CONTROL AND MODELLING OF BRACKEN (*PTERIDIUM AQUILINUM* (L.) KUHN) IN GREAT BRITAIN

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy

by Stephen Paterson.

January 1996

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ACKNOWLEDGEMENTS

I wish to thank Professor Rob Marrs and Doctor Robin Pakeman for supervising this study. I would also like to express my gratitude to Doctor Mike Le Duc for comments on several aspects of the work and field cooperation. Special thanks to Steve Jones for his invaluable assistance with fieldwork. Further thanks are extended to Caroline Jones, Peter Walley, Glynnis Williams, Nick Green, Fay Ashby, and Ann Matthews for their involvement with the fieldwork.

I also wish to thank the land owners and agencies for the provision of, and assistance in selecting, field sites: Colonel de Klee, and Scottish Natural Heritage (Mull); Harry Sangster (MLURI, Sourhope Field Station); Colin Eastham (Lake District National Park Authority); Mike Hughes (Clwyd County Council); Malcolm Wright (English Nature), Norman Baldock (Dartmoor National Park Authority); and Professor Richard Edwards (Blaen Nanmor, Snowdonia).

In addition I thank my family and friends for all their support.

ABSTRACT

Manipulative bracken control field experiments were conducted simultaneously at six geographically distinct locations across Great Britain. The efficacy of (1) cutting, and (2) herbicide (asulam) as bracken control treatments were evaluated in terms of frond performance and rhizome biomass seasonal dynamics, over a three year period. Combinations of cutting with asulam were also considered. The examination of commonly-used bracken management regimes assured results would have practical value to land managers currently controlling bracken-infested land.

The study constitutes the first comprehensive attempt to consider the efficacy of bracken control treatments across a range of climatic zones. This enabled the synthesis of a national overview towards bracken control. Differential hierarchies of bracken control treatment efficacy were identified with respect to the frond and rhizome component of bracken. Asulam affected the greatest recorded reduction in frond performance. Cutting once yearly affected consistently inferior control relative to cutting twice yearly throughout the experiment in terms of reducing both frond and rhizome biomass. Spraying asulam proved the least effective treatment to deplete rhizome biomass. Relative efficacy of cutting regimes, in terms of biomass reduction, contrasted markedly depending on morphological indicator. Regional contrasts in management success were detected when cutting bracken once yearly, however, these were only evident in a single year, after which similar responses between sites were observed.

The nationwide experiments provided test data for two bracken models:
(1) BRACON (BRAcken CONtrol) describes bracken growth following control treatments. The model was validated as a reasonably accurate predictor of bracken stand dynamics in relation to cutting, and spraying with asulam, across the range of climatic conditions which prevail currently across Great Britain. There was a tendency to underestimate the resilience of bracken to cutting treatments, however, a weakness within the model structure was identified which should enable this problem to be rectified. The context within which predictions should be interpreted is discussed.
(2) REBRA (REvegetation after BRAcken control) predicts the direction and rate of vegetation succession in areas where bracken control measures have been implemented. Monitoring of the ground flora within experimental plots in Breckland, and multivariate analysis enabled a novel approach to model evaluation. Divergence between actual and predicted vegetation assemblages increased with time, however, improvements to the model, and the acquisition of test data are discussed.

The use of bracken control treatments to promote establishment of oak seedlings planted under a continuous bracken canopy was also investigated. Oak seedlings continue to grow and establish under untreated bracken, however, bracken control halted seedling mortality observed across the study site. Bracken cutting treatments affected the greatest increase in seedling performance which may have been associated with an earlier removal of the light-limiting bracken canopy relative to asulam treatment.

1. INTRODUCTION

1.1. BRACKEN DISTRIBUTION

Bracken† (*Pteridium aquilinum* (L.) Kuhn) is a fern with a worldwide distribution: it is present on every continent except Antarctica (Page, 1979). Found throughout Great Britain, particularly high concentrations occur in northern and western areas (Watt, 1976). Current estimates of bracken land coverage, within this country, figure between 2880 and 6361 km^2 (1.3 - 2.8% of the land area) with the problem increasing, through the invasion of new land, at a rate of 1 - 3% per year (Bunce *et al.*, 1981; Taylor, 1986). These figures are estimates of the area covered by dense bracken in open countryside which represents the major problem for land use at present.

The 1990 countryside survey assessed the national presence of both dense bracken and non-dominant bracken in both the open and under woodland, as well as bracken present in linear features (Bunce *et al.*, 1992). A figure of 17,073 km^2 (7.3% of Great Britain) was calculated which overestimates the absolute areal coverage under present conditions, but it gives an assessment of the bracken resource from which, given suitable conditions, expansion may occur.

1.2. REASONS FOR EXPANSION

A number of intrinsic and extrinsic factors have operated to enable bracken to achieve its current impact upon the environment. Bracken was originally a woodland plant as are many other ferns in the British flora. However, bracken is almost unique amongst ferns in that it has a high light saturation point enabling it to increase its photosynthetic rate when released

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† *Nomenclature follows Stace (1991) for higher plants and Smith (1978) for mosses.*

from the light-limiting woodland canopy (Hollinger, 1987). Furthermore, bracken is less dependent upon moisture for its life-cycle (Tinklin & Bowling, 1969) than other ferns, thereby facilitating its success in open conditions. Bracken can invade habitats vegetatively (via rhizome extension: Watt, 1940) or sexually (spore dispersal: Conway, 1959; Oinonen, 1967). Dense stands cast a deep shade and produce a smothering litter layer, with reported allelopathic properties (Gliesmann, 1976), to the detriment of other vegetation.

The prevalence of a series of extrinsic factors have permitted bracken to express and take advantage of its competitive traits. Changes in upland agriculture which have magnified the bracken problem include (1) the shift from cattle to sheep farming (Fletcher & Kirkwood, 1979): the lower bulk of sheep relative to cattle inflicts less damage to emerging fronds (Williams, 1980). (2) Drainage of upland areas (Cadbury, 1976): bracken favours well drained soils. (3) Rural depopulation (Fletcher & Kirkwood, 1979) has permitted bracken to invade land formerly under cultivation. Poor land management fails to maintain the vigour and competitiveness of existing vegetation thereby leaving it susceptible to bracken invasion (e.g. Watt, 1947,1970; Marrs & Hicks, 1986), Woodland clearance (Rymer, 1976) and a decline in bracken harvesting (Rymer, 1976) have been cited as contributory factors.

1.3. BRACKEN GROWTH CYCLE

Williams & Foley (1976) characterised bracken growth in terms of carbohydrate fluxes during its annual growth cycle. Bracken is a geophyte perennial with the majority of its biomass below ground in the form of rhizomes. Rhizomes are underground plant stems modified for carbohydrate storage, which can form an extensive system in bracken. This structure has a large number of resting buds situated along its length which given suitable growth conditions are supplied with carbohydrate, enabling their development into fronds. Before frond development losses of rhizome carbohydrate are primarily due to respiration and tissue senescence.

Fronds are the morphological equivalents of leaves which emerge with tightly curled tips giving a typical crosier appearance. During frond development and expansion, despite becoming photosynthetically active, they continue to be primarily fuelled by the rhizome carbohydrate reserves. Once full frond expansion is achieved, photosynthetic production exceeds metabolic demand, and the assimilate is translocated to the rhizome where the reserves are replenished, and the rhizomes grow.

Carbohydrate translocation to the rhizome is terminated upon frond death which is principally determined by the first severe frosts of the autumn. Dead fronds collapse giving rise to a characteristic deep litter layer. The underground storage of carbohydrate in the rhizome enables bracken to survive until the onset of the next period of suitable growth conditions in the spring. It also allows bracken to withstand severe perturbation such as fire, cutting or herbicide application.

1.4. THE BRACKEN PROBLEM

Bracken infestations conflict with several types of land use including agriculture, forestry, conservation, shooting, water collection and recreation. In addition, it poses a potential human health hazard.

1.4.1. Agriculture

In upland agriculture, vigorous bracken growth reduces the quality and quantity of grazing land and can hinder shepherding (Lawton & Varvarigos, 1989). This may lead to over-grazing in other areas thereby increasing the susceptibility of this land to bracken encroachment. Furthermore bracken is toxic to grazing livestock (Evans, 1986) and the litter harbours sheep ticks which transmit Lyme Disease resulting in productivity losses and increased veterinary costs.

1.4.2. Forestry

In forestry plantations, an abundance of bracken often proves problematic as it can limit nutrients, light and water availability to young trees. Furthermore, the collapse of dead fronds may cause direct physical damage. During hot, dry summers, bracken litter dries out and is highly inflammable which constitutes a fire risk (Biggin, 1982).

1.4.3. Conservation

Bracken is generally considered to have little conservation value as it tends to lower species diversity of communities it has invaded. Habitats at risk from bracken incursion include moorland, lowland heath and upland grasslands (Pakeman & Marrs 1992a). Encroachment upon and domination of such habitats would prove disastrous for conservation as many support a rare species complement. However bracken can benefit some species and provide a conservation benefit (Pakeman & Marrs, 1992a). This includes the protection of relict vernal flora where woodland has disappeared and the provision of sites for rare species e.g. *Cornus suecica* L., *Corydalis claviculata* (L.) DC. At moderate densities on Exmoor, bracken provides a replacement habitat (surrogate coppice) for the heath fritillary butterfly (*Mellicta athalia*) following a decline in its former habitat coppiced woodland (Warren, 1991).

1.4.4. Shooting

Shooting of game birds is an important component of the rural economy in upland Britain (Burge & Kirkwood, 1992). Bracken invasion of grouse moors shifts the habitat away from one which is capable of supporting birds to one with virtually none. In addition, bracken litter harbours sheep tick populations which have been associated with outbreaks of louping ill in grouse populations (Hudson, 1986).

1.4.5. Water Industry

In water catchment zones, dense stands of bracken are capable of intercepting up to 50% of incident rainfall. Such an impediment to water throughfall reduces yields leading to increased costs for water collection (Williams *et al.*, 1987).

1.4.6. Recreation

Bracken impedes access to the countryside by virtue of its size and density. For example paths along the Pembrokeshire coast were obscured following bracken incursion (Long, 1988). Rural recreation will be affected indirectly if links between bracken and mammalian health problems are proven. These links could act as a deterrent to public use of the countryside leading to serious implications for the tourism industry.

1.4.7. Human Health Hazard

Bracken can have direct and indirect effects upon human health. The consumption of bracken is very rare in Great Britain however in countries where it is considered a delicacy e.g. Japan, it has been implicated as a factor explaining the high incidence of oesophageal cancer (Hirayama, 1979). Bracken spores are a suspected carcinogen and their inhalation has been identified as a potential hazard (Evans, 1987), however this result remains to be thoroughly verified. During summer 1989, prior to an anticipated period of vigorous sporulation, a press release was issued warning the public to avoid bracken infested areas. Workers in such areas were advised to wear protective face-masks (Taylor, 1989). The indirect effects upon human health include exposure to milk from cows allowed to browse bracken, as the carcinogenic agents of bracken are known to be present (Evans *et al.*, 1972). Water run-off from bracken infested catchment areas also exhibits carcinogenic properties (Evans *et al.*, 1984). Links between bracken and human gastric cancer via contaminated well-water have been identified however at present these are only correlative not causative (Galpin & Smith, 1986). In addition, bracken litter offers a habitat suitable for sheep ticks (*Ixodes ricinus*) which can act as vectors for Lyme disease to which humans are susceptible.

1.5. BRACKEN MANAGEMENT

Bracken has been managed throughout Great Britain for many centuries. It was considered to be a valuable resource and was managed actively to at worst maintain the resource without depletion and at best to encourage and enhance its occurrence and vigour. Bracken has only recently been viewed as a weed species i.e. its presence is undesirable and in conflict with other land-use practices, and suppression rather than enhancement of performance is preferred. Regular frond harvests occurred for use in bedding, thatch and soap-making (Rymer, 1976). Bye-laws were at one point in operation in some areas forbidding harvest before a certain date in order to protect this valued commodity (Crompton & Sheail, 1975).

A wide variety of weed control strategies, including physical, chemical, biological and environmental techniques, have been used and suggested for the management of bracken infested land. During 1982-87, the most common methods for bracken control in the Less Favoured Areas of England and Wales were cutting (13,151 ha yr^{-1}) and spraying with asulam (9,123 ha), at a total cost of £903,510 yr^{-1} (Lawton & Varvarigos, 1989).

1.5.1. Physical Control

Physical control methods include ploughing, pulling, stock-trampling, rolling and cutting all of which are variants on the same theme. The aim is to remove biomass from the system which brings about a net depletion of rhizome carbohydrate stores. Ploughing is the most effective treatment, however it is the least applicable due to problems with access and terrain. Ploughing and pulling directly damage the rhizome whilst the former can have the added advantage of exposing the rhizome to frost damage (Conway, 1959). Cutting of bracken affects all the fronds, and the timing of cuts in response to bracken growth enhances the efficacy of this method (Lowday *et al.*, 1983). Cutting must be maintained for several years in order to gain maximum effect. Mathematical model predictions based upon studies in Breckland, East Anglia indicate that it would be necessary to cut repeatedly 19 to 21 years to achieve bracken eradication by cutting once and twice a year respectively (Lowday & Marrs, 1992a). Rolling is less effective than cutting as only a proportion of the fronds are damaged.

1.5.2. Chemical Control

Several phyto-toxic chemicals are effective against bracken, however most have little practical use. Most of the contact herbicides which have been tried (e.g. sodium chlorate, ammonium sulphamate) are only effective in the year of application (Fletcher & Kirkwood, 1979) and failed to have any impact upon the rhizome. A number of residual herbicides (e.g. picloram, dicamba) when applied to the soil, penetrate the rhizome directly where they can affect a lethal action. Their soil persistence can pose problems for agriculture, although dicamba can be used when applied in strips to aid tree establishment in new forestry plantations (Palmer, 1988).

Asulam and glyphosate are systemic herbicides and have been the most consistently effective and most widely used against bracken. Asulam offers high target specificity (ferns and docks are susceptible), low mammalian and fish toxicity and has (sole) approval for aerial application (Soper, 1986). Applied to the foliar parts of the plant, asulam is translocated to the rhizome system where it accumulates in buds and apices. The active ingredient (methyl 4-aminobenzene sulphonyl carbamate) inhibits RNA and protein synthesis resulting in bud and apex structural degeneration (Veerasekaran *et al.*, 1977). No effect of treatment is visible in the year of treatment, but very few fronds are produced in the season following application. A depletion of rhizome carbohydrate stores results through respiration and a reduction in photosynthetic capability. Glyphosate is a non-specific herbicide favoured where bracken is amongst a number of weeds which all require control. However, where bracken is the only target species then asulam is recommended.

1.5.3. Biological Control

Phytophagous Arthropods

Two species of South African moth, *Conservula cinisigma* and *Panotima* sp. near *angularis*, from a climate equable to Great Britain, have been identified as potential candidates for a biological control programme within this country (Lawton, 1990). Both species are external frond-feeders however during the third instar, *Panotima* larvae burrow into the vascular tissue where they continue to develop as rachis miners. Laboratory feeding trials have indicated that following the release of this alien species a host switch would be highly improbable. This technique offers the possibility of an inexpensive and prolonged period of control following its introduction however potential legal problems persist and government approval is required (Lawton, 1990). Bracken eradication by this method is not expected; it is more likely to form an integrated approach towards management.

Fungal Pathogens

Certain bracken stands have been found to be susceptible to the fungal disease curl-tip. The causative fungi have been identified as *Ascochyta pteridium* and *Phoma aquilina* however most bracken appears to be resistant to attack. Incorporation of these virulent strains to produce mycoherbicides have had limited experimental success and is currently under development (M^cElwee & Burge, 1990).

1.5.4. Environmental Control

This strategy involves the manipulation of habitat to create conditions adverse to bracken vigour. The introduction of desirable replacement vegetation which may successfully compete with bracken leads to a change in resource availability. Over-planting with trees e.g. Douglas Fir (*Pseudotsuga menziesii* (Mirb.) Franco) immediately alters the light regime at the expense of bracken photosynthesis. If heather is kept in a vigorous state (building and mature phases) it is believed that bracken encroachment may be checked (Watt, 1955; Marrs & Hicks, 1986). These examples are only applicable practically where plantations are desirable or in areas where conservation or game is a high priority.

1.6. CLIMATE CHANGE AND BRACKEN MODELLING

It is believed that global warming will change the climate across Great Britain. Current estimates predict an increase in mean summer and winter temperatures of 1.4°C and 1.5 -2.1°C respectively by the year 2030 (United Kingdom Climate Change Impacts Review Group, 1991). The potential for such a climatic shift to exacerbate the current bracken problem requires investigation. It was against this backdrop that bracken models were developed based on the plant's physiology and ecology. These models can predict bracken growth and spread at the site, regional and national level in response to different control strategies, different climate scenarios and their interaction.

1.6.1. COBRA (COntrol of BRAcken)

COBRA is a mathematical model which predicts the growth and spread of a bracken stand (Pakeman *et al.*, 1994). It considers the movement of carbon through the plant by describing the yearly growth cycle in terms of rhizome biomass, carbohydrate content and frond biomass. Several physiological processes are included in the model: rhizome respiration, rhizome senescence, rhizome to frond transport, daily dry matter production and dry matter partitioning. Given a starting value for rhizome biomass and the ambient environmental conditions, the model calculates daily losses and gains via the processes listed above. The environmental variables considered are soil temperature, incident solar radiation, dates of first and last frosts, and rates of actual and potential evaporation. This original model was developed and tested on a site in the Breckland in East Anglia.

1.6.2. COBRA-X (COntrol of BRAcken - eXtended version)

COBRA-X is a refinement of COBRA which considers bracken stand dynamics across Great Britain (Pakeman *et al.*, 1993b). Predictions are made for individual 40 km grid cells based upon the mean environmental conditions operating within that area. A simplified set of readily available meteorological data is used for reference within the model. Daily changes in environmental variables are obtained from sine functions fitted to yearly maxima and minima for soil temperatures and solar radiation. Daily changes in transpiration rates are calculated by assuming a linear increase and decrease between annual maximum and minimum values. Improvements on the original model include a consideration of frond senescence (Pitman & Pitman, 1990), cost of carbohydrate movement (Bloom *et al.*, 1985) and initial allocation of carbohydrate to the rhizome (Al Jaff *et al.*, 1982; Williams & Foley, 1976).

Predictions for Current Bracken Abundance and Distribution

Equilibrium biomass is defined as the maximum attainable biomass in the open under the mean environmental conditions operating at that site (Pakeman & Marrs, 1993b). It is reached when losses through respiration and tissue senescence are balanced by gains via photosynthesis (Pakeman *et al.*, 1994). The use of equilibrium biomass is important as the unit of 'currency' for comparative estimate in different situations. Under current climatic conditions COBRA-X predicts that the highest bracken concentrations occur in the south-west and west of the country (Pakeman *et al.*, 1993b). Equilibrium biomass is high within these regions as a result of long growing seasons uninterrupted by frosts and low soil moisture deficits (max. 3136 g m^{-2} - North Cornwall). Lower equilibrium biomass is predicted for the Welsh interior, northern England and, with the exception of western areas, Scotland. In these areas bracken abundance is limited by shorter growing seasons and their interruption by frost incidents (min. 169 g m^{-2} - Grampians). In south-eastern parts of England, characterised by lower rainfall, bracken is restricted by soil moisture deficits. At higher altitudes, biomass is seen to decrease in relation to the shorter growing season (Pakeman *et al.*, 1993a).

Predictions for Current Bracken Expansion

Under current climatic conditions, bracken fronts are predicted to spread at higher rates in the south-west of England and coastal areas of Wales and southern and eastern England (max. 0.9 m yr^{-1} - Lands End). Lower values have been evaluated for the uplands of England, Wales and Scotland (min. 0.05 m yr^{-1} - Grampians) (Pakeman *et al.*, 1993a).

Climate Change Scenario for Modelling Exercise

In order to model bracken trends by the year 2030 a number of assumptions were made (Pakeman & Marrs, 1993b) e.g. little is known about how a climatic shift might influence the length of frost-free periods. The projected climate scenario considered a 1.4°C rise in summer and winter temperatures, a 7 day extension at either end of the growing season and a 10% increase in potential evaporation. Photosynthetic efficiency was anticipated to increase by 5% due to elevated levels of CO_2.

Modelled Predictions for Future Bracken Abundance and Distribution

Southern and western areas of England and Wales are expected to exhibit a slight decrease (< 10%) in equilibrium biomass at sea-level. The remainder of England and Wales are likely to experience slight increases (< 10%) as will western areas of Scotland. However the majority of Scotland is expected to encounter the largest change in equilibrium biomass within Great Britain. Increases in excess of 30% have been predicted for the Grampians and the Orkney Islands (Pakeman *et al.*, 1993a).

Modelled Predictions for Future Bracken Expansion

Bracken fronts are expected to show little change in their rates of spread following a climatic shift (fluctuations of 15%), however a large increase is expected within the Grampians (Pakeman *et al.*, 1993a). Bracken is expected to increase its altitudinal range following the onset of milder meteorological conditions. The scale of this increase has been modelled for a site in the Grampians where the current altitudinal limit will increase from 350 m to 550 m (Pakeman & Marrs, 1993b). This bracken invasion would threaten former altitudinal refuges for ecologically desirable habitats e.g. upland heath.

1.6.3. BRACON (a model describing the detailed effects of BRAcken CONtrol)

BRACON is a development of COBRA-X which enables predictions of bracken response across Great Britain to a number of control regimes. These regimes include cutting, spraying with asulam, over-planting with trees and release of insect biological control agents.

Modelled Predictions for Current Bracken Control

Suitable data for testing bracken control predictions across the current range of climatic conditions within Great Britain are scarce. The model has been tested against the data used in its development, results from an independent study in the Breckland (Lowday, 1987) and data from a study in the North York Moors (Pakeman & Marrs, 1993a). This limited validation has confirmed the model as a reasonably accurate representation of bracken dynamics however a national appraisal of model performance has not been done.

Modelled Predictions for Future Bracken Control

Under the expected climate scenario for the year 2030, it has been predicted that bracken stands will become increasingly resilient to standard bracken control practices (Pakeman & Marrs, 1992b). The time interval for bracken to recover to 90% of pre-treatment levels will decrease (100% recovery is a less meaningful measure due to the asymptotic nature of recovery as it approaches 100%). In Breckland, modelled bracken stands are observed to recover two years quicker following a single spray with asulam (8 years instead of 10 years) and three years quicker after cutting once yearly for three years (9 years instead of 12 years). Bracken in the North York Moors will respond in a similar manner: one year quicker following asulam (7 years instead of 8 years) and two years quicker following cutting once yearly for three years (8 years instead of 10 years).

Dramatic increases in bracken equilibrium biomass are expected in the Scottish Borders (Pakeman *et al.*, 1993a). Recovery from bracken management is slower in this region relative to the sites modelled in the Breckland and North Yorks Moors due to the shorter growing season. This relative difference will prevail in the year 2030 however recovery times will be quicker (Pakeman & Marrs, 1993b). It will take a bracken stand 15 years to recover from asulam treatment as opposed to 16 years under current climatic conditions. Following cutting once yearly for three years, recovery is achieved 5 years quicker (28 years instead of 33 years).

1.7. VEGETATION RESTORATION

Bracken can dominate its habitat at the expense of the ground flora and its control can prove very expensive. In order to be cost effective the land reclaimed from bracken should be managed to create a productive habitat in order to recoup the initial outlay of capital and the management costs involved in preventing re-invasion or restoring an ecosystem with high conservation value. Success depends upon good initial control maintained by follow-up management and re-establishment of the desired vegetation. Following bracken control, the direction and rate of vegetation succession can be highly variable (Marrs & Lowday, 1992; Pakeman & Marrs, 1992c). A number of factors influence the vegetation dynamics underneath bracken including the initial floristic composition (incorporating established and regenerative phases of life cycle) and its competitive interaction; the potential flora (via seed rain); the ability for bracken litter to suppress growth; method of bracken control; and site management after initial control strategies. In addition weather, climate, soil type and fertility interact with these factors to determine the community composition and its successional trajectory (Lowday, 1986; Sparke & Williams, 1986).

1.7.1. Habitat Manipulation

Bracken suppresses ground vegetation by means of a canopy, which casts dense shade, and its litter, which competes for growing space and hinders germination; effectively the 'Inhibition Model' of Connell & Slatyer (1977). Different bracken control regimes (including frequency, continuity and efficacy) have different effects upon these aspects of plant suppression, which consequently exhibit various direct and indirect effects upon the ground vegetation.

Bracken Cutting

Cutting removes the canopy immediately and can disturb the litter layer via the passage of the cutter; cutting twice yearly is particularly effective in this regard (Lowday & Marrs, 1992a,b). However, regrowth can be problematic and the success of this treatment depends upon repetition in order to maintain a reduced shade, and limit litter inputs. Continual cutting favours low-growing plants and plants with basal meristems (e.g. grasses). Litter cover decreases slowly and increased vegetation cover is primarily through clonal expansion.

Bracken Spraying

Spraying with asulam has no effect upon bracken until the year after application thereby delaying vegetation response. Since very few fronds are produced after a successful application, there are high light levels at the ground layer. There is no effect on the litter present at the time of spraying and decay is slow. However, subsequent litter inputs are small but these increase exponentially as frond production returns to untreated levels (generally 5 - 10 years). Plants range in their sensitivity to asulam with less tolerant species (e.g. ferns, docks and certain grasses) disadvantaged after spraying.

Bracken Litter Disturbance

Without follow-up treatment the results of vegetation development are slow and variable. It is believed that the principal reason for low rates of recovery is that the slowly decomposing litter provides few suitable micro-sites in which seeds can germinate and establish (Pakeman, Hill & Marrs, 1995). Mosses may directly colonise the litter surface and impede the establishment of higher plants (Clément & Touffet, 1990). In order to obtain increased rates of colonisation the litter layer needs to be disturbed (Lowday & Marrs, 1992b). This can be achieved by incorporation, burning or removal of the litter. Each of these litter disturbance strategies have different advantages and disadvantages which influence vegetation recovery. Incorporation (e.g. by rotovation) retains the seed bank, however the high nutrient levels, which favours nutrient-demanding species (potentially problematic) and allelopathic properties are also maintained. Burning may reduce allelopathic substances but the seed bank and the soil nutrient status may be affected. Removed litter obviously removes any allelopathic substances and associated nutrients, but the seed bank is also lost from the habitat. Loss of the seed bank may or may not be a problem depending on the number of seeds and the species present.

1.7.2. Species Introduction

A depauperate seed bank results from long-term bracken dominance, especially where there is little ground flora. An effective remedy to this problem is seeding with the desired species. At an experimental site in Breckland, seeding in conjunction with litter disturbance resulted in significant colonisation of *Calluna vulgaris* (L.) Hull within two years in contrast with four to ten years without seeding (Lowday & Marrs, 1992a,b). This option is needed where the desired species is absent or present as a small proportion in the seed bank, however it can result in a less species-rich community (Lowday & Marrs, 1992b). Seeding and litter disturbance augmented by fertilising and liming is recommended for the creation of productive grassland from reclaimed bracken-land (Sparke, 1985).

1.8. REBRA (REvegetation after BRAcken control)

In order to provide a means of predicting how vegetation would respond following bracken control, a mathematical model (REBRA) was written (Pakeman *et al.*, 1995). REBRA combines BRACON (a model describing the detailed effects of BRAcken CONtrol) with the vegetation model SETSARIO. The latter describes vegetation succession within abandoned arable fields in response to Set-Aside management routines (Hill, 1992).

REBRA considers the individuals of an existing vegetation community under a bracken stand and evaluates how their abundance (percentage cover) will change in relation to the projected micro-environmental conditions. Vegetation composition and dynamics are a function of the micro-environment and the genetic attributes of individuals within the community. The bracken canopy and litter layer are the principal factors considered within the model which determine vegetation status. Bracken litter consists of thin and thick litter (Watt, 1956): the former competes with other plants for space whilst the latter hinders germination. Changes in canopy cover and litter abundance occur either naturally (seasonal) or artificially (management) and create space for vegetation expansion. Bracken control measures have different effects upon litter abundance (Lowday & Marrs, 1992b). Individuals bid for available space and their success is dependent upon their genetic traits described in terms of light tolerance (Ellenberg, 1988) and vegetative/sexual reproductive habits (Grime *et al.*, 1988). Management regimes considered within REBRA are cutting, spraying with asulam, and litter disturbance.

1.9. AIMS OF STUDY

The aim of this work was to investigate the response of bracken within different climatic zones across Great Britain to several bracken control regimes. The approach included an investigation over three years into the seasonal dynamics of the frond and rhizome components of bracken. Experiments were conducted at sites located across the country exhibiting a range of climatic conditions. The experimental protocol was intended to satisfy the criticisms which either singly or in combination placed limitations on previous studies into bracken control:

- restricted to a single control treatment
- failure to consider seasonal attribution of resources
- confined to a single morphological indicator.

In addition, recommendations for further research quoted in (Pakeman & Marrs, 1994a) are accommodated:

- consideration of combined effects of cutting and spraying
- examination of bracken response in different regions of Great Britain.

The experiments were designed to yield test data to investigate the validity of the BRACON model. Although it has given predictions of growth processes within bracken stands at two sites in the east of England, its validity as a predictor of bracken stand dynamics at the national level needs to be considered. In addition, the accuracy of predictions generated by the REBRA model were assessed by monitoring changes in the composition of vegetation under bracken, at a single experimental site.

A further experiment was undertaken in a woodland clearing where planted oak seedlings were growing under a continuous bracken canopy. REBRA does not consider tree and shrub species however the land management objective is often the establishment of these plant life forms. The effects of bracken control strategies are evaluated on the basis of oak seedling performance.

2. Assessment of bracken (Pteridium aquilinum (L.) Kuhn) control throughout Great Britain: outline of the study

2.1. INTRODUCTION

2.1.1. Bracken Problems

As we have seen (Chapter 1.), bracken (*Pteridium aquilinum* (L.) Kuhn) is an aggressive weed species posing problems for land use and mammalian health. It reduces grazing potential and hinders shepherding (Lawton & Varvarigos, 1989); limits resource availability to newly planted trees (Biggin, 1982); and dominates areas at the expense of rare and ecologically desirable flora and fauna (Pakeman & Marrs, 1992). The abundant growth of bracken can depress the recreational and economic value at the site of infestation (e.g. Long, 1988; Hudson, 1986) and can reduce yields in water catchments (Williams *et al*, 1987). Furthermore, it is poisonous to grazing livestock (Evans, 1986) and bracken spores are a suspected carcinogen (Evans, 1987). Links between bracken and human gastric cancer via contaminated well-water have been identified, however, at present these links are only correlative and not causative (Galpin & Smith, 1986). Dense bracken litter provides a suitable habitat for sheep ticks (*Ixodes ricinus* L.) which are vectors for Lyme Disease to which humans and livestock are susceptible (Habicht *et al*, 1987; Hudson, 1986).

Occurring throughout Great Britain, the highest concentrations are to be found in northern and western areas (Watt, 1976). Estimates of land area covered by bracken range between 2880 and 6361 km^2 and is thought to be increasing at 1 - 3% per year (Bunce *et al.*, 1981; Taylor, 1986). The 1990 countryside survey represents a more extensive assessment of national bracken abundance which calculated a considerable bracken resource (17073 km^2), divided into various categories from which, given suitable conditions, expansion may occur (Bunce *et al.*, 1992).

2.1.2. Bracken Management

For centuries, bracken was managed actively as a valuable resource. It was harvested to provide material for a number of purposes including bedding and thatch (Rymer, 1976).

Legal constraints were in operation governing the dates of harvest in order to maintain high yields (Crompton & Sheail, 1975). However, its use fell into decline which contributed to its expansion and perception as nuisance vegetation.

A number of different methods involving mechanical, chemical and biological approaches to bracken control have been proposed or are currently available for management programmes. The most common techniques employed in the uplands of Great Britain are (1) cutting and (2) spraying with the herbicide asulam (Lawton & Varvarigos, 1989).

There are many types of weed cutting machinery available (Cloy, 1984) with the timing of cuts in response to bracken growth enhancing treatment efficacy (Lowday *et al.*, 1983). Several herbicides have proven effective against bracken including asulam, glyphosate, dicamba, picloram and the sulphonyl-urea compounds. Asulam offers high target specificity and low toxicity to mammals and fish which permitted its approval for aerial application (Soper, 1986). This latter feature is the principal reason for its widespread popularity for bracken control, as it enables the large scale treatment of inaccessible terrain. Applied to the bracken fronds in mid-summer, asulam is then translocated to the rhizome system where it accumulates in buds and apices, affecting structural degeneration via the inhibition of RNA and protein synthesis (Veerasekaran *et al.*, 1977).

Despite the range of treatments available and currently in practice, a single management option which yields immediate long-lasting bracken control does not exist. At the moment, effective control relies upon treatment continuity. Moreover, in spite of the long-interest in controlling bracken in Great Britain, it is surprising that there is almost no information available on the efficacy of control treatments across the climatic zones within Great Britain. Nor is anything known about any regional difference in response to these widespread treatment prescriptions.

The aim of the work described in this and the next three chapters was to investigate the response of bracken across Great Britain to several bracken control regimes, to obtain an insight into both the national bracken response and regional trends. It would be foolish to consider that a complete national picture could be obtained in a short-term study. Nevertheless, by applying a range of common-used bracken control treatments simultaneously at six sites located across Great Britain exhibiting a range of climatic conditions we should gain a better insight. This experimental protocol, which included an investigation into the seasonal dynamics of the frond and rhizome components of bracken over three years, was intended to satisfy the criticisms concerning the limitations of previous studies into bracken control and accommodate the recommendations for further research quoted in Pakeman & Marrs (1994) (Table 2.1.).

Table 2.1. Deficiencies in former bracken control studies and recommendations for future research quoted in Pakeman & Marrs (1994) which formed rationale for research within thesis.

Bracken control research
Limitations of previous studies
restricted to a single control treatment
failure to consider seasonal attribution of resources
confined to a single morphological indicator
Recommendations for future study
consideration of combined effects of cutting and spraying
examination of bracken response in different regions of Great Britain

In this chapter, the experimental outline of the study is described, along with details of the statistical analysis used. The results from this study are analyzed in the next two chapters as follows:

- analysis of bracken control treatment across a range of climatic zones in Great Britain i.e. the national response (Chapter 3).

- analysis of bracken control treatments in each region: site responses are presented and regional contrasts identified (Chapter 4).

The results obtained in this study are then compared with predictions from BRACON model output (Chapter 5).

2.2. SITES

Sites were selected to provide a wide geographical spread within Great Britain with the intention that this would reflect a wide range of environmental conditions. Potential sites were inspected before frond emergence. Sites were located where land managers indicated a closed canopy of bracken would occur (Table 2.2. & Figure 2.1.) with experimental plots established on uniform areas of dense litter. Further site details are included in the Appendix (Table A.1.).

2.3. TREATMENTS

Six bracken management treatments were imposed at each of the study sites:-

$\mathbf{t_1}$ Untreated 'control'.

$\mathbf{t_2}$ Cut once yearly (late July).

$\mathbf{t_3}$ Cut twice yearly (mid-June and late July).

$\mathbf{t_4}$ Single application of asulam in 1993 (late July).

$\mathbf{t_5}$ One cut and single application of asulam in 1993 (mid-June and late July respectively).

$\mathbf{t_6}$ Single application of asulam in 1993 (late July) followed by one cut (late July) in 1994.

Cut treatments were applied with a brushcutter and cuttings were left on the plots. The herbicide asulam was applied at 4.4 kg a.i. ha^{-1} in 400 litres of water as the commercial formulation 'Asulox' using a knapsack sprayer. A non-ionic surfactant ('Agral') was added to the spray mixture at 0.1% v/v.

2.4. EXPERIMENTAL DESIGN

A randomised block design with three replicates was adopted at each site. Bracken management treatments were allocated randomly to plots within each block. Each block contained six 8 m × 8 m subplots separated by 2 m wide pathways for access. Each subplot incorporated a 1 m buffer zone.

Table 2.2. Location of experimental sites.

	Location	National Grid Ref.	Altitude (m)
s_1	Mull	1732,7317	40
s_2	Scottish Borders	3859,6216	350
s_3	Lake District	3348,5357	280
s_4	Clwyd	3138,3672	270
s_5	Breckland	5754,2724	15
s_6	Devon	2778,0854	340

Figure 2.1. Map displaying the distribution of experimental sites across Great Britain (for site codes see Table 2.2.).

2.5. SAMPLING METHODS

Between 1993-95, the bracken was sampled each year at three key stages in the annual growth-cycle (cf. Williams & Foley, 1976) to assess impact of bracken treatments. The sampling dates were timed to measure rhizome resources prior to frond emergence (late March/early April); frond status at full expansion and when rhizome resources should be at a minimum (late July); and rhizome resources following replenishment at the end of the season (early November).

The thirty-six 1 m^2 quadrats within the subplot 6 m × 6 m internal sampling area were allocated randomly a position in a sampling sequence to take account of all monitoring foreseen in this study. On each sampling occasion, rhizomes were excavated from all the soil within the central 0.25 m^2 of each quadrat and, when present, fronds were harvested (cf. Pakeman & Marrs, 1994a). This sampling method gave a buffer zone of 0.5 m between samples.

Frond height, density and counts of pinnae exhibiting third-order subdivision of the frond were measured throughout the experiment. Biomass measurements of frond and rhizome samples were determined by drying sub-samples in an oven at 70°C for at least 24 hours. Prior to sub-sampling, soil was removed from rhizome samples using a pressure washer.

In the first year of the experiment, rhizome samples were collected for the six bracken control treatments. This level of monitoring was possible by obtaining samples from one replicate per plot, however, for subsequent sampling visits it was decided that two replicate samples per plot was preferable. With the time constraint imposed upon sampling it was necessary to discontinue the monitoring of some plots. The combination of cutting with asulam treatments were omitted in order to maintain the geographic spread within the study. At each visit during 1994-95, two samples were collected from each plot.

Limited additional sampling of fronds occurred at all sites when mid-June cuts were applied during 1993 and 1995.

The nature of certain bracken control regimes and the intensity of sampling within the study resulted in bracken samples being collected before all treatments had been fully applied

(Figure 2.2.). In summer of the first experimental year, the only treatment effects which could be tested for were those of cutting 5 - 6 weeks earlier in the season. In the second year of bracken management, all treatments had been applied with the exception of the follow-up cut to previously sprayed plots. In the third year of management, all treatments had been applied. This separation of treatments during the course of the experiment was accounted for within the analysis. At any treatment date, all like-treatments were pooled to provide a more accurate measure of the tested effects.

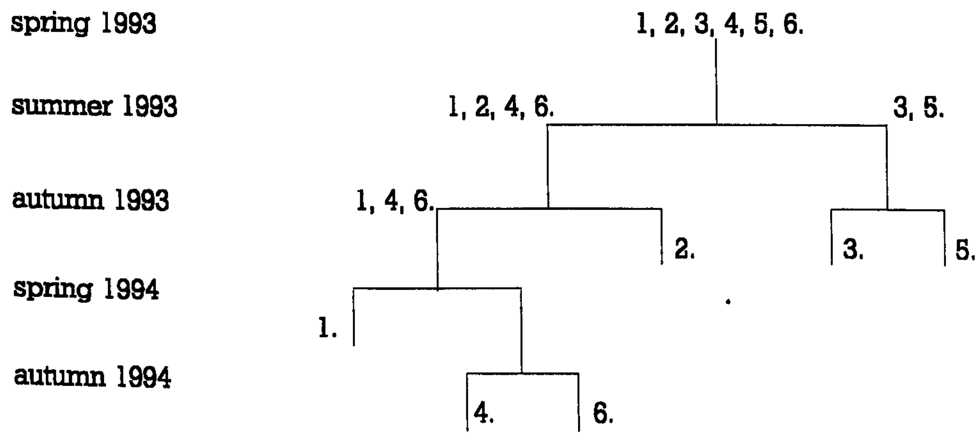


Figure 2.2. Dendrogram displaying division of treatments during the course of the experiment. Treatment codes are: 1, untreated; 2, cut once yearly; 3, cut twice yearly; 4, single application of asulam; 5, cut once 5 - 6 weeks prior to asulam application; 6, cut once in the year following asulam application.

2.6. COMPARISON OF BRACKEN CONTROL TREATMENTS AT A NATIONAL SCALE

2.6.1. Statistical Analysis

Data was subjected to analysis of variance using the GLM procedure in SAS (SAS, 1988). Transformation of the data was considered unnecessary as it failed to increase significantly the variance accounted for within the analysis of variance model. Transformations considered were (a) logarithmic transformation (natural and base 10) for continuous variables and (b) square root and negative reciprocal for discrete variables. Mean separation tests using Fisher's Least Significant Difference were applied. Treatment effects were tested for using a split plot design with sites as whole plot factors and control treatment at the subplot level (Figure 2.3.). In this analysis, the main factor to be considered was the effects of the subplot treatments (Chapter 3.).

2.6.2. Analysis of Variance Model

Source of variation	rhizome *df*	frond *df*
Whole plot		
site	5	5
whole plot error	12	12
Subplot		
treatment	3	5
site × treatment	15	25
subplot error	36	60
total	71	107

df = degrees of freedom

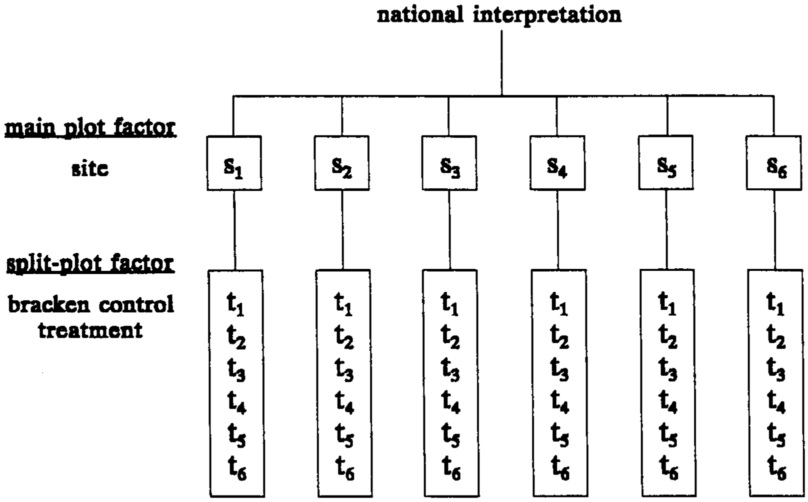


Figure 2.3. Dendrogram identifying levels within analysis of variance model. For site codes see Table 2.2.; for treatment codes see text.

Example of SAS output
Rhizome biomass: spring 1995

General Linear Models Procedure
Class Level Information

Class	Levels	Values
SITE	6	1 2 3 4 5 6
TRMT	4	1 2 3 4
BLK	3	1 2 3

Number of observations in data set = 72

Dependent Variable: DWT

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	35	18079799.49	516565.70	5.77	0.0001
Subplot Error	36	3220587.73	89460.77		
Corrected Total	71	21300387.22			

R-Square	C.V.	Root MSE	DWT Mean
0.848801	20.53020	299.0999	1456.87750

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	5	9606481.622	1921296.324	7.02	0.0028
SITE*BLK (Whole plot Error)	12	3284949.292	273745.774	3.06	0.0046
TRMT	3	3025370.343	1008456.781	11.27	0.0001
SITE*TRMT	15	2162998.231	144199.882	1.61	0.1193

TRMT = treatment; BLK = replicate block; **DWT** = rhizome biomass;
SITE*BLK = site x block interaction; SITE*TRMT = site x treatment interaction.

Example of SAS output
Frond biomass: summer 1995

General Linear Models Procedure
Class Level Information

Class	Levels	Values
SITE	6	1 2 3 4 5 6
TRMT	6	1 2 3 4 5 6
BLK	3	1 2 3

Number of observations in data set = 108

Dependent Variable: DWT

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	47	2811917.182	59828.025	5.22	0.0001
Subplot Error	60	687912.420	11465.207		
Corrected Total	107	3499829.601			

R-Square	C.V.	Root MSE	DWT Mean
0.803444	63.14212	107.0757	169.578889

Source	DF	Type I SS	Mean Square	F Value	Pr > F
SITE	5	116665.2392	23333.0478	2.28	0.1127
SITE*BLK (Whole plot Error)	12	122944.758	10245.397	0.89	0.5581
TRMT	5	2276542.474	455308.495	39.71	0.0001
SITE*TRMT	25	295764.711	11830.588	1.03	0.4447

TRMT = treatment; BLK = replicate block; **DWT** = frond biomass;
SITE*BLK = site x block interaction; SITE*TRMT = site x treatment interaction.

2.7. COMPARISON OF BRACKEN CONTROL TREATMENTS AT INDIVIDUAL SITES

2.7.1. Statistical Analysis

Data was subjected to analysis of variance using the GLM procedure in SAS (SAS, 1988). Transformation of the data was considered unnecessary as it failed to increase significantly the variance accounted for within the analysis of variance model. Independent analyses of variance were conducted for individual sites, testing for treatment and block effects. Mean separation tests using Fisher's Least Significant Difference were applied.

2.7.2. Analysis of Variance Model

Source of variation	rhizome *df*	frond *df*
treatment	3	5
block	2	2
error	6	10
total	11	17

df = degrees of freedom

Example of SAS output

Rhizome biomass: spring 1994

```
---------------------------------- SITE=1 ----------------------------------
                                   (MULL)
                        General Linear Models Procedure
                           Class Level Information

                         Class      Levels     Values

                         TRMT            4     1 2 3 4
                         BLK             3     1 2 3

                  Number of observations in by group = 12

Dependent Variable: DWT
                                      Sum of           Mean
Source                      DF       Squares         Square     F Value      Pr > F

Model                        5   4598136.245     919627.249        2.30      0.1697
Error                        6   2398007.772     399667.962
Corrected Total             11   6996144.017

                      R-Square          C.V.       Root MSE                DWT Mean

                      0.657239      28.53412       632.1930              2215.56833

Source                      DF      Type I SS   Mean Square     F Value      Pr > F

TRMT                         3   2784667.001    928222.334        2.32      0.1747
BLK                          2   1813469.244    906734.622        2.27      0.1846
```

Example of SAS output
Frond biomass, density, height and pinnae number

```
---------------------------------- SITE=4 ---------------------------------
                                   (CLWYD)
                        General Linear Models Procedure
                            Class Level Information

                        Class      Levels     Values

                        TRMT            6     1 2 3 4 5 6
                        BLK             3     1 2 3

                  Number of observations in by group = 18
```

Dependent Variable: DWT

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	7	690292.2813	98613.1830	4.73	0.0139
Error	10	208604.9919	20860.4992		
Corrected Total	17	898897.2731			

R-Square	C.V.	Root MSE	DWT Mean
0.767932	84.30409	144.4316	171.322222

Source	DF	Type I SS	Mean Square	F Value	Pr > F
TRMT	5	591327.8222	118265.5644	5.67	0.0098
BLK	2	98964.4590	49482.2295	2.37	0.1435

Dependent Variable: DNS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	7	1759.753889	251.393413	7.27	0.0029
Error	10	345.835556	34.583556		
Corrected Total	17	2105.589444			

R-Square	C.V.	Root MSE	DNS Mean
0.835754	40.82299	5.880778	14.4055556

Source	DF	Type I SS	Mean Square	F Value	Pr > F
TRMT	5	1633.322778	326.664556	9.45	0.0015
BLK	2	126.431111	63.215556	1.83	0.2106

Dependent Variable: HGT

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	7	27643.03722	3949.00532	4.66	0.0145
Error	10	8467.77889	846.77789		
Corrected Total	17	36110.81611			

R-Square	C.V.	Root MSE	HGT Mean
0.765506	35.13247	29.09945	82.8277778

Source	DF	Type I SS	Mean Square	F Value	Pr > F
TRMT	5	21452.92944	4290.58589	5.07	0.0142
BLK	2	6190.10778	3095.05389	3.66	0.0643

Dependent Variable: PIN

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	7	154.5133333	22.0733333	5.35	0.0090
Error	10	41.2466667	4.1246667		
Corrected Total	17	195.7600000			

R-Square	C.V.	Root MSE	PIN Mean
0.789300	16.69256	2.030928	12.1666667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
TRMT	5	121.0600000	24.2120000	5.87	0.0087

BLK	2	33.4533333	16.7266667	4.06	0.0513

TRMT = treatment; BLK = block; **DWT** = frond biomass; **DNS** = frond density;
HGT = frond height; **PIN** = frond pinnae number

2.8. COMPARISON OF INDIVIDUAL BRACKEN CONTROL TREATMENTS BETWEEN SITES

2.8.1. Statistical Analysis

Data was subjected to analysis of variance using the GLM procedure in SAS (SAS, 1988). Transformation of the data was considered unnecessary as it failed to increase significantly the variance accounted for within the analysis of variance model. In order to determine differences in treatment success between sites, data was expressed as a percentage of untreated plots within respective experimental blocks. Independent analyses of variance were conducted for individual treatments, testing for site effects. Mean separation tests using Fisher's Least Significant Difference were applied.

2.8.2. Analysis of Variance Model

Source of variation	rhizome *df*	frond *df*
site	5	5
error	12	12
total	17	17

df = degrees of freedom

Example of SAS output
Rhizome biomass: spring 1995

```
---------------------------------- TRMT=2 ----------------------------------
                         (CUTTING ONCE YEARLY)
                    General Linear Models Procedure
                        Class Level Information

                      Class     Levels    Values

                      SITE           6    1 2 3 4 5 6

                 Number of observations in by group = 18

Dependent Variable: DWTPCENT
                                      Sum of             Mean
Source                  DF           Squares           Square   F Value      Pr > F

Model                    5       5784.272244      1156.854449      3.71      0.0290
Error                   12       3737.010771       311.417564
Corrected Total         17       9521.283015

                  R-Square              C.V.         Root MSE          DWTPCENT Mean

                  0.607510          21.44662         17.64703             82.2834982

Source                  DF         Type I SS      Mean Square   F Value      Pr > F

SITE                     5       5784.272244      1156.854449      3.71      0.0290

DWTPCENT = percentage of untreated biomass within respective block
```

Example of SAS output
Frond biomass: summer 1994

```
---------------------------------- TRMT=5 ----------------------------------
                         (CUT PRIOR TO ASULAM)
                    General Linear Models Procedure
                        Class Level Information

                      Class     Levels    Values

                      SITE           6    1 2 3 4 5 6

                 Number of observations in by group = 18

Dependent Variable: DWTPCENT
                                      Sum of             Mean
Source                  DF           Squares           Square   F Value      Pr > F

Model                    5       1119.188114       223.837623      1.99      0.1518
Error                   12       1346.465229       112.205436
Corrected Total         17       2465.653343

                  R-Square              C.V.         Root MSE          DWTPCENT Mean

                  0.453911          59.51981         10.59271             17.7969444

Source                  DF         Type I SS      Mean Square   F Value      Pr > F

SITE                     5       1119.188114       223.837623      1.99      0.1518

DWTPCENT = percentage of untreated biomass within respective block
```

2.9. DISCUSSION

The aim of designing this experiment was to investigate bracken control treatment at a range of scales. One of the difficulties in many previous studies was that they were limited to a single site comparison from which it is difficult to extrapolate to national policy. The study used a hierarchial split plot randomised design where all bracken control treatments were applied in the same season and in the same manner. This means that comparison between sites are valid and any differences noted are either because of (1) inherent differences in the bracken present (clonal or historically induced) or (2) differential effects of climate/land use produced in the different regions. The result is that for the first time an assessment of the efficacy of bracken control strategies at the national scale (Chapter 3) and within the different regions (Chapter 4) can be made. The experimental data are then compared against model output (Chapter 5).

3. Efficacy of bracken (*Pteridium aquilinum* (L.) Kuhn) control treatments across a range of climatic zones in Great Britain. I. The national response

3.1. INTRODUCTION

Bracken (*Pteridium aquilinum* (L.) Kuhn) poses an extensive problem for land use throughout Great Britain (Lawton & Varvarigos, 1989; Biggin, 1982; Pakeman & Marrs, 1992a; Long, 1988; Hudson, 1986; Williams *et al.*, 1987; Evans, 1986), and has been implicated as a potential health hazard for humans and wildlife (Evans 1987; Galpin & Smith, 1986; Habicht *et al.*, 1987). Effective control of this weed can prove elusive, with cutting, and spraying asulam, the most common methods of bracken control employed in the uplands (Lawton & Varvarigos, 1989). The current bracken conflict is endemic, with exacerbation of the problem expected during the 21st century (Pakeman & Marrs, 1992b). In order to form policies for a national bracken control programme, policy-makers require access to objective assessments of treatment suitability. Public pressure to instigate such a programme may become greater should links between human health and bracken incidence become substantiated. Therefore, there is a need to construct a national overview of bracken control, and it was against this backdrop that an experiment (Chapter 2.) was undertaken to consider the efficacy of bracken control treatments across a range of climatic zones.

3.2. MATERIALS & METHODS

Full details of sites, treatments, experimental design, sampling protocol, and statistical analysis are given earlier (Chapter 2.). In brief, a series of identical bracken control experiments were conducted simultaneously at six sites across Great Britain. Sites were selected based on two criteria:

- land managers indicated bracken growth was a problem
- representative of the range of climatic conditions prevailing across Great Britain.

The effects of control treatments on the seasonal response of bracken (rhizome and frond components) were evaluated. The four treatments were:

1. Untreated 'control'.
2. Cut once yearly (late July).
3. Cut twice yearly (mid-June and late July).
4. Single application of asulam in 1993 (late July).

The response of bracken to combinations of cutting and spraying asulam was also considered. The assessment of these latter treatments was confined to bracken fronds because of time restraints. The treatments were:

5. One cut and single application of asulam in 1993 (mid-June and late July respectively).
6. Single application of asulam in 1993 (late July) followed by one cut (late July) in 1994.

3.3. RESULTS

3.3.1. Bracken Fronds

June/July 1993

Experimental treatments commenced with the first of two seasonal cuts applied in June 1993. Immediately before this, when all plots were untreated, frond status was assessed. Frond density in untreated plots during mid-June was significantly greater ($P<0.001$) than that of untreated plots 5 - 6 weeks later in the season (Figure 3.1.(a)).

In July 1993, the effects of the mid-June cut upon frond performance were highly significant ($P<0.001$). Frond biomass, density, height and pinnae production were all reduced relative to untreated plots. Moreover, the total number of fronds produced within June-cut plots (i.e. mid-June pre-cut and late July pre-cut) was significantly higher ($P<0.001$) (Figure 3.1.(b)).

(a) (b)

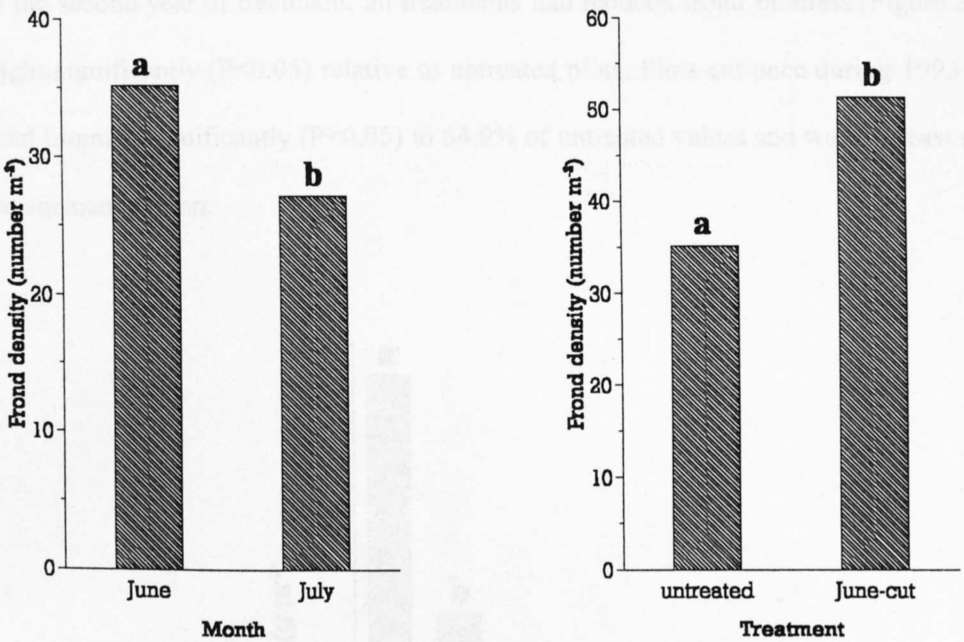


Figure 3.1. Frond densities recorded during 1993; (a) differences within untreated plots between two sampling occasions (b) total number of fronds produced within untreated and June-cut plots, latter determined by adding pre- and post-cut densities. Means are presented: (a) June (n=36), July (n=71); (b) June (n=36); July (n=35). Bars with the same letter are not significantly different (P<0.001). (a) Least significant difference at P<0.05 (LSD) = 4.2 m^{-2} (b) LSD = 6.8 m^{-2}.

July 1994

By the second year of treatment, all treatments had reduced frond biomass (Figure 3.2.) and height significantly (P<0.05) relative to untreated plots. Plots cut once during 1993 reduced frond biomass significantly (P<0.05) to 64.9% of untreated values and was the least effective management option.

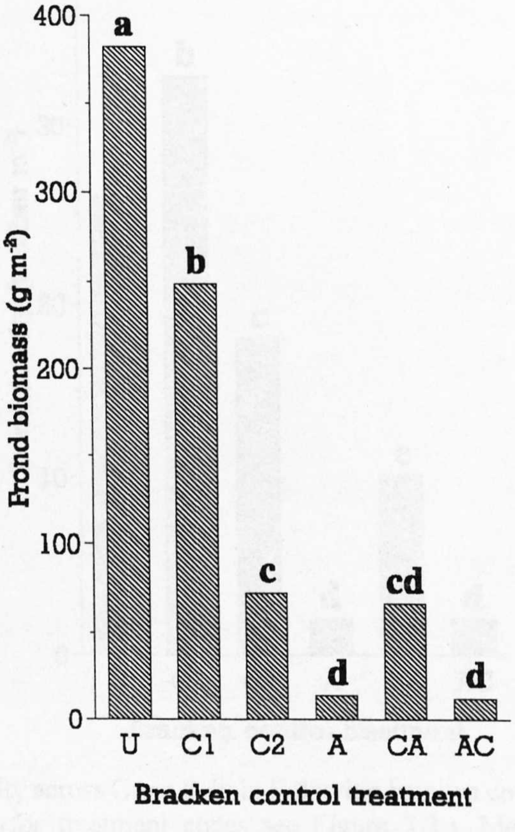


Figure 3.2. Frond biomass across Great Britain following bracken control treatments recorded during summer 1994. Treatment codes are: U, untreated; C1, cut once yearly; C2, cut twice yearly; A, asulam; CA, cut followed by asulam in same season; AC, asulam followed by a cut in the following season. Mean values (n=18) are presented; bars with the same letter are not significantly different (P<0.05). LSD = 58.1g m^{-2}.

This single cut increased frond density significantly (P<0.05) to 126% of untreated plots (Figure 3.3.). Cutting twice yearly reduced frond biomass (18.9% of untreated plots) and density significantly (P<0.05). The most effective method of control was a single application of asulam which reduced biomass to 3.4% of untreated plots. Cutting before spraying asulam was less effective than spraying alone (17.4% of untreated plots), however, the differences were not significant. Frond density was significantly lower (P<0.05) without the cutting pre-treatment.

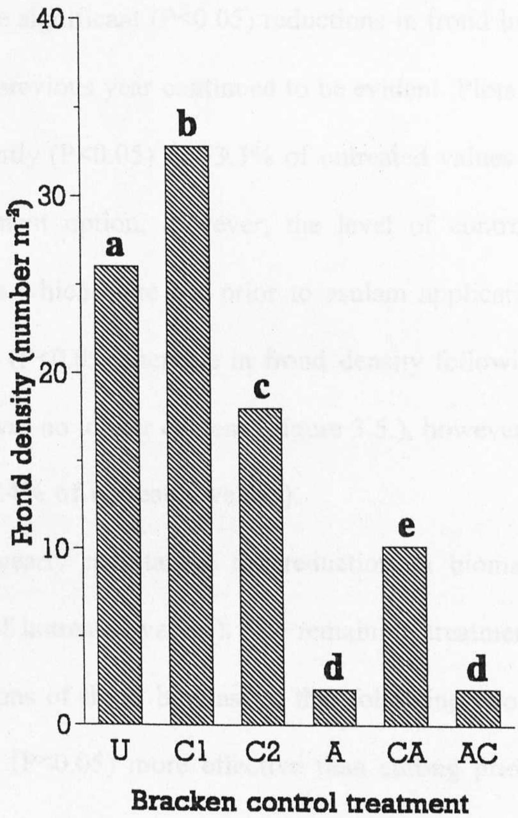


Figure 3.3. Frond density across Great Britain following bracken control treatments recorded during summer 1994; (for treatment codes see Figure 3.2.). Mean values are presented (n=18); bars with the same letter are not significantly different (P<0.05). LSD = 4.2 m^{-2}.

June/July 1995

In June of the third bracken control year, cutting twice yearly for two years resulted in a bracken stand of significantly reduced biomass ($P<0.05$), density ($P<0.05$) and height ($P<0.001$) relative to untreated plots. Cutting had reduced the standing crop of bracken to 29% of the uncut plots.

In July 1995, the significant ($P<0.05$) reductions in frond biomass (Figure 3.4.) and height expressed in the previous year continued to be evident. Plots cut once yearly reduced frond biomass significantly ($P<0.05$) to 53.3% of untreated values and continued to be the least effective management option, however, the level of control was not significantly ($P<0.05$) less than plots which were cut prior to asulam application (37.7% of untreated values). The significant ($P<0.05$) increase in frond density following a single seasonal cut observed in 1994 year was no longer evident (Figure 3.5.), however, they had only returned to untreated levels (100.4% of untreated values).

Cutting twice yearly maintained the reduction in biomass achieved during the previous year (13.1% of untreated values). The remaining treatments incorporating asulam attained similar reductions of frond biomass to that following two cuts per year, however, they were significantly ($P<0.05$) more effective than cutting prior to asulam application. Cutting in the year after asulam treatment produced the lowest recorded frond biomass and density (7.4% and 22.3% of untreated values respectively), however, neither frond variable was significantly ($P<0.05$) different from sprayed plots without the follow-up cut.

Frond height exhibited similar reductions in response to bracken control treatment as those described in terms of biomass, however, cutting twice yearly produced the shortest frond height (30.0% of untreated values) which was significantly ($P<0.05$) less than any other management option.

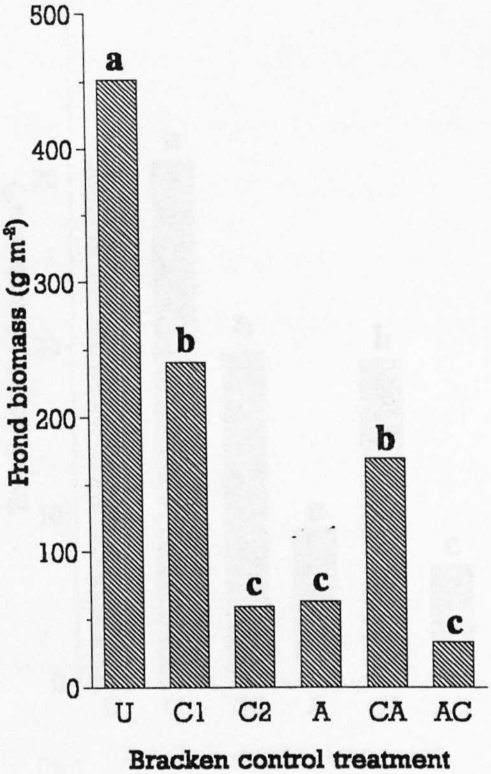


Figure 3.4. Frond biomass across Great Britain following bracken control treatments recorded during summer 1995; (for treatment codes see Figure 3.2.). Mean values are presented (n=18); bars with the same letter are not significantly different (P<0.05). LSD = 71.4g m^{-2}.

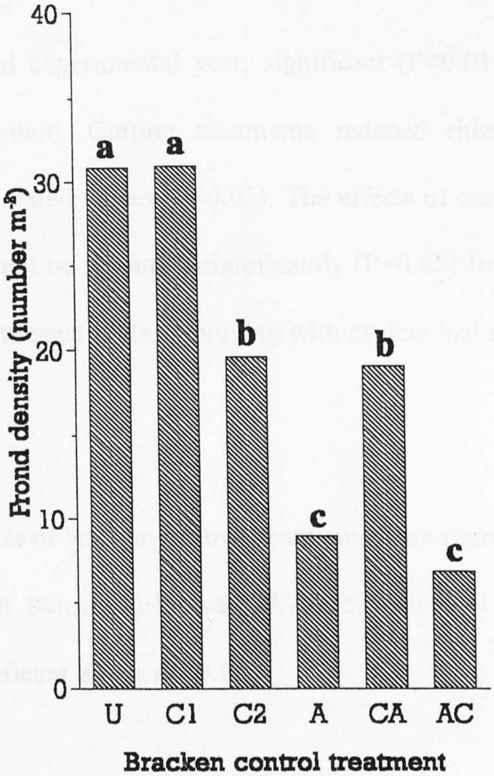


Figure 3.5. Frond density across Great Britain following bracken control treatments recorded during summer 1995; (for treatment codes see Figure 3.2.). Mean values are presented (n=18); bars with the same letter are not significantly different (P<0.05). LSD = 6.4 m^{-2}

3.3.2. Bracken Rhizomes

Spring/Summer 1993

Due to technical difficulties (delayed sampling and sample decay), rhizome samples obtained during the spring and summer 1993 field visits were inaccurate indicators of absolute rhizome biomass. However these samples did permit assessment of comparative rhizome performance which showed no significance with respect to bracken control treatment indicating that all subplots were similar.

Autumn 1993

At the autumn 1993 visit, the six bracken control treatments within each block were sampled. At this stage in the experiment, control treatment had no significant effect on rhizome biomass.

Spring 1994

At the start of the second experimental year, significant ($P<0.01$) treatment effects were evident across Great Britain. Cutting treatments reduced rhizome biomass to levels significantly less than untreated values ($P<0.05$). The effects of cutting twice yearly (78.9% of untreated plots) could not be separated significantly ($P<0.05$) from the effects of a single seasonal cut (84.8% of untreated plots). Spraying with asulam had no significant effect upon rhizome biomass.

Summer 1994

In summer 1994, the effects of bracken control treatments were significant ($P<0.05$). Rhizome biomass within plots cut twice yearly was 78.2% of untreated plots and was the only treatment to have a significant effect ($P<0.05$).

Autumn 1994

At the end of the second year, treatment continued to be a significant factor ($P<0.05$) in determining rhizome biomass. Cutting twice yearly affected the greatest reduction in rhizome biomass (to 68.5% of untreated plots). Its effects could not be separated from that of cutting once yearly, however, it was the only treatment which reduced biomass significantly ($P<0.05$) relative to untreated plots.

Spring 1995

In spring 1995, the third experimental year, effects of treatment were highly significant ($P<0.001$). Both cutting treatments differed significantly from untreated plots with two cuts per year (67.1% of untreated plots) better significantly ($P<0.05$) than one cut yearly (83.2% of untreated plots). After spraying with asulam, differences in rhizome biomass were not significant ($P<0.05$) relative to plots untreated or cut once yearly. However, biomass within sprayed plots (90.1% of untreated plots) did differ significantly ($P<0.05$) from biomass recorded within plots cut twice yearly (Figure 3.6.).

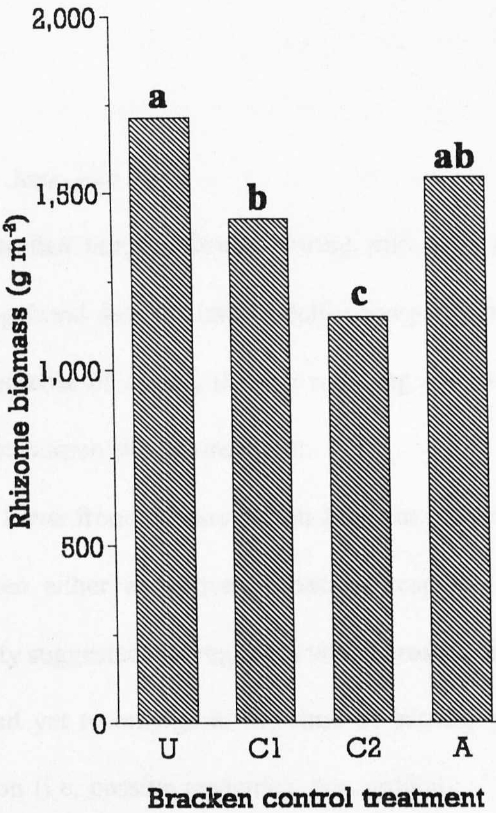


Figure 3.6. Rhizome biomass across Great Britain following bracken control treatments recorded during spring 1995; (for treatment codes see Figure 3.2.). Mean values are presented (n=18); bars with the same letter are not significantly different (P<0.05). LSD = 202.2g m^{-2}

Summer 1995

At the final assessment of rhizome status within the experiment, the trend in biomass decline, identified at the start of the year, continued. Both cutting frequencies reduced rhizome biomass to levels significantly (P<0.05) less than either untreated or asulam-treated bracken. Rhizome biomass in plots cut twice yearly was significantly (P<0.05) less than that detected in plots cut once per year (61.5% and 84.7% of untreated plots respectively). Bracken sprayed with asulam two years earlier, did not sustain the reduction in rhizome biomass evident at the start of the year. This was due to the limited movement of rhizome carbohydrate to fuel frond production in comparison with untreated bracken.

3.4. DISCUSSION

3.4.1. Bracken Fronds

Frond seasonal growth: June-July 1993

Measurements of undisturbed bracken fronds during mid-June and late July identified a seasonal factor regulating frond density. Intra-specific competition may increase growth rate of some fronds at the expense of others, thereby reducing the time interval for bracken to achieve its dominant status upon the environment.

In late July, the lower frond density within June-cut plots represented regrowth. This regrowth may have been either an active or passive response to the cut. The seasonal reduction in frond density suggested that regrowth which arose principally from rhizome buds deep in the soil and had yet to emerge at the time of cutting, or as a result of naturally occurring bud production (i.e. passive response), was unlikely.

Gross frond production within June-cut plots (pre- plus post-cut numbers) indicated that a greater number of buds upon the rhizome were used (severed frond = bud death) by cutting twice yearly than a single cut could achieve in the first season of treatment.

Fronds: July 1993

Cutting during mid-June affected strongly all monitored aspects of frond performance. At this time, frond seasonal growth was recorded in all plots with the exception of those cut twice yearly where regrowth was measured. The problems of interpreting the consequences of this treatment are discussed later.

A 5 - 6 week period of regrowth was insufficient for fronds to return to untreated values, i.e. there is no compensatory increase in frond growth which allows cut plots to catch up. This was to be expected if the timing of the summer visits is correct, i.e. when undisturbed fronds were approaching/at maximum biomass or full expansion.

Fronds: July 1994

In summer of the second experimental year, effects of spraying the previous year became apparent as did those of different cutting frequencies. All management regimes had been fully implemented with the exception of spraying asulam with a single follow-up cut treatment.

Across all the frond variables recorded, there was a clear hierarchy of bracken control treatments. The least effective management regime was cutting once yearly. The imposition of a single cut during 1993 was significant in reducing frond biomass and height, however, superior levels of control were achieved using alternative methods of bracken management. Furthermore, cutting once during the previous season was the only treatment to increase frond density.

Cutting twice yearly produced the shortest fronds and the least pinnae, however, despite the measuremnt being a measure of regrowth it was not the best treatment to reduce frond biomass and density. Treatments which incorporated spraying with asulam had the greatest effect in reducing frond performance. The most successful method of bracken control within this experiment was the single application of asulam.

A single cut 10 weeks before asulam application was shown to increase herbicide efficacy in the Breckland (Lowday & Lakhani, 1987). Within this present study, a similar treatment failed to enhance treatment efficacy across the country. The combination of cutting prior to spraying reduced herbicide efficacy (in terms of frond biomass), however, this reduction was not significant. The possibility that the effect observed in a previous study was site-specific should be discounted, as analysis of data from a single site within the same geographic region as that of Lowday & Lakhani (1987) confirmed the trend observed across the country. The poor results yielded by this combination of treatments was probably due to the reduced time interval between cutting and spraying. Plots were sprayed 5 - 6 weeks after cutting when the fronds were at an early stage of expansion, and a high proportion of the asulam may have missed its target. Postponement of spraying until a replacement canopy had developed which could have intercepted the incident spray mixture may have proven beneficial. This option was less effective than spraying alone and had a significantly higher frond density, although frond biomass values were not significantly different. This may have been attributable to June-cut plots offering an increased ease of passage for the knapsack-operator resulting in more efficient herbicide application.

June/July 1995

The initial success of bracken control treatments was sustained into the final year of monitoring. All treatments continued to suppress frond biomass to levels significantly less than untreated bracken. Cutting treatments improved upon the level of success attained in the previous year, however, the decline in frond biomass relative to untreated plots was greatest in the first year after cutting. Asulam-sprayed plots exhibited some recovery after the expected dramatic decline in frond biomass. A cutting pre-treatment to sprayed plots permitted the greatest frond recovery in contrast with a follow-up cut to previously sprayed plots which retarded frond performance relative to a single application of asulam. However, the advantage of this cutting aftercare treatment was not significant and at this stage of management did not appear to be of practical benefit. It is difficult to consider the recovery of bracken within the confines of a three year study and the benefit of a single cut after spraying may prove significant within a few years.

3.4.2. Bracken Rhizomes

Throughout the first experimental year, bracken control treatment had no effect on rhizome biomass This may have been due to an inadequate sampling protocol which failed to accommodate plot variability, or that a longer time interval is required to affect the rhizome. In spring 1994, the first effects of cutting upon rhizome biomass were observed. They indicated that the first cut at the start of the 1993 season failed to confer any significant advantage over the single cut in late July. Both cutting treatments continued to deplete rhizome resources with cutting twice yearly proving a better treatment than the single annual cut by spring 1995. The effects of spraying asulam, on rhizome performance, were not apparent by the start of the third year of management.

3.4.3. Morphological Indicators and Control Efficacy

The study identified a hierarchy of management options which differed with regard to the bracken variable recorded. Assessment of fronds alone indicated that treatments incorporating asulam offered initial superior control over cutting regimes, however, the rhizome biomass data revealed the converse to be true. This result was expected owing to the different modes of action between cutting and spraying and confirms the hierarchy shown in longer-term experiments (Marrs *et al.*, 1993). The former steadily reduces rhizome resources throughout the cycle of treatment operation with frond production reduced in proportion to the rhizome, whereas the latter destroys rhizome buds and apices resulting in little frond production and limited initial rhizome depletion via respiration and senescence.

3.4.4. Management Success and Problems of Interpretation

In July 1994, the second year of treatment, both frond and rhizome biomass data indicated that cutting twice yearly had a significantly greater impact than cutting once yearly. However, the frond data indicated that cutting twice yearly was ×3 more effective than cutting once yearly, whereas the rhizome data indicated a ×1.2 improvement in efficacy. This highlighted the difficulty in interpreting the impact of cutting twice yearly relative to other management options based upon frond performance. Comparing frond regrowth to frond production within undisturbed plots is valid as regrowth is intrinsically linked to the treatment. However it is misleading in terms of assessing the bracken resource from which bracken will re-establish following the cessation of this treatment.

3.4.5. Bracken Management: National Trends in Relation to Previous Studies

The data obtained from this study may be compared with the results from the few independent examinations into the effects of cutting, and herbicide, upon frond and rhizome performance. Parallels could be drawn with three studies, all of which were conducted in East Anglia, where much of this type of work has been focused.

Cutting treatments have a greater immediate impact upon the rhizome system than spraying asulam, with the effects of herbicide not apparent by the second year after application (Pakeman & Marrs, 1994). These observations were confirmed by this study, however, cutting twice yearly proved more effective than cutting once yearly, and differences between cutting frequency became significant by April of the third year which contradicted the findings of the cited single-site investigation. Frond biomass and density between similar treatments were ranked consistently between the two studies. However, the increase and decrease in frond density and biomass respectively following a single cut in July, which proved significant at the national scale, was not significant in the single-site study. Furthermore, cutting twice yearly was significantly less effective than asulam at suppressing frond biomass, whilst it significantly reduced density relative to untreated plots which contradicted the formerly cited study.

An earlier study monitored rhizomes on a less regular basis than this experiment, sampling started during the fourth year of bracken control (Lowday, 1987). At this stage of treatment, cutting twice yearly had reduced rhizome biomass to the lowest level and ranking of treatments was consistent with the national trend. However, the percentage reduction in rhizome biomass relative to untreated plots was greatly in excess of similar figures obtained in the current study to date. Given that the greatest effects of treatment are achieved during the early stages of control the prospect of achieving similar levels of long-term control within this experiment seemed doubtful.

A further investigation incorporating rhizome sampling (Lowday & Lakhani, 1987) permitted a limited comparison of results. In the second year of treatment, differences in cutting frequencies were significant in their effect upon rhizome biomass, but only two cuts per year significantly reduced rhizome resources relative to untreated plots. The national assessment, reported here, indicated that at this stage of treatment both cutting regimes reduced rhizome biomass significantly relative to undisturbed plots with cutting frequency of little consequence. Later within the same year only plots untreated and cut once yearly may be compared. A significant increase in frond density was observed which is confirmed within this national study.

The single-site studies appeared to underestimate the initial importance of differences between cutting once and twice yearly in depleting rhizome reserves relative to undisturbed plots, whilst the scale of reductions appeared to be over-estimated in relation to national trends. Temporal, spatial and methodological contrasts can obscure comparison between studies, and meaningful extrapolation from a single-site study to the national level is difficult. However, the simultaneous multiple-site approach to bracken control, as illustrated here, avoids some of these problems and, by monitoring rhizome dynamics, the implications of treatment cessation for land management can be better assessed.

3.4.6. Implications of National Bracken Control Appraisal for Site Management

Selection of the most appropriate technique for bracken control should not be based upon weed depletion *per se*. Decisions should be reached with reference to the management objective and the option for treatment continuity. National trends can only prove useful as a guide to treatment effects as site-specific factors inevitably operate to modify management efficacy.

Spraying asulam reduces the standing crop of bracken fronds rapidly after a single treatment, however, the effect upon rhizome biomass is limited, leaving a considerable resource from which re-establishment may commence. If the management objective is to increase access to a site then this option is of value, however, rapid frond recovery would necessitate re-spraying or alternative after-care measures (Robinson, 1986) in order to sustain weed suppression. However, if the objective of control is the protection of desirable species (e.g. relict woodland flora), and herbicide-sensitivity is not an issue, the instant canopy clearance may prove disadvantageous, whereas a reduced canopy would prove preferable. If a protective canopy is not necessary, the open ground created often leads to the establishment of a different weed species (Marrs & Lowday, 1992).

Cutting is slower than spraying asulam at reducing standing crop of bracken fronds, however, as in the previous example of a shade-advantaged flora, this gradual decline in frond vigour can be more suitable. Where the management objective is to improve access to the site of infestation, the increase in frond density following a single annual cut could pose problems for human and animal passage through a bracken stand during the initial stages of this control option. However, the objective can be attained with treatment continuity.

The cutting treatments require continuity over the three year period which the asulam does not. However, the level of control achieved was considerable, especially when cutting is applied twice yearly, albeit a labour-intensive technique. Cutting twice yearly proved more effective than cutting once yearly, in terms of rhizome depletion, and it is this feature which is of prime importance as recovery of the stand to pre-treatment levels would be slowest following cessation of this management option (Marrs *et al*., 1993).

4. Efficacy of bracken (*Pteridium aquilinum* (L.) Kuhn) control treatments across a range of climatic zones in Great Britain. II. The regional response

4.1. INTRODUCTION

Bracken (*Pteridium aquilinum* (L.) Kuhn) is an invasive weed species conflicting with current land use (Lawton & Varvarigos, 1989; Biggin, 1982; Pakeman & Marrs, 1992; Long, 1988; Hudson, 1986; Williams *et al.*, 1987; Evans, 1986; Habicht *et al.*, 1987). It is problematic throughout Great Britain, especially in the uplands of northern and western areas (Watt, 1976). Cutting or spraying asulam are the most common methods of bracken control in the uplands (Lawton & Varvarigos, 1989). The outcome of bracken management operations are conflicting and effective control in all situations has proven elusive. An experiment into bracken control at six geographically distinct sites across Great Britain was described earlier (Chapter 2.). A national overview of bracken control was constructed (Chapter 3.) with experimentally derived data further analyzed within this chapter to describe regional responses to six bracken control treatments (Chapter 2.7.) and compare sites (Chapter 2.8.). The possibility that specific bracken control methods were more effective under different climatic regimes (as represented at the six climatically contrasting study sites) is investigated. In addition, the extent to which individual sites reflect the national response is considered.

4.2. MATERIALS & METHODS

Full details of sites, treatments, experimental design, sampling protocol, and statistical analysis are given earlier (Chapter 2.).

4.3. RESULTS

The nature of certain bracken control regimes and the intensity of sampling within the study resulted in bracken samples being collected before all treatments had been fully applied (Figure 4.1.). In summer of the first experimental year, the only treatment effects which could be tested for were those of cutting 5 - 6 weeks earlier in the season. In the second year of bracken management, all treatments had been applied with the exception of the follow-up cut to previously sprayed plots. In the third year of management, all treatments had been applied.

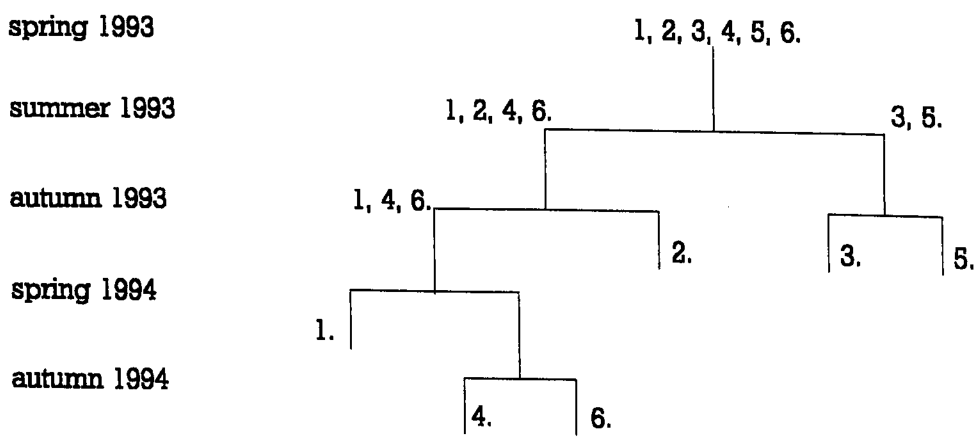


Figure 4.1. Dendrogram displaying division of treatments during the course of the experiment. Treatment codes are: 1, untreated; 2, cut once yearly; 3, cut twice yearly; 4, single application of asulam; 5, cut once 5 - 6 weeks prior to asulam application; 6, cut once in the year following asulam application.

4.3.1. Effects of Bracken Control Treatments at Individual Study Sites

Mull: Bracken fronds

Summer 1993

The effects of cutting in June (5 - 6 weeks earlier in the season) upon frond performance were apparent in the cut twice yearly treatment. Frond biomass ($P<0.05$) and height ($P<0.001$) were reduced significantly (to 11.0% and 37.7% of untreated plots respectively). No significant differences in frond density were observed between cut and uncut plots.

Summer 1994

In the second year of bracken management, all treatments reduced frond biomass significantly ($P<0.05$) relative to untreated plots. Cutting once yearly caused the lowest decline in frond biomass (to 65.7% of untreated values). Cutting twice yearly and treatments incorporating asulam produced a standing crop of bracken significantly less ($P<0.05$) than that achieved cutting once yearly. A single application of asulam produced the lowest biomass (2.0% of untreated plots).

Cutting once yearly was the only treatment which failed to reduce frond density significantly ($P<0.05$) relative to untreated bracken. Spraying with asulam produced the lowest frond number (6.4% of untreated values) and attained superior control relative to bracken cut twice yearly.

All treatments reduced frond height significantly ($P<0.05$) relative to untreated bracken. Cutting twice yearly and treatments incorporating asulam produced significantly ($P<0.05$) lower frond height than plots cut once yearly (77.2% of untreated values).

Summer 1995

In the third year of management, cutting once yearly did not reduce biomass significantly ($P<0.05$) relative to untreated bracken (to 101.0% of untreated values). Cutting twice yearly and treatments incorporating asulam exhibited frond biomass significantly ($P<0.05$) less than untreated plots. These management options produced the same significant ($P<0.05$) levels of bracken control. Bracken cut in the year after asulam application produced the lowest frond biomass (7.6% of untreated values).

Frond density was no longer a significant consequence of bracken control. However, the only treatment that achieved a significant ($P<0.05$) reduction in frond number relative to untreated values was spraying asulam combined with a follow-up cut.

All treatments reduced frond height significantly ($P<0.05$) relative to untreated plots, except cutting once yearly (to 91.0% of untreated values). Cutting twice yearly produced the shortest fronds (21.5% of untreated values), however, the reduction in frond height was not significantly greater than that recorded following treatments incorporating asulam.

Mull: Bracken rhizomes

Throughout the experiment, bracken control treatments did not significantly reduce rhizome biomass in Mull. Prior to frond emergence in the third year of bracken control, cutting twice yearly reduced rhizome biomass to 71.0% of untreated plots. Spraying with asulam reduced rhizome biomass to 91.5% of untreated values, however, cutting once yearly did not deplete rhizome status (107.0% of untreated values).

Scottish Borders: Bracken fronds

Summer 1993

The single cut in June reduced frond biomass ($P<0.01$) and height ($P<0.05$) significantly (to 22.4% and 59.8% of untreated plots respectively) relative to uncut plots. Frond density was lowest in plots that had been cut however the decline was not significant.

Summer 1994

In the second year of bracken management, all treatments reduced frond biomass significantly ($P<0.05$) relative to untreated plots, except cutting once yearly (112.8% of untreated values). Spraying asulam produced the lowest frond biomass (4.2% of untreated values).

Cutting once yearly produced a significant ($P<0.05$) increase in frond numbers (to 243.7% of untreated values) whereas cutting twice yearly had no significant ($P<0.05$) effect upon frond density (100.0% of untreated values). Treatments which incorporated asulam exhibited a significant ($P<0.05$) reduction in frond density relative to untreated plots. All management regimes reduced frond height significantly ($P<0.05$) relative to untreated bracken with the exception of cutting once yearly (to 93.4% of untreated values). Cutting twice yearly produced the shortest fronds (50.6% of untreated values).

Summer 1995

In the third year of bracken control, all treatments reduced frond biomass and height significantly ($P<0.05$) relative to untreated plots. Cutting once yearly was the least effective treatment (52.1% of untreated values). A single application of asulam produced the least standing crop of bracken fronds (8.0% of untreated values) and was the only treatment to reduce frond biomass to a level significantly ($P<0.05$) less than cutting once yearly.

The highest frond density was recorded within untreated plots. Within cut plots, the decline in frond numbers was not significant whereas treatments incorporating asulam exhibited a significant ($P<0.05$) reduction in frond density. A follow-up cut to previously sprayed bracken produced the same frond density as that recorded in plots treated with a single application of asulam (25.9% of untreated values).

All treatments reduced frond height significantly (P<0.05) relative to untreated plots. Cutting twice yearly produced the shortest fronds (35.8% of untreated values) and was the only treatment which reduced height significantly (P<0.05) relative to the least successful treatment, cutting prior to asulam application (to 65.6% of untreated values).

Scottish Borders: Bracken rhizomes

At no stage in the experiment did bracken control treatment significantly reduce rhizome biomass recorded in the Scottish Borders. In the third year of bracken control, prior to frond emergence, the largest reduction in rhizome biomass was detected within plots sprayed with asulam (to 76.6% of untreated plots). Cutting twice yearly achieved a similar level of control (to 79.5% of untreated plots) as spraying asulam, whereas, cutting once yearly reduced rhizome biomass to 94.6% of untreated plots.

Lake District: Bracken fronds

Summer 1993

Plots which had been cut in June produced significantly ($P<0.05$) less biomass (16.0 % of untreated values) and significantly ($P<0.05$) shorter fronds (51.9% of untreated values) than undisturbed bracken plots. However, cutting had no influence upon frond density.

Summer 1994

In the second year of bracken management, all measures of frond performance were significantly influenced ($P<0.001$) by bracken control treatment. Reduction of frond biomass, relative to untreated bracken, was significant ($P<0.05$) for all management regimes except cutting once yearly (to 77.3% of untreated values). Treatments incorporating asulam were significantly ($P<0.05$) more effective at reducing frond biomass than any of the alternative control options. Spraying with asulam affected the greatest reduction in frond biomass (to 1.4% of untreated values). Cutting prior to asulam application conveyed no significant ($P<0.05$) advantage over plots receiving a sole application of asulam.

Cutting treatments had no effect upon frond density, however, treatments incorporating asulam did reduce frond numbers significantly ($P<0.05$) relative to untreated plots. Bracken treated with a single application of asulam exhibited the lowest frond number (7.2% of untreated values) as the cutting pre-treatment appeared to convey no advantage. All treatments reduced frond height significantly ($P<0.05$) relative to untreated plots. Plots cut once yearly or cut prior to asulam application achieved the lowest reductions in frond height. Cutting twice yearly produced fronds significantly ($P<0.05$) shorter than cutting once yearly, however, spraying with asulam produced significantly ($P<0.05$) shorter fronds than any other treatment (40.9% of untreated values).

Summer 1995

In the third year of bracken control, all treatments reduced frond biomass and height significantly ($P<0.05$) relative to untreated plots. Cutting once yearly was the least effective treatment to reduce biomass and height (to 46.6% and 60.2% of untreated values respectively) whereas sprayed plots with a follow-up cut produced the lowest biomass and shortest fronds (5.4% and 38.2% of untreated values respectively).

Spraying asulam without a cutting pre-treatment were the only treatments to exhibit frond density significantly less than untreated plots. A follow-up cut to previously sprayed plots produced the lowest frond number (24.1% of untreated values) however the cut did not convey a significant ($P<0.05$) advantage over a single application of asulam (29.6% of untreated values).

Lake District: Bracken rhizomes

Throughout most of the experiment, bracken control treatment did not reduce rhizome biomass significantly ($P<0.05$) relative to untreated plots in the Lake District. In spring 1995, cutting twice yearly was the most successful treatment to reduce frond biomass (72.8% of untreated plots). Cutting once yearly depleted rhizome biomass to 94.6% of untreated plots whilst treatment with asulam resulted in rhizome biomass 105% of untreated plots.

Clwyd: Bracken fronds

Fronds

Summer 1993

Plots cut in June produced the lowest recorded biomass (13.3% of untreated values), however, this was not significantly lower than the standing crop of undisturbed bracken fronds. The single cut had no effect upon frond density, however, cut plots contained fronds significantly ($P<0.05$) shorter (42.3% of untreated values) than those present in plots which were not cut.

Summer 1994

In the second year of bracken management, all measures of frond performance were significantly influenced ($P<0.01$) by bracken control treatment. All treatments reduced frond biomass significantly ($P<0.05$) relative to untreated plots. Cutting once yearly was the least effective treatment to reduce frond biomass (to 43.6% of untreated plots) whereas spraying asulam offered the greatest reduction in frond biomass (to 5.4% of untreated plots), however, these reductions were not significantly ($P<0.05$) different.

Cutting once yearly or cutting prior to asulam application had no significant effect upon frond density, whereas, cutting twice yearly or spraying with asulam both affected a significant ($P<0.05$) reduction in frond number relative to untreated values. The herbicide treatment produced the lowest frond density (12.3% of untreated values).

All treatments reduced frond height significantly ($P<0.05$) relative to untreated plots. Cutting once yearly affected the least decline in frond height (to 60.3% of untreated values) whilst cutting twice yearly produced the shortest fronds (30.3% of untreated values). Frond height differences between cutting frequencies were not significant.

Summer 1995

In the third year of bracken control, all treatments reduced frond biomass significantly ($P<0.05$) relative to untreated plots. Cutting prior to asulam application was the least effective treatment (39.2% of untreated values) whilst cutting twice yearly produced the least frond biomass (4.0% of untreated values). Differences in frond biomass between these treatments were not significant ($P<0.05$). Bracken control treatment was not identified as significant in determining frond number, however, frond density was greatest in untreated plots and least in plots cut once in the year after spraying asulam (15.7% of untreated values).

Cutting prior to spraying asulam (80.4% of untreated values) was the only treatment which resulted in frond height significantly ($P<0.05$) less than undisturbed bracken fronds. Cutting twice yearly produced the shortest fronds (23.5% of untreated values).

Clwyd: Bracken rhizomes

In the spring of the third year of bracken control, all treatments reduced rhizome biomass to levels significantly ($P<0.05$) less than untreated bracken in Clwyd. Cutting twice yearly reduced rhizome biomass (to 49.1% of untreated values) to a level of control significantly ($P<0.05$) better than spraying asulam (to 73.1% of untreated values). However, there was no significant ($P<0.05$) difference with cutting once yearly (60.7% of untreated values).

Breckland: Bracken fronds

Summer 1993

Cutting 5 - 6 weeks earlier in the season produced a standing crop of bracken significantly ($P<0.05$) less than undisturbed plots (6.2% of untreated values). The lowest frond density was recorded within cut plots (35.5% of untreated values) however the decline in frond numbers was not significant. Fronds within cut plots were significantly ($P<0.05$) shorter than uncut fronds (26.2% of untreated values).

Summer 1994

In the second year of bracken management, all bracken control treatments reduced frond biomass relative to untreated plots. Cutting once yearly was the least effective method of control (to 65.5% of untreated values), and cutting twice yearly or treatments incorporating asulam all offered significantly ($P<0.05$) superior control over the single seasonal cut. Plots sprayed with asulam produced the lowest standing crop of fronds (2.9% of untreated values).

Cutting once yearly was the only treatment which failed to reduce frond density significantly ($P<0.05$) relative to untreated plots. Spraying with asulam affected the greatest decline in frond number (to 4.1% of untreated values).

Spraying with asulam was the only treatment which failed to reduce frond height significantly ($P<0.05$) relative to untreated plots. However, the decline in frond height within sprayed plots with a cutting pre-treatment (to 45.8% of untreated values) was significant ($P<0.05$). Cutting twice yearly produced the shortest fronds (26.6% of untreated values).

Summer 1995

In the third year of bracken control, all treatments reduced frond biomass significantly ($P<0.05$) relative to untreated plots. Cutting prior to asulam application was the least effective treatment (47.8% of untreated values) whilst a follow-up cut on sprayed plots affected the greatest decline in frond biomass (to 7.4% of untreated values). Frond biomass differences between these treatments were significant ($P<0.05$).

Cutting once yearly in the previous two years increased frond density significantly ($P<0.05$) relative to untreated plots (to 171.7% of untreated values). Plots which received a single application of asulam and those which received a follow-up cut exhibited the largest declines in frond density (to 18.9% and 22.6% of untreated values respectively), to levels significantly ($P<0.05$) less than untreated plots.

All treatments reduced frond height significantly ($P<0.05$) relative to untreated plots. No single treatment appeared to offer significantly ($P<0.05$) better height suppression than any other management option. Cutting prior to asulam application was the least effective treatment (50.9% of untreated values) whereas cutting twice yearly produced the shortest fronds (21.1% of untreated values).

Breckland: Bracken rhizomes

In the autumn of the second year of bracken control, cutting twice yearly was the only treatment which reduced rhizome biomass significantly ($P<0.05$) relative to untreated bracken. In spring of the third year, the significance attached previously to rhizome biomass decline, after cutting twice yearly, relative to untreated plots was no longer evident. Cutting twice yearly (65.4% of untreated values) failed to affect superior control over cutting once yearly (70.5% of untreated values). Spraying with asulam appeared ineffective in reducing rhizome biomass at this stage of experimental monitoring (134.3% of untreated values).

Devon: Bracken fronds

Summer 1993

The first cutting treatment, applied in June, produced a standing crop of bracken significantly ($P<0.05$) less than untreated plots (21.7% of untreated values). The lowest frond density was recorded within cut plots (67.9% of untreated values), however, relative to untreated bracken, the decline in frond numbers was not significant ($P<0.05$). Fronds within cut plots were significantly ($P<0.05$) shorter than untreated fronds (54.6% of untreated values).

Summer 1994

In the second year of bracken management, all treatments reduced frond biomass relative to untreated plots. Cutting once yearly was the least effective treatment (49.3% of untreated plots) whereas spraying asulam produced the lowest standing crop of fronds (4.3% of untreated values). However, the contrasting reductions in frond biomass between these treatments were not significantly ($P<0.05$) different. No significant effects of bracken control treatment upon frond density or height were observed at this stage of the experiment.

Summer 1995

In the third year of bracken control, all treatments, except cutting once yearly (62.9% of untreated values), reduced frond biomass significantly ($P<0.05$) relative to untreated plots. Cutting twice yearly and treatments incorporating asulam application produced similar levels of control, however, the cutting pre-treatment to spraying asulam (25.4% of untreated values) offered no significant decline in biomass over cutting once yearly. Cutting once in the year after asulam application produced the lowest frond standing crop (7.8% of untreated values).

Frond density was greatest in plots cut once yearly however neither cutting regime altered frond number significantly relative to untreated plots. Treatments incorporating asulam reduced frond density significantly ($P<0.05$), relative to untreated plots, and achieved similar levels of control. A follow-up cut to plots previously sprayed with asulam produced the lowest number of fronds (12.5% of untreated values).

All treatments produced significant (P<0.05) reductions in frond height relative to untreated bracken. Cutting once yearly affected the least reduction in frond height (to 70.4% of untreated values), whereas cutting twice yearly twice yearly produced the shortest fronds (34.0% of untreated values). Differences in frond height between cutting frequencies were significant (P<0.05).

Devon: Bracken rhizomes

In the spring of the third year of bracken control, both cutting treatments reduced rhizome biomass significantly (P<0.05) relative to untreated bracken. Cutting twice yearly was the most effective treatment (66.7% of untreated values) whilst cutting once yearly affected a decline in rhizome biomass to 68.3% of untreated values. The reduction in rhizome biomass within asulam-sprayed plots (to 88.8% of untreated values) was not significant, however, cutting once yearly did not affect significantly (P<0.05) superior control over the herbicide treatment.

4.3.2. Regional Comparisons of Bracken Control Treatments

Bracken fronds

Summer 1993

There were no significant differences in bracken response to any of the management regimes between any of the sites.

Summer 1994

Cutting once yearly affected significantly (P<0.05) different levels of bracken control between sites. The percentage of untreated frond biomass, density and height after the single cut were all significantly (P<0.05) greater at the Scottish Borders (184.2%, 213.9% and 109.2% of untreated values respectively) than at any other site (Figure 4.1.). The remaining experimental sites appeared not significantly different to one another after a single cut. Of these sites, in terms of frond biomass, bracken in the Lake District (77.1% of untreated values) and Mull (70.4% of untreated values) was most resilient. This treatment was most effective in Clwyd (50.3% of untreated values).

The cutting pre-treatment to sprayed plots showed significant ($P<0.05$) differences in frond height between sites. The lowest decline in frond height was in Devon (68.5% of untreated values) whereas a significantly ($P<0.05$) greater reduction in frond height was observed in Mull (37.7% of untreated values).

(a)

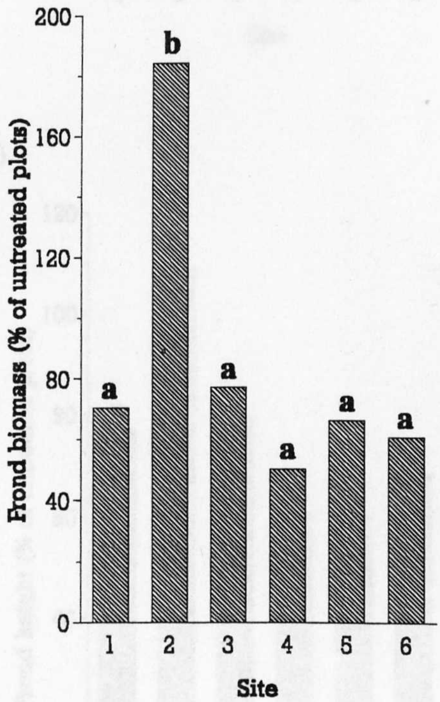
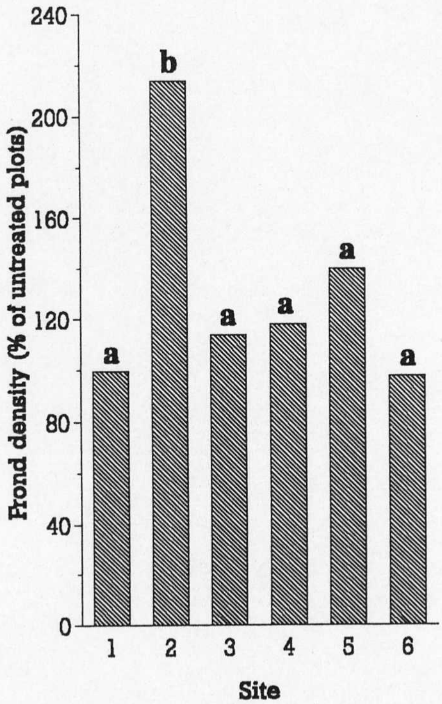


Figure 4.1. Frond performance (expressed as a percentage of untreated plots) after cutting once yearly. (a) biomass (b) density (c) height, recorded at individual study sites during summer 1994. Site codes are: 1, Mull; 2, Scottish Borders; 3, Lake District; 4, Clwyd; 5, Breckland; 6, Devon. Means are presented (n=3); bars with the same letter are not significantly different ($P<0.05$). (a) LSD = 68.7%; (b) LSD = 66.1%; (c) LSD = 24.7%.

(b)



(c)

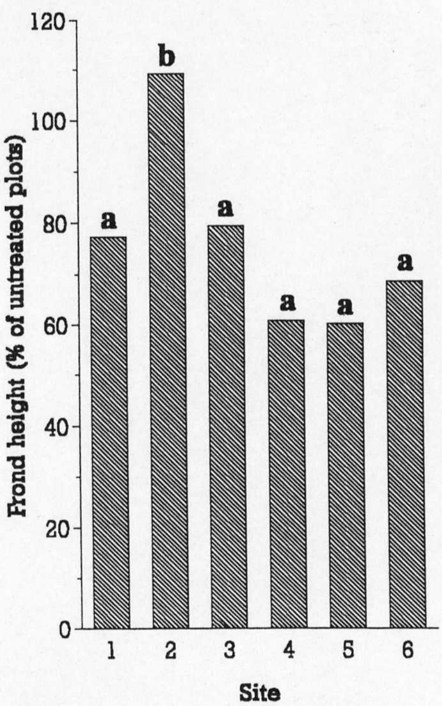


Figure 4.1. continued.

Summer 1995

Cutting once yearly was the only treatment which affected significant (P<0.05) differential control between sites. This could only be detected in terms of frond density (Figure 4.2.). Breckland, Devon and Mull sites were not significantly different in terms of increased frond density relative to untreated plots. The greatest increase was in Breckland (179.0% of untreated values) and was the only site to produce significantly (P<0.05) inferior bracken control relative to Clwyd. The latter site affected the greatest control over frond density after cutting once yearly (52.7% of untreated values).

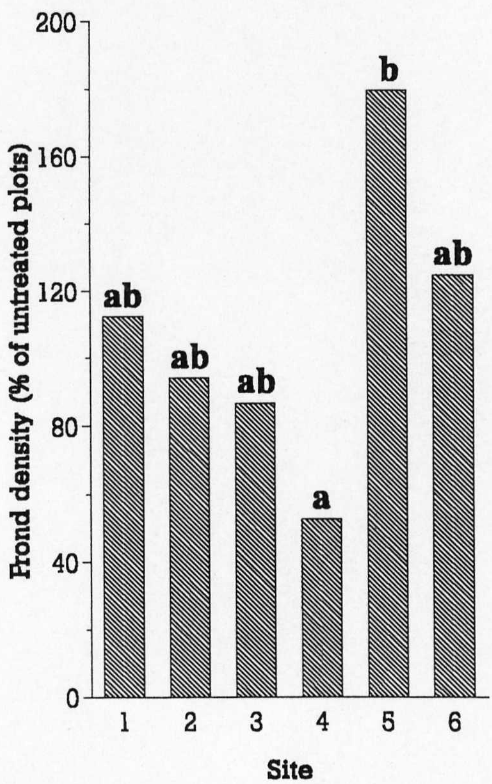


Figure 4.2. Frond density (expressed as a percentage of untreated plots) after cutting once yearly, recorded at individual study sites during summer 1995; (for site codes see Figure 4.1.). Means are presented (n=3); bars with the same letter are not significantly different (P<0.05). LSD = 73.2%.

Bracken rhizomes

No significant differences were observed in the level of control achieved in relation to any bracken control regime between sites during the first two years of the experiment. However, in the third year of bracken control, cutting once yearly affected significantly ($P<0.05$) different levels of control upon rhizome biomass between sites (Figure 4.3.). Alternative treatments did not exhibit significant differences between sites. Cutting once yearly was least effective in Mull (110.8% of untreated values), however, significantly ($P<0.05$) similar levels of control were achieved in Scottish Borders and Lake District (93.9% and 92.0% of untreated values respectively). The remaining sites achieved a level of rhizome biomass suppression significantly ($P<0.05$) greater than that detected in Mull. Cutting once yearly was most effective in Clwyd (59.4% of untreated values) and was the only site to affect significantly ($P<0.05$) superior control relative to that obtained in Scottish Borders and Lake District.

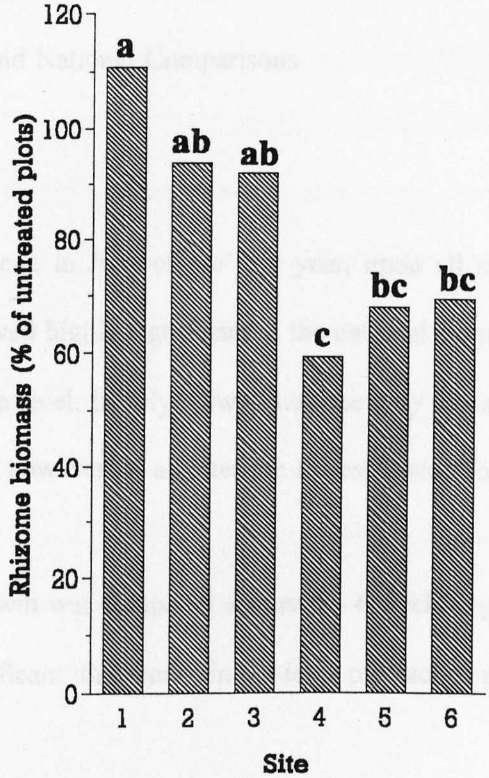


Figure 4.3. Rhizome biomass (expressed as a percentage of untreated plots) after cutting once yearly, recorded at individual study sites during spring 1995; (for site codes see Figure 4.1.). Means are presented (n=3); bars with the same letter are not significantly different (P<0.05). LSD = 31.4%.

4.4. DISCUSSION

4.4.1. Site Responses and National Comparisons

Bracken fronds

Summer 1993

The effects of a single cut, in June of the first year, upon all measures of bracken frond performance, which proved highly significant at the national level (Chapter 3.), were not as clearly defined at the site level. In July, Clwyd was the only site at which the effects of this cut proved insignificant, however, at all sites the lowest frond biomass was recorded within cut plots.

Undisturbed growth was compared against 5 - 6 weeks regrowth. At this early stage of bracken control, significant differences in the level of bracken performance between sites were absent.

Summer 1994

The hierarchy of bracken control treatments identified at a national level was found to apply generally at individual sites. However, the significance of differences in bracken response within sites did contrast.

A single cut in the previous year was the least effective treatment nationally and this agreed at all sites. Cutting once yearly affected a significant decline in frond biomass with a concomitant increase in frond density. Scottish Borders was the only site at which the increase in frond numbers proved significant, however, an increase in frond biomass was associated with this response. Frond density increased at Lake District, Clwyd, and Breckland, however, only the latter two sites exhibited significant declines in biomass. Frond density declined in Mull and Devon, however, only the decline in biomass was significant.

Spraying asulam affected the greatest control over frond biomass and density at all sites, which accurately reflected the national response. Bracken cut 5 - 6 weeks prior to spraying asulam produced consistently inferior control relative to plots without the cutting pre-treatment. This combination treatment was intended to investigate the observation in Breckland that cutting prior to spraying asulam enhanced the efficacy of herbicide treatment (Lowday & Lakhani, 1987). The poor level of control attained in this study is believed to be attributable to a shorter interval between cutting and spraying relative to the 10 week period in the cited investigation. It is believed that fronds produced as regrowth (either as a consequence of management or environmental interference e.g. late frost) may exhibit a change in their morphology to increase their leaf area index and increase photosynthetic efficiency, thereby better facilitating the offset of energy losses. What the current study identifies is that any changes which do occur, within the period of regrowth in this experiment, were not sufficient to promote asulam efficacy. Properties of frond regrowth did not contrast sufficiently to affect differential control between sites.

Summer 1995

At the countrywide scale, cutting once yearly continued to prove the least effective method for controlling bracken. The significant decline in frond biomass continued to be evident, however, frond density was no longer significantly different from untreated frond numbers. All sites except Mull and Devon reflected the significant decline in frond biomass, however, cutting prior to asulam application was less effective than a single annual cut in Clwyd. Scottish Borders site exhibited a one year delay in achieving the reduction in frond biomass observed at all sites in the second year of bracken control. All sites agreed with the national observation concerning frond density in relation to cutting once yearly, except in Breckland where a significant increase in frond numbers was recorded.

As the national cycle of cutting twice yearly continued it appeared to offer increased control relative to the previous year whereas the cutting pre-treatment to sprayed plots exhibited recovery from levels in the previous year. This principle applied generally from site to site.

Nationwide, the follow-up cut to sprayed plots appeared to delay recovery as it was ranked below plots treated with a single application of asulam for all measures of frond performance. However, the relative difference between treatments was not described as significant nationally. In a few instances, different measures of frond performance identified the follow-up cut as a disadvantage in terms of ranked treatments, however, differences between treatments were at no stage significant.

Bracken rhizomes

At the national level, the effects of cutting treatment were first observed in spring of the second bracken management year. However, at individual sites significant effects were first described in spring of the third year of experiments. The highly significant effects of bracken control on rhizome biomass identified at the countrywide scale were not as clearly defined at the regional level. Mull, Scottish Borders and Lake District did not exhibit significant effects of treatment. Of the remaining sites, the analysis of variance model attached greatest significance to Clwyd results. Cutting twice yearly affected the greatest reduction in rhizome biomass at Clwyd, Breckland and Devon, which agreed with the national picture. However, in contrast with the nationwide response, increased cutting frequency conveyed no bracken control advantage and in Breckland the decline in biomass was not significant relative to undisturbed bracken rhizomes. Spraying asulam in Breckland and Devon did not effect a significant reduction in rhizome biomass, which was consistent with national rhizome dynamics. However, the identical treatment produced a significant reduction in rhizome biomass levels in Clwyd.

Interpretation of management success using rhizome biomass

Sampling the rhizome system at the height of the season when fronds have developed can prove misleading in terms of assessing the impact of contrasting bracken control treatments. This is because the seasonal allocation of carbohydrate into frond production is superimposed upon rhizome biomass decline due to treatment. Untreated bracken is expected to show the greatest seasonal decline in rhizome biomass since greater frond biomass is produced which demands a greater investment of resources. This decline places the apparent performance of asulam treatments at a disadvantage as the limited frond investment results in rhizome biomass being similar to untreated plots at this stage in the growth cycle.

4.4.2. Site Comparison

Cutting once yearly was the only treatment which affected significantly different levels of control upon bracken biomass between sites. The significance of site contrasts were evident within both the frond and rhizome component. Bracken was most resilient to a single annual cut in the Scottish Borders, with significantly poorer control evident after the first cut. Significant differences were not identified between the remaining sites, however, in terms of frond biomass, poorer control was affected in Lake District and Mull. Greatest bracken control by cutting once yearly was observed in Clwyd. In terms of frond biomass, significant differences in control efficacy between sites did not continue into the final year of monitoring.

In the third year of bracken control, cutting once yearly expressed significant ($P<0.05$) contrasts in rhizome biomass between sites. Applying one seasonal cut affected poorer control at the northern sites (Scotland and northern England): reductions to >90% of untreated values were achieved). Whilst superior reductions were evident at the southern sites (southern England and Wales): reductions to approximately 66% of untreated values were identified). Sites within the two groups identified were not significantly different ($P<0.05$) from one another. Of the northern sites, significant differences ($P<0.05$) existed only between Mull and all the southern sites. Of the southern sites, significant differences ($P<0.05$) existed only between Clwyd and all the northern sites. Therefore, despite the distinct differences in control efficacy identified, segregation of sites on a north/south basis is not fully vindicated statistically. A longer time period for experimentation may be required before any separation of geographic zones, at this scale, can be identified.

Cutting once yearly was the sole treatment to achieve significantly different levels of bracken control at a site by site basis. This result should not be unexpected due to the unique interaction of bracken with this particular management protocol and climatic conditions.

Management interaction with bracken

Frond production is a vulnerable stage in the bracken growth cycle. The investment of energy required to fuel frond emergence, development, and expansion is repaid within undisturbed bracken stands when photosynthetic production exceeds the energy level required to maintain the frond structure. This 'excess' energy is translocated to the rhizome whereupon carbohydrate stores are replenished. Bracken control can exploit this state of vulnerability by interrupting the movement of plant energy. Damage may be inflicted resulting in both frond and rhizome biomass loss thereby constituting management success i.e. a depletion in weed biomass.

Climate interaction with bracken management

Of the cutting treatments employed, cutting once yearly permitted the longest period of frond expression uninterrupted by management practices. It is this duration of freedom from artificial interference which permits climate to exert a greater influence over frond expression and hence determine the consequences of bracken control. Asulam treatment affected an immediate severe level of control upon bracken fronds, such that differences between sites were not evident. In the absence of follow-up treatments, differential recovery between sites may be detected in future years, however, within the confines of this study such contrasts were not evident.

5. Evaluation of a bracken (*Pteridium aquilinum* (L.) Kuhn.) growth model and the effects of control strategies across a range of climatic zones in Great Britain

5.1. INTRODUCTION

Bracken is a species in conflict with the activities of man. This aggressive weed species presents problems for agriculture (Lawton & Varvarigos, 1989), forestry (Biggin, 1982), conservation (Pakeman & Marrs, 1992a), recreation (Long, 1988), shooting (Hudson, 1986) and water collection (Williams *et al.*, 1987). Moreover, it has been implicated as a human health hazard via suspected carcinogenic spores (Evans, 1987), contaminated well-water (Galpin & Smith, 1986), and provision of a habitat favoured by sheep ticks which transmit Lyme Disease (Habicht *et al*, 1987).

In Great Britain, the highest concentrations are found in northern and western areas (Watt, 1976). Estimates of bracken areal coverage vary, however, the most recent, and most extensive, assessment of bracken abundance, calculated a considerable bracken resource (17073 km^2) divided into various categories (Bunce *et al.*, 1992).

5.1.1. Bracken Control

Physical, chemical, biological and environmental approaches to bracken control have been proposed or are currently available for management programmes. Two of the most common techniques employed in the uplands of Great Britain are cutting or spraying with the herbicide asulam (Lawton & Varvarigos, 1989).

Bracken possesses an extensive rhizome system which stores carbohydrate and has a large number of resting and active buds. Cutting removes frond biomass from the plant system which constitutes a loss of energy from the rhizome network which has provided the initial investment of carbohydrate for frond growth. The efficacy of cutting treatments is enhanced when cut events are applied in relation to bracken growth in order to maximise energy loss (Lowday *et al.*, 1983).

Asulam is applied to bracken fronds in mid-summer, whereupon it is translocated to the rhizome system and accumulates in buds and apices. Degeneration of these structures is affected via the inhibition of RNA and protein synthesis (Veerasekaran *et al.*, 1977). No effect is visible in the year of treatment, but very few fronds are produced in the season following application. A depletion of rhizome carbohydrate occurs because rhizome respiration continues and there is a presumed reduction in photosynthetic production, as a consequence of reduced frond number. High target specificity (ferns and docks are susceptible) and low toxicity to mammals and fish has permitted approval of asulam for aerial application (Soper, 1986).

None of the bracken management options available provide long-lasting control. At present, effective control relies upon treatment continuity.

The current bracken problem consists of three parts:-

- specific problems (i.e. bracken interference with land use and health issues).
- extent of the problem (bracken occurrence and abundance).
- difficulties in alleviating the problem (bracken control is expensive and time consuming).

5.1.2. Bracken Models

Results of bracken management operations are inconsistent and the ability to identify the probable consequences of management would prove valuable in order that finite resources may be better directed thereby facilitating improved bracken control. In addition, it is believed that global warming will change the climate across Great Britain (United Kingdom Climate Change Impacts Review Group, 1991). The potential for such a climatic shift to exacerbate the current bracken problem requires investigation. It was against this backdrop that models based on bracken physiology and ecology were developed (Pakeman *et al.*, 1994). These models can predict bracken growth and spread at the site, regional and national level in response to different control strategies, different climate scenarios and their interaction.

BRACON (a model describing the detailed effects of BRAcken CONtrol)

BRACON is a mathematical model which predicts the response of bracken to a range of climate scenarios and a number of control regimes. These regimes include cutting, spraying with asulam, overplanting with trees and release of insect biological control agents and may be considered individually or in combination.

BRACON considers the movement of carbon through the plant by describing the yearly growth cycle in terms of rhizome biomass, carbohydrate content, and frond biomass. Several physiological processes are included in the model: rhizome respiration; rhizome senescence; rhizome to frond transport; daily dry matter production; dry matter partitioning; frond senescence; cost of carbohydrate movement; and initial allocation of carbohydrate to the rhizome. Given a starting value for rhizome biomass and the ambient environmental conditions, the model calculates daily losses and gains via the processes listed.

Predictions are made for individual 40 × 40 km grid cells based upon the mean environmental conditions operating within that area. A set of readily available meteorological data was used for reference within the model. Daily changes in environmental variables are obtained from sine functions fitted to yearly maxima and minima for soil temperatures and solar radiation. Daily changes in transpiration rates are calculated by assuming a linear increase and decrease between annual maximum and minimum values. The environmental variables considered are soil temperature, incident solar radiation, dates of first and last frosts, and rates of actual and potential evaporation.

Model Predictions

Suitable data for testing bracken control predictions across the current range of climatic conditions within Great Britain were not available. The model has, however, been tested against:

- the data used in its development
- results from an independent study in the Breckland (Lowday, 1987)
- data from a study in the North York Moors (Pakeman & Marrs, 1993a).
- data from a comprehensive study of bracken growth, carbohydrate partitioning and control in Breckland (Pakeman & Marrs, 1994).

This limited assessment confirmed the model as giving reasonably accurate predictions of bracken dynamics, however, to be of any value as a predictive tool, a national appraisal of model performance was required.

Under the expected climate scenario for the year 2030, it had been predicted that bracken stands would become increasingly resilient to standard bracken control practices (Pakeman & Marrs, 1992b). If BRACON can be validated under present climatic conditions, then greater confidence can be attached to predictions for future climate scenarios. Regional differences in bracken response to control regimes have been detected across a range of climatic conditions in Great Britain (Chapter 4.). The ability of the model to accommodate these response contrasts required investigation. The aim of this work was to test the validity of model predictions against data derived from a series of manipulative experiments into bracken control and gauge the accuracy of expected bracken response across several climatic zones in Great Britain.

5.2. MATERIALS & METHODS

The experiments which yielded test data for model predictions were initiated in 1993 and are described in full earlier (Chapter 2.). In brief, a series of identical bracken control trials were conducted simultaneously at six sites (Table 2.2. & Figure 2.1.) which were selected on two criteria:

- land managers indicated bracken growth was a problem
- representative of the range of climatic conditions prevailing across Great Britain.

The seasonal response of bracken (rhizome and frond component) was monitored in response to four control strategies:

1. Untreated 'control'.
2. Cut once yearly (late July).
3. Cut twice yearly (mid-June and late July).
4. Single application of asulam in 1993 (late July).

5.2.1. Model Simulations

BRACON was used to simulate bracken rhizome and frond biomass dynamics in response to the four bracken control treatments at each of the study sites over a three year period.

Bracken status

Initial starting values (rhizome biomass at January 1st, 1993) for all modelled management scenarios at individual sites were extrapolated from the mean biomass figures derived from untreated and asulam sprayed plots within that site during spring 1994 which were effectively untreated at that stage (Figure 2.2.; cutting and spraying combined treatments are not considered within this appraisal of BRACON). Pooling these plot means provided a more accurate assessment of bracken rhizome biomass prior to commencement of treatment.

Rhizome samples from spring and summer 1993 were discarded due to technical difficulties. Autumn 1993 samples despite being accurate measurements of rhizome biomass at the time of sampling were an underestimation for end of season reserves at some sites. This was due to the presence of carbohydrate within the frond bases because sampling had occurred too early at some of the sites. Tissue biomass and carbohydrate biomass for spring 1994 samples were set at 73% and 27% of rhizome biomass respectively (Pakeman & Marrs, 1994a).

Environment

Bracken dynamics were modelled using:

- 40 × 40 km square environmental data applicable to individual sites
- appropriate site altitude
- default settings (i.e. current climatic conditions and no change in photosynthetic efficiency).

Management

Modelled cutting regimes occurred on day 166 and 212 during each year of treatment: these values were unchanged as they were approximate to actual cutting dates (Table 5.1.).

Table 5.1. Divergence (days) between modelling constants and actual dates for bracken cutting. 'Cut date 1' is 16th June; 'Cut date 2' is 31st July.

	Cut date 1			Cut date 2		
Site	1993	1994	1995	1993	1994	1995
Mull	−5	−5	-4	+3	−11	-10
Scottish Borders	−3	−3	-3	+4	−8	+3
Lake District	−2	−2	-3	−7	+2	+5
Clwyd	−1	−1	-2	−6	+4	-6
Breckland	+4	+3	+3	−1	−3	-2
Devon	+2	+1	+2	−2	−5	-4

The 'effectiveness of spray' following a single application of asulam was calculated as proportion of frond biomass present in the year after spraying relative to frond biomass the previous year (Pakeman & Marrs, 1993a). The experiment which yielded test data, considered bracken management regimes which were not modelled: treatments that combined cutting with spraying asulam. The effects of a single cut following a single application of asulam in the previous year was, when frond samples were collected in 1993-94, effectively the same treatment as that applied to sprayed-only plots (Figure 2.2.). Data from this additional treatment was used to calculate the effectiveness of spray in order that a more accurate value of achievable control at individual sites could be calculated.

5.2.2. Model Evaluation

BRACON simulations of rhizome and frond biomass dynamics for the twenty-four different site-treatment combinations (6 sites × 4 treatments) were plotted and overlain with mean recorded biomass, and their associated 95% confidence intervals, collected throughout the three year study. The extent to which simulated biomass was outside the 95% confidence intervals and how clearly the seasonal fluxes in simulated biomass were detectable within collected data were identified. However, this only permitted a subjective assessment of model prediction validity.

Model accuracy was assessed objectively by calculating the correlation coefficient between model predicted biomass and recorded biomass. This enabled evaluation of BRACON predictions for individual treatments at national level and regional levels. In addition, the applicability of the model for evaluating bracken management at individual sites was considered.

5.3. RESULTS

5.3.1. Testing BRACON Frond Predictions

Frond samples collected throughout the experiment were unavoidably subject to decay during the interval between sampling and biomass determination. This was reflected in the comparison between model output and actual biomass, where actual values were less than predicted values (Figure 5.1.). In order to make comparison between treatments, frond decay was assumed equal for all samples. Thus, the effects of bracken control treatments were calculated relative to untreated values for both actual and model data.

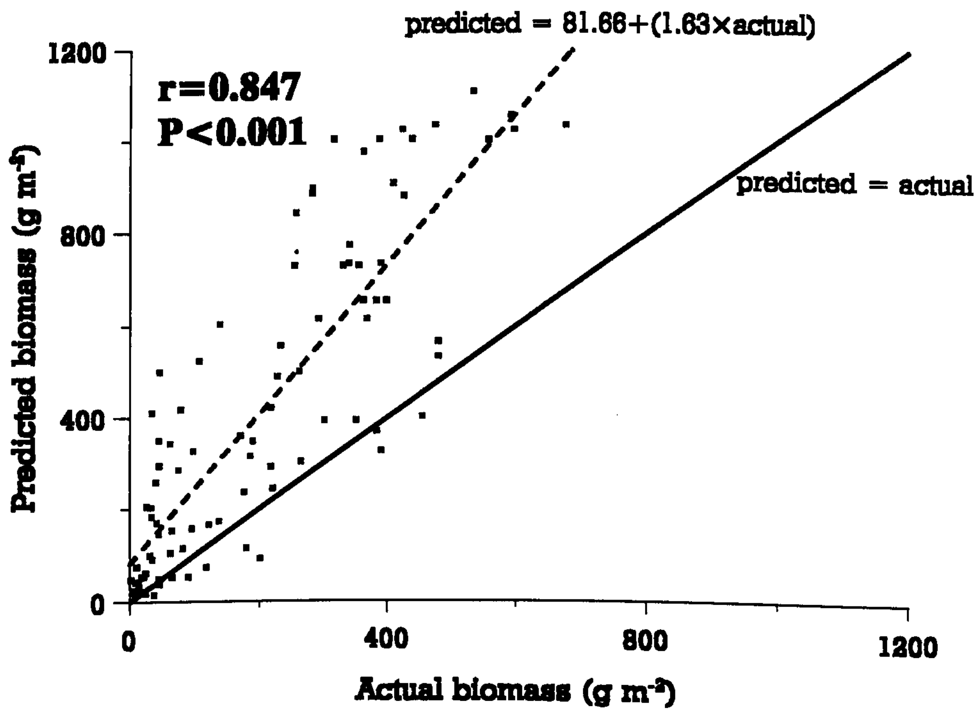


Figure 5.1. Correlation between predicted and actual frond biomass across all experimental sites for all bracken control treatments. Solid line is predicted = actual. Dotted line is fitted regression equation. 'r' = correlation coefficient; 'P' = significance of correlation.

The mean percentage of frond biomass in treatments relative to the untreated 'constant' for all sites (n=6) was calculated for each year throughout the study (Table 5.2.). Similar levels of frond biomass decline were observed between the field data and model predictions following one cut yearly or a single application of asulam. This was to be expected for the latter treatment as the 'effectiveness of spray' within the simulations was calculated directly from actual biomass values. Discrepancies were apparent between harvested and simulated frond biomass when bracken was cut twice yearly. The experimental data, presented in relation to this treatment, is a measure of frond regrowth following the cut 5 - 6 weeks earlier in the season. In the first year, a lower value of frond regrowth is observed in the field following the single initial cut; a value which was maintained throughout the experiment. BRACON expects frond regrowth to be much greater during the first year, however, by the second year frond biomass is consistent between the simulation and the experimental results. In the third year, the model predicts that frond biomass will decline in the field, however, this was not found.

Table 5.2. Predicted and actual mean percentage of untreated frond biomass following bracken control treatment at all experimental sites. Treatment codes are: C1, cut once yearly; C2, cut twice yearly; A, single application of asulam. Standard errors (n=6) are given in parentheses.

Treatment	Year	Mean percentage of untreated frond biomass	
		actual	predicted
C1	1	100	100
	2	69.0 (10.1)	59.1 (4.9)
	3	54.6 (11.0)	46.3 (4.5)
C2	1	15.1 (2.6)	44.9 (2.3)
	2	22.0 (6.8)	16.4 (1.4)
	3	13.8 (3.5)	6.2 (1.4)
A	1	100	100
	2	3.4 (0.6)	5.8 (1.2)
	3	13.9 (4.9)	13.2 (3.3)

5.3.2. Testing BRACON Rhizome Predictions

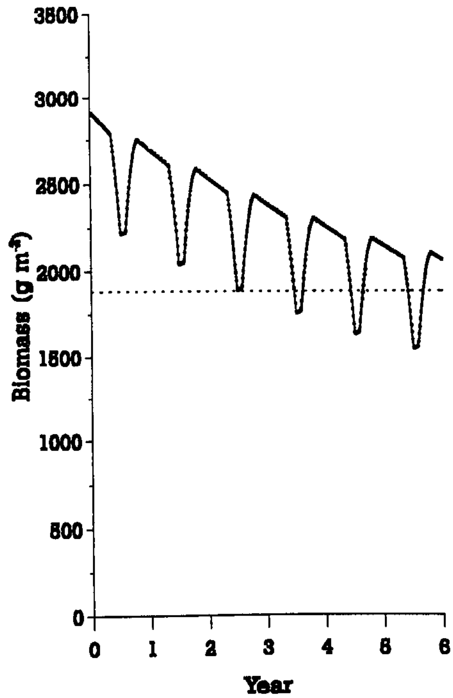
Equilibrium biomass discrepancies

Equilibrium biomass represents the maximum attainable biomass predicted by the model given environmental constraints, given a long enough time for equilibrium to be achieved, and should be reflected in the field data. Predicted equilibrium biomass for the 40 × 40 km squares containing the two Scottish sites was considerably less than actual recorded biomass. This discrepancy manifested itself within model simulations by 'driving' biomass down towards equilibrium (e.g. Figure 5.2.(a)). This decline in biomass must be due to an inappropriate environmental data set for the test sites which placed unrealistic limitations on equilibrium biomass at the sites concerned. This could have obscured subsequent reductions in biomass due to bracken management. In order to compensate for this, new environmental data sets were ascribed to the two sites concerned which produced a relatively stable annual growth cycle for untreated bracken (e.g. Figure 5.2.(b)). This was achieved by selecting pre-existing data sets used in alternative 40 × 40 km grid cells which were capable of supporting recorded rhizome biomass, and had similar growing seasons to those operating at each site. All other sites had sub-equilibrium biomass, which increased towards equilibrium within model simulations.

Predictions and field data: problems of comparison

Model predictions for each site-treatment combination were plotted and overlain with the respective mean sample biomass and associated 95% confidence intervals obtained throughout the study. A consistent feature between all site-treatment scenarios was the high variability attached to biomass samples (e.g. Figure 5.3.; results from only one site presented, however, similar figures for all possible site-treatment combinations are presented in Appendix A.3) which tended to obscure the seasonal fluxes which had determined the sampling protocol.

(a)



(b)

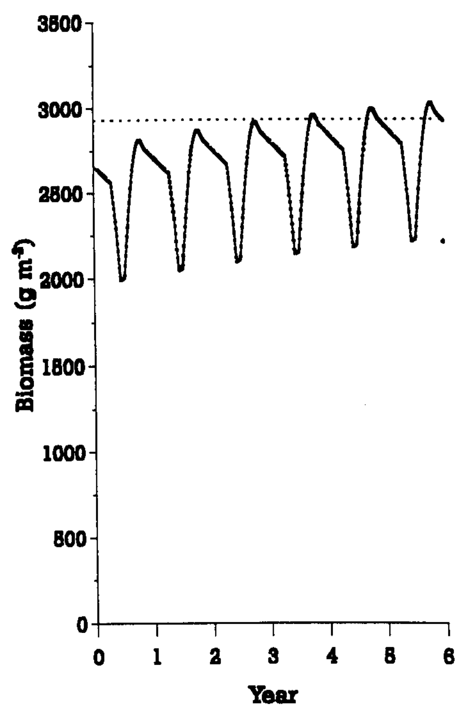
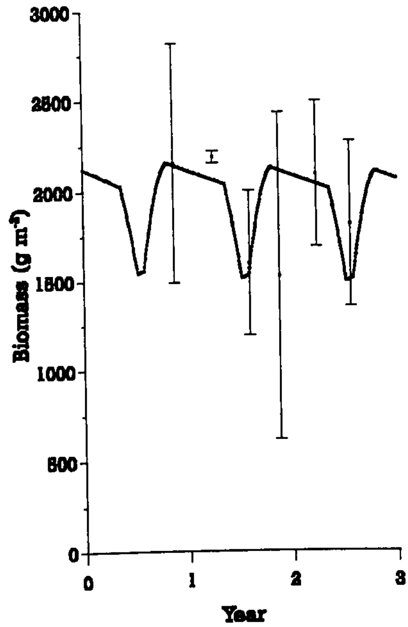


Figure 5.2. BRACON predictions for untreated bracken in Mull with reference to (a) the original environmental data set and (b) the new environmental data set. Dotted line indicates predicted equilibrium biomass. Starting values for both simulations are extrapolated from the spring 1994 field data.

(a)



(b)

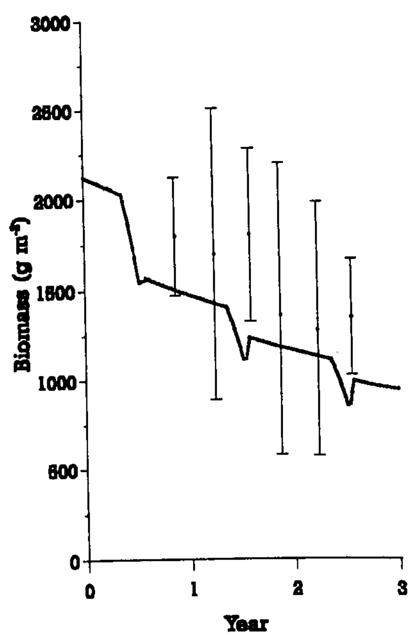
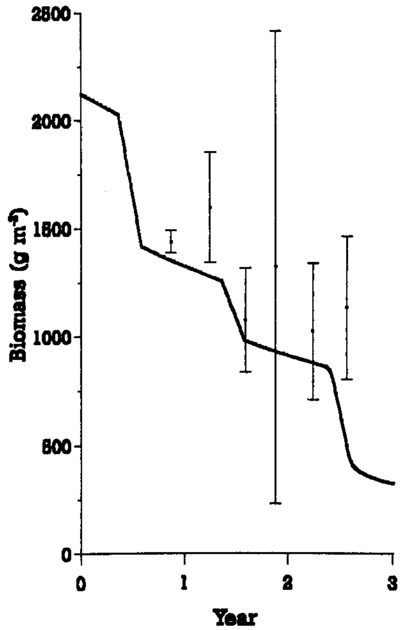


Figure 5.3. BRACON simulations for Clwyd study site following bracken control treatments (a) untreated; (b) cut once yearly; (c) cut twice yearly; (d) asulam. Predictions are overlain with plot means and their associated 95% confidence interval obtained throughout the experiment.

(c)



(d)

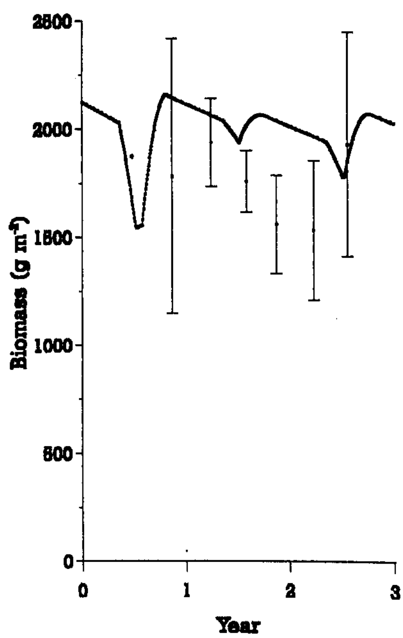


Figure 5.3. continued.

Correlation analysis

All site-treatment combinations

Correlation of actual rhizome biomass samples obtained from all sites in relation to all management regimes throughout the entire study, with model predictions was significant (P<0.001) (Figure 5.4.).

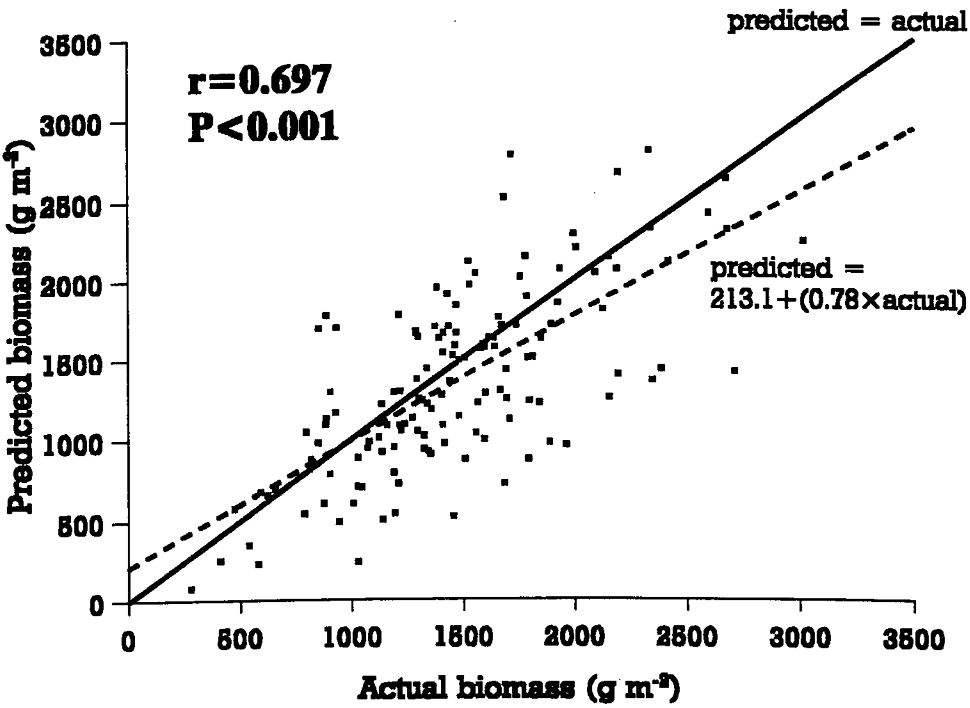


Figure 5.4. Correlation between predicted and actual rhizome biomass across all experimental sites for all bracken control treatments. Solid line is predicted = actual. Dotted line is fitted regression equation. 'r' = correlation coefficient. 'P' indicates significance of correlation.

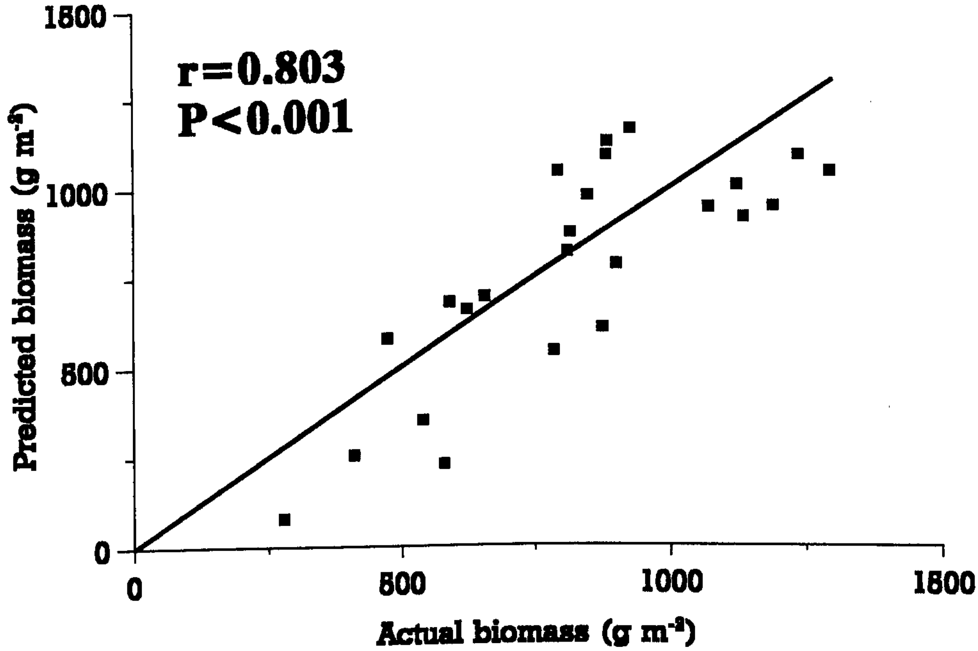
Individual sites (all treatment combinations)

Predicted rhizome biomass was correlated with actual biomass recorded from all experimental plots at individual sites. Modelled predictions for bracken response to combined management treatments in Breckland and Clwyd had the greatest significance (P<0.001). The remaining sites produced significant correlations (P<0.05) with the exception of the Scottish Borders (e.g. Figure 5.5.). Increased significance appeared to be attached to sites which exhibited greater reductions in biomass after cutting (Table 5.3.).

Table 5.3. Percentage of untreated rhizome biomass after cutting treatments (C1, cutting once yearly; C2, cutting twice yearly) recorded during spring 1995. Significance of correlation between predicted and actual rhizome biomass recorded from individual sites (all treatments). *** P<0.001; ** P<0.01; * P<0.05; NS, not significant.

	Percentage of untreated rhizome biomass		Significance of correlation
Site	C1	C2	
Mull	107.0	71.0	*
Scottish Borders	94.6	79.5	NS
Lake District	91.2	72.8	*
Clwyd	60.7	49.1	***
Breckland	70.5	65.6	***
Devon	68.3	66.7	*

(a)



(b)

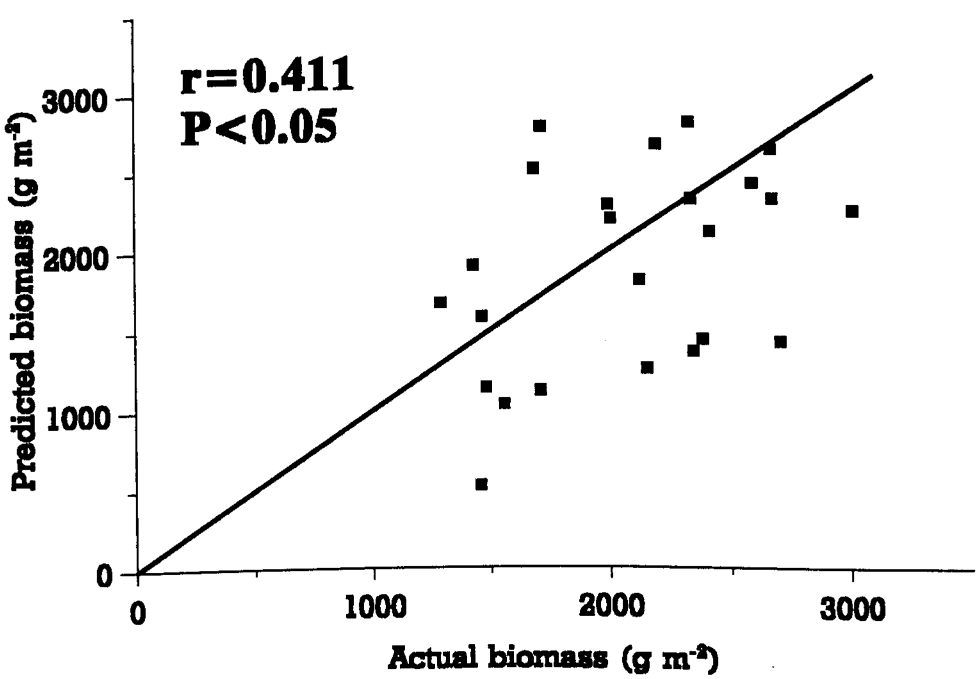


Figure 5.5. Correlations between predicted and actual rhizome biomass for combined treatment scenarios at (a) Breckland and (b) Mull. 'r' = correlation coefficient. 'P' indicates significance of correlation.

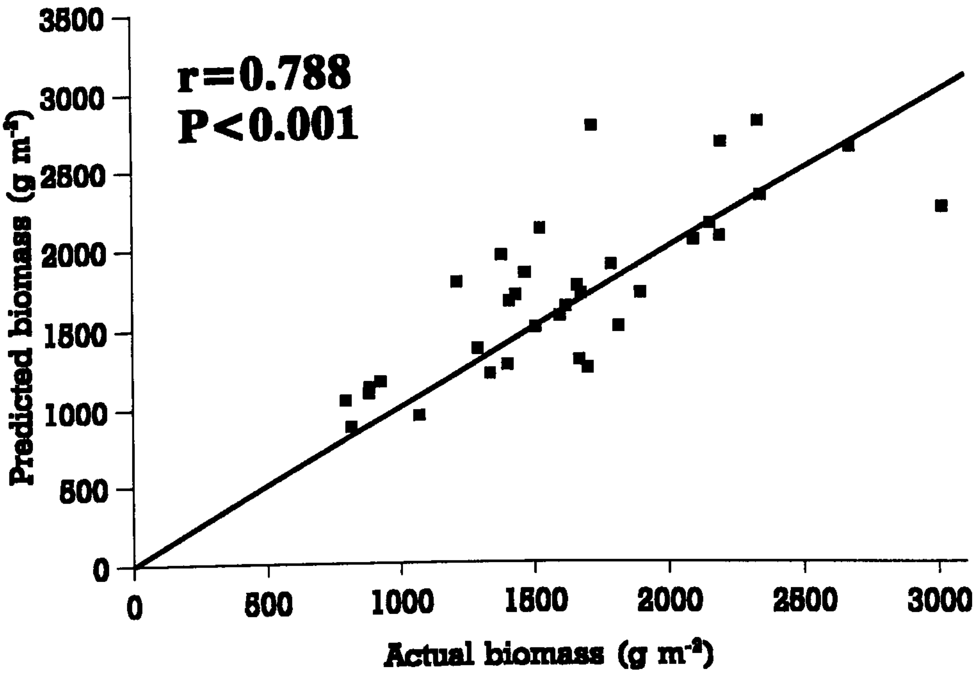
Individual site-treatment combinations

Correlations between model rhizome biomass predictions and actual recorded rhizome biomass were significant (P<0.05) at only one of the twenty-four site-treatment combinations (six sites × four treatments): cutting twice yearly at Lake District. Correlation coefficients were greatest for cutting treatments.

Individual treatments (all sites)

Predicted rhizome biomass was correlated with actual biomass for individual treatments recorded at all sites. BRACON predictions for bracken response to single management treatments across the range of environmental conditions operating at all study sites were significant for all control options (Figure 5.6.). Significant (P<0.001) correlations were identified for untreated, cut twice yearly or sprayed bracken. Cutting once yearly produced a less significant (P<0.01) correlation.

(a)



(b)

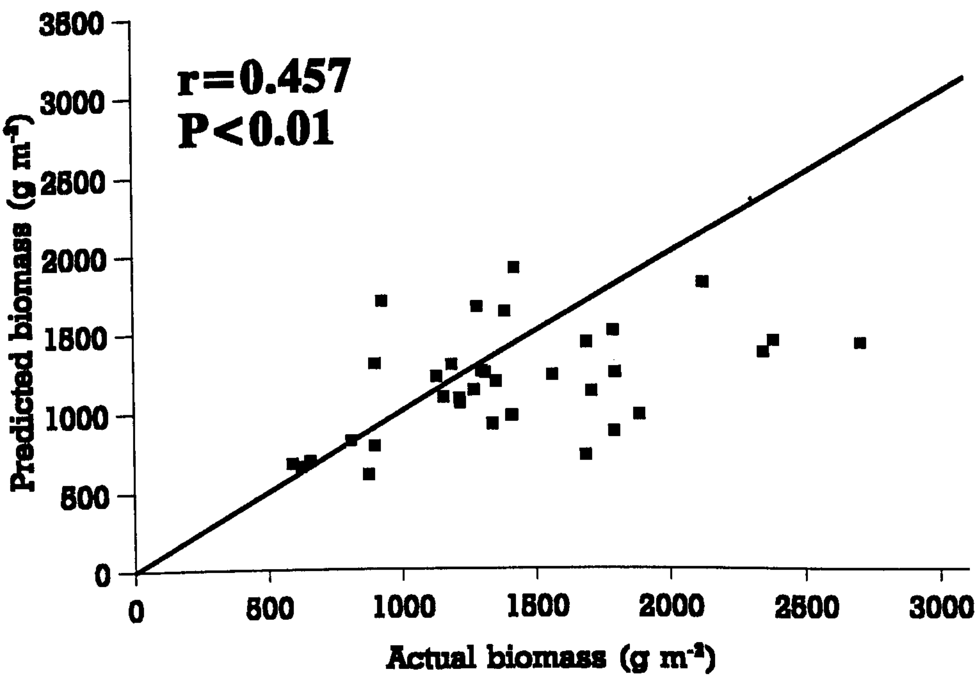
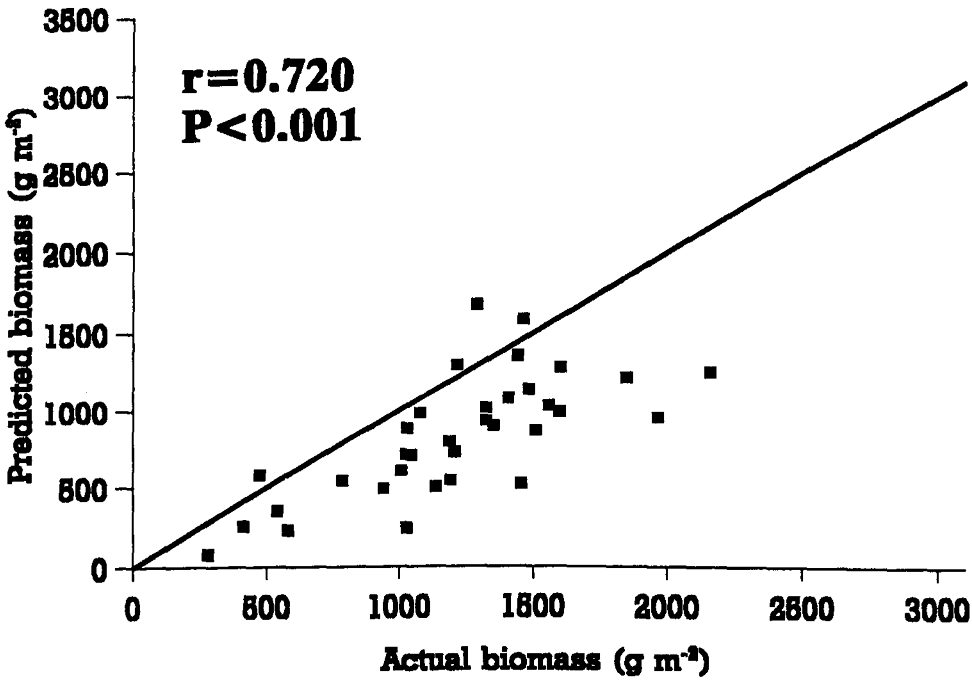


Figure 5.6. Correlations between predicted and actual rhizome biomass across all experimental sites for bracken which was (a) untreated; (b) cut once yearly; (c) cut twice yearly; (d) sprayed with asulam. 'r' = correlation coefficient. 'P' indicates significance of correlation.

(c)



(d)

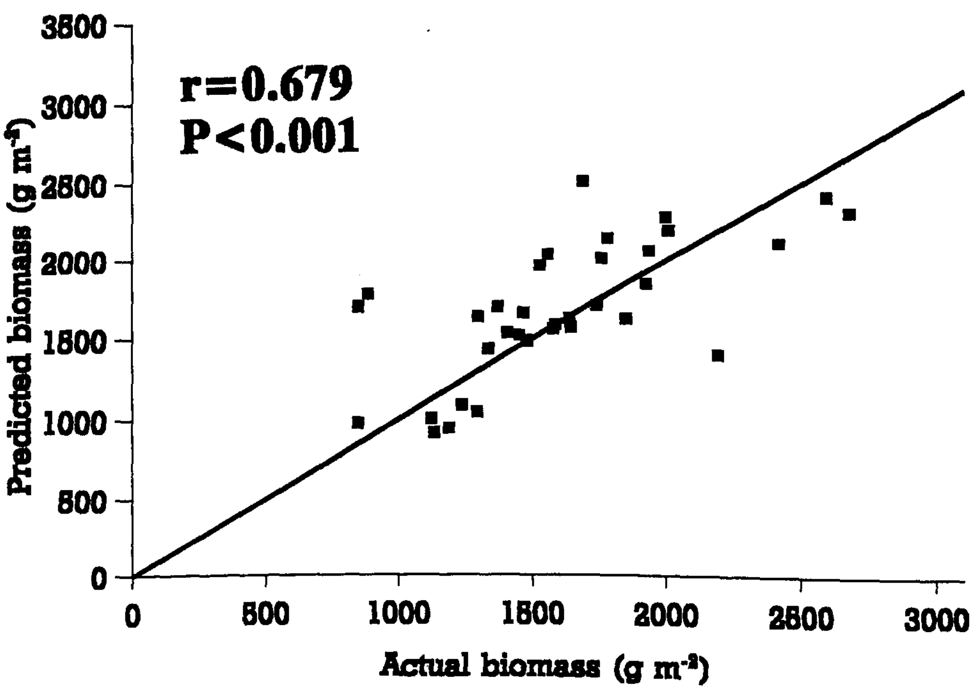


Figure 5.6. continued.

5.4. DISCUSSION

5.4.1. The Role of the Model in Practical Bracken Management

The model is of little practical value as an indicator of frond biomass. Frond production is known to be strongly influenced by annual climatic fluctuations which can distort the accuracy of model predictions regardless of any imposed management regime (Lowday & Marrs, 1992a). The outcome of control operations upon this morphological indicator is therefore of little value in itself. The real value of the model is as a gauge of bracken 'strength' i.e. its resilience to weed control measures. The key to successful bracken control is the depletion and sustained reduction of rhizome biomass. Therefore, it was the accuracy of predictions concerning rhizome biomass which required determination in order to test the practical value of the model. However, to assess model applicability and identify possible deficiencies within its structure, frond dynamics also must be considered.

Modelled predictions of reductions in frond biomass relative to untreated bracken were consistent with the experimentally derived data. A consistent hierarchy of effective bracken management regimes was found at each site: cutting once yearly was less effective in reducing frond biomass than either cutting twice yearly or spraying with asulam which gave similar levels of success. This ranking of treatments was predicted within the model simulations.

The discrepancy in first year frond biomass for bracken cut twice yearly, observed between the model and field data, did not appear important as, in the subsequent two years, very similar values were obtained. However, this excessive simulated regrowth in the early stages of bracken control may explain the differences in predicted and actual rhizome dynamics discussed later.

5.4.2. Interpretation of Model Predictions using Generalised Environmental Data

BRACON uses mean values for climatic data recorded from several meteorological monitoring stations within a 40 × 40 km grid cell, and performs mathematical functions upon them, to interpolate environmental conditions for any particular day. For accurate predictions, values accessed using this procedure will need to be modified to account for site specific factors, e.g. aspect, soil depth, water-logging (Pakeman & Marrs, 1993b), which could alter the micro-climate substantially from the modelled scenario. Where extremes of any single or all these environmental factors occur, predictions will be a distortion of actual events. These discrepancies have to be anticipated when predictions are made at a relatively coarse scale. The collection of such data was outwith the scope of this study.

The scale of regional predictions are determined by the scale of available climatic data (40 km grid). More practical information could be provided for land managers if predictions were made for smaller grid units however this climatic data is not available. If detailed site specific predictions are required then site specific environmental data are also needed and a model to utilise such data already exists. BRACON is only intended as a general tool whose predictions should not be taken as absolute. Predictions require interpretation by users of the model to apply their knowledge of individual bracken-infested sites (e.g. favourable aspect yet prone to water-logging) to evaluate the direction of deviation from a generalised simulation for their local region.

5.4.3. New Environmental Data Sets

Problems with the use of 40 × 40 km square environmental data were encountered within this study. New environmental data sets with similar or corrected frost dates, capable of supporting recorded biomass, were required for meaningful model evaluation of bracken dynamics in Mull and the Scottish Borders. The reason for this is that the actual biomass was greater at these sites than predicted equilibrium biomass. The new climate scenarios increased equilibrium biomass, however, they also included increased soil temperature and incident solar radiation. These figures may have been inappropriate and brought about an improvement of treatment efficacy, within the simulations, by promoting frond growth/regrowth, thereby increasing losses of biomass from the system via cut material. This may in part explain the discrepancy in frond regrowth identified in bracken cut twice yearly. However, this discrepancy would only occur at two of the six study sites and would not invalidate the national trends.

5.4.4. Variability of Experimental Data and its Interpretation

The figures of model simulation dynamics and actual biomass with attached 95% confidence intervals indicated the considerable variability encountered throughout the sampling visits. The variability obscured the seasonal fluxes in rhizome biomass which had determined the sampling protocol. From inspection of the graphs, it was evident that a high variability in rhizome biomass could be detected at the site level and assessment of the model accuracy was difficult and subjective. A method to gauge objectively the accuracy of modelled predictions was required.

5.4.5. Limitations of Correlation

The sensitivity of correlation analysis is increased by the number of observations and the range of observed values. Throughout the course of the experiment, a relatively consistent value for rhizome biomass was exhibited by untreated and sprayed bracken. However cutting bracken, in particular cutting twice yearly, resulted in a steady decline in rhizome biomass. At sites where cutting was most successful at reducing rhizome biomass (relative to untreated plots) a greater range of biomass values are obtained throughout the three years of treatment. Correlation coefficients were greater within cut plots than within untreated or sprayed plots, however, only one of the twenty four possible site-treatment combinations was significant (cutting twice yearly at Lake District).

The variability attached to mean sampled rhizome biomass could obscure differences in bracken response to treatment however this was ignored within the correlation analysis. It was only where large reductions in biomass occurred (after cutting), that trends could be identified. This identification could only be made with confidence when biomass reduction was sufficient to overcome the problems of sample variability (e.g. biomass may have been limited due to soil depth, which varied within plots regardless of imposed management regime).

Modelled predictions for untreated bracken and bracken sprayed with asulam appeared reasonable. The effects of cutting appeared less accurate: the model tended to overestimate the influence of both cutting frequencies. This tendency has been noted previously (Pakeman & Marrs, 1994a). The use of correlation analysis provided a ranking of regional, and treatment prediction accuracy.

Within the short time frame of this study, the apparent discrepancy in the cutting treatment (as a consequence of BRACON failing to consider frond regrowth in the latter portion of the growing season) may be exaggerated in terms of impact on the rhizome system. If any/greater regrowth was predicted in the model, energy losses would be compounded as the follow-up cut removed a greater amount of energy, similar to that which occurs in the field. In addition, the apparent resilience of the rhizome system to cutting may be due to regrowth after the final cut in each season. The model predicts that there is no regrowth after cutting in late July. Field observations show that this is not the case. If regrowth is beneficial, and energy loss via cutting can be offset then this could explain the resilience observed in the field. It has been suggested that a change in frond photosynthetic efficiency occurs and may be the cause of experimentally derived figures for rhizome biomass being consistently in excess off predicted values. However, if regrowth is not beneficial and fronds are terminated prior to returning energy to the rhizome then field values would be expected to be less than the model predicts.

5.4.6. Conclusions

The model gave a reasonable description of rhizome dynamics for all individual treatment scenarios at a national level and combined treatment scenarios at a site by site level. It is least effective for the sites where new environmental data sets were required but this step was necessary to remedy problems in predicting equilibrium biomass for the 40 × 40 km grid cells.

The impact of cutting once yearly upon the rhizome system was found to be significantly different at the individual sites for which treatment scenarios were modelled (Chapter 4.). Despite these differences, the correlation between predicted and actual rhizome biomass obtained from plots cut once yearly at all sites was significant albeit at a lower level relative to other management options. Therefore, within the confines of this test, it can be concluded that given the range of environmental conditions currently prevailing across Great Britain, the model is capable of accommodating these climatic contrasts and synthesising a reasonable description of bracken status following control treatments.

The correlation test was a poor indicator of model accuracy at the site-treatment level due to an apparent greater than expected resilience to bracken control by cutting. In addition, rhizome biomass variability reduced the sensitivity of the model test. Therefore, it was necessary to base judgement upon a subjective interpretation of model simulation graphs.

Despite the accurate predictions at some sites, there was a tendency for the model to overestimate the impact of cutting upon the rhizome system. This study indicates that the intensity of bracken control regimes required to achieve a managerial objective is underestimated. but only if the model is correct in identifying regrowth in the latter stages of the growing season as a minor and unimportant process in relation to management practices.

Continued monitoring of experimental plots would yield data to test modelled predictions for either continuation or cessation of bracken control. This could identify the most effective practical and economic cycle of bracken treatment could be identified at a regional level.

An investigation of the importance of frond regrowth throughout the growing season is required. Furthermore, a study into possible differential response in activation and production of buds on the rhizome following bracken control treatments at a site by site basis could aid understanding into the deviations between modelled predictions and actual rhizome biomass. This could be facilitated further by monitoring carbohydrate fluxes: this data would have proven useful for calculating new model coefficients e.g. initial rhizome carbohydrate reserves, ratio between carbohydrate reserves and frond production. The time required to sample bracken as intensively as this study precluded such analysis.

6. Evaluation of a model describing vegetation succession after bracken (*Pteridium aquilinum* (L.) Kuhn) control

6.1. INTRODUCTION

Bracken (*Pteridium aquilinum* (L.) Kuhn) is an aggressive, invasive weed species which interferes with current land use practices in Great Britain (Lawton & Varvarigos, 1989; Biggin, 1982; Pakeman & Marrs, 1992a; Long, 1988; Hudson, 1986; Williams *et al.*, 1987), and constitutes a potential human health hazard (Evans, 1987; Galpin & Smith, 1986; Habicht *et al.*, 1987). Moreover, if current models of climate change are realised, with an increase in mean summer and winter temperatures of 1.4°C and 1.5 - 2.1°C respectively (United Kingdom Climate Change Impact Review Group, 1991), it is expected that the current bracken problem will intensify as it increases its areal coverage and effective control becomes more difficult (Pakeman & Marrs, 1992b).

6.1.1. Vegetation Restoration

Effective bracken control is expensive. It can necessitate an initial outlay of considerable capital; prove time-consuming; and be labour-intensive (Musgrave, 1993; Pakeman & Marrs, 1994b). If replacement vegetation can become established following good initial bracken control, this may suppress bracken recovery thereby minimising, and hopefully, eventually removing, the need for any form of follow-up bracken management. Factors determining the dynamics of the ground flora in its response to bracken control options are discussed earlier (Chapter 1.7.) and described by the mathematical model REBRA (Chapter 1.8.).

The response of the ground flora within experimental plots which had been subjected to different bracken control treatments (Chapter 2.4.) was monitored in order to provide test data for the revegetation model. The validity of REBRA had been considered previously in terms of six key species and bracken, with predictions for their individual performance assessed (Pakeman *et al.*, 1995). Here, instead of comparing theoretical and actual fluxes in individual species abundance, the accuracy of predicted changes at the community level were assessed. This was facilitated by multivariate analysis of vegetation data.

6.2. MATERIALS & METHODS

6.2.1. Study Site

In April 1993, as part of a national study into bracken control, an experimental site was established at Cavenham Heath (Grid Reference TL 754,724), in the Breckland of East Anglia. The site was inspected before frond emergence and located where the land manager indicated a closed canopy of bracken would occur. Experimental plots were established on a dense litter area.

6.2.2. Experimental Design

The experimental design used at individual sites is described earlier (Chapter 2.4.).

6.2.3. Treatments

Six bracken management treatments were applied:-

1. Untreated 'control'.
2. Cut once yearly (late July).
3. Cut twice yearly (mid June and late July).
4. Single application of asulam in 1993 (late July).
5. One cut and single application of asulam in 1993 (mid June and late July respectively).
6. Single application of asulam in 1993 (late July) followed by one cut (late July) in 1994.

Cut treatments were applied with a brushcutter and cuttings were left within plots. The herbicide asulam was applied at 4.4 kg a.i. ha^{-1} in 400 litres of water as the commercial formulation 'Asulox' (Rhône-Poulenc) using a knapsack sprayer. A non-ionic surfactant ('Agral') was added to the spray mixture at 0.1% v/v.

6.2.4. Assessment of Vegetation

Field data

Measurements of vegetation cover were recorded within two 1 m^2 quadrats located randomly within each experimental plot, during July 1994 and 1995. This provided test data for the model.

Predicted data

A baseline vegetation survey consisting of whole plot assessments of vegetation cover in three plots which were randomly selected was conducted during May 1993. These data provided input for the model, upon which REBRA based its predictions. The model accessed a BRACON biomass file based upon recorded rhizome biomass and described vegetation dynamics using:

- applicable 40 × 40 km square environmental data
- appropriate site altitude (15 m)
- default settings (i.e. current climatic conditions; no change in photosynthetic efficiency).

6.2.5. Multivariate Analysis

Data were analyzed using the ordination technique of DEtrended CORrespondence ANAlysis and the classification procedure Two-Way INdicator SPecies ANalysis. The respective analyses were performed using the FORTRAN programs DECORANA and TWINSPAN (Hill, 1979a,b).

The sample × species data matrix used in both the DECORANA and TWINSPAN analyses consisted of mean replicate cover values converted to a five point scale (1, 0.1 - 5%; 2, 5.1 - 26%; 3, 26.1 - 51%; 4, 51.1 - 76%; 5, 76.1 - 100%).

6.2.6. Model Evaluation

Three data sets were analyzed independently using multivariate analysis to investigate:

- *Changes in the actual vegetation community (based upon field data 1994-95)*

  The species composition data (attributes) from each of the 18 plots (individuals) were represented twice (1994 and 1995) within the data matrix.

- *Changes in the predicted vegetation community (based upon model predictions 1994-95)*

  The species composition data (attributes) from each of the five bracken control treatment scenarios (individuals) were represented twice (1994 and 1995) within the data matrix.

- *Differences between the actual and predicted vegetation community (based upon field data and model predictions 1994 and 1995)*

  The species composition data (attributes) from each of the five bracken control treatments (individuals) were represented twice (actual and predicted) within each of the two data matrices (1994, 1995).

6.3. RESULTS

6.3.1. Changes in Species Composition in the Field 1994-95

Analysis of variance indicated that bracken control treatment had no significant effect upon the percentage cover of any individual species within the ground flora, however, bracken frond cover was affected significantly (P<0.001). Only some of the species recorded (1994-95) can be considered within REBRA (Table 6.1.) predictions as the program confines its description of vegetation dynamics to a short-list of 76 species, and does not have information on non-vascular plants or tree species.

Table 6.1. Species recorded during vegetation surveys at Cavenham Heath in 1994-95. Significance attached to effect of bracken control treatment upon individual species percentage cover was calculated by analysis of variance. Individuals considered within REBRA predictions are also identified.

Species	Probability 1994	Probability 1995
Considered within model		
Carex arenaria L.	NS	-
Deschampsia flexuosa (L.) Trin.	NS	NS
Festuca ovina L.	NS	-
Holcus lanatus L.	NS	-
Rumex acetosella L.	NS	NS
bracken fronds	***	***
bracken litter	NS	NS
(bare ground)	-	NS
Not considered within model		
Betula L. spp.	NS	NS
Calluna vulgaris (L.) Hull	NS	NS
Carex L. sp.	-	NS
Senecio sylvaticus L.	NS	NS
moss spp.	NS	NS

(***, P<0.001; **, P<0.01; *, P<0.05; NS, not significant)

Field data from 1994 and 1995 were merged into a single data matrix and subjected to TWINSPAN analysis. The classification identified two discrete groups at the first level of division. Four treatment-year individuals were categorised within a single vegetation group (cutting twice yearly (1994 & 1995); asulam (1995); asulam with follow-up cut (1995)). TWINSPAN identified bracken litter cover as the indicator species separating group 'A' from group 'B' (Figure 6.1.). DECORANA separated the two vegetation assemblages principally along the first axis of the ordination (Figure 6.1.). This axis may have represented a gradient in the level of bracken control achieved using the different treatments, in terms of litter cover reduction. The ordination of species is presented (Figure 6.2.).

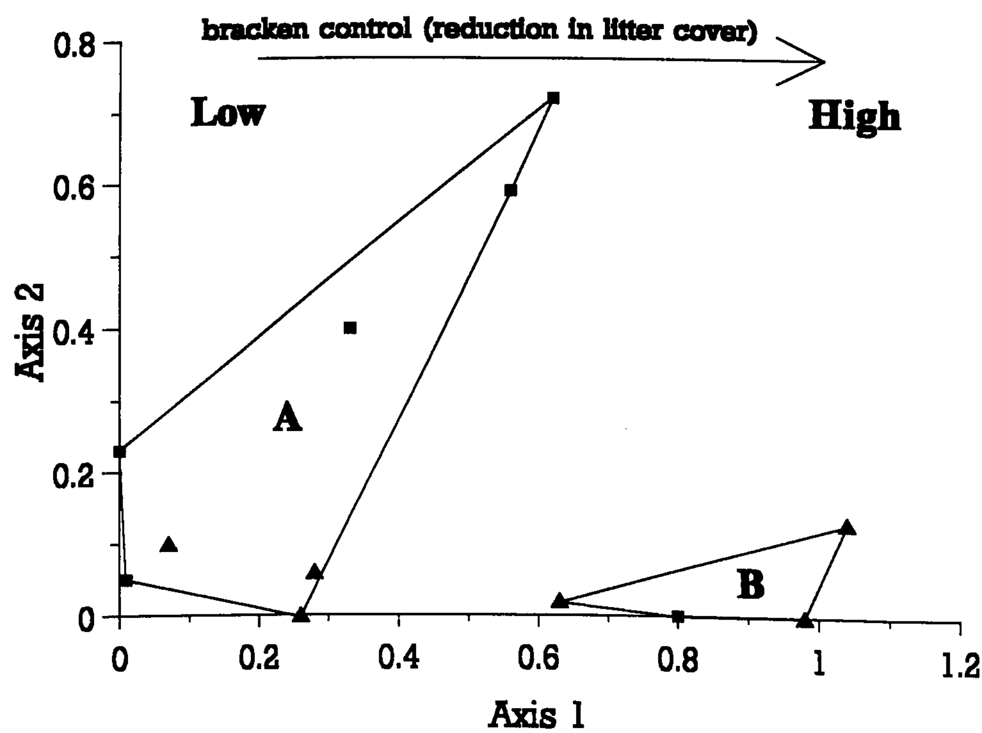


Figure 6.1. DECORANA ordination of 1994 (■) and 1995 (▲) recorded vegetation samples. The two TWINSPAN groups identified at the first level of division are indicated. Axes are in standard deviations of species turnover.

Cutting twice yearly produced the lowest litter cover in 1994 and 1995 (43.7% and 23.2% respectively), and was the only treatment which affected a significant ($P<0.05$) decline in litter cover (to 25.8% of untreated values in 1995) relative to undisturbed bracken. In 1994, spraying asulam affected the greatest initial decline in frond cover, however, the litter layer appeared relatively unaffected. In 1995, spraying asulam with/without a follow-up cut exhibited the lowest litter cover, second only to cutting twice yearly (Figure 6.3.).

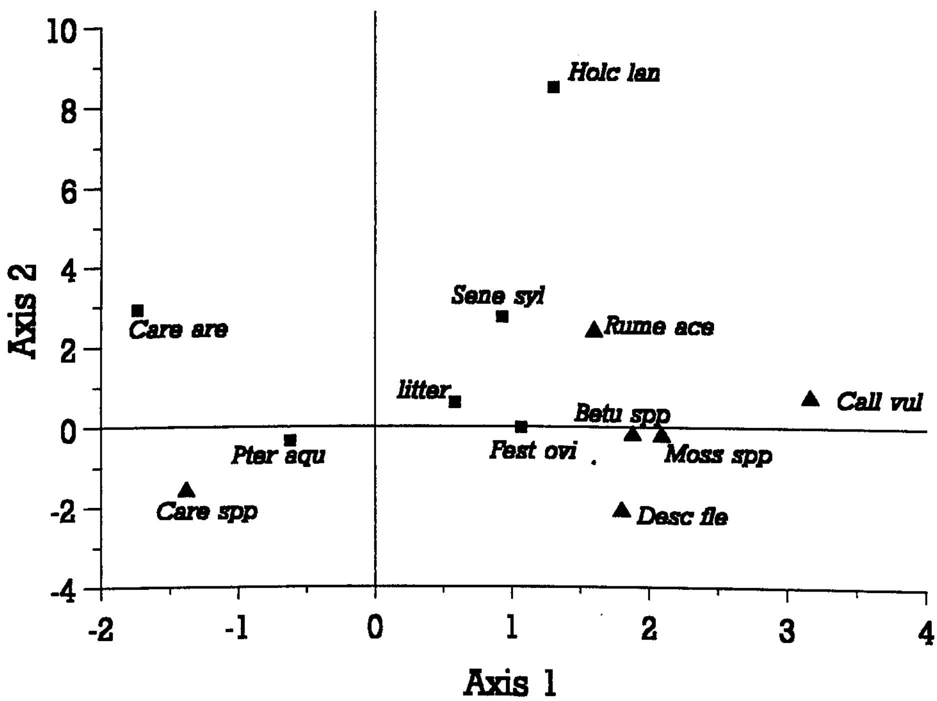


Figure 6.2. DECORANA ordination of species recorded during 1994 and 1995. The two TWINSPAN groups identified at the first level of division are indicated: the negative group (▲); the positive group (■). Axes are in standard deviations of species turnover.
Species codes are: Betu spp = *Betula* species.; Call vul = *Calluna vulgaris*; Care spp = Carex species; Care are = *Carex arenaria*; Desc fle = *Deschampsia flexuosa*; Fest ovi = *Festuca ovina*; Holc lan = *Holcus lanatus*; litter = bracken litter; moss spp = moss species; Pter aqu = *Pteridium aquilinum*; Rume ace = *Rumex acetosella*; Sene syl = *Senecio sylvestris*.

(a)

(b)

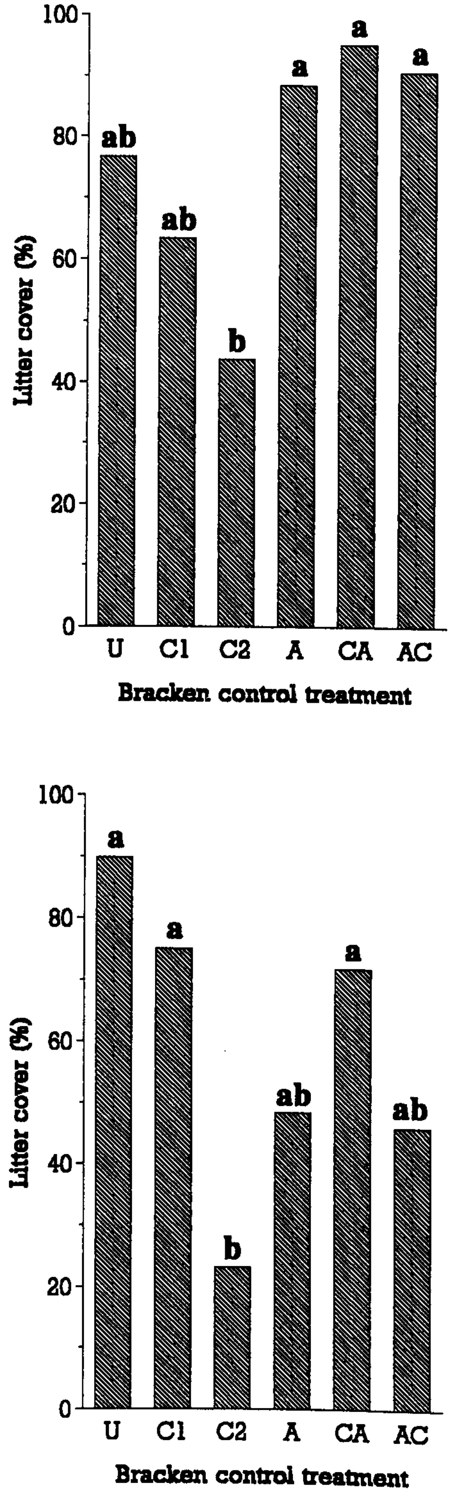


Figure 6.3. Percentage cover of bracken litter recorded during (a) 1994 (b) 1995 at Cavenham Heath. Treatment codes are: U, untreated; C1, cut once yearly; C2, cut twice yearly; A, asulam; CA, cut prior to asulam; AC, asulam with follow-up cut. Mean data is presented (n=3); bars with the same letter are not significantly different (LSD) at P<0.05: LSD (1994) = 34.4%; LSD (1995) = 48.2%.

6.3.2. Model Predictions 1994-95

Species detected at the baseline assessment of floristic composition formed the initial starting conditions from which REBRA generated its predictions. Only some of the species recorded are able to be considered within the successional model (Table 6.2.).

Table 6.2. Mean percentage cover (n=3) of species recorded at baseline assessment of floristic composition at Cavenham Heath study site. Species considered within REBRA predictions are also indicated. This data provided starting conditions for model simulations.

Species	Mean cover
Considered within model	
Vascular plants	
Agrostis capillaris L.	1.67
Calamagrostis epigejos (L.) Roth	3.33
Carex arenaria L.	1.67
Deschampsia flexuosa (L.) Trin.	1.67
Festuca ovina L.	11.67
Galium saxatile L.	0.17
Holcus lanatus L.	1.67
Rumex acetosella L.	0.50
Not considered within model	
Vascular plants •	
Senecio sylvaticus L.	0.67
Stellaria media (L.) Villars	0.50
Non-Vascular plants	
Brachythecium rutabulum (Hedw.) Br. Eur.	0.33
Dicranum scoparium Hedw.	5.67
Hypnum cupressiforme Hedw.	0.33

Predicted vegetation for 1994 and 1995 were merged into a single data matrix and subjected to TWINSPAN analysis. Treatment-year samples were categorised into two groups at the first level of division. REBRA does not readily accommodate cutting 5 - 6 weeks prior to asulam application (cutting and spraying in the same year is not a current option within the BRACON suite of control regimes) and is consequently excluded from this part of the analysis. Predicted vegetation composition within plots untreated or cut once yearly were described as exhibiting a similar floristic composition, whereas cutting twice yearly or treatments incorporating asulam resulted in a divergent form of vegetation development. Separation of the two vegetation assemblages occurred principally along the first axis of the ordination which may be interpreted as a gradient of bracken control (Figure 6.4.). At the first level of division, bracken was the only indicator species (pseudospecies level '3') for predicted vegetation within plots subject to cutting twice yearly or treatment incorporating asulam. Plots untreated or cut once yearly had predicted frond cover at pseudospecies levels of '5' and '4' respectively, whereas plots allocated to the second TWINSPAN group had frond cover at pseudospecies levels of '1' and '2'. Separation of samples appeared to be on the basis of successful bracken control (Figure 6.5.), with the demarkation zone between success and failure quantified as frond cover 26.1 - 51% (i.e. pseudospecies level '3'). The ordination of predicted species is presented (Figure 6.6.).

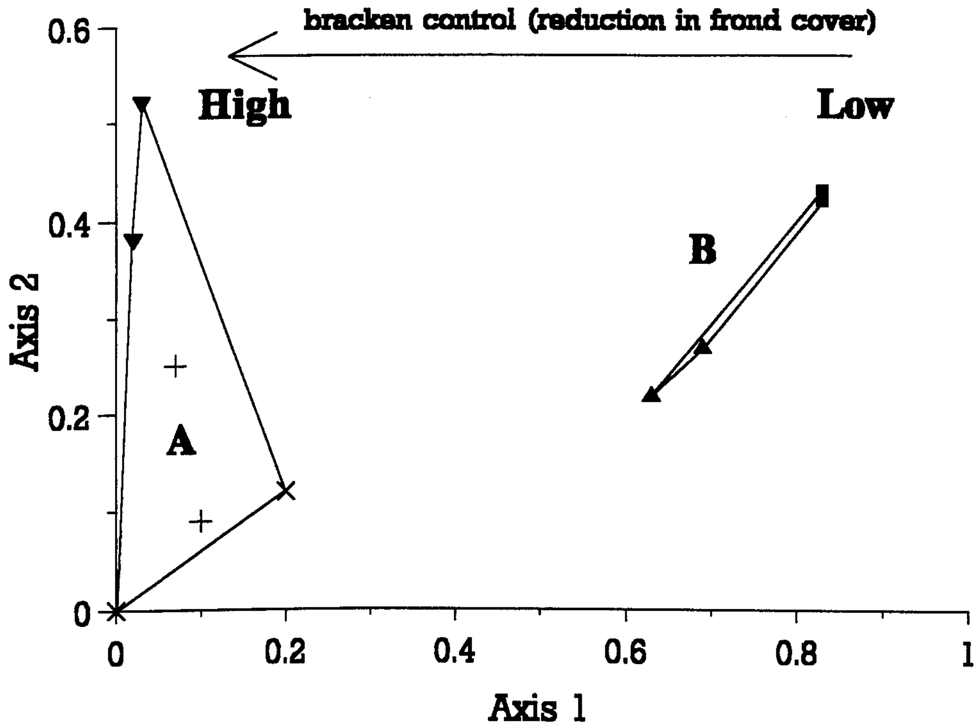


Figure 6.4. DECORANA ordination of predicted vegetation in 1994 and 1995 following five bracken control treatments: untreated (■); cut once yearly (▲); cut twice yearly (×); asulam (▼); asulam with a follow-up cut (+). The two TWINSPAN groups identified at the first level of division are indicated. Axes are in standard deviations of species turnover.

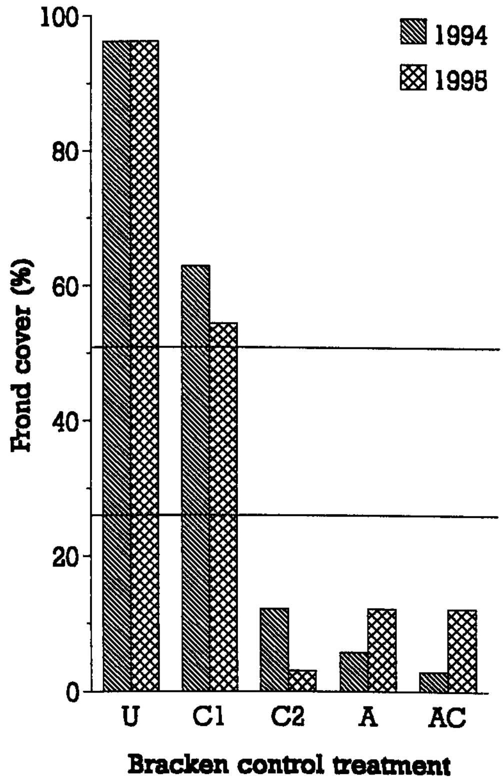


Figure 6.5. Percentage frond cover predicted by REBRA for Cavenham Heath during 1994-95; (for treatment codes see Figure 6.3.). Horizontal lines indicate the hypothetical demarkation zone between treatment 'success' and 'failure' identified by TWINSPAN analysis which corresponds to cover interval 26.1 - 51%.

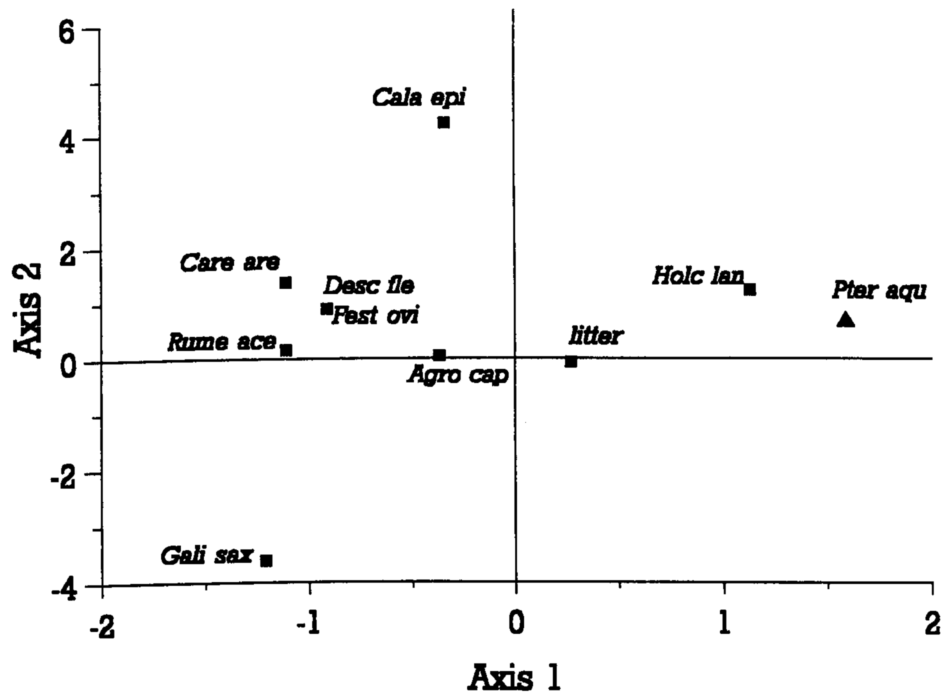


Figure 6.6. DECORANA ordination of predicted species for 1994 and 1995. The two TWINSPAN groups identified at the first level of division are indicated: the negative group (■); the positive group (▲). Axes are in standard deviations of species turnover.
For species codes see Figure 6.2.; additional species codes are: Agro cap = *Agrostis capillaris*; Cala epi = *Calamagrostis epigejos*; Gali sax = *Galium saxatile.*

6.3.3. Comparison of Model Predictions with Field Data

Field data and modelled predictions describing the vegetation community under bracken were merged into a single data matrix for TWINSPAN analysis. Individual years were analyzed independently. In both years, two groups were identified at the first level of division with allocation to discrete groups based upon whether the community was actually recorded or model simulated. *Agrostis capillaris* L. was the indicator species for predicted vegetation groups in both years. In 1994 separation of groups was principally along the second axis of the ordination (Figure 6.7.(a)), with overlapping of the groups evident. The 1994 species ordination (Figure 6.8.(a)) confirms the tendency for species which were only detected to group at the upper end of Axis 2, whereas species which are predicted and absent from the field survey gather at the lower end. In 1995, the two groups were separated along the first axis of the ordination with no overlap between groups (Figure 6.7.(b)). It appeared that the greater the time frame within which REBRA predictions were generated, the greater the divergence between predicted and actual community structure. The 1995 species ordination (Figure 6.8.(b)) confirms this trend with species unique to the field survey forming a distinct cluster (e.g. *Betula* spp., moss spp.) separated from species unique to model predictions (e.g. *Calamagrostis epigejos*, *Galium saxatile*.). Bracken fronds and litter are located at an intermediate location between groups.

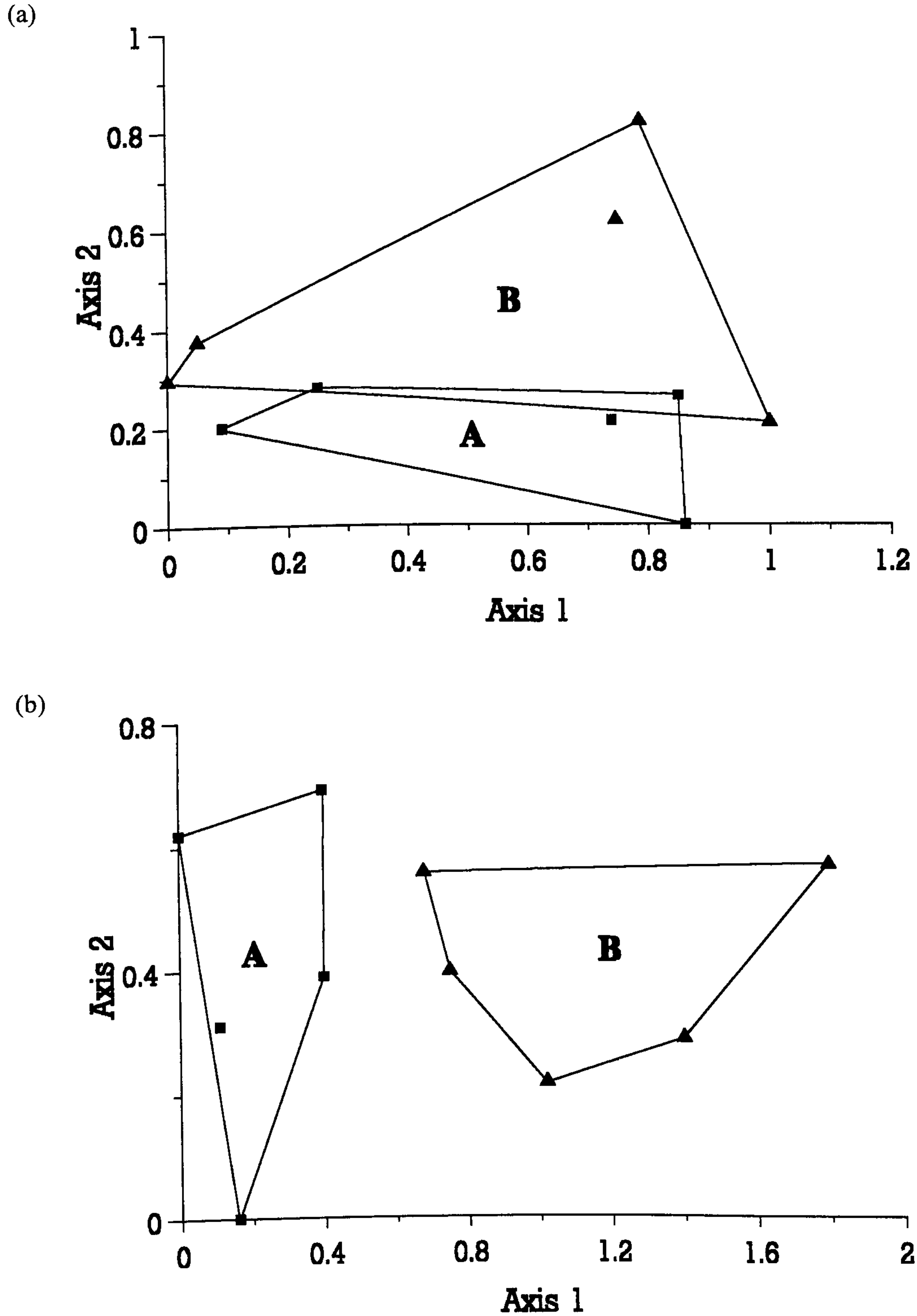
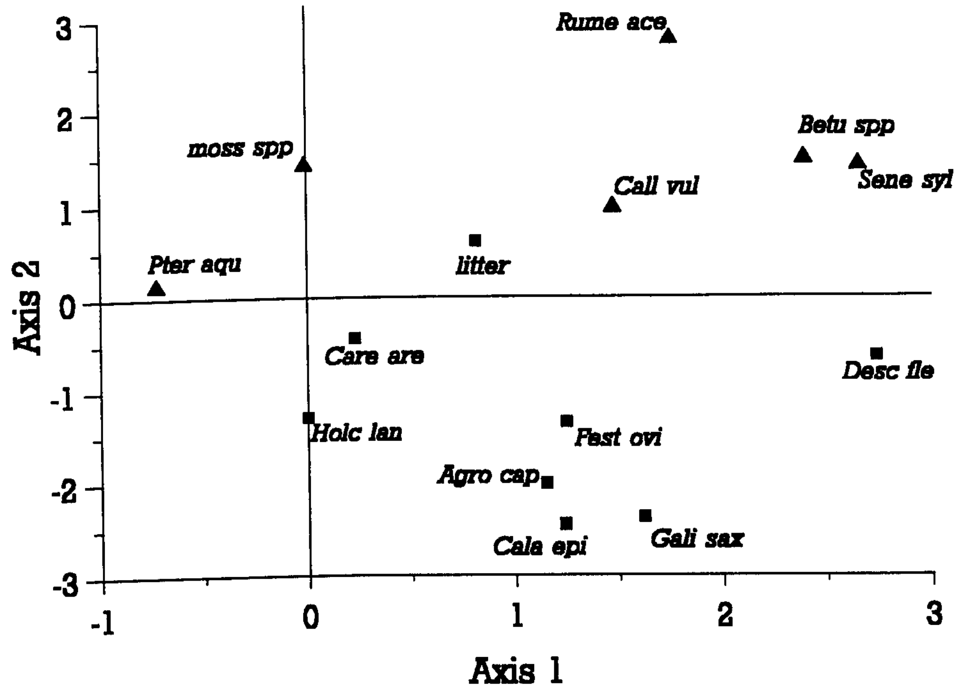


Figure 6.7. DECORANA ordination of recorded (▲) and predicted (■) vegetation samples in (a) 1994 (b) 1995. The two TWINSPAN groups identified at the first level of division are indicated. Axes are in standard deviations of species turnover.

(a)



(b)

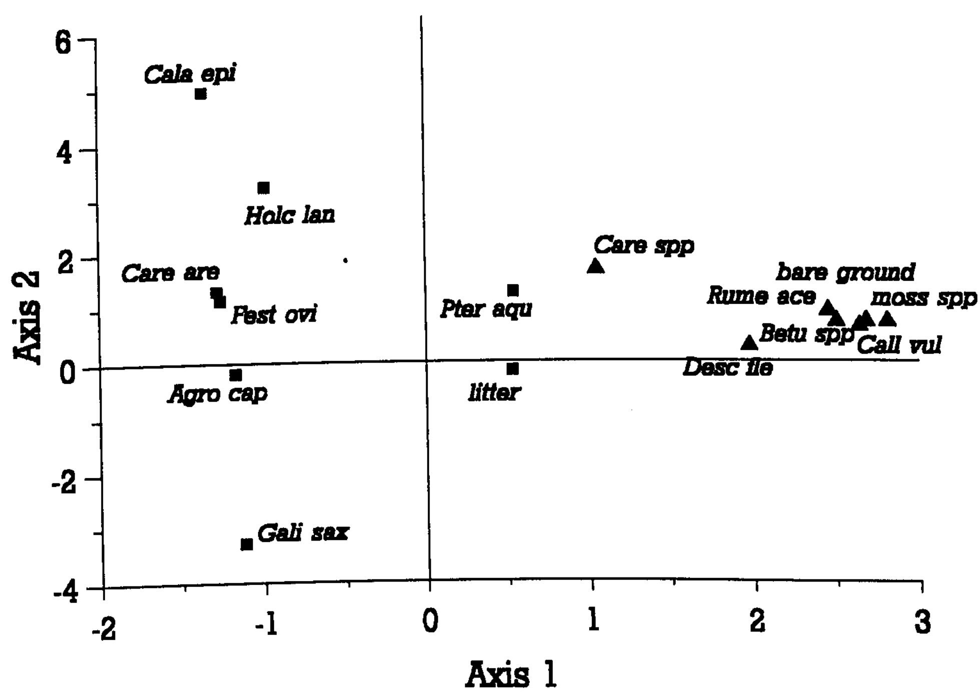


Figure 6.8. DECORANA ordination of recorded and predicted species in (a) 1994 (b) 1995. The two TWINSPAN groups identified at the first level of division are indicated: the negative group (■); the positive group (▲). Axes are in standard deviations of species turnover. Figures 6.2. and 6.6. identify species codes.

6.4. DISCUSSION

Within the confines of this limited assessment of vegetation development under bracken, in a species-poor habitat (at this particular site), analysis of the change in species cover could have been done using analysis of variance. However, within large data sets considering greater species diversity, when predictions and monitoring are considered over a longer time interval, analysis in this manner is more difficult and of limited value. Such analysis may identify a single desirable species associated with a particular form of bracken control, however, it fails to consider the vegetation community as a whole. Initial post-bracken control conditions may favour an individual, however, its continued survival will depend on the composition of the vegetation community which may establish itself at the expense of the initially favoured species. Therefore, it is essential to consider the community within bracken control experiments.

6.4.1. Field Data 1994-95

Cutting twice yearly had the greatest immediate effect upon frond status which created conditions free from light suppression, and reduced litter inputs at an earlier stage of treatment. These conditions are suitable for increased expansion of the ground vegetation. Limited frond production in 1994 reduced competition for light between bracken and the ground vegetation, however, the litter component of the micro-environment constitutes a continued impediment to vegetation development. Litter inputs were low at the end of the 1994 season, and by summer 1995 bracken litter had begun to break up and disperse to an extent which permitted the development of ground flora.

In 1994, *Carex arenaria* L., *Festuca ovina* L., and *Holcus lanatus* L. were detected, however, none of these species were recorded in 1995. This may have been due to the method of data collection i.e. recording vegetation within quadrats prior to destructive sampling (necessitated for bracken sampling). The use of permanent quadrats for assessing vegetation dynamics may have prevented the apparent loss of species from the environment, although permanent quadrats have other limitations: reduced estimates of variation; non-random sampling; and increased recorder bias.

6.4.2. Model Predictions 1994-95

REBRA predicts differences within the vegetation community as a consequence of bracken control treatments. Cutting once yearly was the least effective treatment in reducing frond and litter cover relative to untreated bracken; the litter being a major impediment to the development of the ground flora (Lowday & Marrs, 1992a,b). Cutting twice yearly and treatments incorporating asulam affected a greater decline in frond and litter cover. This was sufficient to permit several members of the vegetation community under bracken to increase their occupancy of the habitat (e.g. *Festuca ovina* L., *Rumex acetosella* L.). Most of the species under bracken which was untreated or cut once yearly were predicted to decline between years. Clearly, where bracken control is undertaken in order to encourage survival of rare or desirable species, the use of treatments which affect the quickest reduction in bracken dominance (litter and frond cover) are preferable. Of the treatments considered it was those allocated to TWINSPAN group 'A' (Figure 6.1.), i.e. cutting twice yearly, and spraying with or without a follow-up cut, which should be applied to maintain the existing species before the stock is further reduced or lost. In alternative situations, the introduction of the desired species may be necessary (Lowday & Marrs, 1992a), however, if bracken dominance is removed quickly, then it may be possible to introduce less seed/cuttings as more of the original stock has been preserved. Some species develop which could be considered undesirable for heathland conservation e.g. *Betula* spp., *Carex arenaria*, and *Calamagrostis epigejos* (Marrs & Lowday, 1992).

6.4.3. Comparison of Model Predictions with Field Data

Several species detected within the initial survey, which formed the basis for model predictions, were not recorded in subsequent visits. This produced clear contrasts between the actual and predicted data sets. It may have been that conditions required for the development of these species under field conditions were not achieved within the limited time of this study. Continued study of the experimental plots may result in apparently lost species reappearing, in which case, the method of assessment was unsuitable. As stated, permanent quadrats would have avoided this problem, as the actual trajectories for the site could have been measured, however, this would have reduced the estimate of error for the treatments. Species which were rare or disappeared in the field situation could have been assessed more accurately if the initial assessment of the vegetation composition of the plots before treatment had been more intensive. This approach would have undoubtedly detected heather (the former dominant vegetation) which was present in experimental plots but not recorded in the baseline assessment.

A fundamental deficiency within the model is its failure to consider tree/shrub species. Birch invasion was occurring in close proximity to the experimental area and seedlings were found within plots. Management objectives often include the establishment of such vegetation types and consideration of these species within the model would only serve to extend its applicability to land management. Bryophytes (mosses were a consistent component of recorded vegetation) are also not considered in REBRA. Mosses may impede the establishment of higher plants (Clément & Touffet, 1990), however, under undisturbed bracken, eventual moss decay may create fertile micro-sites for plant succession, especially in Breckland where frost can break up bryophyte mats (Marrs, pers. comm.). A further contrast between model predictions and field data was the presence of bare ground within experimental plots regardless of treatment, whereas REBRA described all available space as being fully occupied.

A deficiency of the BRACON model (a constituent part of the REBRA program) was its inability to consider regrowth in the latter part of the growing season, after cutting operations. Such regrowth would exert some competition with ground vegetation for light and space, and lead to additional litter inputs (at different stages in the season), which are as yet unconsidered within the program structure, at the inevitable expense of the latter. This may in part explain the contrasts between predicted and recorded vegetation.

6.4.4. Conclusions

Evaluation of the model is difficult within this limited assessment of vegetation and incorporation of the suggested improvements would have better served this purpose. However, the multivariate method for model evaluation is envisaged principally for accommodating analysis of more extensive data sets, incorporating a greater number of sites, more intensive sampling, and over a longer time span. The true value of this approach can only be determined using such information, and it is hoped that this study can be continued for a few more years to investigate this further. This data has served to demonstrate the use of multivariate analysis for model evaluation, a technique which can only be as good as the data provided for its operation.

7. The effects of controlling bracken (*Pteridium aquilinum* (L.) Kuhn) to promote sessile oak (*Quercus petraea* (Matt.) Liebl.) seedling performance

7.1. INTRODUCTION

The aim of this chapter is to investigate whether oak woodland regeneration in woodland areas with a dense bracken understorey can be enhanced by controlling the bracken. Oak woodland has a high conservation value (Streeter, 1974) and there have been many concerns expressed over the apparent inability of native oak woodlands to regenerate naturally (Shaw, 1974). The survival and growth of oak seedlings can be reduced by combinations of climatic, edaphic, and biotic factors (Shaw, 1974).

Light availability is considered to be one of the most important factors determining oak seedling performance in woodland. Optimum growth occurs under shade conditions comparable with coppiced woodland or small clearings (Jarvis, 1964a). Oak seedlings normally exhibit a pronounced tap root which develops into a deep root system. When light availability is reduced, seedling height continues to increase, however, this appears to be at the expense of root development (Jarvis, 1964a). Competition for soil moisture and with the roots of other species (e.g. *Deschampsia flexuosa* (L.) Trin.), also reduces oak performance (Jarvis, 1964b). Fungal infection, and herbivory by arthropod and mammal grazers, have also been cited as contributory factors in limiting oak seedling survival. It has been observed that damage inflicted by small mammals could be greater under dense bracken than damage incurred outside the bracken stand (Shaw, 1974).

In order to try and increase the amount and quality of the existing oak woodland in the Snowdonia National Park, landowners have been offered financial incentives to increase tree cover and regenerate existing woodlands. However, in many woodlands a dense bracken understorey is present, and this can affect the success of such tree planting schemes.

Bracken (*Pteridium aquilinum* (L.) Kuhn) is a weed species in many different land use situations and often causes problems in conservation and forestry. Its abundant growth can dominate areas at the expense of rare and/or more ecologically desirable flora and fauna

(Pakeman & Marrs, 1992a), and can limit the availability of light, water and nutrients to newly planted trees. Moreover, the collapse of dead bracken fronds may cause direct physical damage to trees whilst during hot, dry summers, bracken litter dries out becoming highly inflammable, and may, therefore, constitute a fire risk (Biggin, 1982). Dense stands of bracken can form a continuous canopy casting a deep shade capable of reducing light levels to 4.2% of full sunlight (Humphrey & Swaine, *in press*). Such bracken stands can swamp tree seedlings and weed control is recommended to prevent suppression of young oaks (Penistan, 1974). Moreover, if expected increases in global warming occur (United Kingdom Climate Change Impacts Review Group, 1991), the current bracken problem is predicted to increase (Pakeman *et al*, 1996).

Bracken can be controlled in two ways; by cutting and herbicide use:

1. Cutting

Cutting removes energy from the bracken system bringing about a net depletion of rhizome carbohydrate stores. Cutting should be timed to affect maximum reduction of rhizome reserves, allowing maximum removal from the rhizome and minimum returns of photosynthate (Lowday *et al.*, 1983). Cutting must be maintained for several years in order to gain maximum effect.

2. Herbicide Use

The systemic herbicides asulam and glyphosate have been the most consistently effective and most widely used against bracken. Asulam offers high target specificity and low toxicity to mammals and fish and it is approved for aerial application (Soper, 1986). Applied to the bracken fronds in mid-summer, asulam is translocated to the rhizome system where it accumulates in buds and apices, affecting structural degeneration via the inhibition of RNA and protein synthesis (Veersasekaran *et al.*, 1977). No effect of treatment is visible in the year of treatment, but very few fronds are produced in the season following application. A depletion of rhizome carbohydrate stores results through respiration and a reduction in photosynthetic capability. Glyphosate is non-specific and is favoured where bracken is amongst a number of weeds which all require control. However, where bracken is the only target species then asulam is recommended.

The residual herbicide dicamba when applied to the soil, penetrates the rhizome directly where it can affect a lethal action. It has been applied in strips to aid tree establishment in new forestry plantations (Palmer, 1988).

Weed control measures were not undertaken prior to oak transplant introduction and seedling mortality in the year following planting had suggested bracken was limiting oak survival. In this study, the efficacy of cutting or asulam application to control a dense bracken infestation in an oak woodland clearing is assessed in relation to the performance of transplant oak seedlings. The ultimate aim of this study was to regenerate the oak woodland.

7.2. MATERIALS & METHODS

7.2.1. Study Site

The experimental site was in a clearing in an oak woodland at Blaen Nanmor within the Snowdonia National Park (National Grid reference 2625,3479) where seedlings of sessile oak (*Quercus petraea* (Mattuschka) Liebl.) had been planted in a dense bracken infestation. The aim of introducing these seedlings was to regenerate the oak woodland. Oak seedlings were planted during February 1992 in a regular pattern throughout the clearing at a distance of approximately 1.5 m between individuals. Treeshelters (0.6 m height) were used to protect seedlings against damage and to assist establishment.

7.2.2. Experimental Design

In July 1993, plots were located within the clearing so that each contained 8 - 9 planted seedlings, with the criterion that at least 50% of the transplants had survived. This approach limited the number of experimental plots. Bracken control treatments were then allocated randomly to plots within each of two replicate blocks. Pathways separating plots were kept cut for access.

7.2.3. Treatments

Four bracken control treatments were applied:-

1. Untreated 'control'.
2. Fronds cut once yearly (early July).
3. Fronds cut twice yearly (early July & early August).
4. Single application of asulam in 1993 (early August).

Cut treatments were applied with a brushcutter and cuttings were left within plots. Asulam was applied at 4.4 kg a.i. ha^{-1} in 400 litres of water as the commercial formulation 'Asulox' (Rhône-Poulenc) using a knapsack sprayer. A non-ionic surfactant ('Agral') was added to the spray mixture at 0.1% v/v.

7.2.4. Sampling Methods

Bracken fronds

Eight 1 m^2 quadrats were identified for sampling within each plot and were allocated a position randomly in a sampling sequence to take account of all sampling foreseen in this study. Two quadrats were sampled per plot during early August once fronds had fully expanded. Between 1993-95, all bracken fronds were harvested from the central 0.25 m^2 of each quadrat. Limited additional sampling of fronds occurred prior to application of the early-July cut in 1994.

Frond height, density and counts of pinnae exhibiting third-order subdivision of the frond were measured and frond biomass determined by drying sub-samples in an oven at 70°C for at least 24 hours.

Oak seedlings

Between 1993-95, oak performance was assessed annually using non-destructive sampling methods. Height and leaf number were recorded for all seedlings within all plots after frond senescence.

7.2.5. Statistical Analysis

Data was subjected to analysis of variance using the GLM procedure in SAS (SAS, 1988). Transformation of the data was considered unnecessary as it failed to increase significantly the variance accounted for within the analysis of variance model. Mean separation tests using Fisher's Least Significant Difference were applied.

7.3. RESULTS

7.3.1. Bracken Fronds

Summer 1993

All bracken control regimes commenced in 1993: the first year of monitoring. The early-July cut applied to plots cut twice yearly was the first bracken control treatment at the study site. Frond performance was recorded 5 weeks after this first cut and significant reductions in height ($P<0.05$) and pinnae production ($P<0.01$) relative to untreated plots were found. Mean frond height of the fronds produced after the first cut was less than the 0.6 m treeshelter height (Figure 7.1.). Frond density and biomass were reduced relative to untreated plots (57.1% and 5.6% respectively). The extent of biomass reduction within cut plots was consistent with bracken response at national and regional levels (Chapters 3 & 4).

Summer 1994

Bracken control treatments applied during 1993 appeared to affect no statistical significance over frond biomass and density during early July, however, significant reductions in frond height and pinnae production ($P<0.01$) were evident within plots cut twice yearly and plots sprayed with asulam.

Later in the growing season (early August), bracken cut twice yearly or sprayed with asulam had reduced frond biomass, density and height significantly ($P<0.05$) relative to untreated plots. Two seasonal cuts had reduced frond biomass and height to 0.8% and 27.2% of untreated plots respectively. Both treatments produced fronds less than treeshelter height (Figure 7.1.).

The imposition of a single cut in the previous year failed to reduce frond performance significantly ($P<0.05$) relative to untreated plots. Fronds attained a mean height of 1.2 m (87.7% of untreated frond height) whereas two cuts per season produced fronds 0.38 m high.

However, this latter measurement was an assessment of regrowth from the cut 5 weeks earlier, which can present problems for interpretation of management success (Chapter 3.4.).

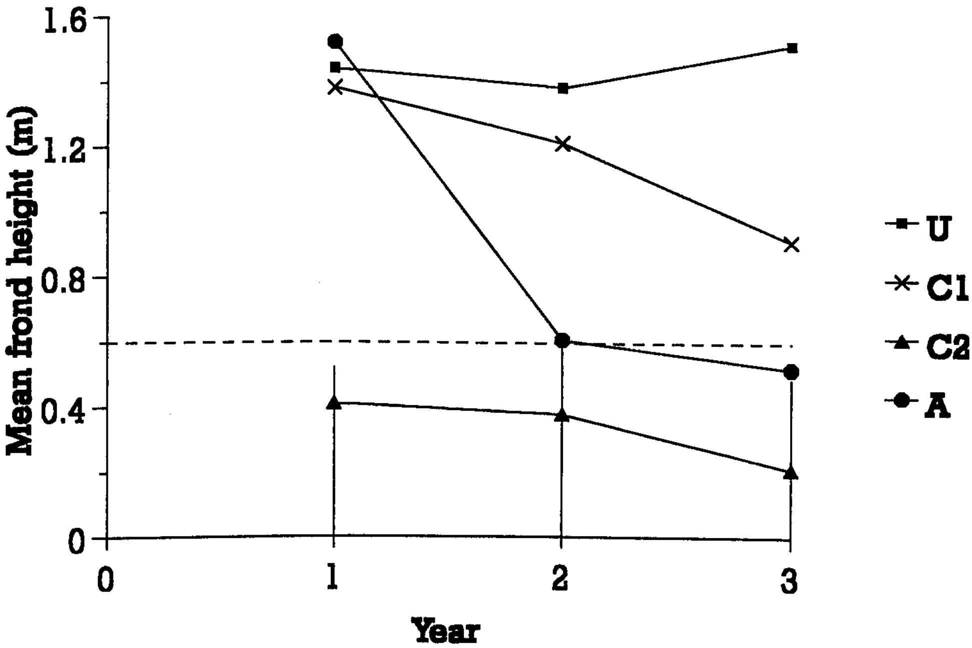


Figure 7.1. Mean frond height (m), recorded during August (n=2), throughout the experiment following bracken control treatments. Treatment codes are: U, untreated; C1, cut once yearly; C2, cut twice yearly; A, asulam. Vertical lines indicate least significant difference (LSD) at $P<0.05$: LSD (year 1) = 0.52 m; LSD (year 2) = 0.60 m; LSD (year 3) = 0.49 m. Dotted line indicates treeshelter height (0.6 m) which constitutes the threshold above which the potential for seedling physical damage exists.

Summer 1995

In early-August, during the third year of bracken management, all control treatments reduced frond biomass and height significantly ($P<0.05$) relative to untreated bracken (Figure 7.2.). Cutting once yearly was significantly less effective in reducing frond height than the regime of increased cutting frequency. Bracken cut twice yearly or sprayed with asulam continued to produce fronds shorter than treeshelter height (Figure 7.1.). Asulam application was the only method of bracken control to reduce frond density to numbers significantly lower ($P<0.05$) than those recorded within untreated plots.

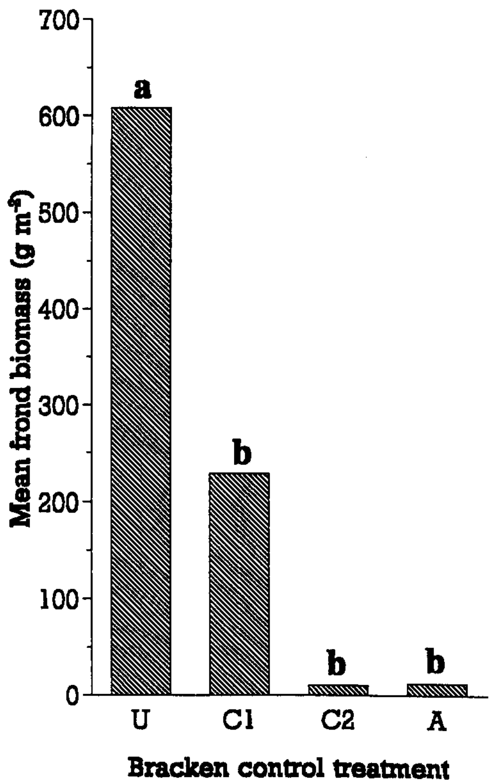


Figure 7.2. Mean frond biomass (g m^{-2}), recorded during August 1995 (n=2), following bracken control treatments; (for treatment codes see Figure 7.1.). Bars with the same letter are not significantly different ($P<0.05$). LSD = 296.4 g m^{-2}.

7.3.2. Oak Seedlings

1993

At the end of the bracken growing season, once fronds had collapsed, control treatments had no significant effects upon seedling height. Mean seedling height was less than 0.6 m in all but one plot (Figure 7.3.). However, some individuals within several plots attained height in excess of this value.

A significantly ($P<0.05$) greater number of leaves were present upon seedlings within cut plots relative to untreated plots. Spraying with asulam had no significant effect upon leaf number.

1994

After two years of bracken management, oak seedling height was not significantly different between treatments, however, seedlings within all bracken controlled plots were taller than those under untreated bracken. Plots which had been either cut or sprayed exhibited oak seedlings with a mean height in excess of 0.6 m (Figure 7.3.).

Significant differences in leaf number were identified ($P<0.05$). All treatments increased leaf number relative to seedlings within untreated plots and differences in cutting frequency were not important within this context.

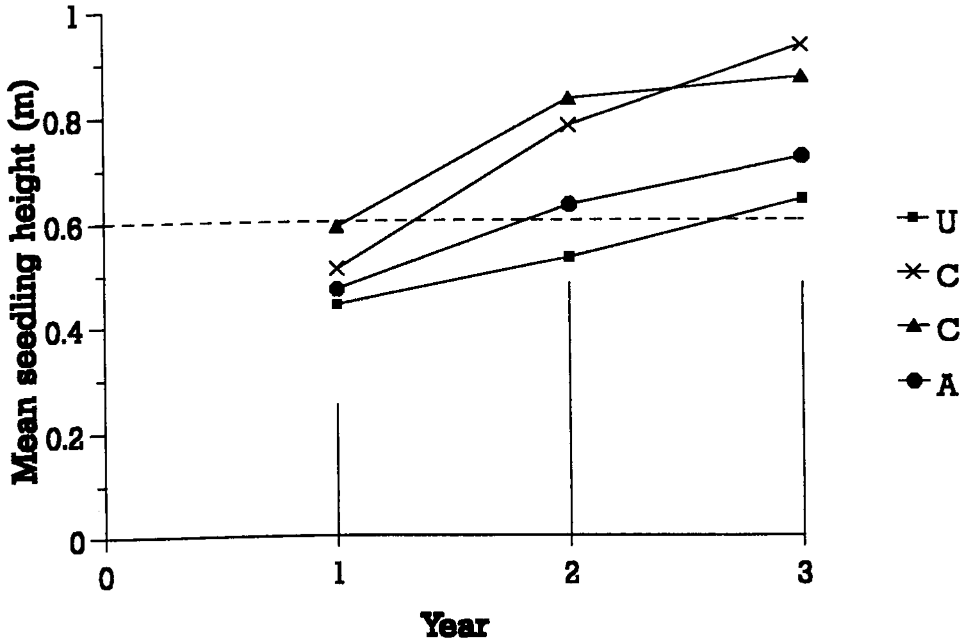


Figure 7.3. Mean oak seedling height (m), recorded during October 1993-95 (n=2), in response to bracken control treatments; (for treatment codes see Figure 7.1.). Vertical lines indicate least significant difference (P<0.05). LSD (year 1) = 0.25 m; LSD (year 2) = 0.48 m; LSD (year 3) = 0.48 m. Dotted line indicates treeshelter height (0.6 m) which constitutes the threshold above which the potential for seedling physical damage exists.

1995

The initial high mortality of oak seedlings which precipitated this study appeared to be stemmed as soon as bracken management commenced (Figure 7.4.). In the final year of bracken control, no significant effect of treatment on seedling height was evident. However, seedlings within plots where bracken had been controlled exhibited a greater increase in height than was observed within untreated plots (Table 7.1.). Mean seedling height, regardless of treatment, was in excess of 0.6 m (Figure 7.3.). Predicted time interval requirement for oak seedlings to overtop the bracken canopy was produced based upon mean height increment during this study. Cutting treatments accelerated this process to a greater extent than that observed within untreated or asulam-sprayed bracken.

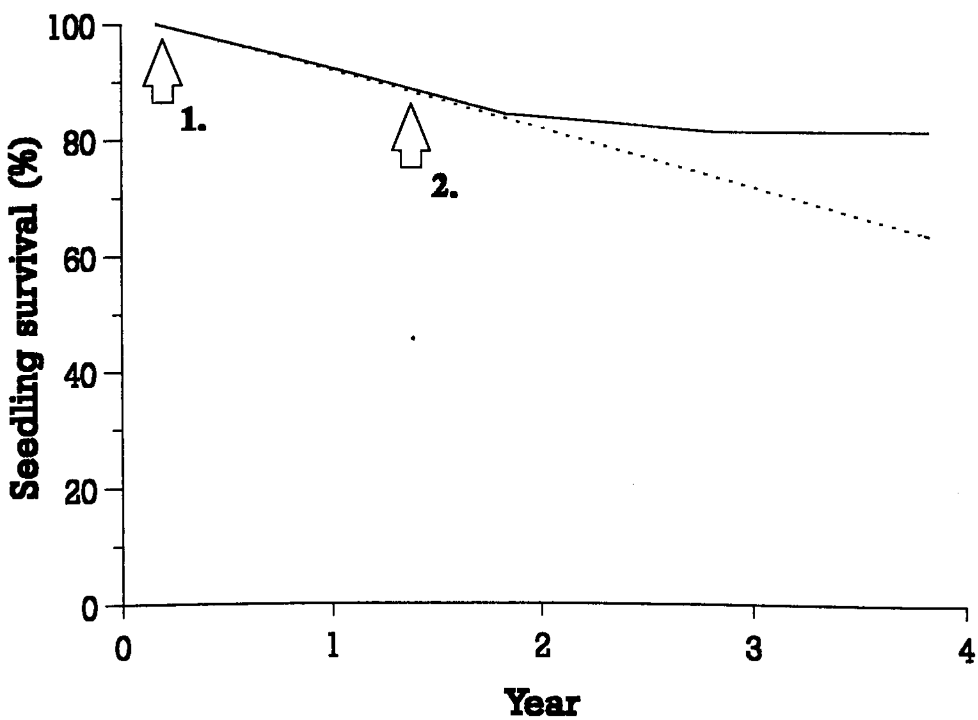


Figure 7.4. Percentage survival of all planted oak seedlings within experimental plots. Solid line indicates recorded survival whereas the dotted line indicates predicted survival had bracken control treatments not been implemented. Arrow (1.) identifies seedling introduction and arrow (2.) identifies the start of bracken control.

Table 7.1 Mean oak seedling height increment (± 1 standard error) during 1993-95 following different bracken control treatments. Time interval until, and year when seedlings would overtop 1.6 m bracken canopy given that height increment is constant and treatments are continued, are presented. Mean height increment values with the same superscript letter are not significantly different ($P<0.05$). LSD = 0.12 m $year^{-1}$.

Bracken control treatment	Mean oak height increment (m $year^{-1}$)	Time interval (years)	Year
untreated	0.10^{a} (±0.03)	10.1	2005
cut once yearly	0.21^{a} (±0.04)	3.3	1998
cut twice yearly	0.14^{a} (±0.03)	5.1	2000
asulam	0.13^{a} (±0.02)	6.9	2002

Seedlings within cut plots produced a significantly ($P<0.05$) greater number of leaves than seedlings within untreated or asulam-sprayed plots, however, cutting frequency was not significant. Spraying with asulam had no significant effect upon this indicator of oak performance (Figure 7.5.).

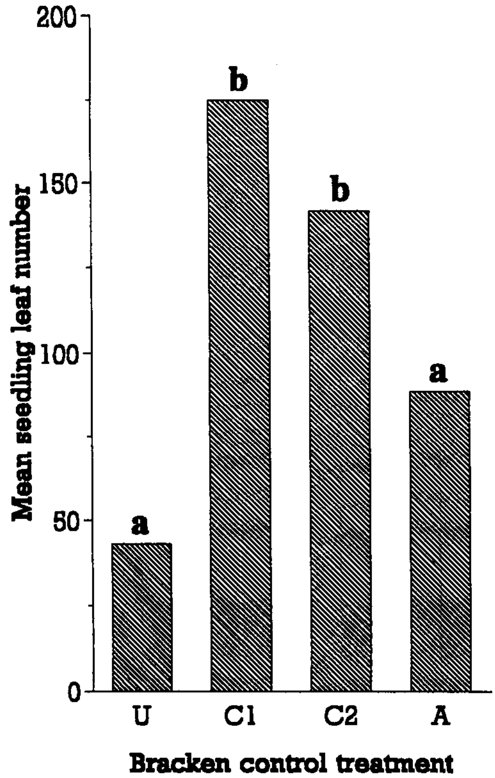


Figure 7.5. Mean seedling leaf number, recorded during August 1995 (n=2), following bracken control treatments; (for treatment codes see Figure 7.1.). Bars with the same letter are not significantly different ($P<0.05$): LSD = 52.2.

7.4. DISCUSSION

This experiment started 17 months after introduction of the transplant seedlings. Initial observations at the site suggested that competition from bracken was killing the trees. As the aim was to regenerate an ageing oak woodland, it was essential to determine whether bracken was indeed responsible for reduced success and whether bracken control could aid seedling survival. Whilst there is no doubt that there was mortality in the immediate post-establishment phase (16% mortality since planting - probably underestimates mortality as measurements were made within a pre-determined location of the study site with a 50% minimum mortality criterion), this factor was reduced considerably over the next three years. However, bracken control is not likely to be the reason for this observation. Failure of the seedlings to develop in their new environment as a consequence of damage during transport or adverse micro-environmental conditions are more probable explanations. Therefore, the prediction which assumed continued decline in seedling numbers is unrealistic (Figure 7.4).

7.4.1. Minimal Management and Oak Performance

Most oak seedlings exhibited increased height and leaf number. This observation appeared to contradict the managerial hypothesis that bracken dominance was responsible for seedling death. However, the result was consistent with observations concerning the natural establishment of a tree species under dense bracken (Marrs & Hicks, 1986). In the cited study, invasion by Scots Pine (*Pinus sylvestris* L.) was independent of bracken canopy density and limited by seed dispersal. In the current study, occurrence of oak seedlings was due to regular planting whilst the provision of treeshelters restricted damage via biotic agents. Seedlings of sessile oak can become established under undisturbed bracken with minimal management input (i.e. planting and treeshelters), however, due to the artificiality inherent within this examination conclusions concerning natural oak invasion and establishment are not possible.

7.4.2. Bracken Control and Oak Performance

1. *Cutting*

Bracken management is intended to alleviate the problems incurred via infestation. Canopy removal increases ambient light levels, however, when cutting techniques are employed, severed fronds collapse and represent a potential source of physical damage to the delicate growing tips of young trees.

Two pre-requisites existed before the identified problem scenario could be realised. Firstly, frond height had to be greater than 0.6 m at the date of cutting in order that collapsing fronds could make contact with the top of the treeshelters. Secondly, oak seedlings had to protrude above the 0.6 m treeshelters thereby exposing their growing tips to collapsing fronds.

Throughout the experiment, fronds attained problematic height within plots cut once yearly. In the first year, seedlings did not emerge above the treeshelter, however, they were prone to damage in the second and third years. Despite the potential for seedling damage the identified problem was not influential within the experiment.

Each year, within plots cut twice yearly, regrowth from the first seasonal cut was insufficient to inflict physical damage upon seedlings. However, in the second year, prior to the first seasonal cut, frond height exceeded the problem threshold. The potential for seedling damage existed as this cutting option proceeded (at a reduced frequency relative to plots cuts once yearly), however, this potential for damage did not appear to be realised. The impact of this control option upon bracken is difficult to determine as it is regrowth which is assessed at the sampling visit however these treatments only require to suppress bracken for a limited period during which oak seedlings can become established.

2. *Asulam*

No effect of spraying upon bracken fronds is evident within the year of application. The delay in canopy clearance constituted a considerable delay within a three year study and may have disadvantaged this management option relative to cutting operations. Potential problems associated with fronds collapsing at the end of the bracken growing season existed within sprayed plots during the first year. However, at this stage of the experiment oak seedlings within sprayed plots were protected inside their treeshelters and damage was not expected.

It has been stated that treatment with asulam results in one weed problem (bracken) being replaced by another (Robinson, 1986). Within sprayed plots, foxglove (*Digitalis purpurea* L.) and bramble (*Rubus fruticosus* L. agg.) were observed, however, these species do not present the problems for young trees which dense bracken stands can pose i.e. deep shade, smothering fronds and possible allelopathy. Neither species need be considered a weed as they do not conflict with the primary management objective i.e. the survival, growth and establishment of oak seedlings.

Bracken suppression using this method of control often requires repeat spraying within a 4 - 6 year cycle, however, as stated above, within the context of seedling establishment, the provision of a period of respite from bracken suppression is the sole requirement of treatment.

7.4.3. Bracken Litter and Oak Performance

Oaks have a long tap-root and are particularly resilient to water shortage, however, competition from wavy hair-grass (*Deschampsia flexuosa* (L.) Trin.) can reduce soil water availability to oak (Jarvis, 1964b). Bracken litter can intercept up to 50% of incident rainfall (Williams *et al*, 1987) and may passively compete with oak for soil moisture. Cutting is more efficient than spraying with asulam at reducing the litter layer, especially cutting twice yearly

(Lowday & Marrs, 1992a,b) and would be the preferred option for alleviating possible water stress on sensitive oak seedlings.

7.4.4. Experimental Conclusions

Oak seedling performance improved when bracken control treatments were imposed. Cutting treatments conveyed the greatest initial aid to seedling establishment which may have been attributed to an immediate removal of the bracken canopy. Damage to seedlings via collapsing fronds through either natural or artificial (cutting) means appeared to have been avoided primarily due to seedling stature and the prompt introduction of bracken management regimes.

If effective bracken control can be achieved and maintained during the sensitive, juvenile oak stages then future bracken management would not be required. Mature oak should affect environmental control over bracken by altering the light regime at the expense of bracken photosynthesis thereby returning bracken to a non-dominant component of the woodland community. The initial high cost of intensive artificial bracken control presents two advantages: (1) the financial, conservational, and health problems associated with bracken infestation are removed or lessened; (2) reduction in the time required to create a new habitat consisting of formerly threatened vegetation.

7.4.5. Future Bracken Control in Woodlands

Predictions concerning the time interval required for oak seedlings to become community dominants, and relieved from physical damage to the growing tips, were produced based upon mean height increment during this study. Cutting treatments accelerated the process to oak dominance of the plant community to a greater extent than that observed within untreated or asulam-sprayed bracken. Predictions made the assumption that treatments are continued, height increment is a constant and that maturing oaks are prone to the same level of suppression as the juvenile phase. Height increment is undoubtedly not a constant and the probability that collapsing bracken fronds will kill all delicate growing tips on an oak transplant should decline with seedling age. Therefore, the predicted time interval until oak dominance is probably inaccurate, however, the ranking of treatments as an aid to this endpoint may be valid. Bracken control accelerates oak dominance, it does not instigate this shift within the plant community. Whether the rate of this natural shift within the community is acceptable must be assessed subjectively by land owners and policy makers.

8. DISCUSSION

8.1. INTRODUCTION

Bracken is a current problem for land use (Lawton & Varvarigos, 1989; Biggin, 1982; Pakeman & Marrs, 1992a; Long, 1988; Hudson, 1986; Williams *et al.*, 1987; Evans, 1986) and has been implicated as a factor detrimental to the health of humans and wildlife (Evans 1987; Galpin & Smith, 1986; Habicht *et al.*, 1987). An extensive underground rhizome network, and the inaccessible terrain infested by bracken, can make large scale, sustained, effective weed control difficult. The bracken problem within Great Britain looks set to continue into the 21st century, with increased occurrence, abundance, and resilience to control treatments predicted (Pakeman & Marrs, 1992b) as a consequence of global warming.

A number of management practices are used to control bracken, throughout the climatic contrasts prevailing within Great Britain. The most common strategies for bracken control in the uplands are cutting, and spraying asulam (Lawton & Varvarigos, 1989). A wealth of experience in bracken control exists within the rural community, however, assessment of treatment efficacy is subjective and relative to individual managerial aims. This work constitutes the first comprehensive attempt to consider the efficacy of bracken control treatments across a range of climatic zones. The value of several management strategies was assessed simultaneously within individual geographic locations over a three year period.

8.2. NATIONAL RESPONSE OF BRACKEN TO CONTROL TREATMENTS

Experimentally derived data enabled the synthesis of a national overview towards bracken control which identified a hierarchy of treatment efficacy. This study excluded several factors which can distort meaningful interpretation of treatment applicability, and plague single-site studies attempting extrapolation to the countrywide scale. Simultaneous monitoring and imposition of bracken control treatments, excluded annual fluctuations in climate from assessment of treatment contrasts between sites. In addition, consistent methodology between sites assessed by the same experimenter enabled a better national interpretation based upon data obtained from the individual study sites.

In order to form policies for a national bracken control programme, policy makers require access to objective assessments of treatment suitability. Public pressure to instigate such a programme may become greater should links between human health and bracken incidence become substantiated. Politicians should not be expected to take policy forming decisions based upon innuendo, hearsay, or anecdotal evidence. The current study, with its scientific protocol, produced the type of data which would facilitate meaningful policy formulation.

The rhizome and frond components of bracken were examined, and identified differential bracken control efficacy with regard to identical treatments. Comparison of cutting frequencies consistently ranked cutting twice yearly above cutting once yearly, however, frond data indicated that the additional seasonal cut increased efficacy ×3, whereas rhizome biomass data indicated a ×1.2 increase in efficacy. The greater suppression of frond biomass is important as it indicates the comparative extent to which the problems associated with swamping bracken growth (e.g. health hazard, public access, interference with desirable vegetation) are alleviated. However, the modest increase in treatment efficacy associated with depletion of rhizome biomass is of greater importance within the context of assessing the longer term implications of bracken management, as the aim should be to identify the time that control needs to be maintained.

The hierarchy of treatments differed with respect to the morphological indicator monitored and emphasised the different methods by which the management regimes employed within this study operate. Spraying with asulam affected the greatest initial control over frond performance, however, this treatment exerted a minimal impact upon rhizome biomass. This is expected via its reported mode of action (Veerasekaran *et al.*, 1977). Cutting twice yearly affected immediate, superior control over frond performance relative to cutting once yearly, which continued throughout the study. This superior control was likewise reflected in rhizome biomass depletion. In conclusion, the effects of cutting treatments on frond performance lag behind the initial success of spraying asulam, however, the continued success of asulam requires repeat treatment (recovery to untreated levels is typically 5 - 10 years). Despite the investment of time, and labour, required to maintain cutting regimes, these treatments can achieve, and maintain, the suppression of bracken fronds. Moreover, a greater reduction of the rhizome resource can be attained, the depletion of which is believed to be the key to successful long term control of bracken-dominated land (Marrs *et al.*, 1993). Cutting once yearly affected a significant increase in frond density in the first year after treatment and is an initial, if only temporary, disadvantage associated with this technique which land managers requiring a rapid removal of swamping bracken growth should be made aware.

8.3. REGIONAL RESPONSES OF BRACKEN TO CONTROL TREATMENTS

The hierarchy of treatments identified at the national scale was found to apply generally within the individual sites. However, several responses of bracken (e.g. increase in frond density in year following first cut) which proved significant at the countrywide level were not as clearly defined at the site scale.

Cutting once yearly was the only bracken control option, examined within this study, which affected a clearly significant contrast in bracken response between sites. These contrasts were evident in both the frond and rhizome component of bracken. The bracken stands which constituted the study site in the Scottish Borders, exhibited elevated levels of frond biomass, density, and height relative to untreated plots. The increased frond density was not unique to the Scottish Borders, in fact most sites exhibited an increase in frond number, however, the scale of increase was significantly greater than that observed at any other site.

The increase in both frond biomass and height was confined to the Scottish Borders. The significant contrasts evident in the Scottish Borders were confined to the second year of bracken management, thereafter, the relative level of control was consistent with that recorded throughout the country. These observations indicate the scale of deviation from national trends which can result, however, this does not discredit the value of the national overview generated within this study. The rhizome data identified significant contrasts between sites, with an apparently superior level of bracken control obtained at the sites in Wales and the south of England relative to that observed in Scotland and the north of England. This perhaps indicates that resources towards bracken control could be evaluated and allocated on a north-south basis in order that finite resources can be better focused at a regional level. Individual cases require to be considered on their own merits, with control costs ascribed from regional funds.

8.4. BRACKEN CONTROL MODEL

In ecology, models can prove valuable if they are accurate representations of biological systems. The BRACON model describes the interaction of the environment and bracken control operations, with a number of physiological processes within bracken to determine plant status in terms of rhizome biomass, carbohydrate content, and frond biomass. Experimentally derived data from this study appeared to validate the model as a reasonably accurate predictor of bracken stand dynamics in relation to cutting, and spraying with asulam, across the range of climatic conditions which prevail currently across Great Britain.

Despite the reasonable accuracy of model-generated predictions, there appeared to be a tendency to underestimate the resilience of bracken to cutting treatments. This may have been attributable to a weakness within the model structure: following cutting treatments, BRACON fails to consider frond regrowth in the latter portion of the growing season. The photosynthetic benefits derived from regrowth may offset energy losses incurred via treatment. Discrepancies between model predictions and actual field data were detected within the initial three years of treatment, however, whether these contrasts will continue to be evident, and to what extent, would require extended monitoring. Therefore, it is possible that current long term predictions which identify the difficulty in attaining effective bracken control are serious under estimates of the actual investment required to achieve management objectives.

The modelling approach is a valuable tool for policy makers and land managers as it can indicate areas where bracken control may be more problematic thereby enabling selection of the most appropriate management technique and identification of the most cost effective cycle of treatment. It is important that the benefits which can be derived from model predictions are made available directly to those currently involved in the management of bracken infested land. Managers should be aware of predictions for land under their jurisdiction and summary charts should be available to individuals actively engaged in bracken management as to the typical consequences of control within their region. The model has the ability to accommodate several contrasting methods of bracken control within a cycle of treatment i.e. the consequence of integrated control are considered within BRACON. In essence, information generated using BRACON could enable finite resources towards bracken control to be better directed.

8.5. VEGETATION SUCCESSION AFTER BRACKEN CONTROL

Effective bracken control is expensive. It can necessitate an initial outlay of considerable capital; prove time consuming; and be labour intensive (Musgrave, 1993; Pakeman & Marrs, 1994b). If replacement vegetation can become established following good initial bracken control, this may suppress bracken recovery, thereby minimising or eventually removing the need for any form of follow-up bracken management. The REBRA (REvegetation after BRAcken control) model was developed in order to predict the direction and rate of succession in areas where bracken control treatments have been implemented. The response of the ground flora within experimental plots at the Breckland study site was monitored in order to provide test data for the revegetation model. Previous assessment of REBRA's validity was limited, and confined itself to the performance of individuals within the ground flora (Pakeman *et al.*, 1993). The current study, instead of comparing theoretical changes against actual fluxes in terms of individual species abundance, assessed the accuracy of predicted changes at the community level. This was facilitated by multivariate analysis of vegetation data. Individual communities were represented twice (model predictions and actual field data) within single data matrices. In the second year of bracken management, actual and predicted communities appeared to exhibit some contrasts, however, ordination indicated that vegetation groups identified by TWINSPAN occupied the same space in a biplot of vegetation samples. In the third year of experimentation, a greater divergence in actual and predicted communities was evident within the biplot of vegetation samples. Some difficulties with REBRA were identified, including its limited set of species available for modelling succession. It does not consider tree, shrub, or bryophyte species, some of which formed an important component of the vegetation within experimental plots. Extension of the model to accommodate these plant life forms may have reconciled some of the disagreements between predicted and actual plant communities.

8.6. BRACKEN CONTROL TO PROMOTE OAK SEEDLING ESTABLISHMENT

An experiment was undertaken in a woodland clearing where planted oak seedlings were growing under a continuous bracken canopy. This experiment constituted a natural development from the work already discussed within the thesis. The principal objective of the thesis was to examine the effects of control treatments upon bracken, with a limited secondary objective of monitoring development of the ground flora. This final part of the thesis advances the study by directly introducing a species whose performance is assessed in relation to common bracken control regimes.

Oak seedlings under untreated bracken continued to grow and establish during the three years of monitoring, however, the commencement of bracken control appeared to halt seedling mortality observed across the study site. Cutting and herbicide management regimes achieved levels of bracken control consistent with national trends. Oak seedling growth improved significantly when bracken control treatments were imposed. The greatest increases in oak height increment were observed within bracken-cut plots. Cutting bracken once yearly exposed seedlings to potential damage from collapsing fronds, however, this did not appear to be an important factor determining seedling status within this study. Cutting may have offered an advantage for seedling establishment by removing the light-suppressing bracken canopy within the first season of treatment, whereas spraying asulam had no effect until the second season. Based upon seedling height increment, it was predicted that seedlings amongst untreated bracken would require a further ten years before it would overtop a 1.6 m bracken canopy, by which stage it could perhaps begin to shade the bracken and eventually become dominant. The scale to which bracken control treatments accelerate oak dominance at this site was predicted.

8.7. SUGGESTIONS FOR FUTURE WORK

- effective control of bracken is a long term undertaking; the continued monitoring of the nationwide experiment would aid the planning of national and regional long term strategies towards bracken management.

- a greater detailed examination into the response of the rhizome system (storage and frond-bearing components; active and dormant bud numbers; carbohydrate levels) in relation to control treatments could explain differences in treatment efficacy between sites.

- future collection of rhizome samples from experimental plots would enable longer term BRACON predictions to be tested. Two possible scenarios are available: (1) predictions for continued control, or (2) predictions for bracken recovery following cessation of control.

- the benefits of frond regrowth in the latter portion of the growing season, as a means to offsetting energy losses incurred via cutting treatments is poorly understood. The collection of such material could be used to improve the accuracy of BRACON predictions.

- a more effective evaluation of REBRA predictions could be undertaken by (1) extending the number of species it can consider, and (2) monitoring vegetation development at several climatically contrasting sites.

- the basic model for predicting when oak seedlings would overtop the bracken canopy could be improved by continued recording of seedling performance. The extent to which the initial three years of bracken control were effective in providing the necessary respite from bracken interference to promote seedling establishment could be determined.

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APPENDIX

A.1. STUDY SITE DETAILS

A.2. SELECTED FROND AND RHIZOME FIELD DATA

Tables A.2 - A.5 present individual site-treatment means for frond density and height during 1994 and 1995. Similar data for frond biomass is not presented due to the problems of sample decay. Table A.6 presents figures for rhizome biomass recorded during spring 1995.

A.3. MODEL SIMULATIONS

BRACON predictions for rhizome biomass dynamics overlain with field data are presented for the study sites at Mull, Scottish Borders, Lake District, Clwyd, Breckland, Devon (similar figures for Clwyd are given in section 5.3.2.).

Table A.1. Site details. Grid reference is given as National Grid easting (km) and northing (km). Meteorological data is derived from relevant 40 × 40 km grid cell for each site.

Site (Grid reference)	Brief description	Meteorological data
Mull (173.2,731.7)	Auchnacraig Estate (altitude 40 m). Slopes easterly. Bracken infestation reduces grazing potential for sheep, deer and cattle. Understorey vegetation includes *Agrostis capillaris* (L.), *Carex pilulifera* (L.), *Corydalis claviculata* (L.) DC, *Ranunculus ficaria* L.	Mean soil teperature (°C) = 3.2 (January); 15.7 (July) Mean incident solar radiation (MJ m^{-2} day^{-1}) = 17.7 (June); 1.1 (December) Day of first and last frost = 121; 319 respectively Ratio of potential to actual evaporation = 0.997
Scottish Borders (385.9,621.6)	Sourhope Estate (altitude 350 m). Slopes south-westerly. Bracken reduces quality and quantity of land available for sheep and goat grazing. Understorey vegetation includes *Agrostis capillaris*, *Festuca ovina* L., *Carex* L. spp., *Potentilla erecta* (L.). Raeusch.	Mean soil temperature (°C) = 3.1 (January); 16.3 (July) Mean incident solar radiation (MJ m^{-2} day^{-1}) = 17.5 (June); 1.4 (December) Day of first and last frost = 130; 288 respectively Ratio of potential to actual evaporation = 0.914
Lake District (334.8, 535.7)	Caldbeck Fells (altitude 280 m). Slopes easterly. Common land grazed by sheep and horses is infested with bracken. Understorey vegetation includes *Agrostis vinealis* Schreber, *Juncus effusus* L., *Galium saxatile* L., *Anemone nemorosa* L.	Mean soil temperature (°C) = 3.6 (January); 16.5 (July) Mean incident solar radiation (MJ m^{-2} day^{-1}) = 18.5 (June); 1.6 (December) Day of first and last frost = 125; 288 respectively Ratio of potential to actual evaporation = 0.953

Table A.1. continued.

Site	Brief description	Meteorological data
Clwyd (313.8,367.2)	Moel Famau Country Park (altitude 270 m) Slopes north-westerly (2 blocks) and north-easterly (1 block). Bracken has proven problematic for grazing and shepherding sheep. Understorey vegetation includes *Agrostis* L. spp., *Potentilla erecta*, *Oxalis acetosella* L., *Ulex europaeus* L.	Mean soil temperature (°C) = 4.3 (January); 17.1 (July) Mean incident solar radiation (MJ m^{-2} day^{-1}) = 19.3 (June); 1.7 (December) Day of first and last frost = 115; 305 respectively Ratio of potential to actual evaporation = 0.844
Breckland (575.4,272.4)	Cavenham Heath (altitude 15 m). Slopes gently north-westerly. National Nature Reserve managed to conserve heathland threatened by invasion from bracken (and birch). Understorey vegetation includes *Calamagrostis epigejos* (L.) Roth, *Calluna vulgaris* (L.) Hull, *Deschampsia flexuosa* (L.) Trin., *Rumex acetosella* L.	Mean soil temperature (°C) = 4.1 (January); 17.7 (July) Mean incident solar radiation (MJ m^{-2} day^{-1}) = 18.5 (June); 1.8 (December) Day of first and last frost = 121; 288 respectively Ratio of potential to actual evaporation = 0.678
Devon (277.8, 85.4)	Pepperdon Down (altitude 340 m). Slopes north-easterly. Bracken dominance reduces the potential recreational value of the site. Understorey vegetation includes *Holcus mollis* L., *Hyacinthoides non-scripta* (L.), *Potentilla erecta*, *Rubus fruticosus* L. agg.	Mean soil temperature (°C) = 5.5 (January); 18.0 (July) Mean incident solar radiation (MJ m^{-2} day^{-1}) = 20.0 (June); 2.6 (December) Day of first and last frost = 105; 298 respectively Ratio of potential to actual evaporation = 0.860

Table A.2. Mean frond density (n=3) following different bracken control treatments recorded at the six study sites during summer 1994. Standard errors are given in parentheses. Treatment codes are: C1, cut once yearly; C2 cut twice yearly; A, asulam; CA, single cut prior to asulam; AC, asulam with single follow-up cut. Site codes are: 1, Mull; 2, Scottish Borders; 3,Lake District; 4, Clwyd; 5, Breckland; 6, Devon.

	Site					
Treatment	1	2	3	4	5	6
U	36.0 (6.1)	26.7 (4.8)	28.7 (3.5)	23.3 (2.4)	26.7 (5.5)	14.7 (2.4)
C1	34.7 (2.4)	65.0† (17.0)	32.0 (2.3)	28.0 (6.1)	35.3 (3.7)	12.7 (3.3)
C2	18.7 (7.0)	26.7 (2.7)	30.7 (4.7)	12.0 (5.3)	8.0 (3.5)	12.0 (5.3)
A	2.7 (0.8)	2.2 (0.3)	2.3 (0.6)	3.0 (1.3)	1.0 (0.1)	0.9 (0.1)
CA	9.3 (0.7)	10.0 (2.3)	7.3 (0.7)	17.3 (2.4)	8.7 (0.7)	8.0 (4.0)
AC	1.9 (0.3)	2.7 (0.4)	2.3 (0.1)	2.7 (0.4)	1.2 (0.1)	1.1† (0.3)

† (n=2)

Table A.3. Mean frond height (n=3) following different bracken control treatments recorded at the six study sites during summer 1994. Standard errors are given in parentheses. See Table A.2 for treatment and site codes.

	Site					
Treatment	1	2	3	4	5	6
U	137.8 (3.0)	87.3 (12.3)	72.3 (0.5)	150.0 (28.2)	74.4 (9.5)	115.3 (7.2)
C1	106.4 (1.0)	81.5[†] (4.6)	57.4 (1.5)	90.5 (16.5)	45.8 (10.4)	78.3 (13.9)
C2	52.5 (7.7)	44.2 (1.2)	42.1 (5.4)	45.5 (13.2)	19.8 (6.4)	58.5 (13.6)
A	54.3 (11.3)	57.5 (18.0)	30.1 (0.5)	49.4 (19.1)	54.8 (12.8)	76.2 (5.2)
CA	52.3 (9.8)	51.2 (5.8)	47.4 (7.1)	86.6 (25.6)	34.1 (1.6)	78.9 (4.7)
AC	42.8 (6.5)	54.6 (17.6)	29.1 (3.4)	75.1 (13.7)	54.8 (12.8)	93.9[†] (20.2)

[†] (n=2)

Table A.4. Mean frond density (n=3) following different bracken control treatments recorded at the six study sites during summer 1995. Standard errors are given in parentheses. See Table A.2 for treatment and site codes.

	Site					
Treatment	1	2	3	4	5	6
U	28.0 (2.0)	36.0 (9.5)	36.0 (6.1)	34.0 (3.5)	35.3 (7.1)	16.0 (3.1)
C1	31.3 (3.7)	29.3 (1.8)	30.0 (7.0)	16.7 (4.7)	60.7 (10.7)	18.0 (2.0)
C2	32.0 (11.7)	20.7 (5.5)	26.0 (8.1)	14.0 (9.2)	15.3 (7.0)	10.0 (2.0)
A	16.0 (5.0)	9.3 (4.4)	10.7 (2.9)	8.7 (1.8)	6.7 (2.9)	2.7 (0.7)
CA	18.7 (6.8)	17.3 (2.4)	23.3 (4.7)	14.7 (9.0)	32.7 (2.7)	8.0 (2.0)
AC	8.0 (1.2)	9.3 (2.9)	8.7 (2.4)	5.3 (0.7)	8.0 (3.5)	2.0 (0.0)

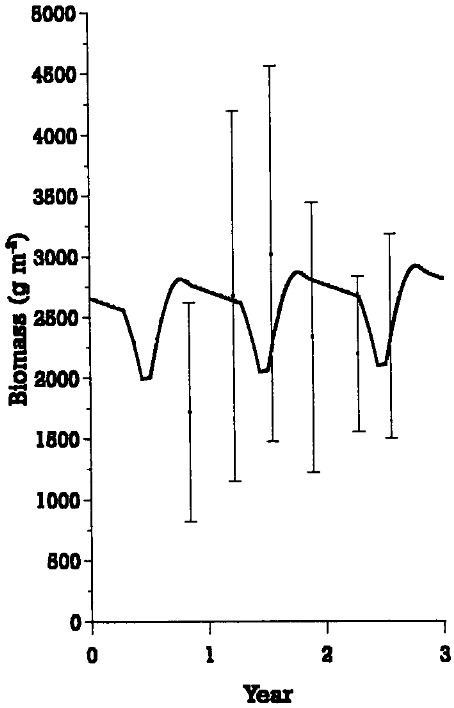
Table A.5. Mean frond height (n=3) following different bracken control treatments recorded at the six study sites during summer 1995. Standard errors are given in parentheses. See Table A.2 for treatment and site codes.

	Site					
Treatment	1	2	3	4	5	6
U	126.1	87.0	70.8	115.9	79.1	110.7
	(23.9)	(18.4)	(2.8)	(21.3)	(7.3)	(10.2)
C1	114.7	52.0	42.6	51.6	32.1	78.0
	(7.3)	(8.4)	(5.5)	(6.6)	(7.2)	(4.3)
C2	27.1	31.1	37.2	27.3	16.7	37.7
	(5.3)	(2.8)	(3.3)	(7.1)	(6.8)	(7.6)
A	64.1	34.8	32.9	39.9	32.3	72.2
	(10.0)	(1.4)	(4.0)	(4.0)	(4.8)	(16.8)
CA	67.1	57.0	40.1	93.2	40.3	61.3
	(7.7)	(14.4)	(5.0)	(8.7)	(11.6)	(7.8)
AC	42.9	40.1	27.0	31.7	31.0	71.7
	(8.5)	(4.4)	(1.9)	(11.7)	(5.8)	(8.2)

Table A.6. Mean rhizome biomass (n=3) following different bracken control treatments recorded at the six study sites during spring 1995. See Table A.2 for treatment and site codes.

	Site					
Treatment	1	2	3	4	5	6
U	2196.1	1897.3	1410.0	2093.9	885.3	1789.1
	(325.7)	(156.2)	(116.1)	(205.2)	(107.7)	(153.2)
C1	2349.4	1795.3	1286.4	1271.6	623.7	1221.1
	(78.1)	(274.7)	(71.4)	(358.3)	(152.5)	(83.0)
C2	1558.7	1509.0	1026.6	1028.2	579.5	1192.5
	(463.2)	(299.1)	(107.4)	(161.0)	(70.9)	(19.8)
A	2009.3	1452.5	1481.1	1530.1	1189.3	1589.2
	(339.8)	(183.7)	(223.7)	(164.2)	(25.8)	(172.8)

(a)



(b)

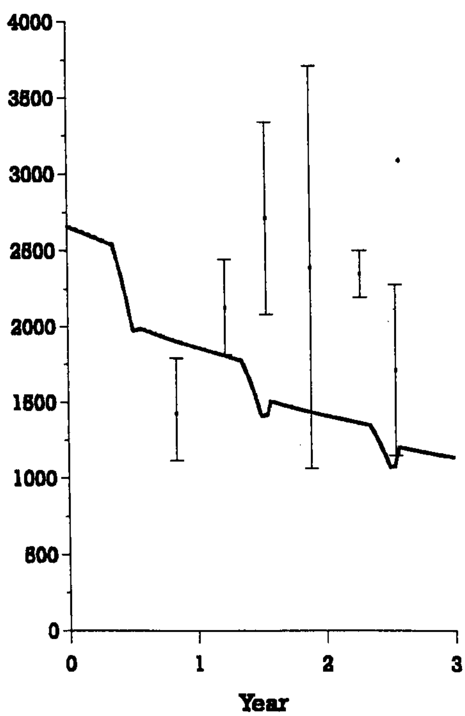
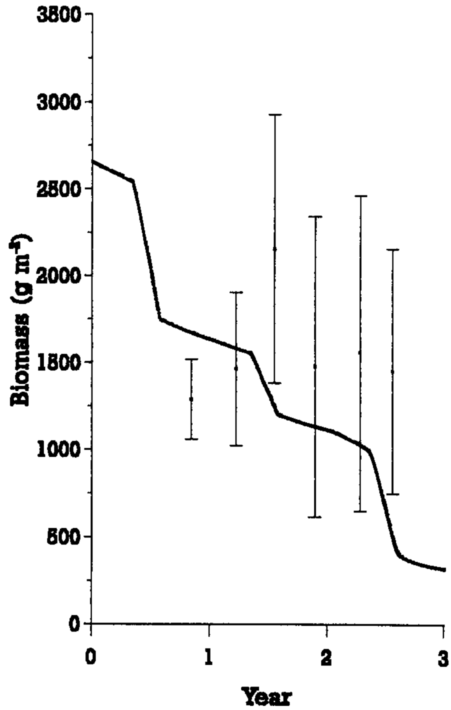


Figure A.1. BRACON simulations for Mull study site following bracken control treatments (a) untreated; (b) cut once yearly; (c) cut twice yearly; (d) asulam. Predictions are overlain with plot means and their associated 95% confidence interval obtained throughout the experiment.

(c)



(d)

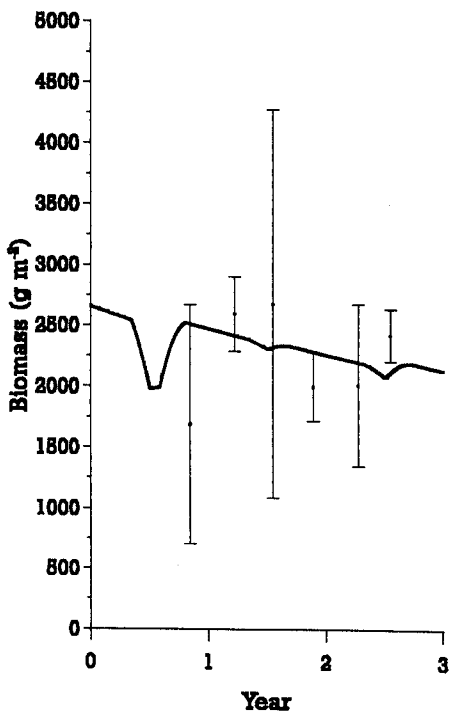
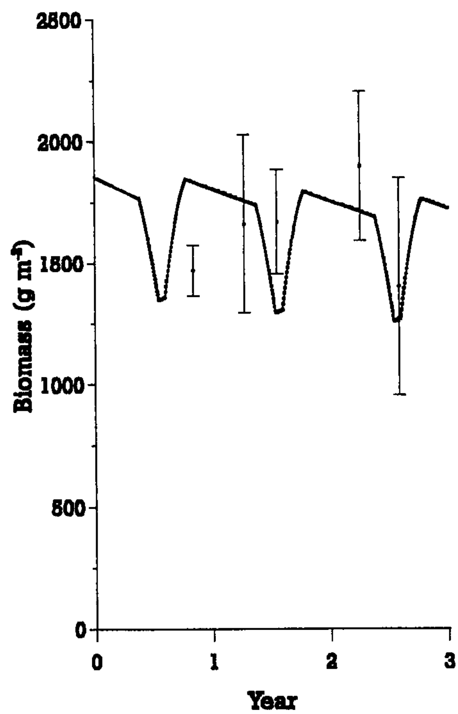


Figure A.1. continued.

(a)



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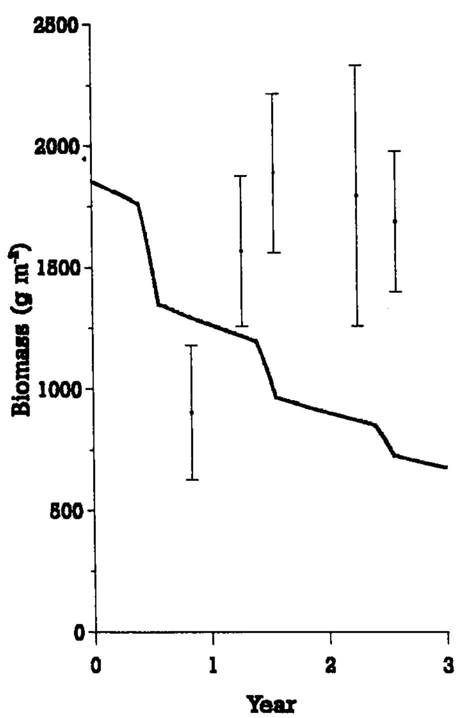
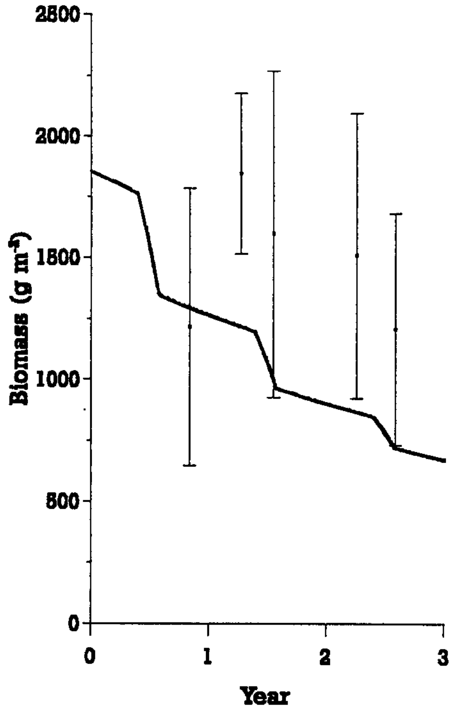


Figure A.2. BRACON simulations for Scottish Borders study site following bracken control treatments (a) untreated; (b) cut once yearly; (c) cut twice yearly; (d) asulam. Predictions are overlain with plot means and their associated 95% confidence interval obtained throughout the experiment.

(c)



(d)

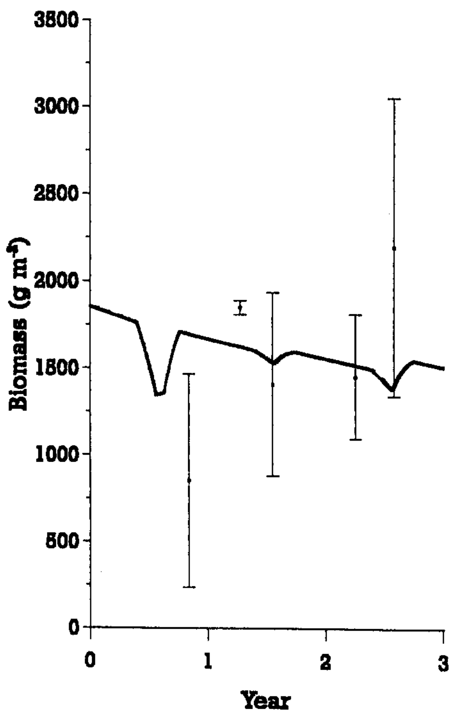
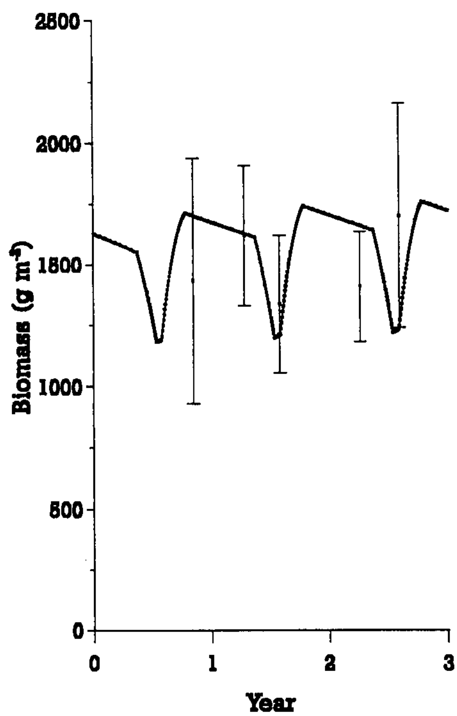


Figure A.2. continued.

(a)



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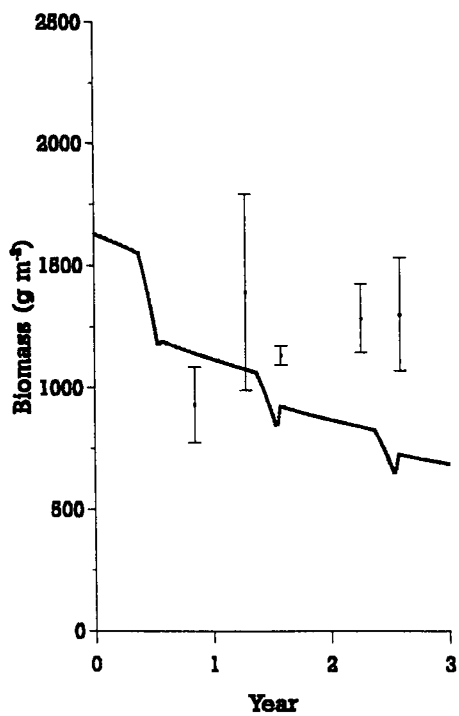
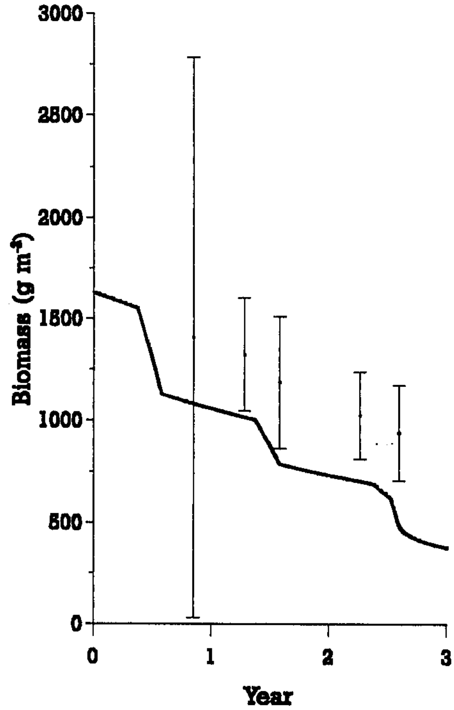


Figure A.3. BRACON simulations for Lake District study site following bracken control treatments (a) untreated; (b) cut once yearly; (c) cut twice yearly; (d) asulam. Predictions are overlain with plot means and their associated 95% confidence interval obtained throughout the experiment.

(c)



(d)

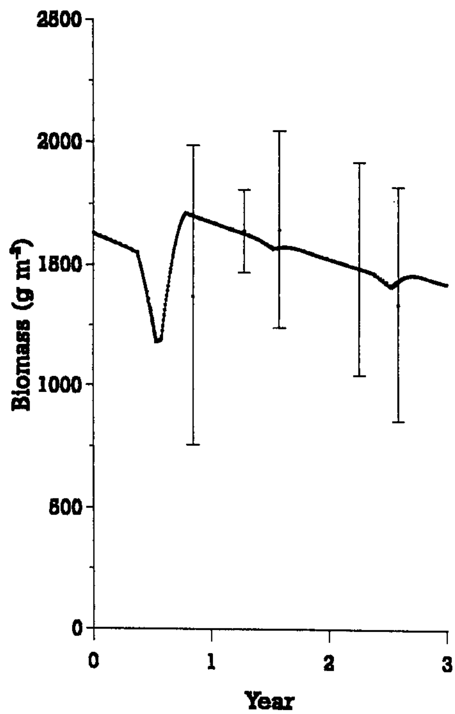
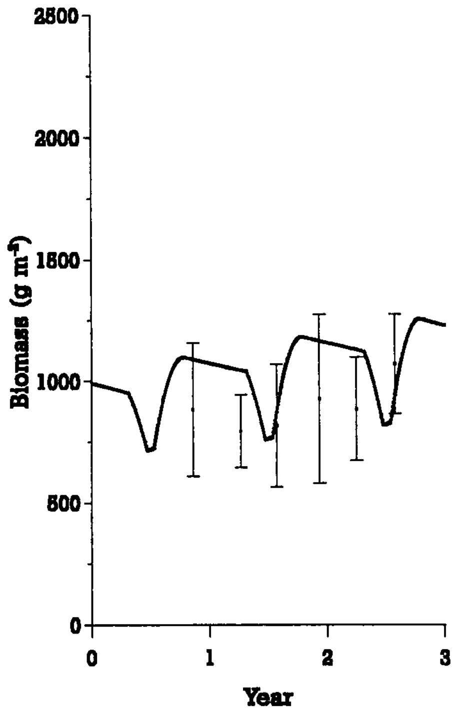


Figure A.3. continued.

(a)



(b)

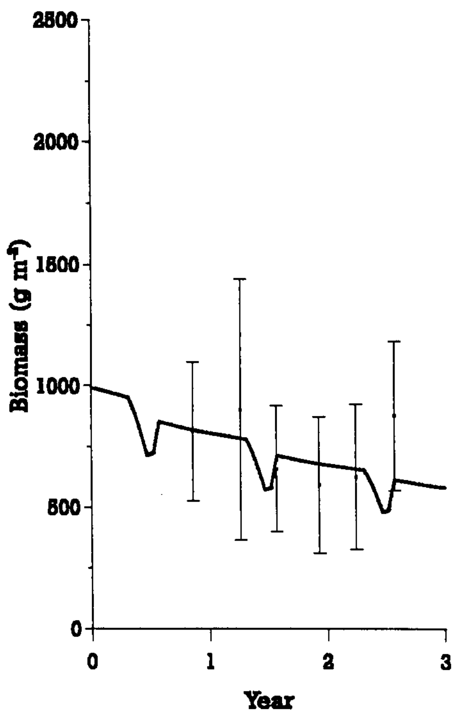
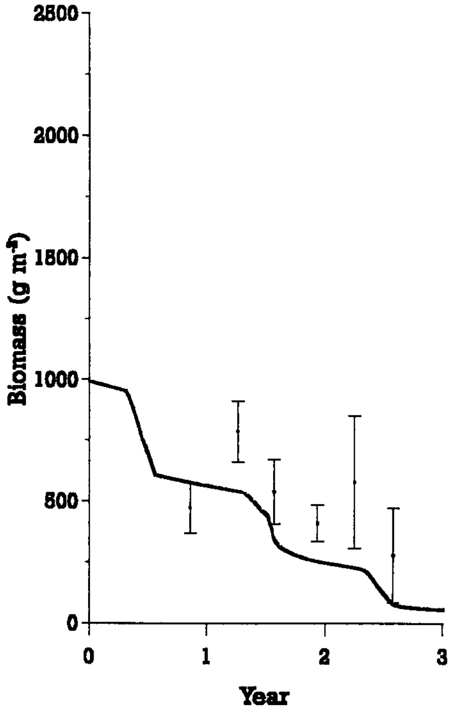
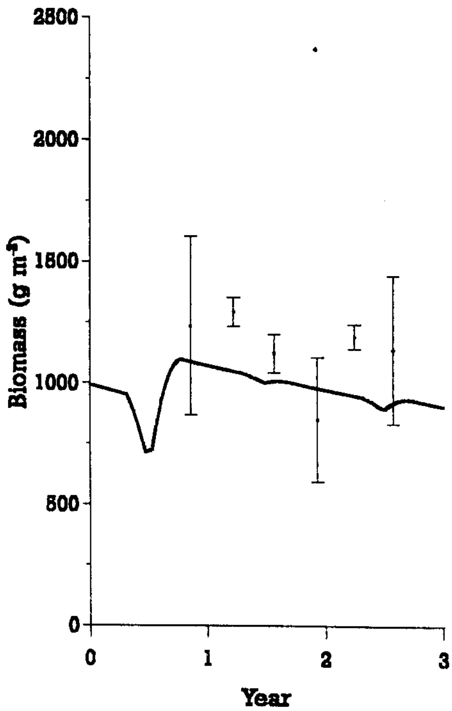


Figure A.4. BRACON simulations for Breckland study site following bracken control treatments (a) untreated; (b) cut once yearly; (c) cut twice yearly; (d) asulam. Predictions are overlain with plot means and their associated 95% confidence interval obtained throughout the experiment.

(c)



(d)



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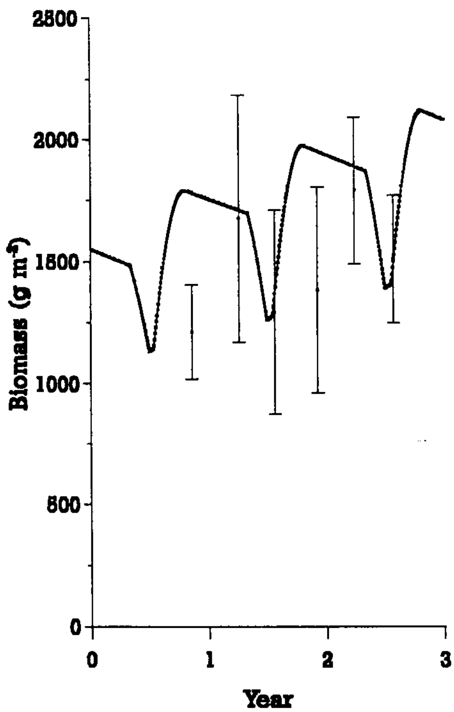
(a)



(b)

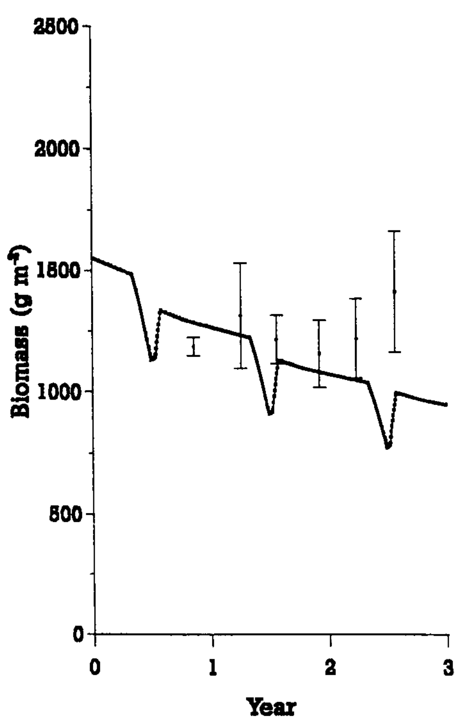
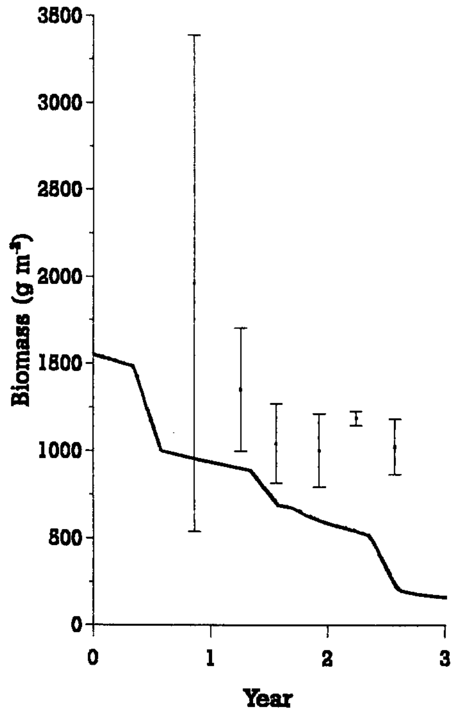


Figure A.5. BRACON simulations for Devon study site following bracken control treatments (a) untreated; (b) cut once yearly; (c) cut twice yearly; (d) asulam. Predictions are overlain with plot means and their associated 95% confidence interval obtained throughout the experiment.

(c)



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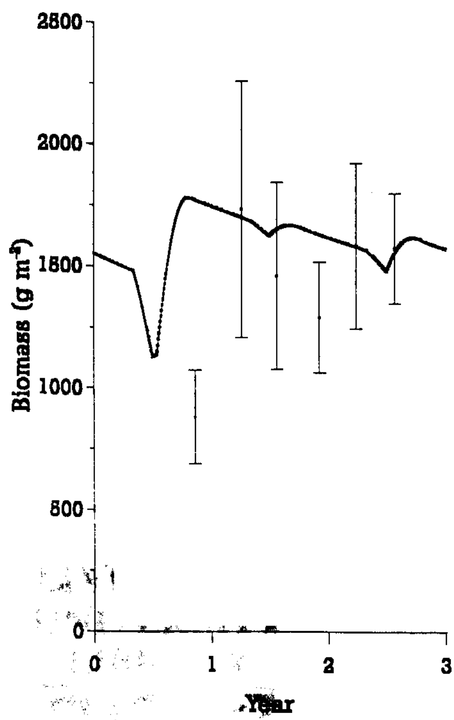

Figure A.5. continued.