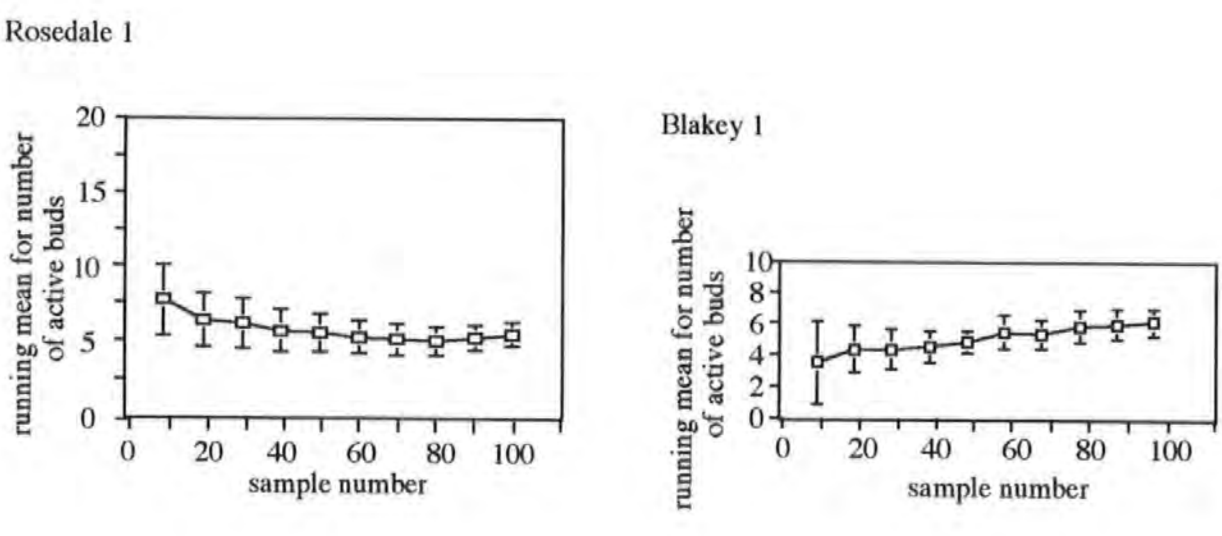


Figure 16 The running mean and 95% confidence interval for activebud number.

The CI continued to decline up to 100 samples. However, the CI at sample size 50 was small enough to justify using this sampling number. Dormant buds had a mean of 17.80 with a 95% probability that μ lay between 13.63 and 21.97 buds. Active buds had a mean of 4.82

sample number	mean	95% confidence limits		95% confidence interval
10	9.00	5.38	12.62	7.24
20	8.20	6.12	10.28	4.16
30	7.53	5.99	9.07	3.08
40	7.15	5.60	8.70	3.10
50	7.62	6.21	9.03	2.83
60	7.48	6.26	8.71	2.45
70	7.77	6.63	8.92	2.29
80	7.73	6.69	8.77	2.08
90	7.86	6.91	8.81	1.91
100	8.00	7.11	8.89	1.77

Table 4.1 The mean, 95% confidence limits and interval for short shoot number at Rosedale 1 for different levels of sampling.

sample number	mean	95% confidence limits		95% confidence interval
10	7.50	3.27	11.73	8.46
20	6.25	3.97	8.53	4.56
30	5.47	3.79	7.15	3.36
40	4.85	3.51	6.19	2.68
50	5.04	3.83	6.25	2.42
60	5.32	4.20	6.44	2.24
70	5.20	4.22	6.18	1.96
80	5.56	4.59	6.53	1.94
90	5.83	4.88	6.78	1.90
100	5.89	4.99	6.79	1.80

Table 4.2 The mean, 95% confidence limits and interval for short shoot number at Blakey 1 for different levels of sampling.

with a 95% probability that μ lay between 3.39 and 6.25. Therefore, if using 50 samples at Blakey 1, it can be ascertained that μ lies between 8.34 and 2.86 buds, respectively.

At Rosedale 1 the use of 10 samples gave a mean of 13.40 dormant buds with a CI of 9.52 and a 95% probability that μ lay between 8.64 and 18.16 (Fig. 15). The mean number of active buds was 7.80 with a CI of 4.44 and a 95% probability that μ lay between 5.58 and 10.02 (Fig. 16). Increasing sampling size to 50 decreased the confidence limits to a more acceptable level. Dormant buds had a mean of 16.54 with a 95% probability that μ lay between 13.52 and 19.56 (Table 5.2). Active buds had a mean of 5.72 with a 95% probability that μ lay between 4.53 and 6.92. Therefore, if using 50 samples at Rosedale 1, it can be ascertained that μ lies between 6.04 and 2.39 buds, respectively.

sample number	mean	95% confidence limits		95% confidence interval
10	28.60	7.72	49.48	41.46
20	19.85	9.22	30.48	21.26
30	17.70	10.39	25.01	14.62
40	17.90	12.35	23.45	11.10
50	17.80	13.02	22.58	9.56
60	18.15	13.98	22.32	8.34
70	17.47	13.82	21.12	7.30
80	18.11	14.73	21.49	6.76
90	18.27	15.18	21.36	6.18
100	18.12	15.22	21.02	5.80

Table 5.1. The mean, 95% confidence limits and interval for dormant bud number at Blakey 1 for different levels of sampling.

sample number	mean	95% confidence limits		95% confidence interval
10	13.40	8.64	18.16	9.52
20	15.30	11.84	18.76	6.92
30	14.80	12.00	17.60	5.60
40	14.50	11.32	17.68	6.36
50	16.54	13.52	19.56	6.04
60	16.48	13.89	19.07	5.18
70	16.77	14.40	19.14	4.74
80	16.23	14.09	18.37	4.28
90	16.49	14.56	18.42	3.86
100	17.14	15.30	18.98	3.68

Table 5.2 The mean, 95% confidence limits and interval for dormant bud number at Rosedale 1 for different levels of sampling.

Although use of the running mean and confidence intervals can be applied to plots that have been sampled on a large scale, ie 50-100 samples per plot, a sample size of 50 may not always be applicable or indeed necessary for some bracken populations. Furthermore, sampling on a large scale (n = 100) is not feasible due to the degree of labour and time involved.

It is therefore useful to be able to determine the optimum number of samples required in order to achieve an accurate estimation of μ for a given rhizome characteristic. This may be accomplished by taking a small number of rhizome samples (n = 20) from a given population of bracken and then using the sample variance, s^2 (Zar 1984). The number of samples required to calculate the CI of a specific width can be determined using the following equation;

$$n = \frac{S^2 t^2_{\alpha(2),(n-1)} F_{\beta(1),(n-1,v)}}{d^2}$$ (Harris, Horvitz & Mood 1948)

By taking 20 samples from Blakey 1 and Rosedale 1estimates of μ were calculated with the 90% probability that the 95% CI will be no wider than specified. Because n was unknown the sample size was determined by iteration. The estimated CI was compared to the actual CI of the 100 sample data to the nearest 10 samples (Table 6 and 7).

For both long and short shoots the level of precision required in the estimation of μ was chosen at 3 shoots. Levels of precision may be altered accordingly. The number of samples of size 30 cm x 30 cm which were required in order to attain a 90% probability that the 95% CI was no more than 3 shoots varied between 36 and 63 (Table 6). If the estimated sample size is compared to the actual CI (calculated to the nearest 10 samples) of the 100 sample data then it can be seen that the stated level of precision had been achieved. The mean did not vary by more than 3 for short shoot number and by 2 for long shoot number.

This gave an upper estimate of the number of samples required to reach a specified precision. The actual confidence intervals for shoot number may be reached by a lower number of samples at Blakey 1 and Rosedale 1, only 20 for long shoots.

For dormant bud number the level of precision required was chosen at 8 buds and for active bud number 3 buds. The number of samples required to achieve these levels were 16-44 samples and 24 - 59 samples, respectively (Table 7). The calculation of the 95% CI from the 100 sample data confirmed that the levels of sampling were adequate for dormant bud number on Rosedale 1 and active bud number on Blakey 1.

The sample estimate of active buds on Rosedale 1, n = 24, had a CI of 3.42. Although this discrepancy seems small, approximately 16 more samples would be required to reduce the

CI to below 3 buds. A large divergence from the precision of 8 dormant buds occurred at Blakey 1. The actual 95% CI of a sample number of 44 (to nearest 10 samples) was 11.10 buds. This may be accounted for by the high confidence intervals on Blakey 1 (Table 2.1). The actual number of samples required to be within a CI of 8 buds was 70 pits. A degree of caution is advisable when evaluating populations of bracken which demonstrate high confidence limits at a small sample size (n $\leq$ 20). Nevertheless, the use of an estimated CI is still a valuable tool upon which to build a sampling strategy for a population of bracken which has been sampled on a small scale.

Plot	Shoot type	Precision of CI required	Sample estimate (n)	95% confidence interval (to nearest 10 samples)	Actual sample number required to reach specified precision
Rosedale 1	short	3	60	2.45	50
	long	3	63	1.65	20
Blakey 1	short	3	53	2.42	40
	long	3	36	1.76	20

Table 6 Estimated and actual sample number required to achieve a specified confidence interval of 3 for short and long shoot numbers.

Plot	Bud type	Precision of CI required	Sample estimate (n)	95% confidence interval (to nearest 10 samples)	Actual sample number required to reach specified precision
Rosedale 1	dormant	8	16	6.92	20
	active	3	24	3.42	40
Blakey 1	dormant	8	44	11.1	60
	active	3	59	2.14	20

Table 7 Estimated and actual sample number required to achieve a specified confidence interval of 8 and 3 for dormant and active bud number respectively.

4.4 Conclusions

Examination of the running means of rhizome shoot and bud numbers in relation to the number of samples has shown that the precision of the population mean, expressed by the confidence interval, increases as the sample number increases. This has implications for both the study of bracken morphology and the monitoring of control programmes. It is important that the high means and large confidence intervals found at low levels ($n \leq 20$) of sampling are avoided as the data will be unrepresentative. A sample number must be chosen where the CI is sufficiently narrow to increase the precision of the estimation of the population mean. On the North York Moors a sampling strategy utilising up to 20 pits was found to be unsatisfactory. This may reduce the value research based on taking a small number of samples (Chapter 1). The use of a small number of large pits is unrepresentative and the derived data invalid due to the high level of rhizome variability.

The rhizomes of bracken, and in particular the number of buds, are highly variable and it is essential to evaluate the number of samples required to predict μ within a stated precision. A more accurate estimate of bracken morphology increases the potential for predicting susceptibility to control measures of a given population.

Because of the variability of bracken within populations, and between populations, a standard sample number cannot be applied across the U.K. A sample size of 50 was found to be practical on the North York Moors but this may have to be increased or decreased according to the particular characteristics of the bracken under examination. A comparison of the estimated sample size and actual sample size required to be within a specified level of precision is informative in forming a suitable sampling strategy.

Chapter 5 Bracken stand morphology on the North York Moors.

5.1 Introduction.

The frond morphology of a bracken stand may give the impression of a uniform Pteridophyte. It is postulated here, however, that no such homogenity exists and that only by examining the variability of bracken and the relationship between the rhizome and frond can effective control management policies be implemented. A stand of bracken has been shown by previous research to comprise either a single clone containing genetically distinct genotypes or consist of a number of clones of different ages and genotypes (Chapter 1). The patterns of bracken re-infestation that often occurs after initial control management have been attributed to application failure or to detrimental environmental conditions without due regard to the possibility of resistant genotypes.

Each stand of bracken needs to be classified in order to define those characteristics of the rhizome that prove difficult to eradicate, as well as identifying those stands which would be susceptible to control measures. If the classification of stands is possible it would be desirable that large-scale control programmes, such as that of the North York Moors National Park, include some form of preliminary ground survey prior to spraying in order to map stand susceptibility and so improve overall control success. Nonetheless, if there is high variability of the rhizome system within separate stands then classification may not be feasible.

By examining bracken stands on the North York Moors, the rhizome and frond morphology found within plots and between plots has been quantified before the implementation of control measures. This identified the likely response to treatment and could be used in general terms as a basic predictive technique for quantifying susceptibility to control.

Relationships were expected to exist between certain rhizome and frond characteristics. The dry weight of the rhizome system was expected to be related to shoot number, and in particular, the number of long shoots because of their storage capabilities. It has been observed by the author, however, that some rhizome systems consist of a dense network of short and intermediate shoots with few long shoots in evidence. It is also recognised that due to the timing of data collection the dry weight of the rhizome will be reduced due to frond production.

The number of dormant and active buds was expected to be related to short shoot number as the short shoots are responsible for bud production. The total number of buds would indicate the potential to produce either fronds or new shoots. The number of each type of bud will also have consequences for control measures. Active buds are sites for the assimilation of asulam whilst dormant buds represent sinks which will be unaffected by asulam, and may require some form of stimulation to become active.

5.2 The morphology of bracken rhizome and frond systems with regard to plot and geographical location.

This section evaluates the morphology of the rhizome and frond on three geographical locations of the North York Moors, the high moor, moor side and low moor. The data presented was taken prior to the 1992 treatment programme. The plots on each location were examined and compared for rhizome and frond characteristics. The findings were related to the potential effect that control treatments may have on each plot. The variability of rhizome and frond characteristics within plots and the differences in variability between plots is discussed in relation to bracken morphology and control.

5.2.1 A comparison of the high moor plots at Blakey 1 and Rosedale 1.

The plots located on the high moor were situated at the present altitudinal extent of bracken growth at Rosedale 1 and Blakey 1 (this may change with global warming). The bracken within these plots, compared to other plot locations, was subject to increased exposure at the summit and lower soil depths (Chapter 3). The litter depth on these plots was high and it was observed that a substantial amount of rhizome growth occurred in the litter layer at Rosedale 1, and to a lesser extent Blakey 1.

The bracken on the high moor plots demonstrated vigorous rhizome growth, particularly on Rosedale 1 (this may be due to Rosedale 1 being located at a lower altitude than Blakey 1). The mean number of dormant buds and active buds on Rosedale 1 was higher than that found at Blakey 1 (Table 8). The rhizome system at Rosedale 1 contained over twice the mean number of dormant buds than at Blakey 1 with 95% of the samples containing between 32.25 and 55.05 buds, with a maximum of 101 buds. At Blakey 1 95% of dormant bud numbers ranged from 14.24 to 23.96 buds with a maximum of 36 buds being recorded. The high mean number of dormant buds on Rosedale 1, approximately 484.56 buds m^{-2}, represented an enormous capacity to produce fronds or new shoots compared to the number of buds at Blakey 1 (212.01 buds m^{-2}).

Dormant buds

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 1	43.65 (±5.45)	32.25	55.05	101	15
Blakey 1	19.10 (±2.32)	14.24	23.96	36	2

Active buds

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 1	15.25 (±1.82)	11.45	19.05	31	5
Blakey 1	11.25 (±1.84)	7.41	15.09	29	2

Table 8. Mean dormant and active bud number and 95% confidence intervals for the high moor plots.

A comparison of active bud number within the plots produced a similar result, although not as extreme, to the dormant bud number (Table 8). The rhizome system at Rosedale 1 contained a higher mean number of active buds compared to Blakey 1 but the maximum number of buds was similar.

Although the percentage of active to dormant buds was lower at Rosedale 1 (25.89% and 74.11%, respectively) compared to Blakey 1 (37.07% and 62.93%, respectively) there was a higher mean number of active buds, and therefore potential sites for frond production or rhizome expansion, and asulam assimilation. This potential was enhanced by the high mean number of dormant buds at Rosedale 1.

The number of buds indicated the potential numbers of frond primordia and new shoots but plant growth was also dependent on the stored carbohydrate in the rhizome, represented in this study by the mean rhizome dry weight. Although frond production was near completion at the time of sampling the rhizome dry weight gave a good indication of the underground vigour of the bracken (Table 9).

The mean dry weight of rhizome and 95% confidence intervals at Rosedale 1 were significantly larger than the rhizome dry weight at Blakey 1. The higher mean number of buds and the mean rhizome dry weight suggested that the bracken at Rosedale 1 was more mature, or growing within more suitable conditions, than the bracken at Blakey 1.

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 1	62.55 (±6.39)	49.17	75.93	107	22
Blakey 1	43.67 (±5.03)	33.15	54.19	80	7

Table 9. Mean dry weight (g) of rhizome and 95% confidence interval for the high moor plots.

In relating rhizome dry weight to shoot number a strong relationship was expected with the number of long shoots. In fact the mean rhizome dry weight demonstrated a relationship with all three shoot types (Table 10) but the levels of significance differed. On Blakey 1 the mean dry weight demonstrated a positive relationship with long shoot number ($P < 0.01$) and a less pronounced relationship with both intermediate and short shoot number ($P < 0.05$). On Rosedale 1 the mean dry weight of rhizome was more significantly related to the number of intermediate shoots [$r = 0.634$ ($P < 0.01$)].

Dry weight (g)	Long shoots	Intermediate shoots	Short shoots
Rosedale 1	0.505*	0.634**	0.407*
Blakey 1	0.919**	0.597**	0.509*

* P< 0.05, ** P < 0.01

Table 10. Correlation coefficients for rhizome dry weight and shoot type on the high moor.

The rhizome system of Rosedale 1 was dominated by a high mean number of short shoots with 95% of samples containing between 10.2 and 17.6 shoots (Table 11). Conversely the rhizome system at Blakey 1 had a higher number of long shoots compared to Rosedale 1.

The shoot data was related to the mean number of dormant and active buds. Rosedale

1 had a high mean number of dormant buds, [43.65 (±5.45)], which demonstrated a significant relationship with the mean number of short shoots, [$r = 0.809$ ($P < 0.01$)], and intermediate shoots, [$r = 0.428$ ($P < 0.05$)]. At Blakey 1 budding frequency was related to the mean number of all three shoot types ($P < 0.01$).

Short shoot

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 1	13.90 (±1.77)	10.20	17.60	32	4
Blakey 1	5.10 (±0.69)	3.66	6.54	12	1

Intermediate shoot

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 1	6.15 (±1.60)	2.81	9.49	35	1
Blakey 1	4.50 (±0.83)	2.77	6.24	12	0

Long shoot

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 1	5.80 (±0.85)	4.01	7.59	13	1
Blakey 1	8.25 (±1.17)	5.81	10.69	19	1

Table 11. Mean number of short, intermediate and long shoots and 95% confidence interval on the high moor plots.

In summarising the rhizome morphology of the high moor plots, major distinctions could be made. Rosedale 1 was found to be comprised of a high mean number of short shoots which was related to the high number of dormant and active buds. The mean dry weight of the rhizome was higher at Rosedale 1 than at Blakey 1 but no relationship was found with either the high number of short shoots or the long shoots. Rhizome dry weight was, however, related to the mean number of intermediate shoots.

Blakey 1 was found to contain a high mean number of long shoots which was related to the mean rhizome dry weight. The number of buds at Blakey 1 was lower than that found at

Rosedale 1. It was postulated that this was due to the lower number of short shoots at Blakey 1; however, it was observed that a high proportion of buds were being produced on the intermediate and long shoots.

In taking the rhizome data into consideration Rosedale 1, with a higher mean number of buds and larger mean rhizome dry weight was expected to have produced a greater biomass of fronds than Blakey 1. Although Rosedale 1 produced fewer fronds than Blakey 1 in 1992 (Table 12), the height data showed that the mean height of fronds at Rosedale 1 was greater than the fronds at Blakey 1 by an average of 9.86 cm. However, the mean length of the pinna and lamina were not significantly different between the plots. Nevertheless, the mean frond biomass (g m^{-2}) on Rosedale 1 was found to be larger than Blakey 1 [1099 (±144) and 799 (±169) respectively].

Blakey 1 had the ability to produce some fronds of a similar height to Rosedale 1 (both maximum denominators differed by only 0.2 cm) but the height range within which 95% of the fronds fell was lower. It was observed by the author that the majority of fronds on Blakey 1 were much shorter and appeared stunted in growth when compared to the fronds growing at Rosedale 1. Nevertheless, the fronds at Blakey 1 did have the potential in some circumstances to grow to heights comparable to Rosedale 1.

Frond number

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 1	31.60 (±1.74)	27.96	35.24	21.00	49.00
Blakey 1	36.60 (±3.32)	29.64	43.56	13.00	69.00

Frond height

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 1	47.40 (±6.85)	33.07	61.73	90.80	15.80
Blakey 1	37.54 (±6.13)	24.70	50.38	90.60	10.80

Table 12. Mean frond number and height (cm) and 95% confidence intervals on the high moor plots m^{-2}.

A comparison of the frond and rhizome system demonstrated that there were no discernible relationships between variables. Most correlations were not significant and only tentative assumptions could be made from those that did demonstrate some relationship. The only consistency between the two plots was the relationship between the mean number of short shoots and the mean frond biomass ($P < 0.05$). The number of short shoots would however have been expected to be related to the number of fronds. Nevertheless, short shoot number and frond number demonstrated no relationship.

The bracken stands on the high moor were significantly dissimilar in rhizome and frond composition. It was considered that the bracken on Rosedale 1 represented a more established stand than the Blakey 1 plot. If comparing the high moor plots to the work of Watt (1947) the plots can be classified within different stages of the life cycle of bracken stands. Rosedale 1, with a more established and complex rhizome system, and taller fronds, is characteristic of the building and mature stages of the cycle. The Blakey 1 plot, however, with a lower number of buds and fewer shoots, consisted of less rhizome dry weight and produced shorter fronds. Blakey 1 was therefore more characteristic of the establishing pioneer phase of the life cycle. On Blakey 1 it was observed that the high density of *Vaccinium myrtillus* appeared to restrict rhizome growth. The long shoots were much thinner than those on Rosedale and the short shoots, by their twisted pattern of growth, appeared to have been out-competed by the dense rhizome mat of *Vaccinium myrtillus*.

The differences between the plots regarding their rhizome and frond morphology was expected to affect the outcome of any subsequent control treatment. The Rosedale 1 plot had a high mean number of dormant and active buds. This has two consequences for asulam control. Firstly, a high number of dormant buds signified that there were a high number of inactive sinks. Consequently, there was the potential to produce a high number of fronds and shoots after control had taken place. Secondly, the high number of active buds on Rosedale 1 compared to Blakey 1 meant there were more sites for asulam assimilation. It is suggested that the importance of bud number is not in how many buds will be affected by asulam, but how many will remain unaffected, as these represent the potential regrowth of the plant. On Rosedale 1, therefore, the high number of dormant buds may cause the use of asulam to be less successful in the long term than Blakey 1.

The number of active buds at Rosedale 1 could have been increased through stimulation of the budding system via mechanical methods of control. This would have also reduced the mean dry weight of the rhizome system at Rosedale 1 through the production of a second stand of fronds. The crushing or cutting of the fronds would have also weakened the rhizome system at Blakey 1.

The positive relationship between mean bud number and mean long shoot number found within Blakey 1 questions the understanding of bracken morphology which indicates that most budding points are located on the short shoot. A substantial number of fronds were observed being produced on the long shoot. If these fronds were sprayed with asulam two effects may occur. Firstly, the translocation of asulam directly into the long shoot system may be beneficial in controlling buds which would normally be remote from the herbicide source. Secondly, the asulam may be less effective because of the diluting properties of the long shoots. Therefore, asulam levels may not be sufficiently high to effect buds located further away from the frond.

5.2.2 A comparison of the moor side plots at Blakey and Rosedale.

The plots on the moor side were less exposed than the high moor plots and were situated at lower altitudes (with a subsequent superior growing season). The mean depth of soil was particularly high on the Blakey 2 plot (Fig. 6, Sec. 3.1.3) due to the local relief, and this anomaly was reflected in the vigorous growth of the fronds. The soil depth of Rosedale 2 was similar to that of the high moor plots. The mean depth of litter was higher on Rosedale 2 than Blakey 2 and it was observed that the litter layer was utilised by numerous short shoots.

The mean number of buds on Rosedale 2 and Blakey 2 were comparable to the high moor plots. The rhizome system of Rosedale 2 had over three times the mean number of dormant buds than the rhizome system of Blakey 2, with 95% of samples containing 38.22 - 53.38 buds (Table 13). In comparison 95% of the samples on Blakey 2 contained between 10.03 and 16.07 dormant buds. The high mean number of dormant buds at Rosedale 2, 508.39 buds m^{-2}, represented a large potential pool for frond and shoot growth compared to the number of buds at Blakey 2, 144.86 buds m^{-2}.

A comparison of the mean number of active buds demonstrated differences between the two plots. The bracken at Rosedale 2 contained a high mean number of active buds compared to Blakey 2. The mean number of active buds on Blakey 2 was particularly low [5.20 (±0.96)]. Although the percentage of dormant to active buds was similar on Rosedale 2 and Blakey 2 (72.96% to 27.44% and 71.51% to 27.51%, respectively) the higher mean number of buds on Rosedale 2 increased its potential over Blakey 2 for frond and shoot production.

Dormant buds

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 2	45.80 (±3.62)	38.22	53.38	90	20
Blakey 2	13.05 (±1.44)	10.03	16.07	28	1

Active buds

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 2	17.15 (±2.49)	11.94	22.36	35	3
Blakey 2	5.20 (±0.96)	3.25	7.25	18	1

Table 13. Mean dormant and active bud number and 95% confidence interval for the moor side plots.

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 2	89.35 (± 9.32)	69.83	108.86	152.50	31.10
Blakey 2	50.06 (±4.67)	40.28	59.84	101.20	0.45

Table 14. Mean rhizome dry weight (g) of rhizome and 95% confidence interval for the moor side plots.

The mean dry weight of rhizome at Rosedale 2 was larger than that at Blakey 2 (Table 14). An examination of the shoot data showed that the rhizome system of Rosedale 2 was dominated by a high mean number of short shoots and the rhizome system of Blakey 2 by a high mean number of long shoots (Table 15). The mean number of intermediate shoots was low on both plots. It was observed by the author that short shoots were particularly absent in many of the samples taken on Blakey 2 and that the majority of fronds were produced directly from the long shoots.

There was a significant relationship ($P < 0.01$) between mean rhizome dry weight and mean long shoot number for both plots (Table 16). Rosedale 2 also demonstrated a significant relationship between mean rhizome dry weight and the mean number of short shoots. The high mean number of short shoots at Rosedale 2, [16.85 (±1.60)], contributed substantially to the mean dry weight of the rhizome and therefore gave an exaggerated indication of the available storage rhizome. Blakey 2 had a lower mean number of short shoots, [3.80 (±0.71)], and consequently demonstrated no relationship with rhizome dry weight.

Short shoot

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 2	16.85 (±1.60)	13.50	20.20	36	7
Blakey 2	3.80 (±0.71)	2.32	5.28	14	0

Intermediate shoot

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 2	5.05 (±0.32)	4.38	5.72	8	3
Blakey 2	2.50 (±0.37)	1.73	3.27	7	0

Long shoot

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 2	6.10 (±0.62)	4.81	7.39	14	2
Blakey 2	8.45 (±0.89)	6.58	10.33	16	0

Table 15. Mean number of short, intermediate and long shoots and 95% confidence interval on the moor side plots.

Dry weight (g)	Long shoots	Intermediate shoots	Short shoots
Rosedale 2	0.649**	0.296	0.686**
Blakey 2	0.704**	-0.185	0.339

** P < 0.01

Table 16. Correlation coefficients for rhizome dry weight and shoot number on the moor side

plots.

The shoot data was related to the mean number of dormant and active buds. The mean number of dormant buds on Rosedale 2 demonstrated a significant relationship with the mean number of short shoots [r=0.608 ($P<0.01$)]. No relationship occurred between mean active bud number and the number of shoots on Rosedale 2. The mean number of dormant buds on Blakey 2 demonstrated a significant relationship with the mean number of short shoots [r=0.432 ($P<0.05$)] and the active bud number demonstrated a significant relationship with the number of long shoots [r=0.467 ($P<0.05$)]. Although the majority of dormant buds were found on the short shoots, few fronds were produced from these shoots.

In comparing the rhizome system with frond production Rosedale 2, with a higher mean number of buds and a larger mean dry weight should have produced either more fronds or fronds of a larger size. Rosedale 2 produced a greater mean number of fronds m^{-2} than Blakey 2; however, the fronds were shorter (Table 17). The mean frond lamina length on Rosedale 2 compared to Blakey 2 [39.29 (±3.21) and 55.31 (±1.66), respectively] and the mean pinna length [39.27 (±2.02) and 51.16 (±1.40), respectively] was also shorter. The mean frond biomass (g m^{-2}) was higher on Blakey 2 than Rosedale 2 [2428 (±1.38) and 1599(±2.08) respectively].

The size and related biomass of the fronds at Blakey 2 may be explained by the relationship between the active bud number and the long shoots. The majority of fronds were being produced from the long shoot. It has been observed by the author that where this occurs on the moorland fronds tend to be much larger than fronds produced on short shoots. Rosedale 2 had the potential to produce fronds >100 cm in some areas of the stand but 95% of frond samples were between 61.68 and 83.11 cm tall. Most of the fronds originated from the short shoots.

Few discernible relationships between frond and rhizome variables existed on the moorland side. The mean number of long shoots at Blakey 2 demonstrated a significant relationship with the mean frond height [$r = 0.427$ ($P < 0.05$)], mean pinna length [$r = 0.485$ ($P < 0.05$)] and mean frond biomass [$r = 0.450$ ($P < 0.05$)]. This may substantiate the hypothesis that a majority of the fronds at Blakey 2 were produced by the storage rhizome rather than the short shoot. No relationship was apparent between the rhizome and frond at Rosedale 2.

Differences were observed in the rhizome and frond morphology of the moor side plots. Both stands were considered established and mature. However, the growth strategies of the rhizome on each plot was found to differ and this could have effected the outcome of bracken control. The plots differed in bud and shoot number, rhizome dry weight and in the production of fronds. The bracken on Rosedale 2 appeared more vigorous in growth compared to the bracken on Blakey 2.

Frond number

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 2	32.40 (±3.75)	24.55	40.25	58	1
Blakey 2	25.40 (±1.29)	22.64	28.06	38	16

Frond height (cm)

Plot	mean	lower and upper C.I		max dn	min dn
Rosedale 2	72.39 (±5.12)	61.68	83.11	102.70	20.30
Blakey 2	117.04 (±3.21)	110.33	123.76	147.00	99.30

Table 17. Mean frond number and height (cm) and 955 confidence intervals for the moor side plots.

The rhizome system of the moor side plot at Rosedale 2 consisted of a substantial number of buds originating on a large number of corresponding short shoots which were observed to mainly grow within the litter layer. No relationship was observed between the mean number of buds and the number of intermediate and long shoots. Frond production was high with the majority of fronds originating on the short shoots.

It was assumed that, although Rosedale 2 had a greater potential for frond and shoot production, and may have been consequently more difficult to control in the long term than Blakey 2, much of the dry weight did not consist of storage rhizome. Therefore, the storage capacity of the bracken on Rosedale 2 was not as great as implied by the mean rhizome dry weight, and a greater proportion of shoot producing rhizome, compared to storage rhizome, may have made the bracken more susceptible to chemical and/or mechanical control.

The mean number of dormant buds at Blakey 2 was related to the mean number of short shoots and the mean number of active buds was related to long shoot number. The majority of fronds were observed to originate from the long shoots and were larger, although fewer in number, than the fronds on Rosedale 2. The bracken on Blakey 2 consisted of more long shoots but fewer short shoots, fewer buds and less dry weight than the bracken on Rosedale 2. The lack of vigorous short shoot growth may be due to the local environment of the Blakey 2 plot. The bracken was growing within a much deeper soil and in less exposed conditions than the bracken on Rosedale 2. Competition from other plant species was at a minimum. Although having a less vigorous rhizome system, the bracken on Blakey 2 may have been more difficult to control. Asulam would have been translocated directly into the long shoots . Although affecting the active buds on the long shoots, dilution factors would be higher than the absorption of asulam into the short shoots. Therefore, fewer buds may absorb lethal concentrations of asulam. There was also the problem of the dormant buds which were located on the short shoot system. These would remain largely unaffected by the application of asulam. The problems of asulam control on Blakey 2 may have been alleviated by the implementation of mechanical control before spraying By removing the fronds the rhizome system may have been stimulated to produce more fronds from the short shoots by breaking bud dormancy. The production of more short shoots, and therefore more buds, may have also been instigated. This would have increased the number of buds available for asulam assimilation and decreased the rhizome dry weight.

Differences were observed in the rhizome and frond morphology of the moor side plots. Both stands were considered established and mature; however, the growth strategies of the rhizome on each plot was found to differ and this could have affected the outcome of bracken control.

5.2.3 A comparison of the low moor plots at Smeathorns.

The plots located on the low moor were situated on the least exposed and lowest elevations compared to the high moor and moor side plots. The depth of soil was significantly deeper than the Rosedale plots, particularly on Smeathorns 3. The depth of litter on the low moor plots was not as substantial as the other plots but there was a high percentage cover of litter. The bracken on the low moor was growing in conditions more favourable for growth and so it was expected that this would be reflected in a more substantial rhizome and frond system.

The mean number of buds on the low moor was found to differ between the plots

(Table 18). The mean number of dormant buds on the Smeathorns 2 and Smeathorns 3 plots was higher than the number of buds on Smeathorns 1 and Smeathorns 4. The rhizome on Smeathorns 4 contained the lowest mean number of dormant buds, [14.20 (±2.11)], and the lowest confidence interval.

A comparison of the mean number of active buds between the low moor plots produced a different pattern to that of the dormant bud number. The mean number of active buds was highest on Smeathorns 2 and Smeathorns 4, 104.34 m^{-2} and 101.57 m^{-2}, respectively, and the highest number of buds within a sample was recorded on Smeathorns 4. The mean number of active buds on Smeathorns 1 and Smeathorns 3 were lower than the other plots by approximately 15-25 buds m^{-2}.

Dormant buds

Plot	mean	lower and upper C.I		max dn	min dn
Smeathorns 1	24.85 (±2.18)	20.29	29.41	47	12
Smeathorns 2	30.45 (±3.68)	22.74	38.16	66	10
Smeathorns 3	30.25 (±2.77)	24.45	36.05	53	13
Smeathorns 4	14.20 (±2.11)	9.78	18.62	39	0

Active buds

Plot	mean	lower and upper C.I		max dn	min dn
Smeathorns 1	7.20 (±1.08)	4.95	9.45	22	2
Smeathorns 2	9.40 (±0.91)	7.49	11.31	17	2
Smeathorns 3	8.05 (±0.92)	6.13	9.97	16	1
Smeathorns 4	9.15 (±1.58)	5.84	12.46	32	3

Table 18. Mean dormant and active bud number and 95% confidence intervals for the low moor plots.

Plot	mean	lower and upper C.I		max dn	min dn
Smeathorns 1	43.10 (±2.62)	37.61	48.59	63	20
Smeathorns 2	53.80 (±4.91)	43.52	64.08	86	8
Smeathorns 3	54.69 (±2.99)	48.42	60.95	74	34
Smeathorns 4	50.06 (±4.90)	34.79	60.33	96	19

Table 19. Mean rhizome dry weight (g) and 95% confidence intervals for the low moor plots.

The mean rhizome dry weight and 95% confidence intervals were larger on Smeathorns 2 and Smeathorns 3 (Table 19). However, dry weight was not found to be significantly dissimilar on Smeathorns 4. The lowest mean dry weight was recorded from Smeathorns 1. There were no consistent relationships found between rhizome dry weight and shoot number (Table 20). The mean number of long shoots demonstrated a significant relationship with mean rhizome dry weight on Smeathorns 1, 3 and 4 ($P<0.01$). The rhizome dry weight on Smeathorns 2 demonstrated a significant relationship with the mean number of intermediate shoots ($P<0.05$) and on Smeathorns 4 with all three shoot types.

Plot	Long shoots	Intermediate shoots	Short shoots
Smeathorns 1	0.802**	0.357	0.338
Smeathorns 2	0.274	0.424*	0.342
Smeathorns 3	0.632**	0.197	0.349
Smeathorns 4	0.804**	0.502*	0.524*

* $P< 0.05$, ** $P < 0.01$

Table 20. Correlation coefficients for rhizome dry weight compared to shoot number on the low moor plots.

An explanation for the lack of any apparent relationship between long shoot number and dry weight on Smeathorns 2 could be found in the size of the long shoots. It was observed by the author that the long shoots on Smeathorns 2, although high in number, had a thin diameter in comparison to the long shoots on the other plots.

The differences in the number of separate rhizome shoots was not as pronounced as those on the high moor and moor side (Table 21). The domination of a rhizome system by one type of shoot was not found to occur; however, the mean number of intermediate shoots was low for all plots. The shoot data was related to the mean number of dormant and active buds. A significant relationship occurred between short shoot number and bud number. The number of active buds demonstrated a relationship with short shoot number on Smeathorns 2, 3 and 4 [$r=0.446$ ($P<0.05$), 0.634 ($P<0.01$) and 0.478 ($P<0.05$), respectively]. The number of dormant buds demonstrated a significant relationship with short shoot number on Smeathorns 1, 3 and 4 [$r=0.617$ ($P<0.01$), 0.751 (P,0.01) and 0.548 ($P<0.01$), respectively]. These relationships were expected due to the bud producing capacity of the short shoot. The number of dormant buds also demonstrated a significant relationship with long shoot number on

Smeathorns 1 and 2 [r=0.436 (P<0.05) and 0.582 (P<0.01), respectively]. Field observation of these plots found that few fronds were produced from the long shoots but that dormant buds were in evidence. Active bud number was not significantly related to long shoot number on the low moor plots.

Short shoot number

Plot	mean	lower and upper C.I		max dn	min dn
Smeathorns 1	10.00 (±0.93)	8.06	11.95	19	3
Smeathorns 2	6.85 (±0.73)	5.31	8.39	13	1
Smeathorns 3	8.65 (±0.74)	7.11	10.19	15	3
Smeathorns 4	5.65 (±0.77)	4.05	7.25	11	1

Intermediate shoot number

Plot	mean	lower and upper C.I		max dn	min dn
Smeathorns 1	4.50 (±0.44)	3.57	5.43	8	1
Smeathorns 2	4.40 (±0.75)	2.84	5.96	16	1
Smeathorns 3	3.15 (±0.34)	2.45	3.85	5	0
Smeathorns 4	3.50 (±0.39)	2.68	4.33	6	0

Long shoot number

Plot	mean	lower and upper C.I		max dn	min dn
Smeathorns 1	9.20 (±0.70)	7.73	10.67	15	4
Smeathorns 2	8.30 (±0.83)	6.57	10.03	17	1
Smeathorns 3	7.10 (±0.56)	5.93	8.28	12	4
Smeathorns 4	6.65 (±0.57)	5.46	7.84	12	2

Table 21. Mean number of short, intermediate and long shoots and 95% confidence interval on the low moor plots.

In summarising the bracken of the low moor plots, distinctions in rhizome morphology could be made but these differences were not as extreme as those found for the high moor and moor side plots. The rhizome of Smeathorns 1 was characterised by a low mean number of active buds and a low mean rhizome dry weight. The mean number of long and short shoots was higher than the other plots. The rhizome system of Smeathorns 2 and 3 was characterised by a high mean number of active and dormant buds and high mean rhizome dry weight. The rhizome of Smeathorns 4 was characterised by a high mean number of active buds and high rhizome dry weight.

The mean number of fronds m^{-2} did not greatly differ between the low moor plots (Table 22). This may have been because Smeathorns is a more homogeneous site than the moor side or high moor sites. However, the height of fronds (cm) were significantly dissimilar. The fronds on Smeathorns 3 and 4 were significantly taller than the fronds on Smeathorns 1 and 2. The fronds on Smeathorns 2 were particularly short with low pinna and lamina lengths. The reason for the stunted growth of the fronds on Smeathorns 2 was not clear. The soil conditions were similar to the other plots. The only difference found was in the lower mean depth of litter on this plot which indicated that frond production had not been as great, or erosion has occurred. The latter is unlikely as no erosional effects were observed. The mean dry weight of the rhizome, which was lower on Smeathorns 2, may have been responsible for the lack of frond size, although no significant relationship was found between the two variables.

Frond number

Plot	mean	upper and lower C.I.		max dn	min dn
Smeathorns 1	49.60 (±1.79)	43.25	54.75	72	41
Smeathorns 2	41.10 (±4.18)	32.30	49.80	76	2
Smeathorns 3	45.90 (±2.44)	40.79	51.01	66	22
Smeathorns 4	46.20 (±2.73)	40.49	51.91	80	29

Frond height (cm)

Plot	mean	upper and lower C.I.		max dn	min dn
Smeathorns 1	75.93 (±1.62)	69.98	81.85	90	64
Smeathorns 2	24.47 (±1.21)	21.94	27.00	38	15
Smeathorns 3	86.37 (±2.82)	80.47	92.27	106	64
Smeathorns 4	96.11 (±3.70)	88.36	103.85	134	69

Table 22. Mean frond number and height (cm) and 95% confidence intervals for the low moor plots.

The differences in the rhizome systems observed between the plots were not as pronounced as those observed on the high moor and moor side. The rhizome morphology was compared with regard to possible susceptibility to control treatments. The bracken on Smeathorns 1 had a low mean number of active buds compared to the other plots. Frond size was smaller and the mean number of fronds was lower than the other plots. Therefore, the absorption and assimilation of asulam would have been expected to be less. Smeathorns 1 had the highest total number of shoots but the lowest rhizome dry weight. The effect of crushing would be to further reduce the amount of dry weight, perhaps to crippling levels, and to increase the number of active sinks by the stimulation of the dormant buds.

The bracken on Smeathorns 3 and 4 may have seemed more susceptible to asulam spray when examining frond morphology however Smeathorns 3 had a high number of dormant buds and large rhizome dry weight. Stands may therefore not be as susceptible as the status of fronds may suggest. High absorption of asulam may occur but the number of active 'sinks' for assimilation may be low.

The low number of dormant buds and the high number of active buds on Smeathorns 4 increased the susceptibility of the rhizome to asulam compared to the other low moor plots. Smeathorns 1,2 and 3 would have benefitted from some form of mechanical treatment in order to stimulate the dormant buds to become active, and to decrease the level of rhizome dry weight.

5.3 The variation in bracken morphology within and between plots.

The previous section described the morphology of the rhizome and frond within different locations on the North York Moors. It was found that the bracken on each plot demonstrated differences in morphology and that these could have consequences for future bracken production and for bracken control. It was considered if the morphology of the rhizome and frond was consistent within plots. This was achieved by examination of the degree of variation of each characteristic (v). The data are presented as the percentage of variation within each plot (Table 23).

The number of active buds demonstrated high variability across the plots. The number of dormant buds was not as variable. The variability in bud number on some plots would seem to be comparable to the variability in number of short and intermediate shoots. The number of long shoots demonstrated a more consistent low variability across the moor side and low moor plots. However, long shoot number variability was high on the high moor plots. The dry weight of rhizome demonstrated the lowest consistent variability across the plots.

The variability in frond size was less substantial on the low moor plots and the moor side plot Blakey 2. On the high moor, and to a lesser extent Rosedale 2 on the moor side, the frond size was highly variable, particularly on Blakey 1. Frond number demonstrated less variability than frond size on the high moor, but was higher than frond size on Rosedale 2 and Smeathorns 1 and 2.

The bracken on Blakey 1 and Rosedale 1 demonstrated a high consistent variability in rhizome and frond characteristics. The reason for the high variation in rhizome and frond morphology between samples taken from the high moor may be explained by the geographical location of the plots. The bracken on the high moor was growing at its present altitudinal extent and may have been less established than the bracken growing on the low moor, and to a lesser extent on the moor side. As bracken colonisation becomes more established then the variability may decline as the stand reaches a mature phase of growth, as demonstrated by the lower variability on Rosedale 2 and Smeathorns 1,2 and 3.

Rhizome variability

Plot	dormant bud	active bud	short shoot	Inter. shoot	long shoot	rhizome weight
Rosedale 1	55.78	53.25	56.83	96.09	65.86	45.71
Blakey 1	54.39	72.98	60.19	82.44	63.15	51.48
Rosedale 2	35.35	64.96	42.43	28.32	45.08	46.66
Blakey 2	49.43	82.88	82.89	65.60	47.46	41.75
Smeathorns 1	39.24	66.81	41.60	44.22	34.13	27.19
Smeathorns 2	54.12	43.30	47.88	75.68	44.58	40.82
Smeathorns 3	40.96	51.06	38.03	47.30	35.35	24.47
Smeathorns 4	66.48	77.27	60.53	50.29	38.19	43.81

Frond variability

Plot	frond number	frond height	frond weight	lamina length	pinna length
Rosedale 1	24.58	64.59	55.78	74.90	57.19
Blakey 1	40.62	73.06	94.49	84.65	61.47
Rosedale 2	51.72	31.63	56.72	36.55	23.07
Blakey 2	22.78	12.25	24.14	13.43	12.25
Smeathorns 1	73.51	23.95	38.28	26.88	23.78
Smeathorns 2	45.50	22.06	25.15	25.83	9.64
Smeathorns 3	23.76	1.16	20.65	13.85	12.21
Smeathorns 4	26.42	17.22	30.34	15.62	10.83

Table 23. The variation (v) in rhizome and frond characteristics 1992.

The bracken on Blakey 2 and Smeathorns 4 displayed high rhizome variability but low frond variability. These plots were characterised by a low mean number of active buds, short shoots and intermediate shoots and similar large means of rhizome dry weight, frond height, pinna and lamina lengths and frond biomass. These similarities were reflected in the level of variation. The stands were considered to be well established and mature thus disputing the previous theory that rhizome variability may decline with the establishment of the stand. If variability is not a factor of bracken establishment then other possibilities must be considered including the local environmental conditions and the possibility of genotype variability occurring within a plot.

The variability in bracken morphology demonstrated a gradient from high rhizome and frond variation on the high moor plots, high rhizome but low frond variation on Blakey 2 and Smeathorns 4, moderate rhizome and frond variation on Rosedale 2 and moderate rhizome variation but low frond variation on Smeathorns 1, 2 and 3 on the low moor. Therefore, the sampling of bracken from the low moor on to the high moor demonstrated a general increase in bracken variation. The consequence for the classification of bracken is that plot characterisation may become more difficult up the moor. Plot characterisation may seem more feasible if consideration is only taken of the frond data, however the frond does not reflect rhizome morphology or variability.

As the morphology of the bracken rhizome and frond can be variable then the application of asulam or the use of mechanical methods of control may also result in variable control success across the plot. For example, if parts of the bracken stand consisted of a low mean number of active buds, a high mean number of dormant buds and a high rhizome dry weight then the use of asulam may be less effective. Conversely, an area of bracken with a high number of active buds, low number of dormant buds and a low rhizome dry weight would be controlled more successfully. The bracken which is more resistant to control may provide a foundation from which bracken may re-establish. This would go towards explaining the patchy result which is often observed in the year after asulam application.

5.4. A comparison of bracken stand morphology between different parts of the North York Moors.

The examination of bracken morphology on the high moor, moor side and low moor demonstrated that bracken in any given area could be variable in both rhizome and frond morphology. By comparing bracken characteristics on each plot to all other plots, the possibility of classification with regard to location and/or control susceptibility could be explored. Except for the long shoot data there was at least one significant difference between the plots for all variables.

The number of short shoots showed marked differences between plots located within different areas of the moor (Rosedale, Blakey and Smeathorns). Rosedale was dominated by a high mean number of short shoots [13.90 (±1.77) and 16.85 (±1.60)], Blakey by a low mean number [5.10 (±0.69) and 3.80 (±0.71)] and Smeathorns by a middle range [5.65 (±0.77) - 10.00 (±0.93)].

Rosedale 1, located on the high moor, and Smeathorns 1, on the low moor were similar in mean short shoot number, [13.90 (±1.77)] and 10.00 (±0.93), respectively]. The Blakey plots were significantly comparable with Smeathorns 2, 3 and 4 for short shoot number. From this it could be seen that there were similarities between plots from different locations. It is postulated that stands of bracken on different parts of the North York Moors cannot be clearly categorised by the comparison of moor type to short shoot number but that there are similarities between plots located within the same location.

The bracken on Rosedale 1 and Blakey had a similar rhizome dry weight to the bracken on the low moor plots. On Blakey and Smeathorns there were no significant differences between the plots within each location regarding rhizome dry weight. The plots on Rosedale were different from one another due to the large mean weight (g) of rhizome at Rosedale 2 [89.35 (±9.32)]. Therefore, the only significant dissimilarity within plots was caused by Rosedale 2. There were no well-defined differences between plots located on separate types of moor.

The number of buds demonstrated a significant relationship with the number of short shoots [$r = 603$ ($P<0.01$)]. The similarities found between plots in the number of short shoots was comparable to the dormant and active bud data, with no significant differences found between bracken growing on plots within each location. There was a comparable number of dormant buds on Rosedale 1 and Smeathorns 3 and between Blakey 2 and Smeathorns 1 and 4.

Unlike the rhizome data, the plots could not be grouped by location on the basis of frond characteristics. The Rosedale plots were similar in frond number and frond biomass whereas the Blakey plots demonstrated no similarity in frond characteristics. On Smeathorns the fronds were similar in size and biomass on plots 1, 3 and 4. On Smeathorns 2, however, the fronds were smaller.

In comparing the frond morphology on the high moor the plots were alike for frond height, biomass and number. The fronds on the high moor showed similarities with the moor side and low moor bracken but these were not consistent. The moor side plots were only comparable to one another in the number of fronds. However, the moor side bracken on Blakey 2 and the low moor bracken on Smeathorns 3 and 4 all possessed large fronds. Smaller fronds were found on the high moor plots, and on the low moor at Smeathorns 2.

Few conclusions may be made about relationships between frond and rhizome variables within all plots regardless of geographical location. Some plots demonstrated a significant relationship between rhizome and frond variables, eg the high moor plot at Blakey 1; however, these associations were not consistent throughout the data. There was high variability of the rhizome and frond system within any given plot, particulary on the high moor. It was therefore concluded that the frond could not be used as an indicator of rhizome morphology.

However, the plots have demonstrated that similarities existed in the rhizome systems of bracken growing in the same location (Rosedale, Blakey and Smeathorns) but not between bracken growing on the same type of moorland (high moor, moor side and low moor). The differences between the bracken plots on each moor type were summarised and related to control success potential. Where bracken was shown to contain a high number of active buds, high frond number/size and low rhizome dry weight it was assumed asulam control would be the most successful. Bracken which demonstrated a low number of active buds but a high number of dormant buds, high rhizome dry weight and small fronds may be less successfully controlled by asulam but would benefit from some form of mechanical control. These two general groupings may not necessarily reflect the true field situation, due to the variability of bracken, but can be used as a guideline for evaluating the control susceptibility of each plot.

Rosedale 1 represented an established bracken stand which consisted of a high number of buds, short and intermediate shoots and a high rhizome dry weight. Frond height and biomass were larger than the fronds at Blakey 1. The bracken on Rosedale 1 had a high potential area for asulam absorption and assimilation and therefore bud 'kill'. Nevertheless, the rhizome dry weight and the number of dormant buds on this plot may reduce the susceptibility of the bracken to asulam and would increase the rate of post-spray regrowth. Crushing before spraying had taken place would have reduced the dry weight levels and therefore decreased asulam dilution. The potential for regrowth would have been reduced through a decrease in the amount of available carbohydrate. The number of active buds would have been increased through dormant bud stimulation. On Blakey 1 the rhizome system carried fewer buds and short shoots and there was less dry weight. However, there was a higher number of long shoots from which fronds were observed to be produced. The fronds on Blakey 1 were smaller, but higher in number.

The bracken on Blakey 1 appeared less established, with fewer buds for asulam assimilation and less surface area for asulam absorption. Smaller fronds naturally have a lower surface area for the absorption of asulam but this effect may have been negated by the high number of fronds found at Blakey 1. Nevertheless, past research has found that fronds of a smaller average size growing on exposed moorland areas may be genetically distinct biotypes which have less penetrable leaf cuticles, thus reducing asulam entry into the plant (West 1992). Therefore, the use of asulam on this plot may not produce a satisfactory result. Crushing may have been used to weaken the rhizome system but it is unlikely that this would have produced a significantly higher number of active buds or larger fronds.

On the moor side the bracken on Rosedale 2 consisted of a high number of buds and short shoots growing in the litter layer, and the largest rhizome dry weight of all the plots. The bracken on Rosedale 2 is similar to the bracken growing on Rosedale 1. Therefore, asulam control may be successful but mechanical control could be used to reduce the rhizome dry weight and to stimulate the dormant buds. Crushing, particularly with ribbed rollers, would be of special benefit on Rosedale due to the growth strategy of the bracken. The majority of short shoots were observed to be growing near the surface in the litter layer. Crushing would therefore break up the short shoots as well as crippling the fronds. Further damage may be caused by the removal of the litter layer, so exposing the short shoots and buds to frost and desiccation.

In comparison, the bracken on Blakey 2 had a low number of buds and short shoots but a higher number of long shoots. The majority of active buds and fronds were produced on the long shoots. The fronds on Blakey 2, although fewer in number, were much larger. Although there was a potentially high area for asulam absorption, the number of assimilation points was low. The susceptibility of the bracken to asulam would have been increased through mechanical control, stimulating the dormant buds on the short shoots.

The differences found between the bracken growing on the low moor plots were not as extreme. Smeathorns 1 was categorised by a low number of active buds and a low rhizome dry weight but a high number of short shoots. Frond number was high but the fronds were smaller than plots 3 and 4. The absorption of asulam on this plot may be high but assimilation would be reduced due to the number of active buds. Mechanical control would be advisable to increase the number of active buds and to reduce an already low rhizome dry weight.

Smeathorns 2 had a high number of active and dormant buds but frond production was poor compared to the other plots. Although Smeathorns 2 has a high number of active buds the spraying of the bracken would not be practical due to the small size of the fronds. In this instance mechanical control would be advisable with spraying being carried out if frond production improved. The bracken on Smeathorns 3 had a high number of buds and produced a large number of tall fronds. Asulam absorption and assimilation would be expected to be high resulting in a good frond 'kill'.

The numbers of dormant buds, short shoots and long shoots were the lowest on Smeathorns 4. However, the fronds on Smeathorns 4 were the tallest on the low moor and contained the largest frond biomass. In comparing the plots on the low moor Smeathorns 4 was considered to be the most susceptible to asulam control with the least potential for post-spray regrowth. However, all the low moor plots would benefit from mechanical control in order to stimulate the dormant buds to become active and to reduce rhizome dry weight levels.

On each type of moors bracken morphology as between plots demonstrated significant differences. However, similarities between plots at the same location have been recognised. The Rosedale and Smeathorns plots were characterised by an established and complex rhizome system. The rhizome consisted of a high mean number of buds and short shoots with the majority of bud and frond production occurring within the litter layer. Although the number of long shoots was low, the rhizome dry weight was high. Much of the rhizome dry weight consisted of a dense network of short shoots. Frond growth was vigorous but not as great as the bracken on the low moor plots or on Blakey 2.

The Blakey plots, and particularly Blakey 2, were characterised by a low number of buds and short shoots and low rhizome dry weight. However, the number of long shoots was found to be higher than the bracken on Rosedale. The majority of fronds, particulary on Blakey 2, were produced from the long shoots. The morphology and number of fronds differred between the Blakey plots. The fronds on Blakey 1 were significantly smaller, but higher in number, than the fronds on Blakey 2.

Comparisons between bracken growing at the same location demonstrates greater similarity than between bracken growing at different locations of the moor. It is not possible to differentiate between the bracken on the high moor, moor side and low moor on the basis of rhizome and frond morphology. The variability of the rhizome was found to be greater than frond variability. A general gradient was observed from high variability on the high moor to low variability on the low moor. The reasons for this may be through environmental stress, the stage at which the bracken has reached in the life cycle, or a response to different historical land management.

Bracken stands which may more be susceptible to control were identified on the basis of their rhizome systems. Bracken which has a high number of dormant buds, a low number of active buds, and consists of a substantial rhizome dry weight, will prove more difficult to eradicate with asulam. What is required in these instances is some form of treatment which will stimulate the dormant buds to become active and to deplete levels of storage rhizome through a reduction in rhizome dry weight. This would effectively weaken the plant and make it more susceptible to asulam control. The hypothesis on bracken susceptibility to control was tested against the actual response of bracken to control on the North York Moors.

Chapter 6. An investigation into bracken susceptibility to control measures on the North York Moors.

6.1 Introduction

It is postulated that an examination of the effect of treatment on the rhizome is fundamentally important to the evaluation of the success of a control programme. The recording of frond number alone may give an incomplete and misleading picture of the bracken response. The rhizome is the section of the plant where asulam assimilation takes place, and where carbohydrate levels are altered, particulary by crushing. It is essential that the 'secondary' effect of control of the fronds is not considered without first inspecting the 'primary' affects on the rhizome system.

In this section the effect of treatment is considered on different geographical locations on the North York Moors and then compared to untreated bracken (see section 3.1.6 for details of spraying and crushing controls). All rhizome means and standard errors are quoted for the sample size taken (30 cm x 30 cm).

6.2.1 The control of bracken on the high moor using asulam.

The high moor plot, Blakey 1, showed a significant decrease in both active and dormant bud number [$F_{1\ 68} = 73.13$; $P<0.000$ and [$F_{1\ 68} = 9.38$; $P<0.003$ respectively] one year after spraying with asulam (Fig. 17). The mean number of dead buds significantly increased [$F_{1\ 68} = 18.22$; $P<0.000$]. The number of shoots and the rhizome dry weight demonstrated little change in the year after spraying (Figs. 18 and 19).

This was consistent with other published studies on the effects of asulam (Pakeman & Marrs 1994). Those parts of the rhizome most susceptible to the herbicide, ie the active buds and apices, were damaged but little effect was observed on the shoots or dry weight. Although dormant buds are generally acknowledged as inactive, a significant number appeared to have been adversely affected by the asulam. It may be that some of these buds were in fact active before treatment had taken place, but were not counted as such because of their external appearance. Although affected by the asulam a high number of dormant buds remained on Blakey 1 in the year after spraying [11.92 (±1.16)]. Although the number of active buds was effectively reduced by asulam, the remaining dormant buds and the unaffected dry weight were the two main problems in effectively reducing bracken vigour on Blakey 1.

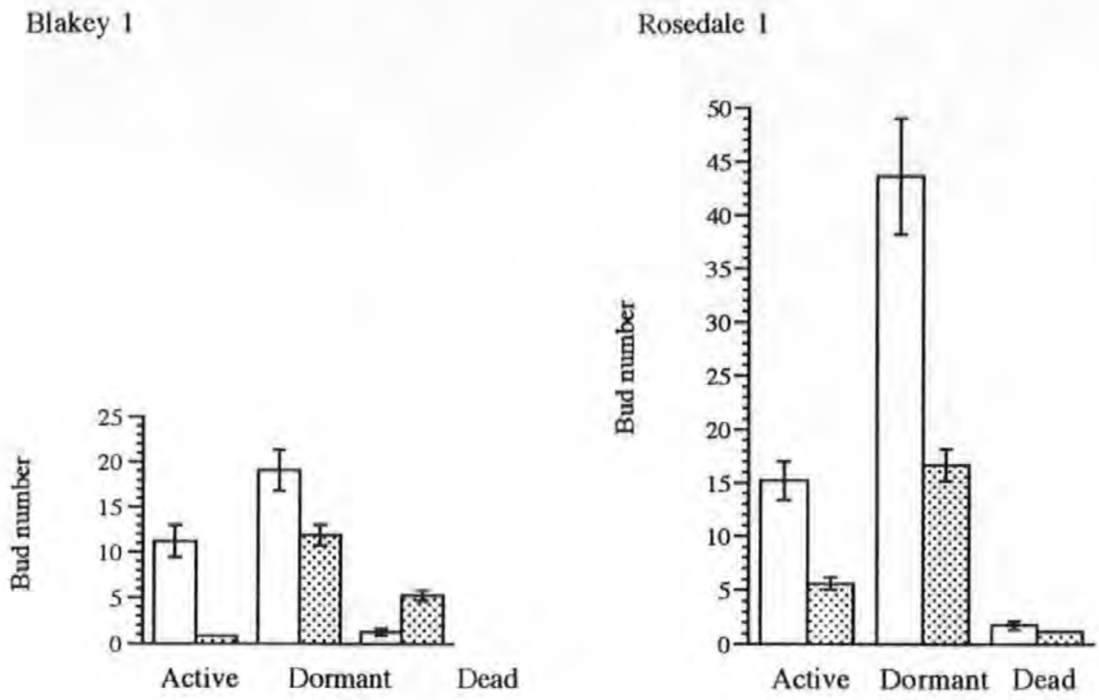


Figure 17 The mean number of buds on Blakey 1 and Rosedale 1 in 1992, ☐ and one year later, ▩ .

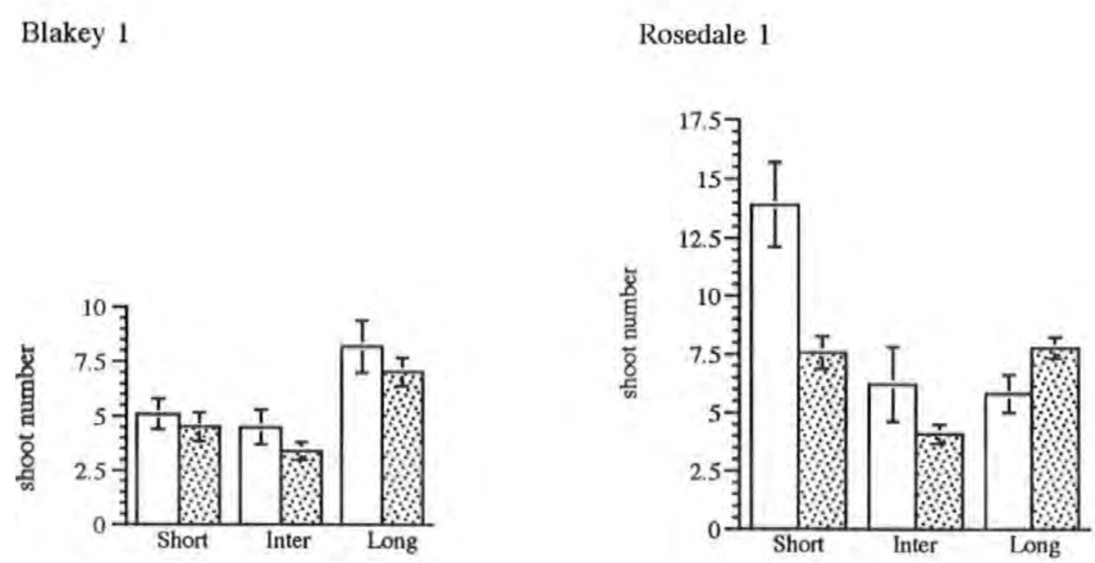


Figure 18 The mean number of shoots on Blakey 1 and Rosedale 1 in 1992 ☐ and and one year later ▩.

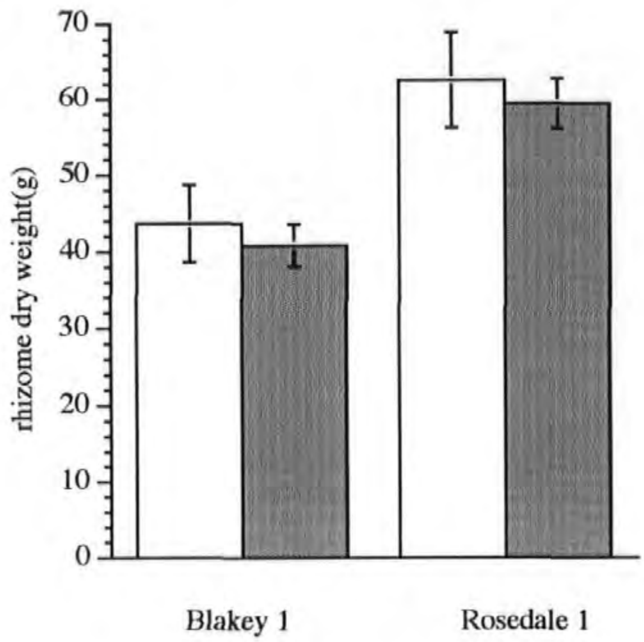


Figure 19 Mean dry weight of rhizome on Blakey 1 before, □ and after, ■ asulam application compared to the untreated bracken on Rosedale 1.

The number, height and size of fronds was significantly reduced in the year following spraying (Table 24). The reduction in frond number represented a 75.9% 'kill' rate which is below that recommended for good bracken control (99%). Frond growth was consistent over the plot but was considered impractical for respray by hand-held applicator or helicopter as the area for asulam absorption was low (Plate 7).

Plot	Frond no' '92	Frond no' '93	Frond ht '92	Frond ht '93	Lamina lgth '92	Lamina lgth '93	Pinna lgth '92	Pinna lgth '93
Blakey 1	36.60 ±3.32	8.80 ±1.30	37.50 ±6.13	12.50 ±0.90	19.90 ±3.77	5.70 ±0.60	23.70 ±3.25	9.20 ±0.80
Rose 1	31.60 ±1.74	21.70 ±6.30	47.40 ±6.84	20.50 ±5.80	20.96 ±3.51	12.60 ±3.60	26.09 ±3.34	13.60 ±3.80

Table 24 The mean and standard error for frond characteristics in 1992 and 1993 on the high moor plots. Blakey 1=asulam treated, Rosedale 1=untreated control. Frond size in cm.

The problems in the year after spraying on the high moor were twofold. Firstly, there was a high number of viable dormant buds and an unchanged rhizome dry weight. The bracken rhizome therefore had a number of potential frond generating buds and the biomass to produce those fronds and to keep the system viable. Secondly, frond growth was consistent over the plot but was considered impractical for respray by hand-held applicator or helicopter as the area for asulam absorption was low. The area was considered unpractical for mechanical removal of the fronds and the area too large for handplucking (Stanton 1990). Therefore the only practical method of follow-up on Blakey 1 would have been to wait until the fronds regained sufficient cover in order to respray with asulam. Nevertheless, the dense mat of *Vaccinium myrtillus* which was present before spraying was observed to be affecting bracken development. It was postulated that the compact growth of *Vaccinium myrtillus* rhizome out competed and restricted bracken rhizome growth.

The untreated high moor plot, Rosedale 1, also demonstrated a significant decrease in active and dormant bud number [$F_{1\,68}=43.09$; $P<0.000$ and $F_{1\,68}=41.84$; $P<0.000$ respectively] (Fig. 17). This reduction may be attributed to the decline in short and intermediate shoot number (Figure 18) as a relationship was found between bud and shoot number (Chapter 5). There was no significant change in the rhizome dry weight (Fig. 19), but long shoot number increased [$F_{1\,68}=4.73$; $P<0.033$].

Although Rosedale 1 was untreated, clearly the bracken has been checked in some way. Unlike the asulam treated bracken on Blakey 1, there had been a significant decline in short and intermediate shoot number [$F_{1\ 68}$ =16.53; P<0.000 and $F_{1\ 68}$ =3.04; P<0.086 respectively] on Rosedale 1 as well as a reduction in the number of buds. This could account for the dead bud number remaining unchanged, though as dead shoots were not recorded, the actual number of dead buds may have been greater than that observed. It is difficult to compare the effects of asulam on Blakey 1 with the untreated bracken on Rosedale 1 because some form of check on stand development had occurred despite no control treatment being applied. Even with the difficulty in comparing the plots, it can be concluded that asulam caused a much greater decline in the number of active buds, and a greater increase in the number of dead buds, than occurred in the untreated plot.

Plate 7 Bracken frond growth one year after asulam spraying. Blakey 1, July 1993.

There are two main possibilities that may have caused this change in the rhizome system. Firstly, Rosedale 1 is situated on the exposed high moor area and was therefore highly susceptible to frost and wind chill damage. The rhizome system consisted of a large number of short shoots which were observed to grow near the shallow soil surface and within the litter layer and these may have been killed by frost. Both high moor plots carried a similar groundflora and had the same depth of litter (Chapter 4) and so protection from frost was assumed to be comparable. However, frost damage on Rosedale 1 may have been exacerbated due to the disturbance of the litter layer caused by sheep in the area. It was observed that the area of the plot was used for feeding sheep during the winter period. Although sheep tend to cause little damage to bracken, the high stocking rate here had a damaging effect. The litter layer was disturbed and almost completely removed in some parts of the plot, exposing the short shoots underneath to frost and to desiccation.

Also the sheep tended to remain in the area well into spring. During this period many young fronds were either trampled or grazed. Browsing by lambs was found to be a particular problem as they removed large numbers of fronds (Plate 8). This is evident in the reduction in number of fronds observed in 1993 (Table 24). This would have stimulated the rhizome to produce more fronds therefore reducing both active and dormant bud number (NB The reduction in frond height recorded on both high moor plots in 1993 may reflect a late spring frost which would have reduced the growing time of the fronds). If stocking had caused the reduction in buds and shoots then overwintering sheep in certain areas where the soils are shallow may have some limited use as a control method. However the problems of bracken as a health hazard to livestock needs to be considered.

Plate 8 Damage to fronds on Rosedale 1 due to sheep browsing. July 1993.

6.2.2 The control of bracken on the moorside using asulam.

The moorside plot, Blakey 2, demonstrated a significant increase in dormant bud number one year after asulam spraying [$F_{1\ 68}$ =1.50; P<0.225] but the number of active buds was unaffected (Fig. 20). The number of dead buds and the rhizome dry weight (Fig. 20 and 22) significantly increased after asulam application [$F_{1\ 68}$ =4.68; P<0.034 and $F_{1\ 68}$ =1.28;

P<0.262 respectively].

The control of the bracken rhizome on the moorside plot was unsuccessful in decreasing bud number and may have stimulated the rhizome system to increase bud number and dry weight levels. To explain the apparent lack of control the rhizome system prior to treatment must be considered. The rhizome system of the Blakey 2 plot consisted of a low number of active buds [5.20 (±0.96)] and therefore few sites for asulam assimilation. Many of the active buds were observed to have been produced on the high number of long shoots (Fig. 21) growing within the deeper moorside soils (Chapter 4). Therefore, many of the active buds would not have been affected by the asulam due to being remote from the herbicidal source, ie the frond. Some active buds may have been affected, as indicated by the rise in dead bud number, but these were on the short shoots.

There were also low numbers of dormant buds, compared to the other sprayed plots, due to the low number of short and intermediate shoots. As bracken undergoes a continuous cycle of frond production within a growing season, a number of dormant buds would be stimulated to become active. Therefore, although counted as dormant due to their external appearance, some buds will have contributed to the overall number of active 'sinks'. Both a low number of active and dormant buds may accordingly result in a poor control result such as that observed on the moorside. Other causes may also be responsible for the lack of control success on Blakey 2. The difficulties of asulam spraying on slopes, even with the use of a helicopter, are great, particularly in achieving an even application. Therefore, some areas of the plot may have received levels of asulam which were significantly lower than the recommended rate.

Although the use of asulam was not successful there were observed changes in the rhizome system following spraying. The increase in dormant bud number and the related increase in the number of short shoots [$F_{1\ 68}$ =1.38; P<0.243] suggested that the rhizome system was increasing the potential to produce fronds nearer the soil surface on the short shoots. The change from a mature, non-aggressive stand to a stand characteristic of an invading front may have been triggered by the asulam or could be a natural progression in the stands growth cycle. In comparison to the rhizome response the fronds demonstrated a significant reduction in number (Table 25). Frond number on Blakey 2 was significantly reduced [$F_{1\ 68}$ =174.06; P<0.000] from 25.35 (± 1.29) to 0.40 (± 0.51) fronds m^{-2}. This constituted a 98.4% reduction in the mean number of fronds which is comparable with other published research on bracken control (Lowday 1987; Lowday & Marrs 1992; Martin 1976;

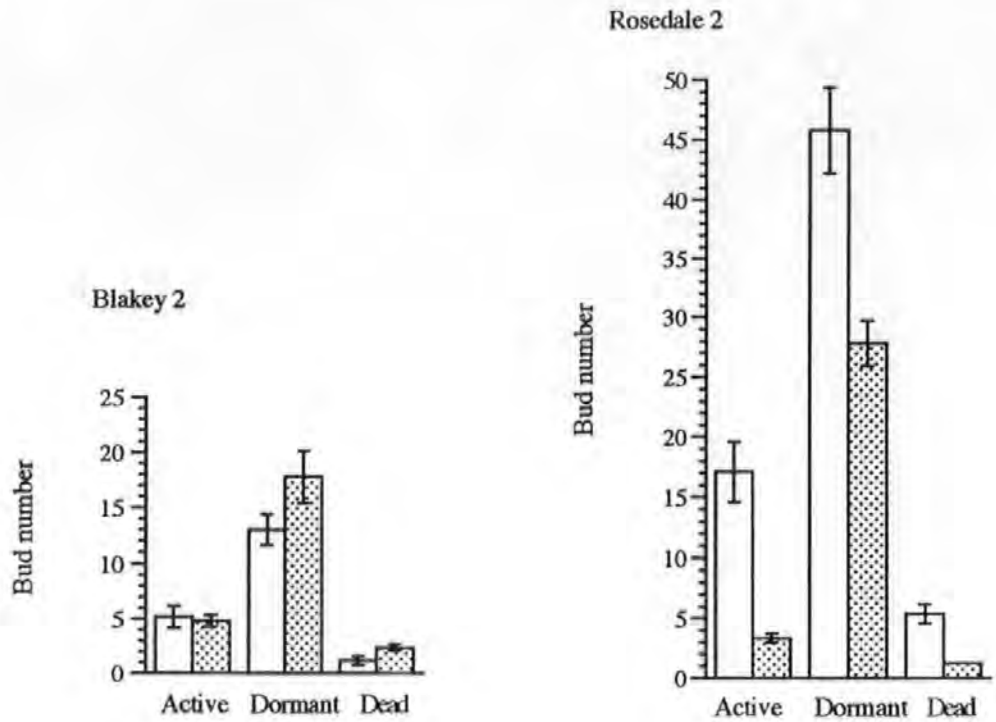


Figure 20 The mean number of buds on Blakey 2 and Rosedale 2 in 1992, ☐ and one year later, ▩.

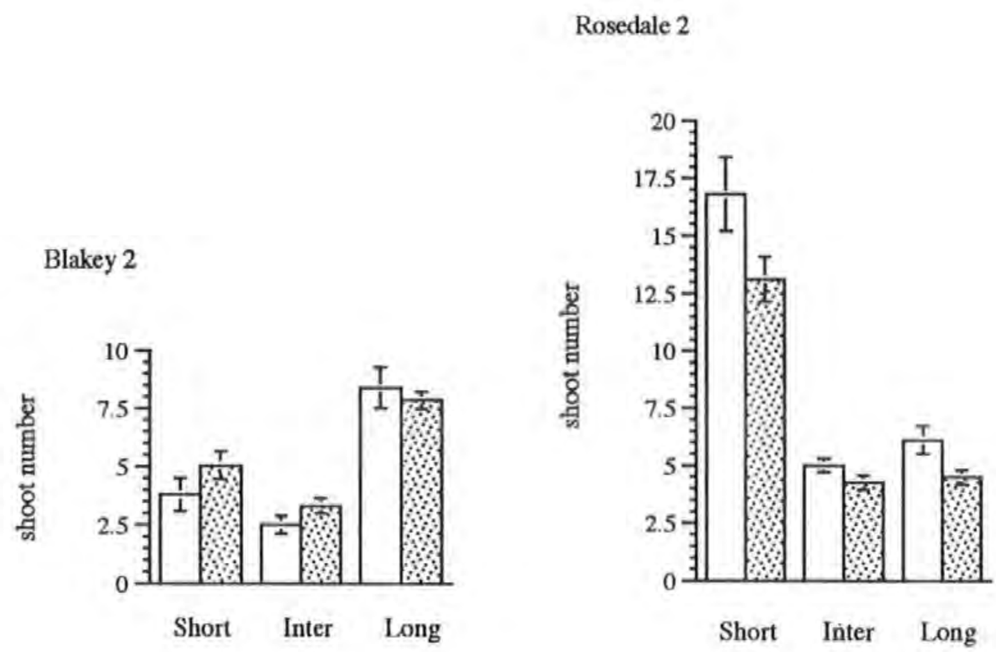


Figure 21 The mean number of shoots on Blakey 2 and Rosedale 2 in 1992, ☐ and one year later, ▩.

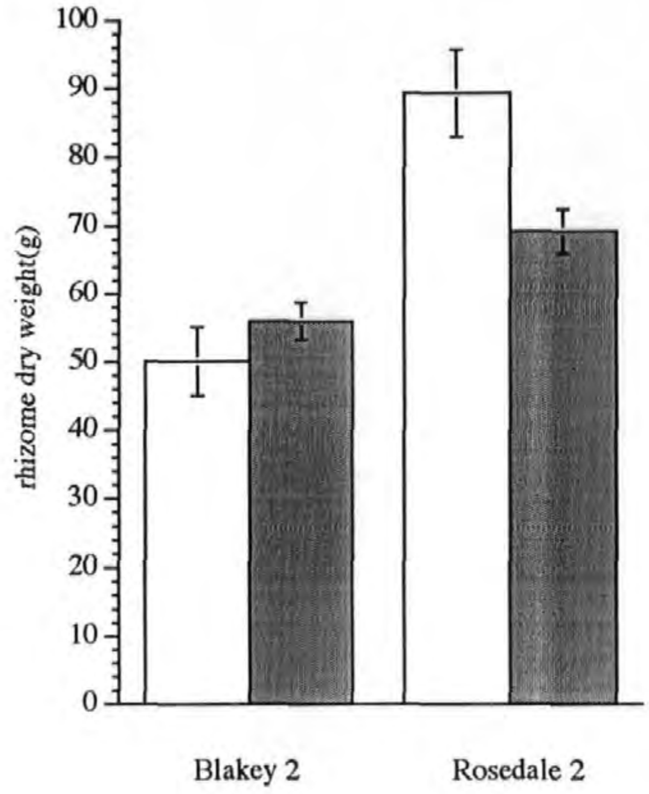


Figure 22 Mean dry weight of rhizome on Blakey 2 before, ☐ and after, ▩ asulam application compared to the untreated bracken on Rosedale 2.

Soper 1986). It was observed by the author that frond emergence in the year after treatment appeared to be related to areas of deep bracken litter (Plate 9). Fronds were rarely found growing in areas which had little or no litter cover. Frond height, lamina length and pinna length was also significantly reduced [$F_{1\ 68}$ =505.67; P<0.000, $F_{1\ 68}$ =389.32; P<0.000 and $F_{1\ 68}$ =377.71; P<0.000 respectively].

The differences between the rhizome and frond response to asulam on Blakey 2 underlay the danger of evaluating asulam control success on some stands by frond response alone. Initial examination of the above-ground effects of asulam on Blakey 2 would have concluded that successful control had been achieved. However, the below-ground effects of asulam were minimal with the rhizome remaining viable and capable of increased frond production.

Plot	Frond no' '92	Frond no' '93	Frond ht '92	Frond ht '93	Lamina lgth '92	Lamina lgth '93	Pinna lgth '92	Pinna lgth '93
Blakey 2	25.35 ±1.29	0.40 ±0.20	117.00 ±3.21	4.70 ±2.40	55.31 ±1.66	2.60 ±1.60	51.16 ±1.40	3.50 ±2.10
Rose 2	32.40 ±3.75	45.00 ±2.60	72.40 ±5.12	40.30 ±1.40	39.30 ±3.21	25.30 ±1.00	39.30 ±2.02	26.00 ±0.90

Table 25 The mean and standard error for frond characteristics in 1992 and 1993 on the moor side plots. Blakey 2=asulam treated, Rosedale 2=untreated control. Frond size in cm.

The moorside untreated plot, Rosedale 2, demonstrated a significant decline in the number of buds, shoots and dry weight in 1993 (Figs. 20, 21 and 22, respectively). This reduction in the rhizome system was similar to that occurring on the high moor plot, Rosedale 1. Therefore, it is assumed that the untreated plots on Rosedale had been adversely affected by some factor associated with location. This factor may have been the number of sheep in the area, which disturbed the litter layer and so increased the potential for frost damage. However Rosedale 2 was situated downslope from the direct feeding area and had a depth of litter greater than Rosedale 1 in 1992 (Chapter 4). Therefore, the potential damage from both sheep and/or frost should have been lower on Rosedale 2. Nevertheless, the reduction in the number of active buds and rhizome dry weight was greater.

The number of fronds on Rosedale 2 increased significantly [$F_{1\ 68}$ =5.53; P<0.026] (Table 25); so it is unlikely that asulam was over-sprayed in the area (which can occur if an operator is testing the nozzles) and could account for a decline in active bud number. The change in the rhizome system was more typical of the effects associated with mechanical methods of control which may stimulate the dormant buds to produce fronds, with a corresponding decrease in rhizome dry weight. As no mechanical control of bracken had taken place, the action of sheep trampling and browsing, with localised frost damage, may account for the effects observed, even though the litter layer was deeper than the high moor plot.

Plate 9 Frond growing within a deep litter 'mound' on Blakey 2. July 1993.

6.2.3 The control of bracken on the low moor using asulam.

The low moor plot treated with asulam, Smeathorns 3, showed a significant decrease in active bud number [$F_{1\ 68}$ =141.79; P<0.001] with a corresponding increase in dead bud number [$F_{1\ 68}$ =10.96; P<0.001] in the year following spraying (Fig. 23). There was also a significant, although small, decrease in the number of dormant buds [$F_{1\ 68}$ =1.28; P<0.263]. Although asulam had been successful in reducing the number of active buds, the large number of dormant buds remaining[26.02 (±2.00)] and the unaffected dry weight (Fig. 25) remain problems for bracken control on this plot.

The reason for this may be explained by the rhizome morphology before treatment had taken place. The Smeathorns 3 plot consisted of a high number of dormant buds [30.45 (±3.68)] compared to the number of active buds [9.40 (±0.91)]. Therefore, although some dormant buds will have been active, there still remained a high number of inactive 'sinks' in contrast to the number of active 'sinks'.

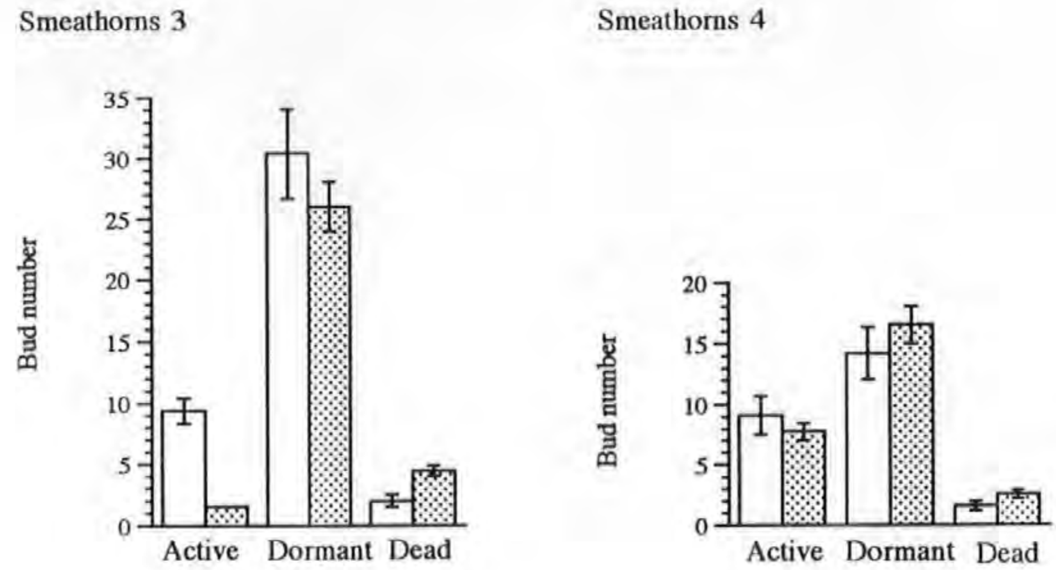


Figure 23 The mean number of buds on Smeathorns 3 and Smeathorns 4 in 1992, □ and one year later, ▩ .

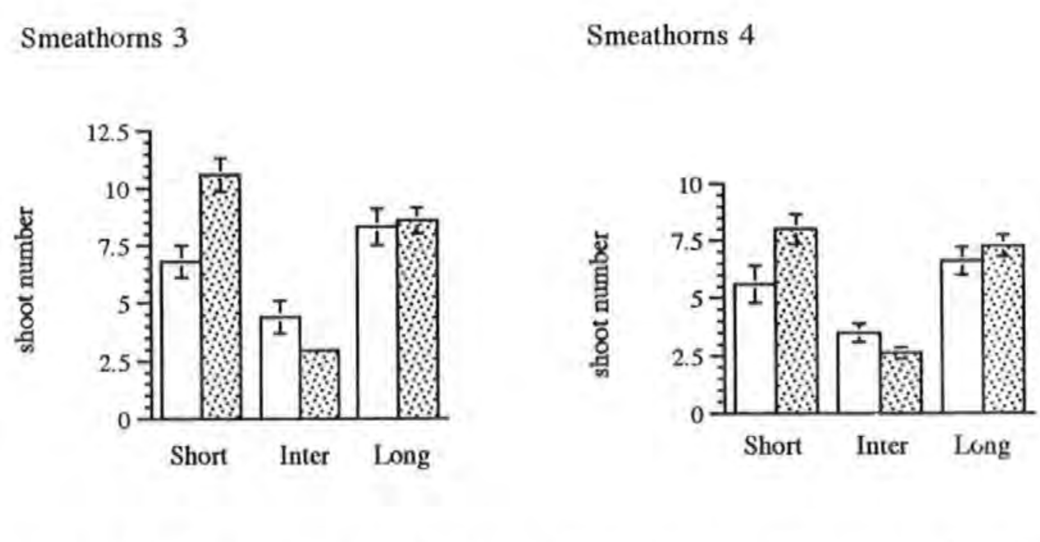


Figure 24 The mean number of shoots on Smeathorns 3 and Smeathorns 4 in 1992, □ and one year later, ▩ .

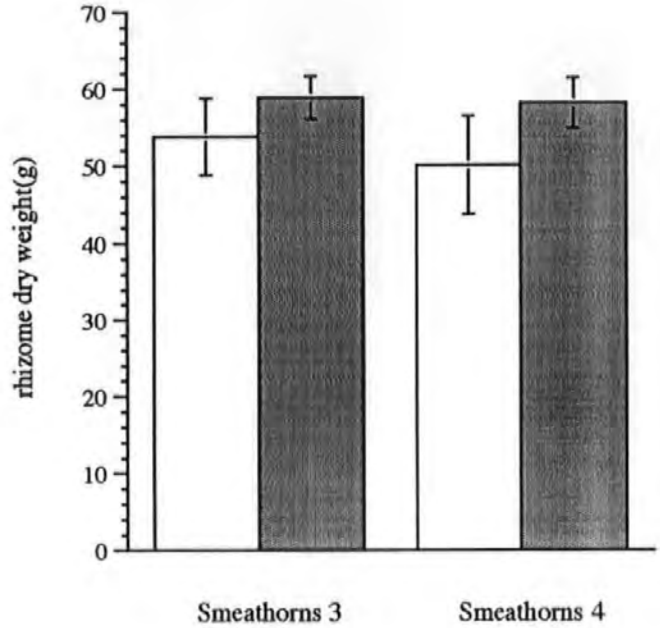


Figure 25 Mean dry weight of rhizome on Smeathorns 3 before, ☐ and after, ■ asulam application compared to the untreated bracken on Smeathorns 4.

There was a significant decrease in the number of intermediate shoots [$F_{1\ 68}$ =6.17; P<0.015] and an increase in the number of short shoots [$F_{1\ 68}$ =9.14; P<0.004] following spraying (Fig. 24). The increase in short shoot number may have been a partial response to the action of asulam. Within mature, non-invading bracken stands the rhizome system, if not competing with other rhizomous species such as *Vaccinium myrtillus*, may reach a state of equilibrium appropriate to the local growing conditions, eg soil depth, nutrient availability, soil moisture potential and microclimate. If disturbance of the rhizome, such as that caused by asulam, occurred then the bracken may produce more short shoots in response, and therefore increase the capacity to produce fronds, in order to 'recover'.

The significant reduction in frond number [$F_{1\ 68}$ =41.13; P<0.000] represented a 96.1% 'kill' (Table 26). Both the height of the fronds and the lamina and pinna lengths were also significantly reduced [$F_{1\ 68}$ =55.70; P<0.000, $F_{1\ 68}$ =36.69; P<0.000 and $F_{1\ 68}$ =18.38; P<0.000 respectively]. Of the fronds that did appear in the year after spraying, a high number were observed to grow from within deep litter mounds, as with Blakey 2. Fronds also appeared to be associated with clumps of heather on Smeathorns 3 (Plate 10). The overall frond and rhizome response to asulam spray was similar to that observed on the moorside plot. Although above-ground kill would seem to be good the below ground effects on the rhizome system were minimal.

Plot	Frond no'		Frond ht		Lamina lgth		Pinna lgth	
	'92	'93	'92	'93	'92	'93	'92	'93
Smeath 3	41.00 ±4.18	1.60 ±0.50	24.50 ±1.21	7.60 ±2.00	13.30 ±0.76	4.40 ±1.30	19.30 ±1.28	8.60 ±2.60
Smeath 4	46.20 ±2.73	39.90 ±1.70	96.10 ±3.70	36.50 ±2.20	56.00 ±1.95	19.80 ±1.30	49.50 ±1.20	26.60 ±1.70

Table 26 The mean and standard error for frond characteristics in 1992 and 1993 on the low moor plots. Smeathorns 3=asulam treated, Smeathorns 4=untreated control. Frond size in cm.

In comparison, the untreated plot, Smeathorns 4, showed no significant change in active or dormant bud number (Fig. 23). There were, however, significant increases in the number of short shoots [$F_{1\ 68}$ =4.28; P<0.042] (Fig. 24) and the rhizome dry weight [$F_{1\ 68}$ =1.58; P<0.214] (Fig. 25) in 1993. A significant decrease was observed in the number of intermediate shoots [$F_{1\ 68}$ =3.41; P<0.069]. No outside influence, which could have caused the change in the rhizome system, was observed on these plots. The changes observed were probably due to both alterations in the sampling strategy between the two years and to an increase in stand growth and development. The bracken within the plot, although appearing to be mature, may still be expanding. Therefore, an increase in shoot numbers and rhizome dry weight would be expected. There is also the possibility of seasonal fluctuations in the rhizome system.

Plate 10 Fronds growing within heather one year after spraying on Smeathorns 3. July 1993.

6.3 The use of crushing as an alternative to asulam, and as a pre-treatment, on the low moor.

The use of mechanical methods of control provides another way in which bracken may be controlled. In particular, cutting and crushing has been used in conjunction with asulam to increase control success by stimulating dormant buds to become active and to reduce the dry weight (Chapter 2). On the North York Moors National Park, mechanical control of bracken is often not feasible due to both the terrain and the availability of suitable machinery and labour. However, on fringe areas of the moor, such as the Skelton and Brotton Estate, the relatively even terrain allows the use of machinery. As a complement to the study on asulam, a subsidiary study was carried out on the possible advantages and disadvantages of implementing the crushing of bracken.

6.3.1 The control of bracken on the low moor by crushing once per year.

The number of active and dormant buds on the crushed plot, Smeathorns 1, did not significantly change one year after treatment (Fig. 26). The number of dead buds, however was found to have significantly increased [$F_{1\ 68}$ =17.71; P<0.000]. This may be due to both the crushing effect of the tractor and the rollers or to the effect of frost. The short shoot system also appeared to be damaged (Fig. 27), evident in the significant reduction in shoot number [$F_{1\ 68}$ =20.35; P<0.000] but this did not affect bud number.

The significant reduction in rhizome dry weight [$F_{1\ 68}$ =18.90; P<0.000] from 43.10 g (±2.60) to 34.64 g (±1.86) was caused by the removal of the frond, and therefore the source of rhizome dry matter accumulation, from the bracken plant (Fig. 28). The dry weight of rhizome would have been further reduced by the production of a secondary stand of fronds during August, 1992.

The ability of the Smeathorns 1 bracken to retain the number of active and dormant buds in the year following crushing demonstrates the ability of bracken to recover the potential to produce fronds rapidly after physical disturbance has occurred. Additional crushing may have further reduced rhizome dry weight with the result that frond growth may have been weakened. Nevertheless, if the number of buds cannot be reduced, this form of control will remain largely ineffective on Smeathorns 1.

There were significantly fewer short and long shoots on Smeathorns 1 in the year after crushing (Fig. 27). An element of this difference may again have been due to the differences in sampling between 1992 and 1993 (Chapter 5). Although the reduction in short shoot number can be explained by factors such as frost action and tractor damage, the reasons for the reduction in long shoot number cannot be so readily defined. One possible hypothesis is that those long shoots which were already in a weakened state, with low levels of carbohydrate, may have been expended in the production of the second stand of fronds in 1992. It is not possible, however, to differentiate between shoots that may have died since crushing and those which were already dead.

The crushing of bracken significantly increased [$F_{1\ 68}$ =48.69; P<0.000] the average number of fronds by 59 m^{-2} in the following year (Table 27). The frond height, and pinna length were significantly shorter in the year after crushing [$F_{1\ 68}$ =2.89 (P<0.100) and $F_{1\ 68}$ =3.72 (P<0.064), respectively].

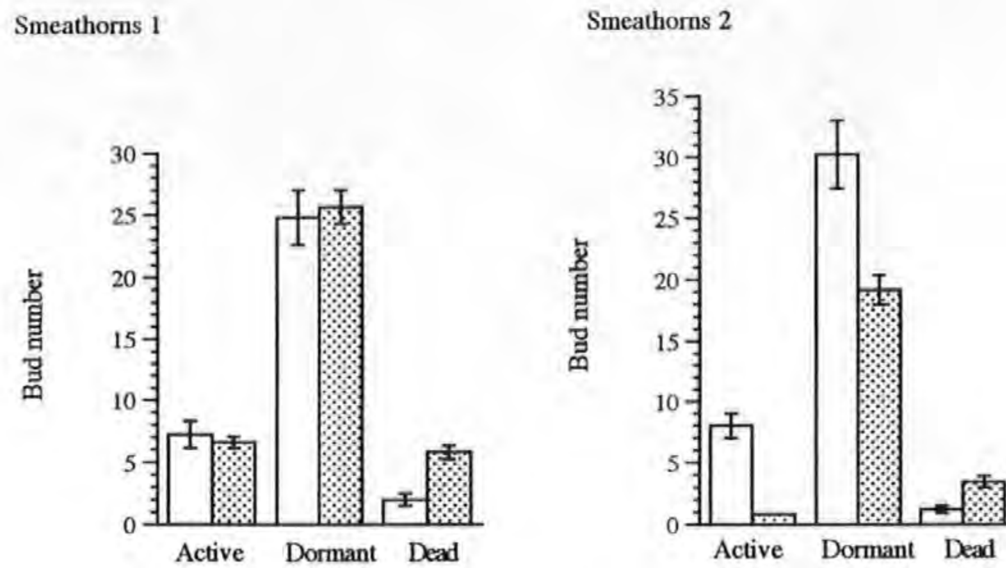


Figure 26 The mean number of buds on Smeathorns 1 and Smeathorns 2 before, ☐ and one year after, ▨ crushing and crushing followed by asulam

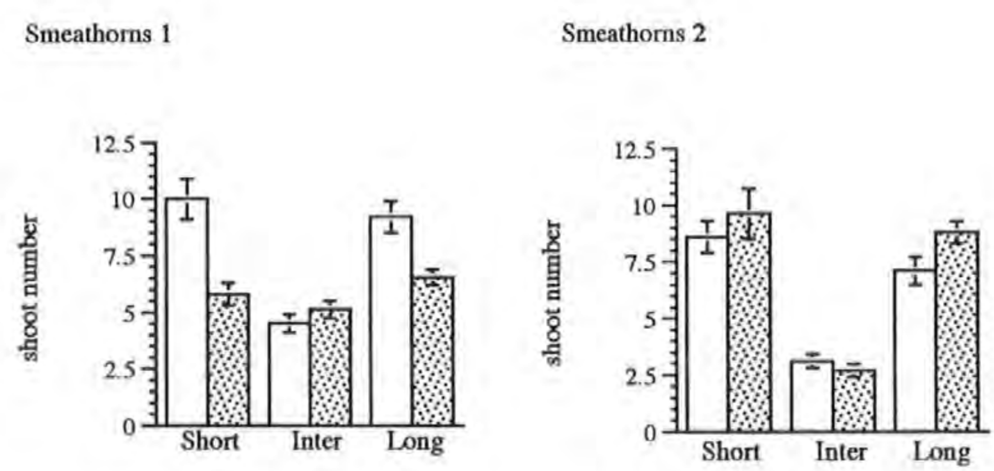


Figure 27 The mean number of shoots on Smeathorns 1 and Smeathorns 2 before, ☐ and one year after, ▨ crushing and crushing followed by asulam application.

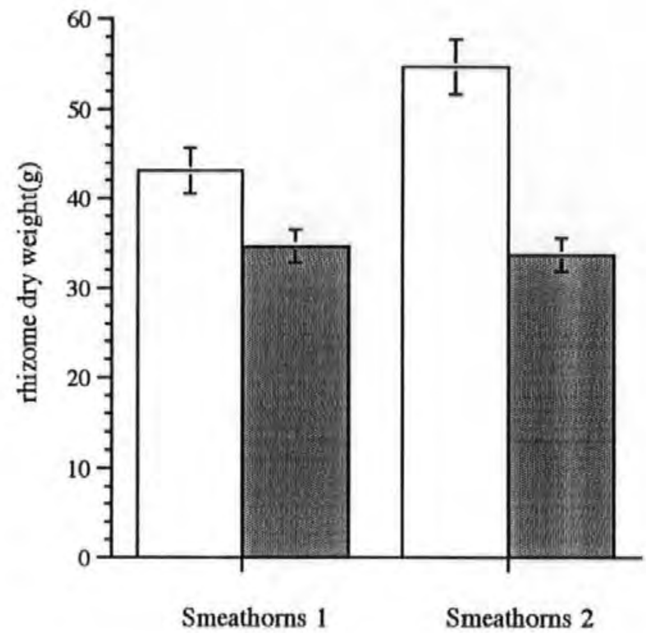


Figure 28 Mean dry weight of rhizome on Smeathorns 1compared to Smeathors 2 before, and one year after, crushing and crushing followed by asulam application.

The increase in the number of fronds can be explained by the stimulation of dormant buds that is the bracken reacted to crushing by sending up more fronds increasing the capacity to produce photosynthate, and thus replenishing the reserve of carbohydrate.

Plot	Frond no.		Frond ht.		Lamina lgth		Pinna lgth	
	'92	'93	'92	'93	'92	'93	'92	'93
Smeath 1	29.00 ±4.89	88.00 ±7.10	27.70 ±1.52	23.80 ±1.10	12.35 ±0.76	16.50 ±0.90	18.90 ±1.03	16.10 ±0.50
Smeath 2	45.90 ±2.44	5.40 ±1.50	86.40 ±2.82	7.60 ±1.30	48.70 ±1.51	4.90 ±0.80	45.30 ±1.24	8.10 ±1.20

Table 27 The mean and standard error for frond characteristics in 1992 and 1993 on the low moor plots. Smeathorns 1=crushing, Smeathorns 2=crushing followed by asulam. Frond size in cm.

Although crushing or cutting has been used previously in order to stimulate bracken to produce a second stand of fronds within the same growing season, which may then be crushed or sprayed with asulam, the large increase in frond number observed on Smeathorns 1 may not occur within the same growing season. This is because a second stand of fronds will have originated mainly from the available active buds. The data from Smeathorns 1 indicates that , if left after a single crush, bracken may be stimulated in the following year to greatly increase frond numbers but frond height and pinna length will be shorter. Therefore, the use of tractor mounted sprayers will be more feasible on moorland of suitable terrain. Furthermore, the rhizome dry weight was significantly reduced (Fig. 28) by the removal of fronds in the first year and the increase in frond number in the second year, therefore rendering the bracken more vulnerable to control. Mechanical control also has the benefit of fragmenting the litter layer, so creating a more favourable habitat for other vegetation species to colonise.

Continuous annual crushing or cutting has proved to be labour-intensive, costly and unsuccessful in completely eradicating bracken, even after 12 years (Marrs *et al* 1992). Crushing once in the year before spraying may increase the success of asulam spray but this would be limited to areas of suitable terrain.

6.3.2 The control of bracken by crushing once followed by asulam.

The application of asulam on Smeathorns 2, once a second stand of fronds had established following crushing, proved to be more effective than crushing alone in weakening the rhizome system. The number of active and dormant buds were significantly reduced [$F_{1\ 68}$ =141.46; P<0.000 and $F_{1\ 68}$ =18.28; P<0.000 respectively] and the number of dead buds increased [$F_{1\ 68}$ =9.15; P<0.004] (Fig. 26). The rhizome dry weight significantly decreased [$F_{1\ 68}$ =36.68; P<0.000] (Fig. 28).

Therefore, a combination of mechanical and herbicidal control successfully reduced both the dry weight of rhizome and the number of viable buds on Smeathorns 2. However, the number of dormant buds one year after treatment remains high [19.18 (±1.21)] and so ensures the eventual recovery of the bracken.

The number of long shoots increased significantly [$F_{1\ 68}$ =3.85; P<0.054] from 7.10 (± 0.60) to 8.80 (±0.49) shoots (Fig. 27). This was unexpected, particulary as the dry weight had been significantly reduced. Although some of the difference may be accounted for by the change in the sampling methodology, it is considered that this cannot account entirely for this increase.

The weakening of the rhizome system is evident in the poor frond regrowth observed in the year after treatment (Table 27). The number of fronds was significantly reduced [$F_{1\ 68}$ =122.97; P<0.000] and represented an 88.2% 'kill'. A greater rate of success was expected due to the large area of absorption provided by the high number of large fronds. However, the figures are for fronds present before crushing had taken place. Those fronds growing after crushing were smaller and fewer in number due to the reduction in available carbohydrate and the short period of growth before spraying was carried out. Also the fronds growing after crushing were observed to be in different stages of growth.

Active buds, within a given sample, differed in their stage of development before crushing. Some were the same size as the dormant buds whilst others had already developed into small croziers. This was observed on all the plots studied on the North York Moors but was particularly evident on the low moor and moor side. Frond emergence had been observed on the untreated plots until the end of September. Therefore, it appears that there is a continuous cycle of fronds being produced throughout the growing season. This phenomena has been noted in previous research publications (Wilson 1985).

After crushing had taken place on Smeathorns 2 those buds/croziers which were the most developed reached maturity ahead of those which were underdeveloped. Consequently, when spraying was carried out, fronds which were younger and therefore shorter, were protected by the overlying canopy of more mature fronds. This would have resulted in a reduced 'kill'. Because of the production of a second stand of fronds the number of active buds, and therefore potential sinks, may also have been reduced after crushing.

6.4 An evaluation of the control of bracken on the North York Moors.

Previous to spraying the high moor plot, Blakey 1 recorded a lower number of buds than the Rosedale 1 plot. It was postulated that this, along with a high mean number of active buds and smaller fronds being produced on long shoots, would reduce the effectiveness of asulam on Blakey 1.

In the year after spraying the mean number of shoots and the rhizome dry weight were not significantly effected by asulam on Blakey 1. However, the mean number of active and dormant buds decreased significantly and the mean number of dead buds increased. It was observed that the decrease in active bud number was more substantial than the decrease in dormant bud number. Although dormant buds do not assimilate asulam, some buds which appeared dormant before spraying were probably active due to the continual production of fronds observed throughout the growing season. Bud number was reduced but there remained high numbers of dormant buds, 132.31 m^{-2}. In the year after spraying 8.80 m^{-2} fronds were present on Blakey 1. This is below the desired rate of frond 'kill' which can be achieved with asulam spraying.

On the moor side the bracken on Blakey 2 demonstrated an increase in mean dormant bud number with little change in active bud number. The Blakey 2 plot, before spraying, had a low number of active buds and dormant buds compared to the bracken on other plots. The majority of active buds and fronds were observed to be produced from the long shoots. Although the active buds on the long shoots appeared to have been effectively killed, recovery occurred from the dormant buds on the short shoots. Prior to spraying few fronds were produced from the short shoots; therefore a high number of dormant buds were remote from the point of asulam entry. It was observed in the year after spraying that the short shoots were producing more active buds. Frond production, although reduced by 98.4% to 0.40 fronds m^{-2}, was mainly occurring from the short shoot under areas of deep litter and not from the long shoot.

Asulam did not inhibit rhizome growth on Blakey 2. However, the bracken appeared to have been stimulated to i) increase active bud production on the short shoot; ii) increase frond production on the short shoot; iii) increase the number of short shoots and dormant buds and iv) increase the rhizome dry weight. The reasons for this reaction to asulam may be twofold. Firstly, due to the majority of fronds being produced on the long - shoot, dilution effects may have been greater than if asulam was translocated directly into the short-shoot system. Secondly, bud production on the long shoot differed compared to bud production on the short shoot. Whereas buds were only a slight distance apart on the short shoots, eg between 3 - 10 mm, the buds present on the long shoot were infrequent and separated by approximately 2 - 5 cm (explaining why there were fewer fronds on Blakey 2 than the other plots). Therefore, the translocation of asulam from a frond into the long shoot system had less potential to reach a high number of buds and/or shoot apexes.

Asulam was effective in reducing frond production from the long shoot. However, it is proposed that asulam also had a stimulatory effect on the rhizome system. The short shoots in the year after spraying increased in number and in the number of buds they carried. In general terms, the stand has been mobilised from a relatively non-vigorous rhizome system to one which is indicative of being invasive. This demonstrates an ability of bracken in some circumstances to react rapidly to a stimulus, in this case asulam.

The rhizome characteristics of the bracken on Blakey 2, described before spraying, may also be indicative of a clone or genotype variation which is significantly different to other bracken plants on the moor. It has been proposed by previous published studies that, because of the potential genetic variability of bracken, some clones or genotypes may be resistant to certain control treatments. These genetic traits may manifest in a similar way to the bracken on Blakey 2, with fronds being produced on long shoots, and the short shoots remaining relatively dormant, compared to other bracken plants.

The phase of growth may also be an important factor in ascertaining asulam susceptibility. Stands of bracken which appear to be more established, eg Blakey 2, may be more difficult to effectively control using asulam than more active pioneer stands, eg Blakey 1, due to their respective assimilation capabilities.

The bracken on the low moor plot, Smeathorns 3, was also considered to represent a mature established stand. The bracken, before spraying, had a higher mean number of active and dormant buds than Blakey 2 and a greater mean rhizome dry weight. There were more fronds on Smeathorns 3 than Blakey 1 or 2, however frond size was greater than Blakey 1.

The reduction in the number of active and dormant buds on Smeathorns 3 was comparable to Blakey 1. There was no stimulation of the rhizome system as observed on Blakey 2. The percentage 'kill' of fronds on Smeathorns 3 (96.1%) was similar to Blakey 2.

The response of the frond and rhizome to asulam has been observed to differ between the plots. The most successful 'kill' of fronds occurred on the moor side, followed by the low moor and then the high moor. The frond 'kill' demonstrated a positive relationship with frond biomass and a negative relationship with the number of active buds. Blakey 2 on the moor side had the highest frond biomass and the lowest number of active buds of the three plots before the application of asulam. Conversely, Blakey 1 had the lowest frond biomass and the highest number of active buds. Nevertheless, bud reduction was greatest on Blakey 1 and Smeathorns 3. Therefore, the observed frond 'kill' did not reflect the reduction in bud number when comparing the sprayed plots. This again questions the use of frond 'kill' as an indicator of asulam control success. On Smeathorns 3 frond 'kill' was good and this reflected the reduction in active bud number. However, the poorer frond 'kill' on Blakey 1 and the good frond 'kill' on Blakey 2 contradicted the reduction in active bud number on the rhizome.

On the sprayed plots the rhizome dry weight was not significantly reduced and increased slightly on Blakey 1 and Smeathorns 3. The number of dormant buds which remained in the year after spraying was high. Crushing was used on the low moor in order to explore the possibilities of reducing dormant bud number, increasing the number of active buds and decreasing rhizome dry weight.

One year after crushing, the bracken on Smeathorns 1 showed a reduction in rhizome dry weight but the number of dormant buds did not significantly decrease. The number of active buds demonstrated little change before and after crushing and was comparable to the low moor control plot. An increase in the number of dead buds occurred but this was considered a result of the tractor and rollers crushing buds and shoots near the soil surface. The increase in dead bud number did not affect the number of active and dormant buds.

Crushing was therefore considered to be of little use if carried out once a year on the established mature stand of bracken on Smeathorns 1. Rhizome dry weight was reduced compared to the sprayed plots but bud number remained unchanged. Frond number was observed to increase in the year after crushing with a corresponding decrease in frond size. The advantages of this are twofold; i) more fronds increases the number of points for asulam absorption and; ii) a reduction in frond size makes the use of tractor-mounted sprayers more feasible.

The combination of crushing followed by asulam was expected to reduce both bud number and rhizome dry weight, therefore weakening the plant more effectively than a single treatment. The number of active and dormant buds and the rhizome weight were significantly reduced compared to the low moor control plot. The reduction in active bud number was comparable to that of the sprayed plots on the high and low moor. The application of crushing followed by asulam was more effective than asulam alone in reducing the number of dormant buds.

The use of a combination of crushing and asulam was more effective than a single treatment in weakening the rhizome system. Nevertheless, there were still a high number of remaining dormant buds, 212.89 m^{-2}. Frond growth in the year after treatment was poor, represented by a low number of small fronds. The frond 'kill', 88.2%, was not as high as the sprayed plots on the moor side and low moor.

Differences were observed in rhizome morphology in 1992 and one year later on the control plots on the high moor and moor side. In 1992 Rosedale 1 and 2 contained high mean numbers of active and dormant buds. However one year later both plots demonstrated a decrease in bud number. The decrease in the number of dormant buds was greater than that observed on the sprayed plots. The dry weight of rhizome was found to have decreased on Rosedale 2. These changes were not apparent on the low moor control plot.

It was assumed that a location effect had caused the change in the rhizome on the Rosedale plots. If a frost had occurred on Rosedale, and was severe enough to damage the rhizome buds, then a similar effect would have been expected on the Blakey plots. However, the growth strategy of the bracken on the two locations was different. On Blakey the majority of buds were located deeper within the soil. On Rosedale bud growth mainly occurred on short shoots growing within the litter layer near the soil surface. This would have two effects. Firstly, buds located nearer the soil surface would be more susceptible to frost damage than buds deeper in the soil. Secondly, soil near the surface, and in particular the litter, warms up in the spring earlier than the deeper layers. This would stimulate the buds to begin growth earlier in the year, and because of the low depth, emergence would be quicker than buds located deeper in the soil. If a late spring frost occurred, active buds and/or croziers at or near the soil/litter surface would have been killed or crippled. On the Blakey plots, frond emergence may not have occurred at the time of the frost. The buds on Rosedale were further exposed by the action of sheep on the plots.

Frond size decreased on the control and treated plots. It is postulated that this was due to a later growing season in 1993, therefore the fronds were not as fully developed. This was confirmed by observations in the field. The majority of fronds had not unfurled the last pairs of pinnae at the time of sampling. Frond number in the year after treatment was related to the type of control. On the plots sprayed with asulam frond number was reduced and on the crushed plot frond number increased. Frond number decreased on the high moor and low moor control plots but increased on the moor side control plot.

The control success of bracken on the North York Moors was found to depend on the treatment, the location of the bracken and the morphology and growth phase of the rhizome system. On the low moor, where crushing was feasible, this form of treatment followed by the application of asulam, gave the best control of bracken. A single application of asulam provided good control of active buds on the pioneer bracken of the high moor and the established bracken on the low moor. However, control on the moor side was not successful. This was attributed to the production of active buds and fronds on the long shoots.

Asulam did not affect rhizome dry weight or shoot numbers. The only discernible effect was a decrease in the number of buds and fronds. The bracken was therefore weakened, with a reduced capability to produce fronds in the year following spraying, but not eradicated. The main problem for after-management was the high number of dormant buds remaining viable. Crushing reduced the numbers of short and long shoots and the rhizome dry weight but bud numbers were not affected. Crushing followed by asulam demonstrated the best reduction in rhizome buds and weight.

Chapter 7 General discussion, recommendations and conclusions.

This study has generated one of the first large-scale examinations of bracken rhizome systems in the uplands, with special reference to stand description and the effects of control treatments. It is of value in providing an insight into the dynamic properties of bracken on the North York Moors and provides a standard against which other areas of the U.K. can be compared. It also complements and substantiates other published research on bracken variability and control.

7.1 A revised rhizome sampling methodology

The present study highlights the need for a move from bracken research dominated by frond evaluation to research concentrating on the rhizome system. This arose from an evaluation of rhizome sampling methodologies which led to an understanding of more reliable sample sizes (Chapter 4). There have been no published studies on the methodology of rhizome sampling, which is reflected in the varied approaches that have been used since the early studies by Watt (Section 1.6.3.1). It is uncertain how representative such studies are of the characteristics of field bracken rhizome systems. There is a requirement, therefore, for Pteridologists to establish a method of rhizome sampling which can increase data reliability, be adaptable to account for the variation observed in the field, and be comparable with other bracken studies. In this way samples taken from different areas may be more easily compared and compiled into a national database of bracken morphology. Until this is achieved the varying, and mostly untested, sampling methodologies still in current use cannot be considered reliable and any comparisons between areas of bracken will be, at the very least, tentative.

Bracken, forming large, dynamic stands which have the potential to incorporate a heterogeneous population, cannot be reliably described or categorised by the use of small-scale sampling. This was demonstrated by the high level of variability observed on the North York Moors plots when taking a low number of samples (Chapter 5). At a sample number of ≤10 the variation within plots in rhizome bud and shoot number was too high for any definite conclusions to be drawn (Section 4.3). A review of sampling methodologies used in other studies (Section 1.6.3.1), demonstrated that sampling conclusions were often drawn using a sample number of less than five, or in many instances, only one sample per plot. To draw conclusions on field bracken morphology and management from such sampling, and to convert those recommendations on a national scale, is unsatisfactory.

By examining the rhizome on a wide scale (sample number = 100) it was found that rhizome shoot and bud variability within a plot decreased substantially when using fifty or more samples, (of size 30 cm x 30 cm). This figure is not absolute but can be used as a guideline for future studies. Some bracken stands may demonstrate consistently high levels of variation beyond fifty samples whilst other stands may require less intensive sampling. This may also be influenced by the specific requirements of the researcher. A study on dormant bud number for example may require the taking of a greater number of rhizome samples than a study on the number of long shoots, eg Blakey 1 (Figs. 13 and 15). There are two main consequences of under-sampling. Firstly, a sample number ≤10 could exaggerate the number of active buds, and therefore assimilation points, and under-estimate the number of dormant buds, before treatment had taken place, eg Rosedale 1. This could result in an over-estimation in the potential for asulam control. Secondly, after treatment has taken place, under-sampling could give a inaccurate estimate of the effectiveness of the control treatment.

It was recognised that the taking of 50 rhizome samples may not be practical, or indeed necessary, for some bracken stands. It is also not practical to undertake intensive rhizome excavation, in order to find a satisfactory level of sampling, for every plot of bracken under study. However, the sample variance, using the calculation of Harris *et al* (1948), was found to be a useful tool with which to determine the number of samples required in order to achieve a specified confidence interval (Section 4.2). By using this method, the accuracy of rhizome data can be defined within specified limits, and it is postulated that this would increase the reliability of the data collected and the validity of any conclusions.

The sampling methodology presented in this study is considered to be a positive move to understanding and describing the rhizome system of bracken more thoroughly on the North York Moors and on other upland locations of the U.K. The increase in understanding of rhizome dynamics, through more reliable sampling, will enable selective control programmes to be more efficient.

7.2 The characterisation of bracken and its implications for control.

Previous published research has demonstrated that bracken is a highly diverse plant. Although frond appearance may seem homogenous there is the possibility that a stand, or plot, will contain multiple clones which may exhibit a high degree of genetic variation (Wolf *et al* 1988, 1990). A stand may also consist of numerous individual plants (Sheffield *et al* 1989). There are changes in frond and rhizome morphology which correspond to the different phases of the bracken life cycle (Watt 1947) and annual changes in rhizome biomass and frond characteristics (Lowday 1986; Lowday & Marrs 1992). It has also been postulated that there are differences in frond morphology associated with the degree of exposure (climate) on moorland areas (West 1992).

This study has established that bracken stands on the North York Moors are distinct from one another and demonstrate intrinsic variation. These differences could effect a differential response to control treatments (Cook, Stephen & Duncan 1982). For example, a population of bracken may be more resilient to herbicide because of the presence of resistance genes (Wolf *et al* 1988) or because of variation in the gross morphology of the rhizome and frond system. Although the potential for variation within bracken has been recognised it has not been effectively related to the field situation. The present study highlights the differences found within the rhizome system on different plots, and this has been related to the potential for differential response to control treatments. An explanation of the reasons for these differences is, however, beyond the scope of the present study and can only be presumed.

Evaluation of bracken biology, in relation to control potential, must consider certain key characteristics of the rhizome. These must include analysis of the number, and location, of active and dormant buds, the dry weight, the structure of the rhizome shoots and the point of origin of the fronds.

The number of buds on the rhizome system is one of the most fundamental elements of stand description as it indicates the potential for future frond production and for control. The mean number of active buds on all plots was found to be much lower than the mean number of dormant buds. Although it is useful to establish how many buds would be affected by control, it is considered that this is not as important as the number of buds which would remain viable after control has taken place.

The number of dormant buds was highly variable between plots (Table 28). On Rosedale there was a high mean number of dormant buds, compared to the other plots, which gives the potential to be resistant to asulam control. Although the plots on Rosedale also had a higher number of assimilation points, the bracken would have been able to demonstrate rapid recovery due to the number of viable buds which would remain. Control would have also been impeded by the high volume of rhizome on Rosedale. This could dissipate asulam concentrations and impede mechanical control. However, the majority of the dry weight at Rosedale consisted of short-shoot rhizome and not storage rhizome. The bracken on Blakey and Smeathorns 4 sustained a much lower number of dormant buds and had a lower dry weight than the bracken on Rosedale. It is postulated that these plots would be much easier to control on both a short-term and long-term basis because there would be fewer viable buds remaining after control had taken place.

Bud number and rhizome dry weight demonstrated the variability that occurs in rhizome characteristics on particular locations of the North York Moors. It is suggested that bracken from other upland areas of the U.K. is also likely to demonstrate similar variability and therefore it is important, when considering the implementation of a control programme, to account for the potential differences in stand susceptibility. It would be practical to avoid areas of high dormant bud numbers and rhizome dry weight unless an intensive and long term strategy of follow-up could be implemented.

Plot	Dormant buds	Active buds	Dry Weight (g)
Rosedale 1	43.65	15.25	62.55
Blakey 1	19.10	11.25	43.67
Rosedale 2	45.80	17.15	89.35
Blakey 2	13.05	5.20	50.06
Smeathorns 1	24.85	7.20	43.10
Smeathorns 2	30.45	9.40	53.80
Smeathorns 3	30.25	8.05	54.69
Smeathorns 4	14.20	9.15	50.06

Table 28 A summary of the mean number of buds and the mean rhizome dry weight, before treatment per pit (30 cm x 30 cm).

It is also important to know where the majority of active and dormant buds, and fronds, originate in order to ascertain the susceptibility of the rhizome to control. The majority of fronds, and buds, at Rosedale were produced from the short shoots growing near, or within, the litter layer. It is postulated that control using asulam would affect the majority of active buds, and some dormant buds, as the concentrations of asulam would be high in the short shoots. The Smeathorns plots also demonstrated similar rhizome characteristics to Rosedale, although the short shoots on the low moor grew deeper within the soil and not in the litter layer. On Blakey the long shoots were observed to carry the majority of fronds and active buds. This type of rhizome structure was unique to Blakey and was not consistent with previously published studies on rhizome morphology (Daniels 1981; Lee *et al* 1986). It is considered that, because the fronds were originating directly from the long shoots, the effect of asulam would be reduced due to the potentially high dilution factor of the storage rhizome. Furthermore, only the active buds on the long shoots would be affected as the short shoots were remote from the herbicide source and produced mainly dormant buds. Clearly, the dormant buds on the short shoots would need to be stimulated to become active and to produce fronds, therefore increasing the potential for asulam absorption and assimilation. Mechanical control may be one method through which stimulation may be achieved, although this has limited use on upland terrain.

An interpretation of the rhizome structure on Blakey was made difficult by the differences found in gross morphology between the two plots. The high moor bracken on Blakey 1 was the most exposed to frost and desiccation. The production of buds, near the surface on short shoots, would have been unproductive due to the high risk of frost damage. Furthermore, short shoot growth and frond production were observed to be hindered by a dense mat of *Vaccinium myrtillus* rhizome (Section 3.1.5.2 and 5.2.1). A high proportion of frond production was occurring from the long shoots. On Blakey 2 there was less competition from vegetation and the rhizome was observed to be of a less invasive nature compared to Blakey 1. Rhizome growth was dominated by long shoots which produced the majority of fronds and active buds. This growth pattern was absent on Rosedale and Smeathorns and may therefore be an attribute of a distinct local, clonal adaptation.

Due to the differences in the underground structure of bracken, classification of the plots, according to rhizome characters, was not possible. Similarities were observed between plots but these were not consistent. This confirms speculation that, because of the ability of bracken to demonstrate differences in rhizome characteristics, either through genetics, stand age or environmental adaptation, no two plots or stands will be the same. Although treatments such as asulam would have the same basic effect on bracken from different stands, ie reducing frond and bud number, those stands with a higher number of dormant buds, a greater dry weight of rhizome and the production of fronds from long shoots, may have the ability to recover more quickly. The requirement, if characterising stands with regard to asulam susceptibility, is to identify those stands with the highest number of assimilation points and a low number of dormant buds and low rhizome dry weight.

Nevertheless, certain traits were observed in the rhizomes of bracken from the same locations. On Rosedale the bracken was characterised by high numbers of buds and dry weight. The majority of shoots were short, indicative of bracken in the building and mature phases of growth, and these tended to grow near or within the litter layer. On Blakey the number of buds was much lower. The long shoots were dominant, which is indicative of bracken in the pioneer phase of growth, and produced the majority of active buds. On Smeathorns the structure of the rhizome system was similar to that of Rosedale but with less production of short shoots. The reasons for these differences may be environmental, genetic or due to the age of the stands. However, the fact that these differences exist is important in upland stand evaluation. If similar stands of bracken from other upland locations are identified then a national classification may become more feasible.

An interesting pattern in rhizome variability, within each plot, was discovered (Section 5.3). It is postulated that this was due to a gradient in the suitability of growth conditions up the moor and that this may be linked to stand age and growth cycle phase. On Smeathorns, and Rosedale 2, the bracken appeared to consist of more established stands comprising complex rhizome systems which were in a non-invasive phase of growth. The samples of rhizome tended to display less variability than the bracken further up the moor. The stands appeared to have reached an equilibrium, ie the bracken had made full use of the available resources to maximise growth potential on the low moor with further growth only possible by the death and decay of degenerate rhizome (it may be that the control of bracken within such stands may actually increase bracken vigour through the death/weakening of some rhizomes). This was not completely consistent as demonstrated by the high rhizome variability observed on Smeathorns 4. It is postulated that this may be due to the plot location, and the phase of growth cycle, of the bracken on this plot. Smeathorns 4 was situated adjacent to a lowland grass area and may be demonstrative of the degenerate phase of growth as described by Watt (1947). This may have led to the beginning of rhizome fragmentation, indicated by a lower total number of buds and shoots than the other low moor plots and the observation of a high amount of dead shoot material. However, frond growth was vigorous, and the dry weight of rhizome was comparable to the other plots. The height and number of fronds indicated, in comparison with fronds measured by Watt (1947) that Plot 4 was characteristic of mature, and not degenerate or pioneer, bracken.

In comparison to Smeathorns and Rosedale 2, the bracken on Blakey and Rosedale 1 demonstrated higher rhizome variability (Table 23). This is attributed to a number of factors which affected the characteristics of the rhizome and frond system. The rhizomes on Blakey 1 were considered to be representative of young, pioneer bracken stands which were not as established as the mature bracken on the low moor plots. The rhizomes mostly consisted of long shoots growing in one direction up the moor, there was no dead rhizome material, and the fronds were smaller than those associated with more mature stands. On Rosedale 1 the bracken demonstrated similar characteristics of rhizome growth but the stand was more established, indicated by the higher number of shoots and buds and the presence of dead shoot material.

The principal factors inhibiting growth, and increasing variability, were considered to be high levels of exposure, poorer soil conditions and an observed increase in competition from other vegetation species. The bracken, particulary on Blakey 1, was growing at its present limit but its range will increase with the continued decline in heather management, and may be affected by global warming and an increase in the frost-free period (Pakeman, Marrs & Jacob 1994). The bracken on Blakey 2 however was in a less exposed location, was further down the moor, had little vegetation competition and better soil conditions. Nevertheless, rhizome variability was high. It is postulated that the bracken was representative of pioneer conditions as it demonstrated characteristics comparable to Blakey 1 and the work of Watt (1947).

The gradient of low rhizome variability at Smeathorns on the low moor to much higher levels of variability at Blakey on the high moor may affect the evaluation of bracken. As rhizome variation increases, it may become more difficult to classify the rhizome system within a given area. This would mean that the number of samples may have to be changed to account for the higher variability on top of the moor, utilising the sampling programme put forward by the present study (Chapter 4).

7.3 The control of bracken on the North York Moors and its implications for upland bracken management.

The control of bracken using asulam and crushing demonstrated a variable effect on the rhizome and frond systems of the plots. This study found that, although the bracken on any given plot was not eradicated, some plots appeared more susceptible, and some treatments more effective.

Crushing, followed by the application of asulam, demonstrated the best overall reduction in bracken rhizome growth (Section 6.3.2). This is comparable with the recommendations of Pakeman & Marrs (1994) who concluded that a combination of cutting and asulam was the most effective treatment for bracken. Crushing, followed by asulam gave the best control due to the removal of the first stand of fronds, and therefore dry matter, from the system, and then asulam effecting a good reduction in the number of buds on the weakened rhizome. The reduction in rhizome dry weight was particulary high compared to the other plots in the study (Fig. 28). It is uncertain how much dry matter is lost due to crushing, from the production and senescence of a second stand, and from respiration of the rhizome. Further weight loss was expected due to respiration exceeding photosynthate gains in the second year after treatment.

In comparison, the crushed plot, Smeathorns 1, did not demonstrate such a large reduction in rhizome dry weight. This was because the second stand of fronds which emerged after crushing was allowed to develop to maturity and therefore translocated photosynthate back to the rhizome. It is postulated that on both plots which underwent crushing a percentage of the dry matter lost from the rhizome system was due to the damage caused to the shoot system, near the soil surface, by the rollers and tractor wheels.

On Smeathorns 1 the bud number did not significantly change in the year after treatment (Fig. 26). An initial change in bud number may not be apparent in the first year after mechanical control but may decline in subsequent years in comparison to untreated bracken (Pakeman & Marrs 1994). It was observed that crushing did not significantly stimulate the dormant buds to become active (therefore making the bracken more susceptible to site-selective herbicides). The number of buds was retained despite the production of a second stand of fronds in 1992 and a high number of fronds in the following year (Table 30). Observation of the rhizome system on Smeathorns 1 showed that the majority of fronds in the year following crushing were being produced from new buds on the shoot apexes. Some of the dormant buds had become active but these had not reached a stage of growth capable of producing fronds.

The implications of using crushing, or crushing followed by the application of asulam, is that rhizome dry weight will be reduced. The effect of asulam may be improved by crushing, or cutting, before application, and then spraying the second stand of fronds. Absorption and translocation of asulam may also be increased in the year after crushing due to the significant increase in frond numbers observed on Smeathorns 1. However, mechanical methods of controlling bracken have a limited use in upland situations due to the difficulty of the terrain and the lack of suitable equipment. There is also an increase in the potential damage to ground nesting birds and other plant species. Where mechanical control of bracken in the uplands is feasible, it should be included as part of a control programme using asulam.

Asulam caused severe localised damage to the buds and apices of the rhizome system and reduced frond number due to its mode of action (Veerasekaran *et al* 1978). It is postulated however that this represented only short-term control. In the year after asulam application the rhizome systems from the separate plots demonstrated differences in their response but total eradication did not occur (Table 29).

The control of bracken using asulam was most successful on the high moor at Blakey and the low moor at Smeathorns where there was a reduction in the number of buds and fronds, and an increase in the number of dead buds (Section 6.2.1 & 6.2.3). It is postulated that the success of asulam on these plots was greater than that on Blakey 2 because of the characteristics of the rhizome systems. The rhizome systems on Blakey 1 and Smeathorns 3 carried a higher numbers of buds. On Smeathorns 3 the majority of active bud production and frond origination came from the short shoots. Therefore, asulam was translocated into the region of the shoot where the bud concentrations were highest. On Blakey 1 the location of bud and frond production on the rhizome was similar to Blakey 2; however, asulam was more effective in reducing bud number. This was probably due to the smaller rhizome system of Blakey 1, and its active state of growth. Although asulam was mainly translocated into the long shoots, the shoots were much thinner than those on Blakey 2, and therefore the effect of dilution would have been reduced.

The bracken on the moor side at Blakey 2 appeared to have been stimulated to produce more dormant buds and shoots with no apparent effect on active bud number (Section 6.2.2). An explanation for the effect of asulam may be the production of active buds and fronds on the long shoots, due to the previously discussed reasons of environmental and/or clonal adaptation. On this plot the short shoots, and the dormant buds, were remote from the herbicide source, and were therefore not affected. It was observed in the year after spraying that active bud production, and the growth of shoot apexes, originated from the short shoots but that the long shoots did not show any signs of active growth.

The study demonstrates that asulam may not be appropriate for controlling bracken within some stands, and may in fact stimulate it to more vigorous growth. Bracken, adjacent to heather fronts, which has a high number of active buds and low dry weight, eg Blakey 1, may be more effectively controlled in upland regions using aerially applied asulam. Those stands which do not appear invasive, and would be difficult to effectively control due to their rhizome characteristics, should remain untreated unless there is a specific requirement to do so (eg conservation or landscape purposes).

It was apparent that high numbers of dormant buds, and high rhizome dry weight, remained on all the sprayed plots one year after asulam application. However, the number of dormant buds was affected; on Blakey 1 and Smeathorns the number of dormant buds declined. It is suggested that this was caused by; i) dormant buds which were in fact active, despite their outward physical appearance (Section 7.4), and were therefore susceptible to asulam, and/or; ii) the stimulation of dormant buds to become active after treatment had taken place. It was observed that the majority of active buds observed in the year after spraying originated from dormant buds and not from growing shoot apexes or from new bud production (Figure 17 and 23). In most circumstances shoot apex growth had been checked by asulam, probably due to an increase in assimilation at these points.

The levels of rhizome dry weight would be expected to decline further, two years after spraying, due to respirational losses being greater than the photosynthate gains, ie a decline in net production. This would depend on the number, and size, of the fronds produced It was observed, in the year after spraying, that areas of rhizome remained where little effect due to treatment could be ascertained, and that these often possessed large rhizome dry weights. For example, on Smeathorns 3 the mean dry weight of rhizome was 58.92g ±3.45 but weights up to 134.20g were recorded in some samples. These areas were often associated with frond production in the year after spraying and could be identified by large mounds of accumulated litter. It is postulated that these areas could be difficult to eradicate, even with repeated spraying, and could act as a locus for bracken stand regrowth.

Of interest was the effect that the treatments had on frond regrowth (Table 30), and how this related to the condition of the rhizome. At Smeathorns, and Blakey on the moor side, the reduction in frond numbers after applying asulam was comparable to that recorded by other published studies, (Martin *et al* 1972; Soper 1972; Pink & Surman 1974; Ball & McCavish 1980; ADAS 1983, 1988), but not to the level of one frond per $10m^{-2}$, deemed acceptable by Heywood (1982). On Blakey 1 the control of bracken using asulam resulted in a 75.9% 'kill' which was below acceptable levels.

Plot	Active bud no.		Dormant bud no.		Dead bud no.		Rhizome dry wt.	
	'92	'93	'92	'93	'92	'93	'92	'93
Blakey 1	11.25	0.82	19.10	11.92	1.25	5.28	43.67	40.87
(asulam)	±1.84	±0.26	±2.32	±1.16	±0.42	±0.57	±5.03	±2.78
R'dale	15.25	5.58	43.65	16.66	1.75	1.20	62.55	59.37
(control)	±1.82	±0.59	±5.45	±1.52	±0.40	±0.22	±6.39	±3.29
Blakey 2	5.20	4.82	13.05	17.80	1.15	2.38	50.06	55.94
(asulam)	±0.96	±0.51	±1.44	±2.38	±0.41	±0.32	±4.67	±2.71
R'dale 2	17.15	3.38	45.80	27.82	5.40	1.26	89.35	69.20
(control)	±2.49	±0.37	±3.62	±1.89	±0.84	±0.21	±9.32	±4.61
Sm'horn 1	7.20	6.60	24.85	25.62	1.95	5.80	43.10	34.64
(crushed)	±1.08	±0.46	±2.28	±1.35	±0.54	±0.54	±2.62	±1.86
Sm'horn 2	8.05	0.80	30.25	19.18	1.15	3.44	54.69	33.68
(crush/as)	±0.92	±0.13	±2.77	±1.21	±0.32	±0.46	±2.99	±1.84
Sm'horn 3	9.40	1.56	30.45	26.02	2.00	4.46	53.80	58.92
(asulam)	±0.91	±0.21	±3.68	±2.00	±0.53	±0.42	±4.91	±3.45
Sm'horn 4	9.15	7.76	14.20	16.52	1.60	2.54	50.06	58.13
(control)	±1.58	±0.71	±2.11	±1.52	±0.44	±0.34	±4.90	±3.56

Table 29 Summary of rhizome characteristics

On all plots sprayed with asulam frond height, lamina and pinna lengths were reduced. On the crushed plot, Smeathorns 1, there was a large increase in frond number in the year after treatment. This is comparable to the work of Pakeman & Marrs (1994) who demonstrated that cutting once caused an initial increase in frond density in the following year.

If change in frond number is taken as the only means by which control was assessed then the bracken on Blakey 2 demonstrated the most successful control (98.4%) followed by Smeathorns 3 (96.1%), Smeathorns 2 (88.2%) and Blakey 1 (75.9%). However, the control of fronds did not reflect the apparent stimulation of the rhizome system on Blakey 2 to produce more buds and increase rhizome dry weight, and was not indicative of the large number of remaining buds and rhizome dry weight on Smeathorns 3. The increase in frond number on Smeathorns 1, after crushing, was not reflected in stimulation of dormant buds. In comparison, the lower rate of frond reduction on Blakey 1 did not indicate the better rate of rhizome 'kill'. Again this stresses that the condition of the rhizome system, and the effect of control, cannot be assessed by frond number alone.

It became apparent through the study of the control plots that bracken stands within upland regions have a highly dynamic structure. This may be due to the effects of clones and/or genotypes within a stand, seasonal weather conditions, groundflora, stocking rates and fluctuations in the growth cycle of bracken. A low degree of seasonal fluctuation, such as that observed on Smeathorns 4 (Section 6.2.3), would not greatly affect the outcome of bracken control, and is probably due to seasonal variation. On Rosedale, however, significant differences in the rhizome system were observed between the two sampling dates (Section 6.2.1 & 6.2.2) which were greater than the recorded effects of asulam on Blakey (Table 29). Discussion with the Spaunton Estate gamekeeper revealed that Rosedale was being overstocked with sheep in an attempt to reduce the bracken cover (Wass *pers. comm*). Low levels of sheep grazing have little effect on bracken cover, but, the driving and overwintering of sheep in the area appeared to have an impact. Croziers were observed to be trampled in the spring, with a high number browsed off (Section 6.2.1). Litter disturbance also occurred, increasing frost damage to shoots and buds near the surface.

Increasing stocking rates may be a possibility for inclusion within a bracken control programme but this would be limited to very small areas. However, the negative effects of overgrazing are substantial in terms of soil structure and vegetation cover and there is the added hazard of stock poisoning.

Plot	Frond no. '92	Frond no. '93	Frond ht. '92	Frond ht. '93	Lamina lgth. '92	Lamina lgth. '93	Pinna lgth. '92	Pinna lgth. '93
Blakey 1	36.60	8.80	37.50	12.50	19.90	5.70	23.70	9.20
(asulam)	±3.32	±1.30	±6.13	±0.90	±3.77	±0.60	±3.25	±0.80
R'dale 1	31.60	21.70	47.40	20.50	20.96	12.60	26.09	13.60
(control)	±1.74	±6.30	±6.84	±5.80	±3.51	±3.60	±3.34	±3.80
Blakey 2	25.35	0.40	117.00	4.70	55.31	2.60	51.16	3.50
(asulam)	±1.29	±0.20	±3.21	±2.40	±1.66	±1.60	±1.40	±2.10
R'dale 2	32.40	45.00	72.40	40.30	39.30	25.30	39.30	26.00
(control)	±3.75	±2.60	±5.12	±1.40	±3.21	±1.00	±2.02	±0.90
Sm'horn 1	29.00	88.00	27.70	23.80	12.35	16.50	18.90	16.10
(crushed)	±4.89	±7.10	±1.52	±1.10	±0.76	±0.90	±1.03	±0.50
Sm'horn 2	45.90	5.40	86.40	7.60	48.70	4.90	45.30	8.10
(crush/as)	±2.44	±1.50	±2.82	±1.30	±1.51	±0.80	±1.24	±1.20
Sm'horn 3	41.00	1.60	24.50	7.60	13.30	4.40	19.30	8.60
(asulam)	±4.18	±0.50	±1.21	±2.00	±0.76	±1.30	±1.28	±2.60
Sm'horn 4	46.20	39.90	96.10	36.50	56.00	19.80	49.50	26.60
(control)	±2.73	±1.70	±3.70	±2.20	±1.95	±1.30	±1.20	±1.70

Table 30 Summary of frond characteristics.

7.4 The possibility, and feasibility, of follow-up and after-care management on bracken controlled areas.

It is important to consider the problems involved in follow-up and after-care, of the moorland post-bracken control. This study has re-emphasised that primary control of bracken is not entirely successful and that there remains the potential for future frond production through bud reserves.

Within one year of spraying, fronds were present on the plots (Chapter 6). The production of fronds, after control, assumed two modes. On the high moor at Blakey, fronds were produced evenly across the plot but were few in number and small (Table 24). On the moor side and low moor, frond growth after treatment was associated with deep clumps of litter (Plate 11) and/or with shrub growth such as *Calluna vulgaris*. In either instance aerial spraying would not have been a practical method of follow-up because of the low area for absorption. A possible solution would have been to wait for two to three years until a suitable canopy of fronds had built up (therefore the primary spraying was an inefficient use of time and resources) or to spot spray the fronds, achieved through the use of asulam applied by hand held sprayers such as Micron Ulva+ or Selectokil spot gun. This may be a practical solution on areas which consist of a few hectares. However, in dealing with the thousands of hectares which have undergone primary spraying on the North York Moors (Section 1.7) the problem is self evident.

It is proposed that rather than undertake wholesale spraying of large areas of mature bracken, control should be concentrated on the boundary between the invading bracken front and the vegetation communities which need to be protected, and encouraged, for example at Blakey 1. This method of containment, rather than eradication, has not been widely accepted by landowners, who, with the promise of substantial grants, have tended to spray areas on an extensive basis. On some areas of the moor the use of boundary spraying has been put into practise and early results have proved promising (Ideson *pers. comm*). The advantages of marginal bracken control are that costs are kept low, the advance of bracken is checked and follow-up and after-care management are more feasible.

The author observed that bracken control on Blakey 1 benefited from having a dense understorey of *Vaccinium myrtillus* (Section 6.2.1). This rhizomatous dwarf shrub is tolerant of shading and moderately heavy grazing and provides valuable winter forage for sheep and grouse. It is less invasive than bracken and was often found co-existing with *Calluna vulgaris* and *Deschampsia flexuosa*. Taking this into account it is suggested that control in the boundary between heather and bracken, where appropriate, could make use of bilberry as a management tool. This would have the advantage that bracken would not be in direct competition with heather, thus allowing heather burning to be carried out up to the edge of the bilberry, without encouraging bracken invasion. However, some colonisation into heather burnt areas may occur from the bilberry rhizomes (Ritchie 1956), particulary if heavy grazing occurs (Edgell 1971). The large mats of bilberry may also encourage increased species diversification of fauna and flora. However, bilberry may encourage an increase in sheep tick infestation (Brown 1994; Sheaves & Brown 1994).

Bracken could be periodically sprayed along the bilberry edge, and further down the moor, sprayed to encourage sward growth for grazing. Therefore the emphasis would be placed on the containment of bracken within a zone on the moor side with control occurring on the high moor for the encouragement of heather growth. This could be put into practice where bilberry is already established. However, because of propagation and establishment difficulties, the cultivation of new stands of bilberry is not presently possible (Welch, Scott, Moss & Bayfield 1994).

Other problems, associated with after care, also need to be addressed. On the moor side plot at Blakey the removal of bracken resulted in little vegetation cover protecting the soil surface. Of those understorey species which were previously present, few, apart from bilberry, remained in a vigorous state. Other species such as *Oxalis acetosella* and *Galium saxatile* appeared weakened due to increased exposure. Therefore, some species of vegetation, such as chickweed wintergreen, which are considered of conservation value, may be adversely affected due to widescale bracken control.

The removal of litter was observed to be rapid, when not replenished by frond senescence. Within two years the surface of Blakey 2 was observed to be eroding, exposing the peat layer, in those areas which were not protected by a sufficient layer of litter and/or vegetation. This problem was not apparent on the high moor where a sufficient vegetation layer kept erosion to a minimum. At Smeathorns 3, however, soil erosion was apparent.

Where there is an insufficient understorey of species to protect the soil surface the problem of erosion on some plots may be greater than the disadvantages caused by bracken infestation. This potential problem needs to be identified, before bracken control takes place, with areas susceptible to erosion being avoided. Also, bracken stands which have a deep litter layer should be controlled with care because of the problems of vegetation establishment once control has taken place. A deep litter layer suppresses the colonisation of vegetation by reducing germination and by the proposed effects of allelopathic compounds. The litter layer therefore needs to be removed or fragmented by mechanical means. This may be achieved through the indirect action of mechanical control, as observed on the crushed low moor plots (Section 6.3.1). On the more inaccessible, sprayed areas of the high moor and moor side, litter disturbance or removal would not be feasible.

Establishment of vegetation was observed to be impeded on the North York Moors due to overstocking of sheep, particulary on Rosedale and Smeathorns. The clearance of bracken made the understorey vegetation more accessible to sheep which tend to congregate on such areas, and establishing ground cover species such as heather and bilberry were severely grazed. Overgrazing has been a contentious issue for a number of years on the North York Moors, particulary on the Spaunton Estate near Hutton-le-Hole. The result of early trials in excluding sheep from penned areas has already shown that the growth of vegetation is rapid (Plate 11). Nevertheless, the species which benefit from the exclusion of grazing may not be what the gamekeeper requires, ie *Deschampsia flexuosa*. Furthermore, the fencing of large areas of moorland is not feasible due to common land law and conflicts over rights between sheep farmers and grouse interests. Small scale, rotational fencing may, however, be feasible, and desirable, on heavily grazed, eroding areas such as Blakey 2.

There are also problems concerning the colonisation of bracken controlled areas by other weed species. By removing the bracken canopy opportunistic species are often the first to colonise. On the North York Moors this is commonly by *Campylopus introflexus*, a species of moss which was recorded on most of the study plots (Section 3.1.5.2). Where spraying had been carried out on other moorland areas, and particulary on areas of heavy grazing, extensive mats of *Campylopus introflexus* now exist (Plate 12) (Equihua & Usher 1988, 1993; Pakeman & Marrs 1992). This moss, which is fragmentary in nature, will often inhibit growth of herbaceous species, although *Calluna vulgaris* and *Ulex europaeus* have been observed to grow.

Colonisation by herbaceous weed species such as *Rumex acetosella* and *Digitalis purpurea* has also been been observed to occur. Therefore, further weed control will be required in order to encourage the desired species of vegetation. On the North York Moors heather brash is placed on areas of cleared bracken in order to encourage re-seeding. This is only viable over small areas and should be concentrated on the heather/bracken boundary.

Plate 11 Trial plot at Hutton-le-Hole, which excludes sheep grazing, showing the rapid growth of Deschampsia flexuosa after one year. July 1994.

Plate 12 Camplylopus introflexus infestation on the Spaunton Estate after bracken control using asulam in 1988. July 1994.

The number of plant species growing beneath bracken was not found to be great on any of the study plots. However, certain species were found to be more successful in their growth, and would provide suitable cover, once control had taken place. On the North York Moors bilberry was found to be particularly prevalent on the high moor plots where it formed dense mats underneath the bracken. *Festuca rubra* was also commonly found. On all of the plots the cover of *Calluna vulgaris* was poor and appeared as isolated clumps. It must be remembered that the bracken under study was controlled for the purpose of heather conservation. With little or no heather cover, after-care programmes, to encourage heather growth, would have to be intensive and long-term.

The vegetation composition on Blakey 1 was observed to be similar two years after treatment. Vegetation cover was high with vigorous growth of *Vaccinium myrtillus*, *Calluna vulgaris*, *Empetrum nigrum*, the grasses *Festuca rubra*, *Anthoxanthum odoratum*, *Nardus stricta* and *Deschampsia flexuosa* and the sedge *Luzula campestris*. The growth of bracken fronds was low. It was also observed that the percentage cover of litter on Blakey 1 was reduced to negligible levels and was absent in most areas. From these observations it is postulated that the under-storey vegetation prior to spraying was sufficient to ensure successful vegetation growth and bracken suppression, without the requirement for intensive follow-up (apart from minimal spot spraying).

On Blakey 2, however, the lack of a sufficient under-storey of vegetation before spraying, was reflected in poor post-spray growth. After two years the plot was observed to consist of high levels of litter interspersed with areas of serious erosion. The vegetation that did occur after spraying demonstrated poor growth, ie *Luzula campestris*, *Holcus mollis*, *Oxalis acetosella* and *Deschampsia flexuosa*. Bracken cover levels were minimal. Where *Vaccinium myrtillus* was present, litter and erosion levels were reduced and species number tended to be higher.

On Smeathorns 3 the depth and cover of litter remained a problem two years after spraying. The plot had a low number of plant species dominated by *Festuca rubra* and *Vaccinium myrtillus* and bracken growth was low. The same result would have been expected if the bracken on Smeathorns 1 had been sprayed, as these plots demonstrated a similar species composition before treatment. On Smeathorns 1 however the implementation of crushing increased the number of bracken fronds. The under-storey vegetation was not observed to be greatly changed by crushing but litter fragmentation occurred due to the action of the rollers and the tractor. This opened up areas for colonisation by *Rumex acetosa*. Colonisation by *Rumex acetosa* has been observed by the author to occur frequently on recently crushed areas.

On the plot combining crushing with spraying, the reduction in litter cover was the highest and bracken frond growth was low. The plot was heavily grazed but this did not seem to unduly affect the composition of the under-storey vegetation. The further growth and establishment of shrubs such as *Calluna vulgaris* may be inhibited by high grazing levels. As with the Smeathorns 1 plot there was a high level of *Rumex acetosa*.

The control plots demonstrated no change in their species composition. The low moor plot, Smeathorns 4, was dominated by grasses with patches of *Vaccinium myrtillus*. This plot, if sprayed, may have become heavily grazed. The vegetation on Rosedale 1, if spraying had taken place, would have been similar to Blakey 1 due to a similar composition of under-storey species. There was, however, a high cover of *Campylopus introflexus* on this plot. Nevertheless infestation by this moss may not be too problematic if vegetation competition is kept high. On Rosedale 2, the depth of litter and species poor under-storey, would have resulted in poor colonisation if spraying had been carried out.

The follow-up and after care of the majority of plots, treated for bracken infestation on the North York Moors, would need to be comprehensive and long-term. To create, and maintain, a vegetation cover would require the regulation of stocking rates, the follow-up treatment of bracken, litter fragmentation and/or removal, further control of other invasive weed species and mosses, heather re-seeding, and ultimately a change in the land-use which led to the initial infestation of bracken.

The establishment of vegetation to create a habitat suitable for either grouse production or for sheep grazing, would be thwarted by the low success rate of bracken control, the large area which has already undergone primary spraying, the inaccessibility of much of the treated moor, the low levels of labour and capital available, the low growth rate of *Calluna vulgaris* as well as the problems of managing and regulating land with rights of common. Where control of the bracken rhizome is more successful, and where the under-storey vegetation cover is good, (ie Blakey 1) the amount of after-care required would be reduced. However, on stands such as that represented by Blakey 2 the removal of the bracken canopy can result in erosion of the soil surface, little vegetation growth and invasion by other species such as *Campylopus introflexus*. The vegetation that does exist is damaged by sheep grazing. If there is little possibility of effective after-care management taking place, the widescale control of bracken, in situations such as that represented by the Blakey 2 plot, should be avoided and control restricted to containment along the heather/bracken border.

7.5 Contributions to research

This study:

i) Demonstrates that previous sampling methodology is inadequate for evaluating the rhizome, within the upland field situation, due to the variability of rhizome characteristics within separate bracken stands, and the differences in gross rhizome structure between different locations on the North York Moors.

ii) Stresses the importance of the rhizome for stand description and control evaluation. The frond has been used in previous research to illustrate the effectiveness of control treatments. This study has demonstrated that there is little or no relationship between the effect of treatment on frond production and the effect on the rhizome system.

iii) Suggests general models of bracken control by evaluation of the rhizome system with regard to the number of dormant and active buds, and the rhizome dry weight. This may be related to the cycle of growth, as originally described by Watt (1947), although the distinctions between phases may be difficult to discern within upland regions.

iv) Provides the first large-scale examination of the rhizome in an upland area in relation to control strategies on an operational scale, and a baseline for future research.

v) Highlights the differences in the gross morphology of bracken stands and the effect this has on control. It enables the identification of bracken stands which have the potential to be more successfully controlled using either asulam or mechanical means of control.

vi) Demonstrates that the poor control using asulam comes from the inability of dormant buds to assimilate lethal levels of the herbicide, and also from high levels of rhizome dry weight. There is a requirement to break bud dormancy and reduce rhizome dry weight. However, mechanical control was not found to stimulate dormant buds to become active.

vii) Questions the use of large-scale bracken control programmes in upland regions due to the apparent ineffectiveness of asulam on the rhizome system, and the difficulty of implementing a programme of successful follow-up and after-care management.

viii) Contributes to explaining the lack of control success using asulam.

ix) Contributes to the knowledge of basic bracken biology.

7.6 Critique of the present study

The present study has highlighted some of the major problems associated with bracken research. These problems are identified as potential areas of future research, through which, bracken description and control may be improved.

i) The use of asulam demonstrated that a number of dormant buds are in fact active, despite their outward, physical appearance. Also, asulam may stimulate dormant buds to become active, as observed on Blakey 2. Rhizome bud differentiation was difficult because those buds which were newly active were similar in appearance to dormant buds, and could only be distinguished by going down to the cellular level of examination. One solution would be to consolidate active and dormant bud number. However, the author felt that this was not practical when describing bracken with the intention of evaluating susceptibility to asulam. Currently, there is no quick method, other than through evaluation by eye, to differentiate the condition of rhizome buds.

ii) In order to gain a better understanding of the relationship between rhizome dry weight and shoot type future research should weigh each shoot type individually. This will give an improved estimation of the dry weight distribution within the rhizome system, so indicating more accurately the amount of dry weight which is composed of storage rhizome.

iii) It is recognised that only short-term data are available and that bracken control is long-term. However, the effect of control after one year is highly important in evaluating the immediate effects on the bracken frond and rhizome system. The number of fronds following treatment are used as a yardstick from which conclusions on control success are drawn. Most quotations from published research, and manufacturer directions for use for asulam control, are given for one year after treatment. The present study places emphasis on the rhizome indicating control success rather than the frond.

iv) The study included a small number of plots, but these were of a size which were deemed suitable for a representative bracken sampling programme in the field. Ideally, replicates for each treatment should have been available for each category of moor. The purpose of this study, however, was not to produce a definitive statement on bracken control, but to demonstrate that differences in bracken morphology exist in the field and that these differences can lead to a variable response to control which must be taken into account if programmes are to be successful. The bracken on the North York Moors, and in other upland areas, may be treated as heterogeneous stands from which the plots represent matrix samples. Each area of bracken demonstrates particular characteristics, such as a high number of buds, which may be used as indicators of control susceptibility.

v) There was difficulty in the determination of the number of dead buds due to the problem of distinguishing buds which were already dead due to natural causes and those buds which have been affected by the treatment. The number of dead buds have been shown to increase after asulam treatment, but not substantially so, and did not reflect the reduction in dormant and active bud number. This was probably due to the fact that any short shoots (and the buds which they carried), which may have been killed, were not included in the study. The total number of dead buds after asulam application was therefore probably greater than reported.

vi) The initial selection of plots used frond characteristics to identify stands of bracken which were assumed to be mature and similar in composition (Section 3.1.1). As the study progressed it became obvious that, because of the lack of association between the frond and rhizome, the plots contained bracken which demonstrated characteristics of different stages of the life cycle. For instance, the bracken on Blakey 1 was more characteristic of the pioneer stage of the life cycle. On the basis of the rhizome and frond demonstrating no consistent relationships it is acknowledged that this method of locating plots was unsatisfactory. There must be greater emphasis placed upon consideration of the rhizome system in the selection of plots in future studies. This may be difficult due to the high variation of rhizome characteristics, as discussed in section 7.1.

7.7 Conclusions.

A distinct classification of bracken, in relation to rhizome morphology, was not possible due to the diverse characteristics of upland bracken. It is postulated that this may remain the case even if an infinite number of plots were examined. This conclusion is extremely important in stressing the variability of bracken stands in upland regions of the U.K. Bracken should not be considered as a single homogenous species, but rather as a plant with diverse characteristics, which can affect the outcome of a control programme.

The reasons for the differences in the composition of bracken stands from distinct locations are outlined in Fig. 29. It can be seen that a number of main factors affect the composition of bracken, from the genetics of the plant itself through to land management, the local environment, the phase of growth and competition form other plant species. To recommend that a given stand of bracken should for instance be treated with asulam at a specified rate, may not be appropriate unless a tested method of sampling the rhizome is applied beforehand. The sampling methodology put forward by this study can be used to identify general trends in rhizome composition within upland regions and to relate these to control susceptibility.

A broad classification of upland bracken, based on the rhizome, was recognised. This needs to be strengthened by further research in other upland areas of the U.K., where bracken infestation has become a problem, ie Wales, Scotland, Peak District and the moors and heaths of the South-West. Further research should not only be based on the techniques of rhizome evaluation described within this study but should include information on the economics of control and the possibility of practical follow-up taking place, should account for aspects of conservation, landscape aesthetics and the use of the land once control has taken place. It will require the co-operation and co-ordination of all those concerned with bracken and its control, ie ecologists, land managers, conservationists, biologists and agronomists, as well as environmental bodies such as the Countryside Commission, English Nature and the National Park Authorities. Collaboration will be essential if long term success is to be achieved.

One of the main aims of the present study was to quantify the success of the North York Moors National Park bracken control programme and to relate it to upland bracken management in the U.K. Complete eradication of the rhizome was never achieved in the study, although frond 'kill' was good. If frond 'kill' alone is used as a control indicator then the bracken control programme may be considered a short term success. However, the problems of follow-up, the lack of growth of other vegetation species, the remaining litter layer and erosion on the moor side negate any benefits of bracken frond removal.

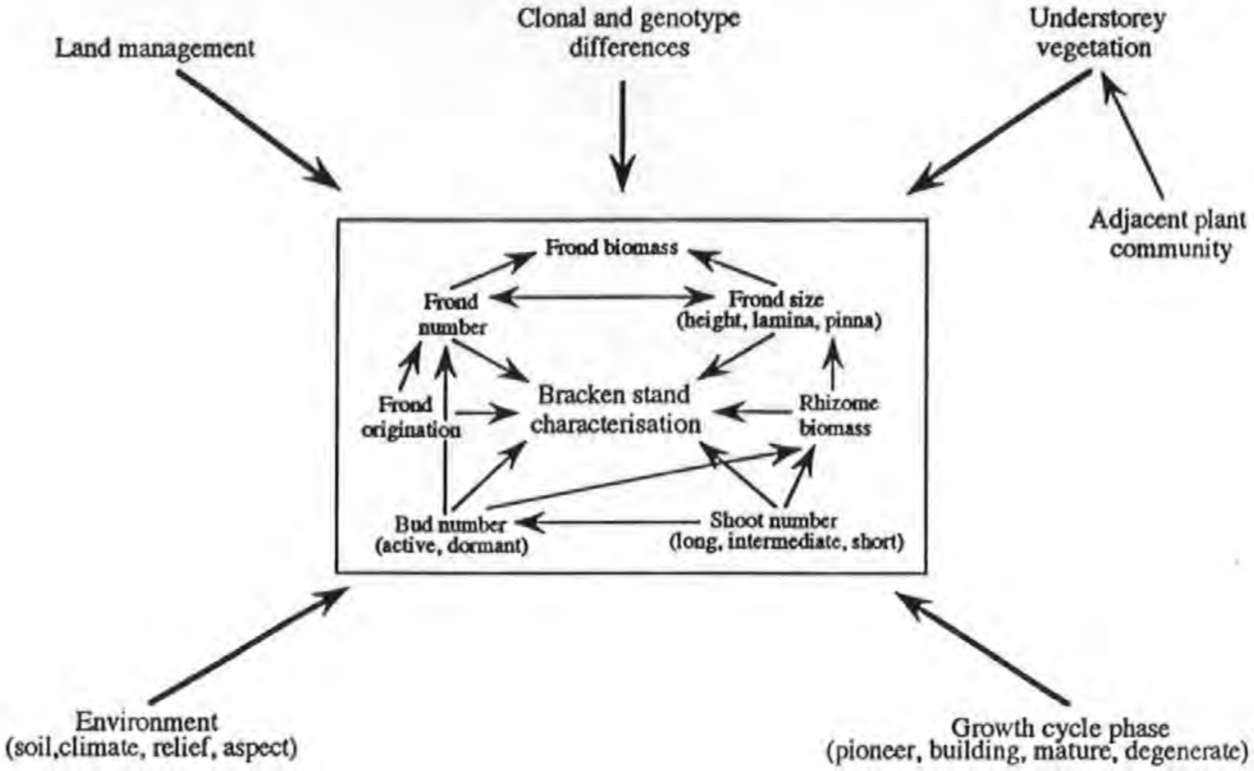


Fig. 29 A simplistic model of the main factors governing the structure of a bracken stand in the uplands.

Throughout the study the frond and rhizome demonstrated no consistent, significant relationships. It has been discussed previously that frond growth is an important indicator of when to treat bracken because it absorbs and translocates asulam to, and removes dry matter from, the rhizome system (Section 1.4.1 and 1.4.2). However, it is postulated that as an indicator of rhizome morphology, or the effects of treatment on the rhizome, the frond could not be used. This was particularly evident on the sprayed plots where the percentage of frond 'kill' one year after treatment did not reflect rhizome damage.

If the effect of control on the rhizome is considered then the author feels that control, on the scale applied on the North York Moors, is perhaps not the best solution to the problem on upland areas. Containment is preferable to attempted eradication.

Dormant buds and rhizome dry weight were not greatly affected by asulam and remained a source of potential bracken re-colonisation. On bracken with a high number of dormant buds, but low number of active buds, the suitability of site-selective herbicides must be questioned. Stimulation of the rhizome system was clearly required on most plots in order to increase the number of assimilation points. Presently, the only means through which to achieve this is mechanical control methods which also reduce the dry weight of the rhizome. However, although dry weight did decline after crushing, there was no stimulation of the dormant buds to become active. This may of course be an isolated reaction of the bracken on the low moor plot. Bracken crushed on the heather/bracken boundary may, for instance have reacted in a manner which did in fact stimulate the dormant buds. Even if this was true the use of mechanical control would be unsuitable on many upland areas due to the difficulties of terrain. Stimulation of the dormant buds by chemical or biological means may provide an answer.

It would be more practical to target pioneer bracken which has a higher susceptibility to asulam control, a greater potential for the growth of other vegetation species once control has taken place and is capable of more cost-effective follow-up treatments. It is also postulated that a buffer zone could be set up between bracken and heather using swards of bilberry which seemed to inhibit the invasion of bracken. This would allow appropriate burning of the heather to take place without the danger of bracken competition.

This study has investigated a key issue about bracken and its control, that is, can the large-scale control of bracken, using presently available techniques, be justified when long-term control, which requires a high degree of follow-up, is often not possible in upland regions? The answer must be yes, and no. Clearly the rapid infestation of the North York Moors, and other upland regions of the U.K., by bracken must be contained, and due to the scale of the problem control must also be achieved on a large scale. However, selective spraying along the heather/bracken boundary would be far more practical, and follow-up easier to implement. The spraying of large, mature stands of bracken with little understorey vegetation, results in large expanses of the moor remaining unproductive and liable to erosion, therefore reducing the capital value of the land.

At the present time asulam is the main method available for bracken control, but this study has demonstrated that its limited effect is due to the resistance of the rhizome system. The eradication of bracken from the North York Moors, and other upland areas of the U.K. is not a possibility, and nor should it be desired. There must be a move to more site specific control of bracken which recognises those stands which will be more susceptible to control and places emphasis on containment rather than eradication.

This requires knowledge of the actual distribution of bracken and adjacent plant communities. This could be achieved using a combination of remote sensing (Weaver 1986) and ground survey to produce target area maps for each upland area before bracken control is implemented. The ground survey would also include regular sampling of bracken, before and after treatment, using a recognised, and validated, methodology in order to build a database on stand composition, phase of growth and susceptibility to control. A target area map would also require information on terrain (particulary slope data), local stocking rates, areas of conservation value such as SSSI's, bracken litter cover and depth, and the presence of understorey vegetation. Consideration must also be taken into the requirements of bracken control. If control, for example, is for the purpose of grouse management then there must be the possibility for heather establishment afterwards.

Stands of bracken which would not demonstrate successful control could be avoided in favour of bracken stands which could be more effectively contained, and would require minimal after-care. In this way selective control would be achieved, reducing the problem of erosion and the remaining litter associated with large-scale programmes and rendering follow-up more feasible and bracken control more cost-effective.

However, much of the information required is held by different agencies, and therefore the key to future success may well lie in closer collaboration and co-ordination of biological, technical and management information through a neutral, professional clearing agency. This could be managed through the International Bracken Group.

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Appendix I TWINSPAN classification for the North York Moors vegetation data, June 1992.

TWINSPAN (Hill 1979) is a method of phytosociological numerical classification which groups quadrats of similar species together. Despite the apparent complexity of the final classification table (Figure 1), it is simply a two-way sort of the input data so that quadrats (columns) and species (rows) are placed next to those judged to be most similar. The quadrats are sorted vertically and the species sorted horizontally which tends to concentrate entries down the diagonal from top left to bottom right. The quadrat numbers are printed vertically at the top of each column and are as follows;

Rosedale 1	1-30	Smeathorns 1	121-150
Blakey 1	31-60	Smeathorns 3	151-180
Rosedale 2	61-90	Smeathorns 2	181-210
Blakey 2	91-120	Smeathorns 4	211-240

Species names and numbers are printed down the left hand side with species number followed by the latin binomial. The figures in the main table represent a 6 point scale on the percentage occurrence of species with - equalling 0% and 5 equalling 100% cover. The classification groups and classification hierarchy information is contained in the binary codes of 0's and 1's at the bottom of the table for quadrats and to the right for species.

Figure 1 The TWINSPAN classification table, North York Moors 1992.

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              1145555666777778811333464555566677899234443923223333344567788889122346035662222333334467778111111122222222333347788880948557556744507991346790090110344555666735566900244708993908881111   23   1111222223  1222912802300119491 9001126901900890
              0480127014136791437248495346835704037892491924346234592834191569056721600757158935789039258312568901246793677356024788578697580856094282693344772791801124268005928028306219191635731248123515790357013890686467182235550134756439504016692476 86

 2 BRAC RUTA  2--------------2-3-----------------------------------------------------------------------------------1------22-------32-2-----------------------2---------------------------2---1-------4-------------------------------------------------------  000
 8 FEST RUBR  35425554455554535555533333323242223325255555555----3----3--2--2-23-12224445555455-5555545555555555555555555555555-443234-3-5-4--2------3------------------------------------------255555554-55535354253334-3451-42-5353--------52--------345-3-3  000
18 PTER AQUI  55455555555535555545555454555555555555555545--554455555545355555555555555555--5555553444555455555555555545555555555553455555555553455555555555555534445555544455455555555555553555555555545545555555555--55555435455555435555454345 4-552-445555  0010
20 RUBU FRUT  --------------------------------------------------------------------------------------------------------------3-------------------------------------------------------------------------------------------------------------------------------  0010
21 RUME ACET  --11-----------1----------------------2145-----------------------------------------------------1---------1-2-----------45--------------------------------------------------3-25--------------------------------------------------------------2-  0010
23 TRIE EURO  -------------------------------------------------------------------------3-------------------------------------43----1---3545444--1--2-2--2------------------------------1-------------------------------1-----2--------------------------------  0010
14 OXAL ACET  ------------------------------------------------------------------------------------------------------------------------------------ -244535244352-------------------------1-----------------------------------------2------44-----433------------  0011
24 VACC MYRT  -4----------------------2----------122-2--41-35555555454455554443544355553545334535555555553454445555454455545555545555545555555555-224354221255452----31--2---1-----------1------555555555555555555555555555555555555--555--255354515---531----  01
 3 CALL VULG  ---3--2-----------------------------------555525----------------------------------------------------------------------------------------------------------------------------------------------5555-3-----5---4----5---------------  10
 4 CAMP INTR  5--------------------------------------------------------------------------2-------------------3--------------13-4533-5-2-----2--2-----3--3---11--2----------------------15341-1---455333----------5--------------------5545253555---3554-5-----  10
13 NARD STRI  34-----------------2-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------4-5-------------------------  10
 5 CARE MONT  ----------------------------------------------------------------3------------------------------------------------------------------------------------------------------------------------------------------------1--4----3-------------------------  1100
 6 EMPE NIGR  -------------------------------------------------------------------------------------------------------------2---------------------------------------------------------------4----3-------------------------5-2---------------------------------  1100
 7 FEST OVIN  -------------------3---------------2------1-----------------------------------------------2---------3--------2-----2---------------------------------------------------2---------5555-1-4-55455535-45555554555554-354-----3-----2-----------  110100
12 LUZU MULT  -------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------3-----------------------  110100
19 RHIZ GEOG  -------------------------------------------------------------------------------------------------------------------------------------------------------------------------------3-----------------------------------------------------------  110100
26 BARE ROCK  -------------------------------------------------------------------------------------------------------------------------------------------------------------------------------3-----------------------------------------------------------  110100
17 PSEU PURU  ------------------------------------------------1--1----2-----------------2--------------------------------------------------------1-----1------------------4----------------------3-445-443355-5553554555455545--5----------------------------  110101
11 LUZU CAMP  -----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------5------------------------43--254----2--1--------2----------------------4  11011
 9 GALI SAXA  --------------2-----------------------------------------------------------------4----------------------------4-------------1----------3----------------------------------------2534----5455-5-5523-44-2-32-55-5--223--14-33545435--------5-3-544  11100
10 JUNC EFFU  -------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------3----------------5545-2-  11101
15 POLY COMM  ----------------------------------------------------------------------------------------------------------------------------------------5-------------------------------------------2---1-1---54445----2--142--------------124----31-234-554-55-2-5  11101
16 POTE EREC  ----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------1------------------------------3  11101
22 SOLI CANA  -----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------3----  11101
 1 ANTH ODOR  ----------------------------------2-4-----------------------------------------5-22--5-----2-5----------------------------------------------------5232--------1------------------------2-335-4-3--3--241-2-2335315444-554------2-53525545345545555  1111
25 BARE _GND  ---------------------------------------------------------------------------------------------------------------------------------------------5-----------------------------------------------------------------5-----------------------5----  1111

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Appendix II GLM Anova calculations for bracken characteristics 1992 and 1993

1. Rhizome anova

Rosedale 1 Dead buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	4.321	4.321	4.321	1.62	0.208
Error	68	181.75	181.75	2.67		
Total	69	186.07				

Rosedale 1 Active buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	1335.80	1335.80	1335.80	43.09	0.00
Error	68	2107.90	2107.90	31.00		
Total	69	3443.80				

Rosedale 1 Dormant buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	10407.00	10407.00	10407.00	41.84	0.00
Error	68	16914.00	16914.00	249.00		
Total	69	27320.00				

Rosedale 1 Long shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	54.88	54.88	54.88	4.73	0.033
Error	68	788.32	788.32	11.59		
Total	69	843.20				

Rosedale 1 Intermediate buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	60.04	60.04	60.04	3.04	0.086
Error	68	1345.05	1345.05	19.78		
Total	69	1405.09				

Rosedale 1 Short shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	547.22	547.22	547.22	16.53	0.00
Error	68	2362.12	2362.12	34.74		
Total	69	2936.34				

Rosedale 1 Rhizome weight

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	144.90	144.90	144.90	0.23	0.63
Error	68	42048.90	42048.90	618.40		
Total	69	42193.80				

Rosedale 2 Dead buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	244.85	244.85	244.85	44.00	0.00
Error	68	378.42	378.42	5.57		
Total	69	623.27				

Rosedale 2 Active buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	2708.80	2708.80	2708.80	68.47	0.00
Error	68	2690.30	2690.30	39.60		
Total	69	5399.10				

Rosedale 2 Dormant buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	4618.30	4618.30	4618.30	22.82	0.00
Error	68	13760.60	13760.60	202.40		
Total	69	18378.90				

Rosedale 2 Long shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	37.49	37.49	37.49	6.70	0.012
Error	68	380.28	380.28	5.59		
Total	69	417.77				

Rosedale 2 Intermediate shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	8.92	8.92	8.92	2.26	0.138
Error	68	268.57	268.57	3.95		
Total	69	277.49				

Rosedale 2 Short shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	198.76	198.76	198.76	4.12	0.046
Error	68	3281.83	3281.83	48.26		
Total	69	3480.59				

Rosedale 2 Rhizome weight

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	8379.00	8379.00	8379.00	7.41	0.008
Error	68	76910.00	76910.00	1131.00		
Total	69	85289.00				

Blakey 1 Dead buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	232.01	232.01	232.01	18.22	0.00
Error	68	865.83	865.83	12.73		
Total	69	1097.84				

Blakey 1 Active buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	1554.10	1554.10	1554.10	73.13	0.00
Error	68	1445.10	1445.10	21.30		
Total	69	2999.20				

Blakey 1 Dormant buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	736.46	736.46	736.46	9.38	0.003
Error	68	5341.48	5341.48	78.55		
Total	69	6077.94				

Blakey 1 Long shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	20.92	20.92	20.92	0.92	0.342
Error	68	1553.67	1553.67	22.85		
Total	69	1574.59				

Blakey 1 Intermediate shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	17.29	17.29	17.29	1.83	0.181
Error	68	643.00	643.00	9.46		
Total	69	660.29				

Blakey 1 Short shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	4.81	4.81	4.81	0.26	0.613
Error	68	1268.28	1268.28	18.65		
Total	69	1273.09				

Blakey 1 Rhizome weight

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	112.30	112.30	112.30	0.27	0.607
Error	68	28583.30	28583.30	420.30		
Total	69	28695.70				

Blakey 2 Dead buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	21.61	21.61	21.61	4.68	0.034
Error	68	314.33	314.33	4.62		
Total	69	335.94				

Blakey 2 Active buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	2.64	2.64	2.64	0.18	0.669
Error	68	975.13	975.13	14.34		
Total	69	977.77				

Blakey 2 Dormant buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	322.30	322.30	322.30	1.50	0.225
Error	68	14649.00	14649.00	215.40		
Total	69	14971.30				

Blakey 2 Long shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	4.97	4.97	4.97	0.52	0.471
Error	68	644.97	644.97	9.49		
Total	69	649.94				

Blakey 2 Intermediate shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	9.61	9.61	9.61	2.03	0.159
Error	68	321.88	321.88	4.73		
Total	69	331.49				

Blakey 2 Short shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	21.97	21.97	21.97	1.38	0.243
Error	68	1079.12	1079.12	15.87		
Total	69	1101.09				

Blakey 2 Rhizome weight

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	494.50	494.50	494.50	1.28	0.262
Error	68	26260.10	26260.10	386.20		
Total	69	26754.60				

Smeathorns 1 Dead buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	211.75	211.75	211.75	17.71	0.00
Error	68	812.95	812.95	11.96		
Total	69	1024.70				

Smeathorns 1 Active buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	5.14	5.14	5.14	0.37	0.546
Error	68	951.20	951.20	13.99		
Total	69	956.34				

Smeathorns 1 Dormant buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	8.47	8.47	8.47	0.09	0.762
Error	68	6250.33	6250.33	91.92		
Total	69	6258.80				

Smeathorns 1 Long shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	101.08	101.08	101.08	14.70	0.00
Error	68	467.62	467.62	6.88		
Total	69	568.70				

Smeathorns 1 Intermediate shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	5.49	5.49	5.49	0.83	0.365
Error	68	448.28	448.28	6.59		
Total	69	453.77				

Smeathorns 1 Short shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	252.00	252.00	252.00	20.35	0.00
Error	68	842.00	842.00	12.38		
Total	69	1094.00				

Smeathorns 1 Rhizome weight

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	19633.00	19633.00	19633.00	18.90	0.00
Error	68	70650.00	70650.00	1039.00		
Total	69	90283.00				

Smeathorns 2 Dead buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	86.45	86.45	86.45	10.96	0.001
Error	68	536.42	536.42	7.89		
Total	69	622.87				

Smeathorns 2 Active buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	878.08	878.08	878.08	141.79	0.001
Error	68	421.12	421.12	6.19		
Total	69	1299.20				

Smeathorns 2 Dormant buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	280.40	280.40	280.40	1.28	0.263
Error	68	14939.90	14939.90	219.70		
Total	69	15220.30				

Smeathorns 2 Long shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	1.12	1.12	1.12	0.07	0.79
Error	68	1064.38	1064.50	15.65		
Total	69	1065.50				

Smeathorns 2 Intermediate shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	29.62	29.62	29.62	6.17	0.015
Error	68	326.72	326.72	4.81		
Total	69	356.34				

Smeathorns 2 Short shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	200.89	200.89	200.89	9.14	0.004
Error	68	1494.55	1494.55	21.98		
Total	69	1695.44				

Smeathorns 2 Rhizome weight

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	374.50	374.50	374.50	0.66	0.418
Error	68	38325.30	38325.30	563.60		
Total	69	38699.80				

Smeathorns 3 Dead buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	74.92	74.92	74.92	9.15	0.004
Error	68	556.87	556.87	8.19		
Total	69	631.79				

Smeathorns 3 Active buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	750.89	750.89	750.89	141.46	0.00
Error	68	360.95	360.95	5.31		
Total	69	1111.84				

Smeathorns 3 Dormant buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	1750.60	1750.60	1750.60	18.28	0.00
Error	68	6513.10	6513.10	95.80		
Total	69	8263.80				

Smeathorns 3 Long shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	41.29	41.29	41.29	3.85	0.054
Error	68	729.80	729.80	10.73		
Total	69	771.09				

Smeathorns 3 Intermediate shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	2.89	2.89	2.89	0.84	0.361
Error	68	233.05	233.05	3.43		
Total	69	235.94				

Smeathorns 3 Short shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	13.44	13.44	13.44	0.28	0.6
Error	68	3284.33	3284.33	48.30		
Total	69	3297.77				

Smeathorns 3 Rhizome weight

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	6305.40	6305.40	6305.40	36.68	0.00
Error	68	11689.40	11689.40	171.90		
Total	69	17994.80				

Smeathorns 4 Dead buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	12.62	12.62	12.62	2.38	0.128
Error	68	361.22	361.22	5.31		
Total	69	373.84				

Smeathorns 4 Active buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	27.60	27.60	27.60	0.86	0.357
Error	68	2179.67	2179.67	32.05		
Total	69	2207.27				

Smeathorns 4 Dormant buds

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	76.90	76.90	76.90	0.71	0.401
Error	68	7327.70	7327.70	107.80		
Total	69	7404.60				

Smeathorns 4 Long shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	5.32	5.32	5.32	0.52	0.472
Error	68	690.17	690.17	10.15		
Total	69	695.49				

Smeathorns 4 Intermediate shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	11.06	11.06	11.06	3.41	0.069
Error	68	220.78	220.78	3.25		
Total	69	231.84				

Smeathorns 4 Short shoots

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	78.89	78.89	78.89	4.28	0.042
Error	68	1254.55	1254.55	18.45		
Total	69	1333.44				

Smeathorns 4 Rhizome weight

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	929.90	929.90	929.90	1.58	0.214
Error	68	40131.80	40131.80	590.20		
Total	69	41061.60				

2. Frond anova

Rosedale 1 Frond number

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	702.20	702.20	702.20	4.06	0.054
Error	27	4671.00	4671.00	173.00		
Total	28	5373.20				

Rosedale 1 Frond height

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	5352.70	5352.70	5352.70	7.32	0.012
Error	27	19742.90	19742.90	731.20		
Total	28	25095.60				

Rosedale 1 Lamina length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	565.80	565.80	565.80	2.77	0.108
Error	27	5520.30	5520.30	204.50		
Total	28	6086.10				

Rosedale 1 Pinna length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	1181.90	1181.90	1181.90	6.18	0.019
Error	27	5165.90	5165.90	191.30		
Total	28	6347.80				

Rosedale 2 Frond number

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	1170.90	1170.90	1170.90	5.53	0.026
Error	27	5714.40	5714.40	211.60		
Total	28	6885.30				

Rosedale 2 Frond height

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	6570.20	6570.20	6570.20	17.61	0.00
Error	27	10073.50	10073.50	373.10		
Total	28	16643.70				

Rosedale 2 Lamina length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	1225.50	1225.50	1225.50	8.28	0.008
Error	27	3994.60	3994.60	147.90		
Total	28	5220.10				

Rosedale 2 Pinna length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	1203.00	1203.00	1203.00	20.00	0.00
Error	27	1624.40	1624.40	60.20		
Total	28	2827.40				

Blakey 1 Frond number

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	5229.70	5229.70	5229.70	32.99	0.00
Error	27	4280.50	4280.50	158.50		
Total	28	9510.20				

Blakey 1 Frond height

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	4591.80	4591.80	4591.80	9.06	0.006
Error	27	13683.60	13683.60	506.80		
Total	28	18275.40				

Blakey 1 Lamina length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	1465.60	1465.60	1465.60	7.61	0.01
Error	27	5202.10	5202.10	192.70		
Total	28	6667.60				

Blakey 1 Pinna length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	1543.50	1543.50	1543.50	10.85	0.003
Error	27	3839.80	3839.80	142.20		
Total	28	5383.30				

Blakey 2 Frond number

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	4015.90	4015.90	4015.90	174.06	0.00
Error	27	622.90	622.90	23.10		
Total	28	4638.80				

Blakey 2 Frond height

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	83052.00	83052.00	83052.00	505.67	0.00
Error	27	4435.00	4435.00	164.00		
Total	28	87487.00				

Blakey 2 Lamina length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	18191.00	18191.00	18191.00	389.32	0.00
Error	27	1262.00	1262.00	47.00		
Total	28	19452.00				

Blakey 2 Pinna length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	14564.00	14564.00	14564.00	377.71	0.00
Error	27	1041.00	1041.00	39.00		
Total	28	15605.00				

Smeathorns 1 Frond number

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	22807.00	22807.00	22807.00	48.69	0.00
Error	27	12646.00	12646.00	468.00		
Total	28	35453.00				

Smeathorns 1 Frond height

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	97.06	97.06	97.06	2.89	0.1
Error	27	905.63	905.63	33.54		
Total	28	1002.69				

Smeathorns 1 Lamina length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	110.28	110.28	110.28	11.52	0.002
Error	27	258.41	258.41	9.57		
Total	28	368.69				

Smeathorns 1 Pinna length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	53.26	53.26	53.26	3.72	0.064
Error	27	386.79	386.79	14.33		
Total	28	440.05				

Smeathorns 2 Frond number

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	9820.50	9820.50	9820.50	41.13	0.00
Error	27	6446.50	6446.50	238.80		
Total	28	16267.00				

Smeathorns 2 Frond height

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	1890.00	1890.00	1890.00	55.70	0.00
Error	27	916.30	916.30	33.90		
Total	28	2806.30				

Smeathorns 2 Lamina length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	520.19	520.19	520.19	36.69	0.00
Error	27	382.80	382.80	14.18		
Total	28	902.99				

Smeathorns 2 Pinna length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	802.73	802.73	802.73	18.38	0.00
Error	27	1179.46	1179.46	43.68		
Total	28	1982.19				

Smeathorns 3 Frond number

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	1094.00	1094.00	1094.00	122.97	0.00
Error	27	2402.00	2402.00	89.00		
Total	28	13342.00				

Smeathorns 3 Frond height

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	40056.00	40056.00	40056.00	368.54	0.00
Error	27	2935.00	2935.00	109.00		
Total	28	42990.00				

Smeathorns 3 Lamina length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	12400.00	12400.00	12400.00	368.40	0.00
Error	27	909.00	909.00	34.00		
Total	28	13308.00				

Smeathorns 3 Pinna length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	8971.90	8971.90	8971.90	346.92	0.00
Error	27	698.30	698.30	25.90		
Total	28	9670.10				

Smeathorns 4 Frond number

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	315.70	315.70	315.70	2.91	0.10
Error	27	2931.40	2931.40	108.60		
Total	28	3247.20				

Smeathorns 4 Frond height

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	24622.00	24622.00	24622.00	136.21	0.00
Error	27	4881.00	4881.00	181.00		
Total	28	29503.00				

Smeathorns 4 Lamina length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	8901.30	8901.30	8901.30	177.62	0.00
Error	27	1353.10	1353.10	50.10		
Total	28	10254.40				

Smeathorns 4 Pinna length

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C1	1	3533.60	3533.60	3533.60	122.57	0.00
Error	27	778.40	778.40	28.80		
Total	28	4312.00				