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The implications and effects of bracken (*Pteridium aquilinum* (L.) Kuhn) control on species diversity, re-vegetation and bracken preformance

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

By

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Some of the work in this thesis and, additional work outside the formal scope of this thesis but allied to it, has been published in refereed journals or is in press. All of this material is provided in an Appendix, for completeness.

Declaration of work carried out

I declare that all of the work presented in this thesis, which was conducted at the School of Biological Sciences, University of Liverpool, is my own work, unless otherwise stated. This thesis is submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor of Philosophy.

Work in Chapters 2, 3, 4, 5, 8 & 9 in this thesis is based on data collected from a series of long-term experiments set up by Dr. Mike Le Duc & Prof. Rob Marrs at the University of Liverpool in 1993, which was funded by the Ministry of Agriculture, Fisheries and Food and then the Department for Environment Food and Rural Affairs. Field work between 1993 and 2003 was conducted by Dr. Le Duc. This project was funded mainly by Department for Environment Food and Rural Affairs with additional support from Moors for the Future (www.moorsforthefuture.org.uk) and the Royal Botanical and Horticultural Society of Manchester and the Northern Counties.

Work in Chapter 3 was carried out in collaboration with Dr. Gavin Stewart and Prof. Andrew Pullin at the University of Birmingham. Dr. Stewart carried out the meta-analysis presented in Chapter 3.

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Abstract

The implications and effects of bracken (*Pteridium aquilinum* (L.) Kuhn) control on species diversity, re-vegetation and bracken productivity

Emma Cox

Pteridium aquilinum is the most widely distributed of all the pteridophytes; it is present throughout the world with the exception of hot and cold desert regions. Originally a component of open woodland communities its range has extended markedly as a result of mans' activities. The problems caused by bracken infestation are many and varied. Bracken infestation can cause considerable loss of revenue for farmers in terms of the reduction in available grazing land and through additional expenses such as veterinary fees and control costs. The quality of grazing is reduced due to the shading out of understorey vegetation. It also competes effectively with *Calluna* and other heath and grassland species, at best reducing their cover but in some cases eliminating them. The control of *Pteridium aquilinum* requires a long-term strategy and when planning to undertake control at least a five year programme should be considered. One of the reasons bracken is so hard to control is its extensive rhizome system that can potentially live for more than 50 years. Segments as small as 9 cm are able to grow.

A fundamental limitation in vegetation management and restoration ecology is the ability to predict, with some degree of precision the likely outcome of a proposed treatment across a range of sites. A great deal of money and effort is being placed into controlling invasive weeds as part of international and national policies, for example within the UK agri-environment schemes and Biodiversity Action Plans. One of the major issues highlighted in *Pteridium aquilinum* control is the high variability in success rates, and a cost-effective control strategy has proved elusive. Alongside this, the need for long-term, fully replicated experiments is often highlighted in restoration ecology.

In this thesis long-term, multi-site bracken control experiments were analyzed to assess efficacy of various control treatments and subsequent re-vegetation. The experiments assessed the efficacy of five treatments designed to control *Pteridium aquilinum* relative to an untreated comparison in a range of contrasting ecological situations. These control treatments were also combined with site-specific treatments designed to restore appropriate heathland or grassland vegetation. In addition two methods of bracken control, bruising and the current manufacturers' guidelines for Asulox application, previously untested in formal experiments were studied.

Long-term control of bracken at all sites was best achieved using a continuous cutting treatment, preferably twice per year. As expected re-spraying previously treated bracken with asulam caused a reduction in all bracken response variables at both sites tested. The rate of recovery after ten years of bracken control is dependent of the initial degree of control, which presumably reflects the starting rhizome biomass of the bracken. It is difficult to develop a one-size-fits-all policy for vegetation restoration within a *Pteridium aquilinum* control strategy, with analysis finding a considerable number of spatial effects between sites of similar vegetation type and located <2.5 km apart. Few bracken control treatment effects were found and where they were detected it was only at single sites. Thus, the development of target vegetation requires a combination of control and restoration treatments that take into consideration the aspects of that site.

After only one year of treatment, the results show support for the theory that bruising is less effective than cutting as a mechanical control. All bracken response variables in August and *Pteridium aquilinum* cover in June increased in the rolled three times per year plots compared with the untreated control, rather than the desired decrease. Bruised fronds were found to remain alive and green for up to seven weeks after the initial bruising treatment, with no significant difference between the photosynthesis and transpiration rates in bruised and untreated fronds. Even in severely damaged fronds key structures such as the xylem vessels remaining intact, despite extensive damage to other tissues. However there was no evidence of the 'rhizome being bled dry' as none of the bracken control treatments had any impact on the rhizomes.

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Chapter 1

General Introduction

1. General Introduction

The control of undesirable invasive plants requires cost effective and ecologically-based methods (Wiles, 2004). In Australia and New Zealand policy has moved away from the emphasis on purely weed control towards consideration for long-term effectiveness based on a 'strategic, integrated and ecological' approach (Williams & West, 2000). In Britain, such approaches have been developed for *Molinia* control in the uplands (Milligan *et al.*, 2003). Such management usually involves a combination of control treatments and specific treatments designed to restore vegetation. Together they can control the problematic weed and create a more desirable target habitat (DiTomaso, 2000). This is particularly important when weed infestation is high (Simmons, 2005), and the aim is to establish vegetation that increases resistance to invasion and prevents the weed infestation from recurring (Blumenthal *et al.*, 2003). Although, restoration management that involves a weed control phase often produces mixed results (Le Duc *et al.*, 2000, 2003; Hytonen & Jylha, 2005).

In the UK there is an increasing need for applied ecologists to be able to assist in the development of national weed control strategies, to meet the conservation objectives of Biodiversity Action Plans (Anon, 1995 a, b). The Common Agricultural Policy developed by the European Union provides financial incentives to farmers to carry out environmentally beneficial measures (Ovenden *et al.*, 1998). Management prescriptions, in the UK, are implemented through agri-environments schemes, such as Countryside Stewardship Schemes and Environmentally Sensitive Areas (MAFF, 1993, 1996) or through management agreements with conservation bodies.

A good example of such a problem is *Pteridium aquilinum* (L.) Kuhn control in the UK. *P. aquilinum* occurs throughout the world with the exception of hot and cold desert regions (Page, 1976). *P. aquilinum* tends to be found on acidic (Grime, 1988; Koedam *et al.*, 1992), well drained soils, and is thought to have originated in woodlands. However, this does not mean it is confined to them, as bracken has been found in soils with a pH of 8.6 (Willis *et al.*, 1959a, b), nor is it absent from waterlogged ground (Marrs & Watt, 2006; Poel, 1951), although soil aeration is a limiting factor, (Poel, 1948, 1951, 1961). It shows maximum vigour on deep productive brown earths (Grime, 1988). *P. aquilinum* is know to be a strong competitor for water (Gordon *et al.*, 1999; Smith & Lockwood, 1990) and can absorb nutrients effectively (Evans & Gaplin, 1990).

Part of the reason for the success of *P. aquilinum* is its ability to restrict water loss more effectively than other ferns; it is possible that the presence of vessel members could indicate *P. aquilinum*'s increased water efficiency (White, 1963). Originally a component of open woodland communities (Marrs & Watt, 2006), the plant's ability to restrict water loss has resulted in expansion outside woodlands, creating mid-successional communities between grassland/heath and woodland in open areas (Marrs *et al.*, 2000). Although a mid-successional species it can persist for long periods and appears in some cases it represents a highly resilient stable state (Marrs *et al.*, 2000; Suding *et al.*, 2004; Marrs & Watt, 2006).

1.1 Is bracken expanding?

Large-scale land clearing has been followed by an increase in *Pteridium* spp. in many parts of the world including; Europe (Rymer, 1976), America (Stewart *et al.*, 1979), Australia (Thomson *et al.*, 1986; Hamilton *et al.*, 1990) and New Zealand (Taylor, 1986). *P. aquilinum* appears in 42 communities and as part of 153 sub-communities in the UK (Rodwell, 1991a, b, 1992, 2000), where it is found as a component species in woodland, heath, grassland, maritime and open habitats. An estimated total of 17073 km^2 (7.3%) of Britain contains some bracken, with 4762 km^2 (2.0%) being dense bracken in the open (Pakeman *et al.*, 1995). The UK Countryside Survey data showed a reduction in land formerly dominated by bracken from 4200 km^2 to 3800 between 1984 and 1990 (Barr *et al.*, 1993). The main communities that replaced bracken over this period were managed grassland and dwarf-shrub dominated vegetation. However, there were 600km^2 of land that changed its dominant cover to bracken in the same time period (Barr *et al.*, 1993). Alternatively, Taylor (1999) suggests encroachment rates of bracken in the UK ranges from 1 to 3% per annum, with similar results found in grassland surveys conducted by Hopkins *et al.* (1988). Exclusion of very low density bracken from remote survey followed by the inclusion of bracken when the same area is resurveyed, after an interim increase in density, could account for some of the encroachment (Taylor, 1985). However, this is not true encroachment but regeneration of already established bracken (Marrs & Hicks, 1986).

Modelled predictions by Pakeman *et al.* (1995) suggest bracken encroachment may be a problem in the south-west and Wales, in the future it may become denser in Wales, the Pennines and western Scotland as a result of less intensive management. On a local scale *P. aquilinum* has been noted to advance on to lowland grass heath at an average rate of 43 cm per year (Watt, 1954) increasing to 87 cm per year on upland *Calluna* heath treated with asulam (Pakeman *et al.*, 2002).

Improving climate (Pakeman & Marrs, 1996) and increased nutrient supply (Caporn *et al.*, 1999) are likely to have the greatest influence on bracken in upland areas of the UK, rather than increased levels of CO_2 (Caporn *et al.*, 1999). The largest effects of climate change on bracken vigour are predicted to occur in northern Scotland where climate is currently limiting to bracken growth.

1.2 Why control bracken?

P. aquilinum was originally a component of open woodland communities (Marrs & Watt, 2006), and its range has extended markedly as a result of mans' activities (Marrs & Watt, 2006) with attitudes towards bracken changing with changes in farming and the economy in the 20th Century.

The problems caused by bracken infestation are many and varied. Bracken infestation can cause considerable loss of revenue for farmers in terms of the reduction in available grazing land and through additional expenses such as veterinary fees and control costs (Varvarigos & Lawton, 1991). The quality of grazing is reduced due to the shading out of understorey vegetation (Pakeman & Marrs, 1992). As well as having a negative effect on the development of tree seedlings in the USA (Engelmen & Nyland, 2006). It also competes effectively with *Calluna* (Gordon *et al.*, 1999) and other heath and grassland species, at best reducing their cover but in some cases eliminating them (Pakeman & Marrs, 1992). Thus, a reduction in land suitable for grazing and habitat for game is seen. In areas like New South Wales, Australia dense bracken (*Pteridium esculentum*) stands are a potential fire hazard due to the amount of fuel that builds up in the persistent litter layer (Thompson *et al.*, 1986).

1.2.1 The toxicity of bracken

P. aquilinum contains a large number of secondary plant compounds including; terpenoids (sequiterpenoids), the insect moulting hormones ecdysone and ecdysterone, cyanogenic glucosides, tannins and phenolic acids (Cooper-Driver, 1976). These compounds are thought to reduce herbivory, increase disease resistance or provide an allelopathic effect (Marrs & Watt, 2006). When eaten the bracken frond can cause livestock health problems (Hopkins, 1990), these include thiamine deficiency in horses and pigs (Evans, 1976), acute haemorrhagic syndrome and chronic enzootic haematuria in cattle (Fenwick, 1989). It has been linked to incidences of stomach cancer in humans either from consuming bracken as food (Hirono *et al.*, 1970, 1972) or from bracken in the environment with risks from contaminated milk and water (Alonso-Amelot *et al.*, 1996; Gaplin *et al.*, 1990). Bracken spores have also been linked to gastric tumours and leukaemia (Evans & Galpin, 1990). Ptaquiloside a carcinogen compound isolated from *P. aquilinum* has been found to be responsible for >50% of mutagenic activity (van der Hoeven *et al.*, 1983). The compound is readily soluble in water (Ojika *et al.*, 1987) and it is relatively stable at neutral pH (Saito *et al.*, 1989). It has been found in topsoil and organic soil horizons below bracken stands in Denmark, indicating possible contamination of watersheds (Rasmussen *et al.*, 2003). However, to date there is no proven causal link or transfer pathway between bracken and human cancers (Marrs & Watt, 2006).

The tick *Ixodes ricinus* is found in most bracken invested areas (Hodgson, 1991); it is the main vector for transmission of the spirochaete *Borrelia burdorferi* (Nathwani *et al.*, 1990). *B. burdorferi* causes Lymes disease in humans with a characteristic rapidly expanding rash. Symptoms can include; fever, headaches, neurological and cardiac problems and in the long term arthritis if left untreated (Hodgson, 1991). The number of reported cases is thought to be increasing, although the numbers may vary regionally (Hodgson, 1991; Nathwani *et al.*, 1990). Other tick borne diseases, including louping-ill, can affect grouse and sheep (Hudson *et al.*, 1995).

1.2.2 Impact on biodiversity

Dense *P. aquilinum* is a problem species for conservation as well as agriculture, as it is a long-lived robust clonal species (Le Duc *et al.*, 2003) that produces a dense litter layer (Frankland, 1976) associated with low floristic diversity (Grime, 1988). There is often a considerable reduction in conservation value especially when heath and moorland is invaded (Pakeman & Marrs, 1992). The presence of deep litter can impede the growth of other vegetation as it struggles to grow under or penetrate the litter (Humphrey & Swaine, 1997; Engelmen & Nyland, 2006). It is a strong competitor (Grime, 1988), competing effectively with heathland and grassland species, at best reducing their cover but in some cases eliminating them leaving a very depauperate flora (Pakeman & Marrs, 1992). This eventually leads to impacts on seed banks which are also depauperate under bracken (Pakeman & Hay, 1996) leading to potential problems when trying to restore the desired target vegetation post-bracken-control.

1.2.3 The importance of bracken

P. aquilinum used to be an important resource within the rural economy (Pakeman & Marrs, 1992). The importance of bracken is illustrated by the laws that used to govern annual cutting times (Rymer, 1976). Records of the sale of bracken and the need to preserve areas with bracken date back 500-700 years (Rymer, 1976). Uses of bracken over the years have included; use as a source of potash, for use in glass and soap manufacturing, for bleaching, thatch, animal bedding, compost, food and in medicine (Rymer, 1976). For some the aesthetic value of bracken, particularly in the autumn and winter, is an integral part of the countryside (Pakeman & Marrs, 1992; Taylor, 1999). Bracken is also an important part of folk-lore (Rymer, 1976).

In certain circumstances bracken can act as a substitute for a woodland canopy (Pakeman & Marrs, 1992). Species such as *Viola riviniana,* an essential food plant for the currently declining fritillary butterflies eg. the high brown fritillary (*Argynnis adippe*) or the heath fritillary (*Mellicta atthalia*), can be found under bracken. It is often managed to create an optimal frond density or litter depth (Broome, 2007). Other woodland species such as bluebell spp. (*Hyacinthoides* spp.) and wood sorrel (*Oxalis acetosella*) can be found under bracken (Broome, 2007; Pakeman & Marrs, 1992). It is also important for birds such as whinchats (*Saxicola rubetra*) and nightjars (*Caprimulgus europaeus*), whose other natural habitats are declining (Pakeman & Marrs, 1992).

Marrs *et al.* (2007) have recently argued that there is a potential dilemma between controlling a mid-successional invasive species for conservation purposes to achieve Biodiversity Action Plan targets, and the potentially negative effects due to increasing the environmental impact in terms of carbon accounting and water quality. Dense bracken has a large carbon stock and elements such as calcium, magnesium and phosphorus appear to be retained in high quantities in the rhizome; control releases these elements into the ecosystem.

1.3 Controlling bracken

P. aquilinum is dormant over winter, with fronds senescing from late August to October. The fronds collapse in October/ November contributing to a persistent litter layer (Watt, 1976). Fronds emerge in spring between April and June from active rhizome buds, reaching a peak in dry frond mass in August (Watt, 1976). The rhizome system is the main carbohydrate reserve, which has the ability to extend very quickly (Whitehead & Digby, 1997a, b). Storage rhizome mass reaches an annual low in late June/ early July, after frond expansion but before fronds become net importers, and peaks just before senescence (Williams & Foley, 1976). Frond density is variable and can range between 0.1 to 75 fronds m^{-2}, frond height is also very variable with a mean of 63 cm in rough grazed land but a maximum of 4.4m has been recorded (Marrs & Watt, 2006). Reproduction can either be vegetative via the rhizomes or by spores (Marrs & Watt, 2006), although, regeneration by spores is rare in Britain (Dyer, 1989).

1.3.1 Control methods

The control of *P. aquilinum* requires a long-term strategy (Lowday & Marrs, 1992a; Marrs *et al.*, 1998a) and when planning to undertake control at least a five-year programme should be considered (The Southern Uplands Partnership, 2001). One of the reasons bracken is so hard to control is its extensive rhizome system (Le Duc *et al.*, 2003), that can potentially live for more than 50 years (Watt, 1940) and regenerate from segments as small as 9 cm (Daniels, 1985).

The difficultly of controlling *Pteridium* spp. has generated a lot of research both in the UK (Lowday & Marrs, 1992a; Marrs *et al.*, 1998a, Le Duc *et al.*, 2000), the USA (Engelmen & Nyland, 2006; Stewart *et al.*, 1979) and in Australia (Dutkowsli & Boomsma, 1990). Work in the UK has been centred on government policy and developing a cost effective methodology for the reversion of succession of *P. aquilinum* using various mechanical and chemical treatments. Work in the USA on *P. aquilinum* var. *pubescens* and in Australia on *P. esculentum* has focused on the efficiency of different chemicals to control bracken (Dutkowsli & Boomsma, 1990; Engelmen & Nyland, 2006; Stewart *et al.*, 1979) in areas of cleared forest where the development of tree seedlings is desirable. Although, limited testing of mechanical methods (cutting) was done by Englemen & Nyland (2006).

There are three strategies that are generally used to control *P. aquilinum* in the UK:

1. *Herbicidal control.* Herbicide action is unlikely to have a direct effect on the amount of rhizome carbohydrate reserves in the short term, and herbicides which attack frond buds on the rhizome are most successful. Asulam [methyl (4-aminobenzenesulphonyl) carbamate] is the most widely used herbicide; it is translocated into the rhizome and accumulates in both active and dormant buds and kills them (Veerasekaran *et al.*, 1976, 1977a, b, 1978). It has a relatively narrow spectrum (compared with general herbicides such as glyphosate) affecting mainly other ferns, docks (*Rumex* spp. Horrill *et al.*, 1978, Sheffield *et al*, 2001) and bryophytes (Rowntree *et al.*, 2003). However, asulam can also affect some fine grasses including *Holcus* spp., *Poa* spp. and *Agrostis solonifera* (Cadbury, 1976). Herbicide action has little impact of bracken litter (Marrs *et al.*, 2007). Asulam frequently produces a very good reduction in fronds in the year after spraying, but there is often rapid frond recovery (Robinson 1986; Lowday & Marrs, 1992b). Research and practice has shown that a single application of asulam is not sufficient (Cox *et al.*, 2007a; Lowday & Marrs, 1992a; Marrs *et al.*, 1998a; Pakeman *et al.*, 1998), unless other treatments are applied in subsequent years (Lowday & Marrs, 1992b). The current manufacturer's guidelines recommend following the initial spray with annual spot spraying until fronds no longer appear in the spring (Anon, 2005; Robinson, 2000; The Southern Uplands Partnership, 2001), although, this has yet to be formally tested.

2. *Mechanical control.* Fronds are cut or bruised during early summer, before and up to the point of maximum frond expansion, with the aim of withdrawing the maximum amount of carbohydrates and nutrients from the rhizome reserves (Hunter, 1953; Williams & Foley, 1976). When a cutting strategy is used it is advisable to cut the fronds when dry weight and carbohydrates in the rhizome are at an annual low (Williams & Foley, 1976). Normally mid-June to late-July in the UK (Anon, 2005; Southern Uplands Partnership, 2001), before the new assimilates start being translocated from the fronds to the rhizomes in large amounts in late July/early August (Williams & Foley, 1976). Cutting can be carried out one, two or three times annually (Braid, 1959; Williams, 1980). Mechanical control in the form of cutting also has an important additional benefit, in that it breaks up and fragments the litter layer, hence assisting other species to colonize (Lowday & Marrs, 1992b). Recently, however, there has been a resurgence of interest in the use of bruising as an alternative for mechanical control. Bruising is a generic term and includes crushing and rolling the bracken; the technique is an old one,

but it fell out of favour in the middle of the 20th Century with the development of mechanically-driven cutters (Braid, 1948). Although bruising bracken is considered a less effective control method in comparison to cutting (Anon, 2005), because of the reduced damage to the litter layer, it is especially suitable for difficult terrain which might damage a cutter (Marrs & Watt, 2006). To some extent the increase in popularity of bruising in recent years can be attributed to claims made by the manufactures of bruisers. There is a belief among some practitioners that this practice allows the fronds to remain alive, and "bleed the rhizome of resources – water, carbohydrate and nutrients". The efficacy of bruising as a bracken control treatment has not yet been formally tested and neither have claims over the physiological impacts of bruising on bracken fronds and rhizomes.

3. *Inhibition by other vegetation.* Usually where dense bracken is to be controlled, managers want to remove the bracken and replace it with some other vegetation. There is some evidence that when competitive vegetation develops during a *P. aquilinum* control program, there is a reduction in frond performance (Watt, 1955; Lowday & Marrs, 1992a; Le Duc *et al.*, 2000, 2007a).

1.4 Restoration of desired vegetation

Control treatments alone may have little effect in creating the desired species community (Pakeman *et al.*, 1997). Jacquemart *et al.* (2003) found although cutting as a control treatment reduced the problem species (*Molinia*), it had little impact on overall vegetation composition. The current agricultural and conservation policy in the United Kingdom for *P. aquilinum* infestation is delivered through Agri-Environment Schemes (MAFF, 1993, 1996) and Biodiversity Action Plans (Anon, 1995a, b). The policy aim is to reduce the *P. aquilinum* infestation reversing succession towards early-successional communities thus restoring heathland or grassland vegetation (Marrs *et al.*, 2000). Thus, ecological restoration of dense *P. aquilinum* patches to alternative vegetation requires at least two, preferably integrated, treatment strategies: control of the *P. aquilinum*, and restoration of suitable target vegetation. Possible restoration treatments tailored to the desired target and site include; litter disturbance, desired species seeding, grazing management, surface disturbance and fertilizer addition (Marrs & Lowday, 1992; Le Duc *et al.*, 2000).

From a theoretical perspective restoration involves development along a desired trajectory (Hobbs & Norton, 1996). Ecological restoration, where one community is transformed to another, aims to overcome the resistance and resilience of the treated community and move it towards a new community with sufficient resistance and resilience to prevent a return to the original state. Thus, essentially creating an alternative stable state (ASS) or basin of attraction (Beisner *et al.*, 2003). This can be done in two ways: by altering either the state variables of the system (e.g. species composition), or its ecosystem parameters (e.g. removal of grazing by fencing), the aim being to force the existing ecosystem to follow a trajectory towards an ASS. If the resilience (Beisner *et al.*, 2003; Mitchell *et al.*, 2000) of the existing system is low, the perturbation may be enough to allow the successional trajectory to reach a new set of state variables, and thus an ASS. However, where the starting state has high resilience, the original community could re-establish rapidly (Marrs & Le Duc, 2000), thus wasting restoration effort. Where ecosystem parameters are changed then we would expect any effect to be a permanent one. However, where state variables are altered the process can be described as two types (see Bender *et al.*, 1984); (1) a "one-off" treatment would be classified as a "pulse-treatment", and (2) a treatment that is applied continuously is described as a "press-treatment". Where a "pulse" treatment has been applied and a new stable ecosystem is formed then we would expect it to be an ASS. However, where a "press treatment" is applied then it is creating a continuing pressure to maintain the new system, and under those circumstances it is not known whether that new state is stable without the continued application of treatment.

1.4.1 Assessing restoration success

A problem in assessing how successful restoration has been is knowing what we want to restore and knowing when the goal has been achieved (Hobbs & Norton, 1996). In order to set restoration goals two principles are suggested. The first is to create a new habitat at the restoration site with the aim of replicating what has previously existed there by using a non-degraded system as a model template. However, ecosystems are naturally dynamic and setting restoration goals in terms of static compositional or structural attributes is problematic (Hobbs & Harris, 2001). The second is the recognition that ecosystems are dynamic and accept that there is a range of potential short- and long-term outcomes (Hobbs & Harris, 2001), some of which might reflect non-damaged systems and some that might be novel.

Measurement of ecosystem components and comparison with the reference components to determine how close projects come to meeting the restoration goal is necessary (Hobbs & Norton, 1996). Monitoring restoration plays a key role determining end points and assessing effectiveness (Davis *et al.*, 2004). If results indicate restoration treatments have met goals then such treatments or activities can be replicated elsewhere (Block *et al.*, 2001). Absence of or a poor monitoring scheme not only decreases the effectiveness of restoration but provide little evidence of success or failure to support further efforts or refining of methodology (Davis *et al.*, 2004). Restoration can take a long time and monitoring of a project can be an extremely long-term procedure (Davis *et al.*, 2004). When management plans are being produced and resources allocated, these resources must be targeted towards restoration that will be easiest and thus most cost effective (Mitchell *et al.*, 1997).

1.4.2 Problems for restoration on land previously infested with bracken

Under experimental conditions, and in practice, *P. aquilinum* control is often highly variable and gives conflicting results (Le Duc *et al.*, 2000) and vegetation development during bracken control is often slow and unpredictable, especially in upland areas of the UK (Marrs *et al.*, 1998b; Marrs, 2004). The variability in the success of bracken control and vegetation restoration has been highlighted as a major issue for bracken control/vegetation restoration schemes. Part of the reason for this variability might be due either to regional effects, or to localized effects interacting with the management applied. Localized effects might be ascribed to (1) local microclimate or soil conditions, (2) local standing vegetation, (2) its derived seed rain, (4) recruitment from the soil propagule bank, and (5) potential seed rain derived from the surrounding landscape. Thus, the development of target vegetation requires a combination of control and restoration treatments that take into consideration the aspects of that site. This may include management for more than one factor, for example, soil condition and the present seed bank (De Graaf *et al.* 1998).

Once bracken control has ceased, recovery of *P. aquilinum* can be rapid if management is not maintained. Recovery to untreated levels, after a single application of asulam, has been found to take six or seven years (Marrs *et al.*, 1998a; Pakeman & Marrs, 1993). Recovery can be variable from site to site; dependent on local factors (Pakeman *et al.*, 2005). Rapid recovery for bracken cuts once per year for six years was noted by Marrs *et al.* (1998a). Whereas cutting twice per year has seen more effective control (Le Duc *et al.*, 2000; Cox *et al.*, 2007a) and a slower recovery (Marrs *et al.*, 1998a). Pakeman *et al.* (2005) observed two trajectories for recovery after asulam treatment with management of grazing a key factor; (1) the dominance of *Vaccinium myrtillus* where grazing is low and *V.myrtillus* is already present under the bracken or (2) a mix of bryophytes dominated by *Campylopus introflexus* and grasses especially *Deschampsia flexuosa* and *Rumex acetosella* on more heavily grazed areas.

In areas where bracken has been controlled, the area tends to be invaded by "weedy" non-target species. These include; *D. flexuosa, Holcus mollis, Chamerion angustifolium, Digitalis purpurea* and *Urtica dioica* (Cadbury, 1976). Additional problems when trying to regenerate *Calluna* heath include; evidence that *Calluna* establishment from seed can be hindered by competition (Allison & Ausden, 2004), as it is able to establish and grow well on arable soil in the absence of other species (Lawson *et al.*, 2004). The establishment of *Calluna* from seed may also be hindered by the presence of bracken litter, experiments conducted on old *Pinus* plantation land found the removal of the litter and humus layers increased *Calluna* establishment (Allison & Ausden, 2006).

Seed banks are often depauperate under bracken (Mitchell *et al.*, 1998; Pakeman & Hay, 1996). Impoverished seed banks are known to hinder restoration of heath and grassland (Bakker & Berendse, 1999), with seed for grassland species being relatively short-lived in comparison to heathland species (Bossuyt & Hermy, 2003). The regional and local seed pool, dispersal of seed on to a given site, which will depend on micro-climatic factors, the site propagule bank and site conditions all interact and affect the number of seeds arriving and whether they begin to germinate (Harper, 1977). Deep and dense bracken litter can act as a potential barrier for seed rain from surrounding vegetation preventing seed entering the soil seed bank (Ghorbani, 2005).

Desired target communities such as *Calluna* heath and acid grassland tend to occur on low fertility soil but nutrients tend to increase with succession (Mitchell *et al.*, 1997). Bracken is a mid-successional species in open habitat (Marrs *et al.*, 2000) thus soil nutrients must be considered when trying to restore a characteristically nutrient poor community. Experiments aimed at restoring oligotrophic heathland in the Netherlands found mixed results, after 25 years of cutting there had been an increase in target species but the community still resembled the original one, typical of eutrophic conditions (Bakker *et* *al.* 2002). The reduction of pH to levels thought suitable for heath vegetation establishment may not be as important as competition from other species, and the reduction of soil nutrients (Allison & Ausden, 2004).

1.5 Long-term, multi-site data

It is well known that accurate prediction is difficult when treatments may have to be applied over wide bio-climatic conditions, and where the restoration objectives may vary according to ecosystem being treated. An obvious solution is to carry out multi-site experiments where the same treatments are applied contemporaneously. In spite of the need for good experimentally-derived information to guide restoration policies there have been surprisingly relatively few attempts to carry out large-scale, long-term, multi-site experiments for the control of pernicious weeds. Most studies are either single-site or short-term (Pywell *et al.*, 2002; Pakeman, 2004; Marrs *et al.*, 2004). Where multi-site studies have been reported in restoration ecology a mixture of analytical techniques have been used. Pywell *et al.* (2002) used standard ANOVA with repeated measures to assess the factors limiting success when attempting to restore species-rich grassland on arable land in a four-year experiment. Pakeman (2004) preferred a combination of Residual Maximum Likelihood (REML) analysis to test for complex relationships between species response and measured covariables in a 7-year study. In contrast, Marrs *et al.* (2004) used a combination of univariate and multivariate analyses of variance to describe a multi-site experiment on *Molinia caerulea* control.

Here, we used a series of statistical techniques to analyse long-term multi-site data;

1. Analysis of variance using repeated measures with polynomial contrasts to analyse both bracken data (Chapter 2) and the understorey vegetation data (Chapter 8). The value of this approach is that it is possible to test for treatment effects as in ANOVA, but the trend of these treatment effects can also be identified. This approach becomes more useful with longer-term datasets.
2. Meta-analysis and meta-regression to assess treatment effectiveness of the bracken control treatments across all six sites with the same treatments applied. This was done using the bracken data (Chapter 3).

3. Multivariate analysis of the developing understorey vegetation to assess trajectories through time, and to assess whether alternative stable states were produced by applied treatments (Chapter 9).

1.5.1 *The Experimental sites*

With the exception of Chapters 6 and 7 the results presented in this thesis are based on long-term multi-site experiments. Six experiments were set up at four different regional locations in the UK (Fig. 1); Cannock Chase in the English midlands; Hordron Edge, North Peak Environmentally Sensitive Area in the Peak District National Park, northern England; the Carneddau Estate in Snowdonia National Park, North Wales; and Sourhope in the Cheviot Hills, on the England/Scotland border. Sites are referred to hereafter as Cannock, Carneddau, Peak and Sourhope. If the bracken patch was large enough three blocks were used, otherwise two blocks were used and the entire experiment was replicated nearby (< 2.5 km distant). Site details are provided in Table 1.

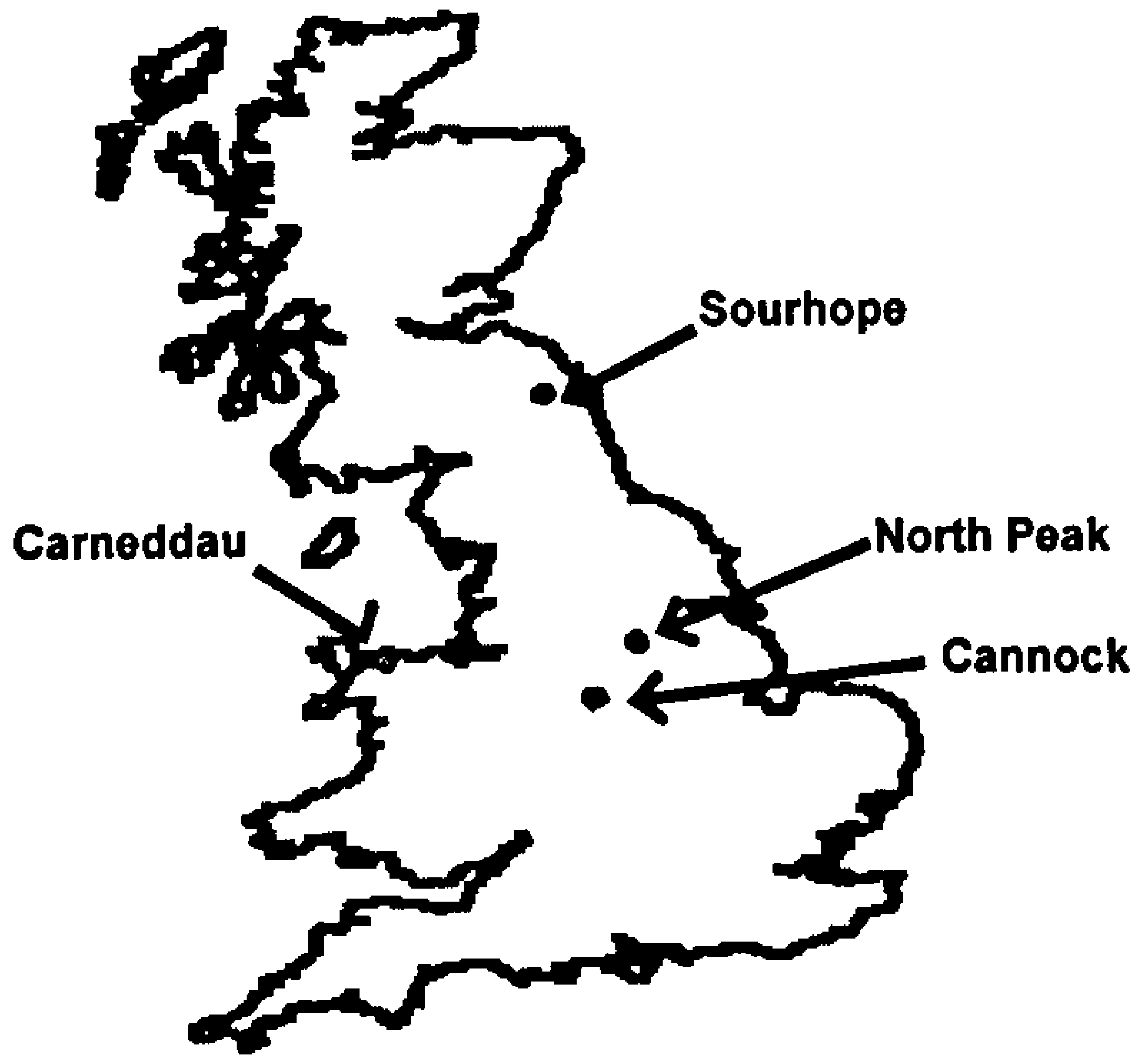


Fig. 1. Map of UK showing the location of the sites.

The sites cover two main types of target vegetation; acid grassland and *Calluna* heath. The untreated control plots give an estimate for initial conditions at the six sites (Table 2). The acid grassland sites, Sourhope 1 & 2 and Carneddau (Fig 2), were the most species-rich sites with the *Calluna* heath sites, Cannock 1 & 2 and Peak (Fig. 3), having the lowest number of species. The lowest *P. aquilinum* cover was recorded at Sourhope 2 (41 %) and Carneddau (48%) the most species-rich sites. The species-poor

Cannock sites had the highest *P. aquilinum* cover. Despite having the highest bracken litter cover (84%) and the deepest litter (18 cm) Peak had the smallest rhizome mass.

Fig. 2. The Carneddau acid grassland site in 2003. This picture was taken from above Block B.

Fig. 3. The Peak *Calluna* heath site in 2003. This picture was taken from an adjacent moor.

Table 1. Description of the experiments. Entries for experimental designs represent: number of blocks/number of plots per block/number of sub-plots per plot/number of sub-sub-plots per sub-plot. These codes are truncated from the right when lower experimental levels do not exist. More than one design for a single experiment indicates successive splitting in time. The National Vegetation Classification (NVC, Rodwell, 1991a, b, 1992) descriptions (the codes are explained in the footnote) represent the pre-treated condition, the data in brackets being the results obtained when bracken was left out of the calculations. The measured fit was obtained using the computer program TABLEFIT version 1.0 (Hill, 1996), and are rated: > 80 very good, > 70 good, > 60 fair, < 60 poor. † - additional fertilizer was added at Cannock 1 in 1996.

Location	Sourhope Estate		Hordron Edge	Carneddau Estate	Cannock Chase	
Latitude:	2° 14' W				2° 2' W	
Longitude;	55° 28' N		1° 41' W 53° 23' N;	3° 58' W 53° 13' N	52° 46' N	
Experiment:						
- Name	Sourhope 1	Sourhope 2	Peak	Carneddau	Cannock 1	Cannock 2
- Started	1993	1994	1993	1993	1993	1993
- Design	1994-03 = 2/6/2	1995-03 = 2/6/22/6/2	1994-02= 2/6/23/6/2/3	1993=3/6 1994-97 =3/6/3 1998-03 =3/6/3/2	1994-03= 2/6/3	1994-03= 2/6/3
National grid reference	NT 861 202	NT 846 210	SK2187	SH6871	SJ 976 200	SJ 987 181
- Main treatments (bracken control)*	All + weed-wiping	All	All	All	All	All + weed-wiping
- Sub-treatments	Grass seeding		Stock fencing	Grass seeding & fertilizer	Harrowing & fertilizer†	
- Sub-sub-treatments	-	-	*Calluna* seeding (brash & litter)	Spot-spray	-	-
Physical:						
- altitude (m)	325	285	290	350	145	165
- aspect (°)	280	130	275	190	140	125
- slope (°)	16	22	9	20	20	18
Vegetation:						
- NVC class	U4e (U4e)	U4a (U4a)	U20 (H18)	U4a (U4a)	W16 (U2b)	W16 (U2b)
- fit	75 (77)	61 (64)	77 (83)	74 (79)	78 (67)	61 (55)

NVC classes represented are:

U2b	*Vaccinium myrtillus* sub-community of *Deschampsia flexuosa* grassland
U4a	Typical sub-community of *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland
U4e	Vaccinium myrtillus-Deschampsia flexuosa sub-community of *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland
U20	*Pteridium aquilinum-Galium saxatile* community
H18	*Vaccinium myrtillus-Deschampsia flexuosa* heath
W16	*Quercus* spp.-*Betula* spp.-*Deschampsia flexuosa* woodland

*Main treatments: (1) Untreated control; (2) Cut once per year; (3) Cut twice per year; (4) Cut in year 1 and sprayed with herbicide in year 2; (5) Sprayed only; (6) Sprayed in year 1 and cut in year 2.

Table 2. Species richness (number of species m^{-2}) in standing vegetation, *P. aquilinum* cover and litter abundance and the total rhizome mass in untreated control plots at each of the experiments. Back-transformed means are in bold and transformed means ± SE in parentheses ($Y' = (Y+0.5)^{0.5}$ for species richness and litter depth; $Y' = \text{Ln}(Y+1)$ for *P. aquilinum* cover and litter cover). Mean total dry mass of rhizomes are presented in bold, SE in parentheses (Le Duc *et al.*, 2003).

Site	Species richness	*P.aquilinum* Cover (%) August	Litter cover (%)	Litter depth (cm)	Rhizome Mass (kg m^{-2})
Calluna Heath Sites					
Cannock 1	2.88	96.23	69.13	11.74	5.14
	(1.84±0.01)	(4.58±0.02)	(3.97±0.96)	(3.28±1.24)	(±0.16)
Cannock 2	3.43	83.65	61.46	15.82	2.67
	(1.98±0.01)	(4.44±0.03)	(3.86±0.92)	(3.81±1.35)	(±0.08)
Peak	5.19	80.60	84.02	17.56	1.85
	(2.39±0.01)	(4.67±0.05)	(4.41±0.28)	(4.2±0.64)	(±0.04)
Acid Grassland Sites					
Carneddau	9.59	47.75	33.59	7.63	4.58
	(3.18±0. 01)	(3.89±0.20)	(3.54±0.13)	(2.79±0.05)	(±0.08)
Sourhope 1	10.76	59.99	6.48	2.54	2.89
	(3.35±0.02)	(4.11±0.08)	(1.21±1.18)	(1.64±0.6)	(±0.09)
Sourhope 2	12.14	41.48	3.77	1.96	3.00
	(3.56±0.02)	(3.75±0.16)	(1.15±0.94)	(1.96±0.88)	(±0.11)

1.5.2 *Experimental Design*

Use of all-terrain vehicle (ATV) equipment to apply the treatments constrained the layout of the experiments. A basic split-plot design was used throughout, with the main plots receiving one of six bracken control treatments, and the sub-plots receiving vegetation restoration treatments in addition.(Table 1).

Within each experiment each block (70 x 40-m) was divided into six plots (10 x 40-m) separated by 2-m untreated buffers. Each plot was divided into two (10 x 18-m) or three sub-plots (10 x 12-m) according to the experiment, with 4-m or 2-m buffer zones. Further splitting was carried out in a similar fashion, dividing sub-plots into two or three sub-sub-plots (10 x 5-m). As an example, the experimental lay out of the split-split plot design at Carneddau can be seen in Fig. 4.

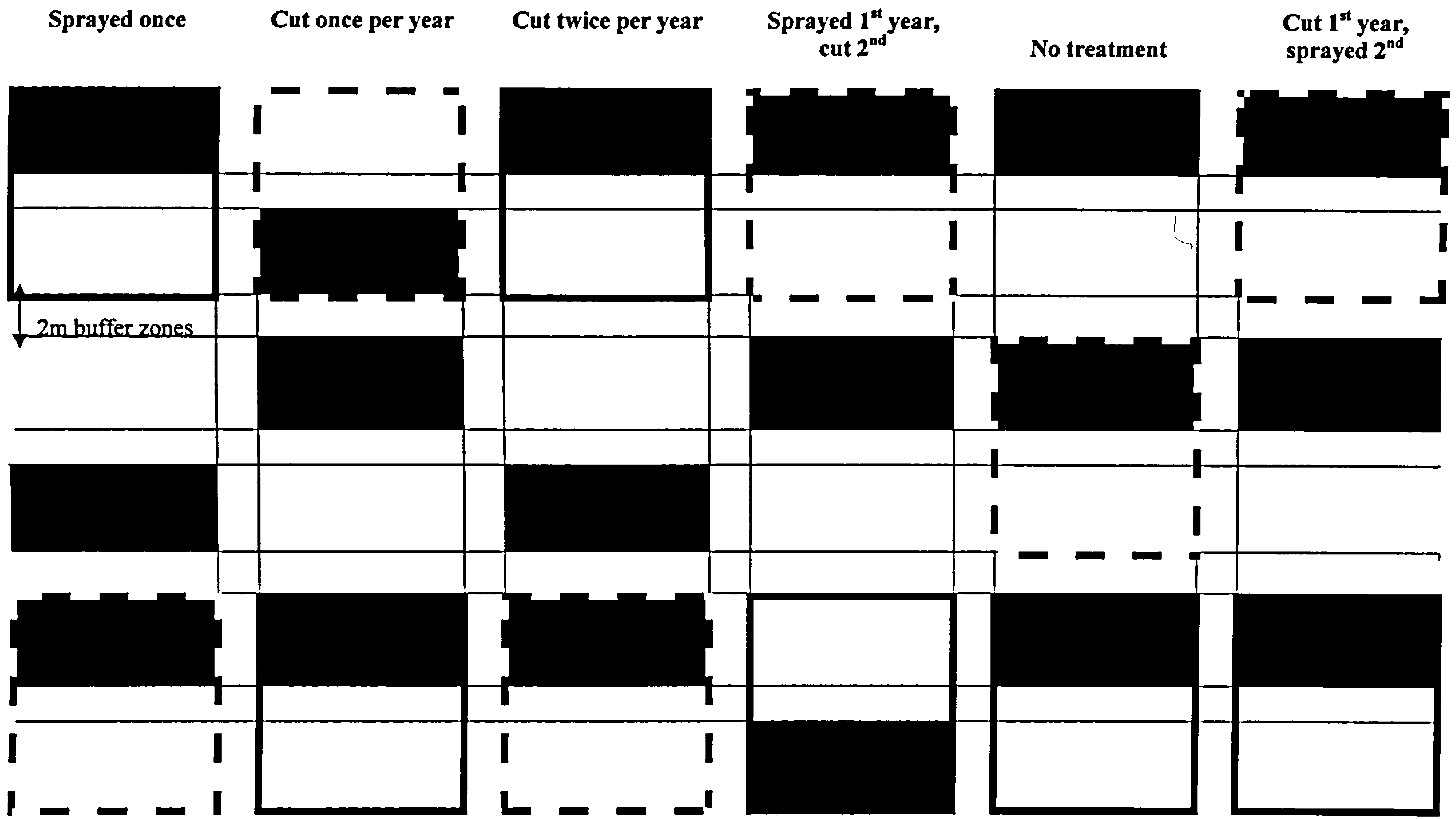


Fig. 4. The experimental lay out of the split-split plot design at Carneddau, Block A. Bracken control treatments (start 1993) in columns: Sub-treatment (1995) boxes: None = no treatment; Dashed = fertilizer addition; Solid = Fertilizer + grass seed: Sub-sub-treatment (1997) colour intensity: White = no treatment; Black= spot-sprayed with asulam. All sub-sub plots are 10m x 5m with 2m buffer zones.

1.5.3 *Treatments*

Six main-plot, bracken control treatments were applied to all experiments: (1) untreated (experimental control); (2) cut once per year in June (Cut1pa); (3) cut twice per year in both June and August (Cut2pa); (4) a single June cut in year one followed by asulam spraying in year two (CutSpray); (5) asulam in year one only (Spray); (6) asulam in year one followed by a single June cut in year two (SprayCut). In two experiments (Sourhope 1, Cannock 2, Table 1) plots treated to a single application of herbicide were re-treated with asulam in 1996, three years after first treatment. On that occasion the herbicide was applied using a weed wiper. Details and a full description of methods have been published in Le Duc *et al.* (2000).

Unlike the main treatments, the sub- and sub-sub-treatments were site-specific vegetation restoration treatments which were designed to match individual site characteristics (Table 1). The sub-treatments and sub-sub-treatments were all associated with vegetation restoration (with the exception of spot-spraying, see below). They included: grass seeding with the mix *Festuca ovina*:*Agrostis capillaris*:*Poa pratensis* at a ratio of 5:4:3, plus a small quantity of *Rumex acetosa*, at an application rate of 60 kg ha^{-1}; *Calluna vulgaris* seeding with brash comprising 20 cm stems at 13 t ha^{-1} and nurse crop, *Agrostis castellana*, at 12 kg ha^{-1}; *Calluna vulgaris* seeding with *Calluna* litter at 1.2 t ha^{-1}, sucked from under mature heather, together with the same nurse crop; stock-proof fencing; fertilizer (ENMAG, Zeneca) application at 150 kg ha^{-1}; harrowing (ATV small chain harrow, Logic).

In addition, spot-spraying with asulam was applied, as a sub-sub-treatment, at Carneddaau in late summer 1997. The spot-spraying was applied strictly within the experimental design with each sub-plot being split into two sub-sub-plots whether it had been sprayed with asulam earlier or not. In June 1997 flash flooding prevented access to Sourhope 2. Consequently, that year the cutting treatments were both replaced by a single cut in August.

1.5.4 *Monitoring*

All experiments were monitored twice per year in June and August. In each case these were carried out before application of bracken control treatments. Quadrats were placed at pre-selected random co-ordinates on 1-m grids within each sub- (sub-) plot. Using a 0.5 x 0.5-m quadrat bracken performance was measured; all fronds were cut at ground level, counted and length measured. Vegetation was monitored in June each year using 1 × 1-m quadrats, placed at pre-selected random co-ordinates on 1 m grids within each sub- (sub-) plot and cover of all plant species present was estimated visually. Generally experiments split to the sub-plot level were monitored using three quadrats per sub-plot in June and two in August. When further split, experiments had two quadrats per sub-sub-plot in June and one in August.

All raw data was entering into a bespoke database and is available at www.appliedvegetationdynamics.co.uk (Le Duc *et al.*, 2007b).

1.6 Aims

The aims of this project were;

- To assess the effectiveness of bracken control treatments on *P. aquilinum* on long-term experiments at different sites throughout the UK.
- To assess the effects of bracken control treatments on *P. aquilinum* using formal meta-analysis.
- To assess the efficacy of the current manufacture's recommended guidelines for asulam in two contrasting long-term experiments over a three year period.
- To assess bracken fronds on three contrasting sites after 10 years of control followed by three years recovery.
- To assess the effectiveness of bruising as a method for bracken control.
- To answer the question; does bruising 'bleed the rhizomes dry'? By assessing the physiological effect of bruising on bracken fronds.
- To assess the effectiveness of bracken control treatments and treatments designed to restore vegetation in the restoration heathland and acid grassland on *P. aquilinum* – infested land on long-term, multi-site experiments across the UK.
- To find out whether or not different bracken control treatments would result in different trajectories and varying rates of success for the restoration of heathland and acid grassland.

Nomenclature throughout follows Stace (1997) for higher plants; Hill *et al.* (1991, 1992 & 1994) for bryophytes and Coppins (2002) for lichens.

Chapter 2

A multi-site assessment of bracken control effectiveness across the UK

2. Introduction

There is an increasing need for applied ecologists to be able to assist in the development of national weed control strategies, for example in the implementation of agri-environments schemes developed by the European Union (MAFF, 1993, 1996) or the delivery of Biodiversity Action Plans to meet conservation objectives (Anon, 1995 a, b). Advice to policy-makers needs to be cost-effective and must apply to a wide range of situations where weeds need to be controlled.

Restoration management which involves a weed control phase often produces mixed results (Le Duc *et al.*, 2000, 2003; Hytonen & Jylha, 2005). Such management usually involves a combination of control treatments and specific treatments designed to restore vegetation. Together they can control the problematic weed and create more desirable target vegetation (DiTomaso, 2000). This is particularly important when weed infestation is high (Simmons, 2005), and the aim is to establish vegetation which increases resistance to invasion and prevents the weed infestation from recurring (Blumenthal *et al.*, 2003).

A good example of such a problem is *Pteridium aquilinum* control in the United Kingdom, where the policy objective is to reduce the *P. aquilinum* infestation and restore a vegetation type with a greater conservation value (Pakeman & Marrs, 1992). *P. aquilinum* is a serious invasive weed of upland and marginal land in many parts of the world (Page, 1995; Pakeman & Marrs, 1992). In the UK dense *P. aquilinum* is a problem species for agriculture and conservation in most situations, as it is a long-lived robust clonal species (Le Duc *et al.*, 2003) that produces a dense litter layer (Frankland, 1976), which competes effectively with heathland and grassland species, at best reducing their cover but in some cases eliminating them leaving a very depauperate flora (Pakeman & Marrs, 1992). This eventually leads to impacts on seed banks which are also depauperate under bracken (Pakeman & Hay, 1996).

One of the major issues highlighted in *P. aquilinum* control is the high variability in success rates (Le Duc *et al.*, 2000, 2003), and a cost-effective control strategy has proved elusive. In order to investigate this problem and develop a national policy a multi-site experiment is needed to ensure that results apply to: (a) a broad geographical coverage of situations, and (b) a reasonable coverage of the types of restoration problem likely to be encountered. Surprisingly there have been relatively few attempts to carry out such large-scale, multi-site experiments in ecological restoration especially over the longer-term, and none on *P. aquilinum* control. Most multi-site studies have been either single site or of short duration (< 8 years) (Pywell *et al.*, 2002; Pakeman, 2004; Marrs *et al.*, 2004).

2.1.1 *Techniques for bracken control*

There are three strategies that are generally used to control *P. aquilinum*, these are:

1. *Mechanical control.* Fronds are cut or bruised during early summer, before and up to the point of maximum frond expansion, with the aim of withdrawing the maximum amount of carbohydrates and nutrients from the rhizome reserves (Hunter, 1953; Williams & Foley, 1976). When this strategy is used it is advisable to cut the fronds before the new assimilates start being translocated from the fronds to the rhizomes in large amounts (late July/early August in Britain) (Williams & Foley, 1976). Cutting can be carried out one, two or three times annually (Braid, 1959; Williams, 1980). This strategy also has important benefits in that it breaks up and fragments the litter layer, hence assisting other species to colonize (Lowday & Marrs, 1992b).
2. *Herbicidal control.* Herbicide action is unlikely to have a direct effect on the amount of rhizome carbohydrate reserves in the short term, and herbicides which attack frond buds on the rhizome are most successful. Asulam [methyl (4-aminobenzenesulphonyl) carbamate] is the most widely used herbicide; it is translocated into the rhizome and accumulates in both active and dormant buds, where it effects a lethal action (Veerasekaran *et al.*, 1976, 1977a,b, 1978). Asulam frequently produces a very good reduction in fronds in the year after spraying, but there is often rapid frond recovery unless other treatments are applied in subsequent years (Robinson, 1986; Lowday & Marrs, 1992a). Herbicide action has a limited impact of bracken litter (Marrs *et al.*, 2007).
3. *Inhibition by other vegetation.* Usually where dense bracken is to be controlled, managers want to remove the bracken and replace it with some other vegetation. There is some evidence that when competitive vegetation develops during a *P. aquilinum* control program, there is a reduction in frond performance (Watt, 1955; Lowday & Marrs, 1992a; Le Duc *et al.*, 2000, 2007a).

2.1.2 *The multi-site study*

Here we present some results from the multi-site study described in chapter 1, carried out with the objective of testing techniques to help develop a national policy for bracken control in the UK. The experiments assessed the efficacy of five treatments designed to control *P. aquilinum* relative to an untreated control in a range of contrasting ecological situations. Moreover, these *P. aquilinum* control treatments were combined with site-specific treatments designed to restore appropriate heathland or grassland vegetation. Thus, the experiments were a compromise to assess bracken control at the national scale and the impact of potential control/restoration practices at the local scale. In this chapter we only consider the effects on *P. aquilinum* performance.

We tested the following hypotheses:

(1) Geographical location (locally between and within sites) affects the control of *Pteridium aquilinum* through time.

(2) Are the *P. aquilinum* control treatments successful at all sites, and if so which ones?

(3) The treatments applied at the individual site level to restore vegetation influences the performance of *P. aquilinum* through time.

Our study started in 1993 or 1994 and has been monitored twice per year for 9 or 10 years. With six experiments and multiple, replicated treatments a voluminous dataset has been produced. The analysis is, therefore, large and complex and presentation of such data in published form is difficult. To accommodate this we have developed a stepwise series of electronic outputs to minimize presentation problems and to make these data and results available for inspection to ensure quality assurance and quality control as well as an audit trail through the analyses (Le Duc *et al.*, 2007b).

2.2.3 *Data analysis and presentation*

Data were transformed using standard procedures (Sokal & Rohlf, 1995), number of fronds per quadrat using $(Y + 0.5)^{0.5}$, and individual frond length, and cover estimates using $\ln(Y + 1)$. After transformation the mean frond length per quadrat was calculated. Estimates of values per treatment combination per block were obtained by combining data per quadrat after transformation by sub- (sub-) plot.

Individual variables were analyzed for change through time for each site individually. As our objective was to measure the shape of response curves through time, we used repeated-measures ANOVAs with the method of polynomial contrasts (Gurevitch & Chester, 1986). Time was denoted as elapsed time

(ET), with the start year designated year=0. This was carried out by means of PROC GLM in SAS version 8.02 (SAS, 1989). The value of this approach is that it is possible to test for treatment effects as in ANOVA, but the shape of the temporal trends of these treatment effects can also be identified. This approach becomes more useful with longer-term datasets (Le Duc *et al.*, 2007a). For each site we used the appropriate analysis of variance model; however for Cannock and Sourhope we initially analyzed both experiments together, with experiment included as the first level in a split-split-split plot design.

The analysis of variance model changed when new treatment combinations were added into an experiment, usually changing the design from a split-plot to a split-split-plot one; thus different segments of the time series were analyzed using different models. At Sourhope there was an additional problem in 2001 because data could not be collected because of the Foot and Mouth epidemic in Britain. At this site the experiments were also started in different years, and accordingly the loss of the 2001 data resulted in the loss of two years information from the repeated measures analysis. Where a gap in temporal data was present this is indicated graphically as a dashed line.

Bonferroni correction was used to adjust for the Type I error rate (Cabin & Mitchell, 2000; Sokal & Rohlf, 1995). For the June sampling there were a large number of comparisons done as all species identified were analyzed, i.e. 144, 85, 44 and 131 analyses at Cannock, Carneddau, Peak and Sourhope respectively. With $\alpha = 0.05$ the critical probability levels of 0.0006, 0.0004, 0.0005 and 0.0004 were used to assess significance. For August the number of comparisons at all sites was 3, with $\alpha = 0.05$ the critical probability level of 0.0167 was used to assess significance.

Both the June and August data was analyzed separately. Here, we concentrate on results from the late-summer, August sampling, the point when *P.aquilinum* reaches maximum frond expansion with all significant results being described. The early-summer June samples should have provided better comparison between-treatments, but this early sampling proved problematic for two reasons. First, *P. aquilinum* performance was affected by late frosts in some years, and secondly the staggered sampling times between-experiments would have introduced a considerable bias as sampling is occurring in the most active part of the frond expansion phase (Marrs & Watt, 2006). The June results more or less supported those from August, and where they diverged the differences are discussed in the text. Graphs of all significant results, for both June and August, can be found in Electronic Appendix 1.

The analyses allowed the three hypotheses to be tested on data collected in early- and late-summer, as follows:

(1) Geographical location (locally between and within sites) affects the control of *Pteridium aquilinum* through time. This was assessed by the significance between (a) the different experiments (Cannock and Sourhope) and the interactions between these experiments and applied treatment, and (b) significant block effects at Carneddau and Peak.

(2) Are the bracken control treatments successful at all sites, and if so which ones? This was assessed by the significance of bracken control treatment effects and interactions through time.

(3) The treatments applied at the individual site level to restore vegetation influences the performance of *P. aquilinum* through time. This was assessed by significance of restoration treatments through time.

2.3 Results

2.3.1 *Effects through time*

Significant mean variations over time were found for *P .aquilinum* cover at all sites; for frond density at all sites except Cannock; and frond length at all sites except Sourhope (Chapter 1, Table1). However, where these overall significant mean effects were found there were also significant bracken control treatment effects, suggesting that the mean variation is not independent of treatment effects.

Table 1. Bracken response variables which showed significant variation through time (mean effects).

	Site	Other significant treatments	df	Effect	n	F Value
Pteridium aquilinum Cover	Cannock	Experiment x Bracken Control	1,24	3rd	72	117.77
Pteridium aquilinum Cover	Carneddau 98-03	Bracken Control x Spot Spray	1,36	1st	108	41.98
Pteridium aquilinum Cover	Peak	Block & Bracken Control	1,48	1st	108	1859.93
Pteridium aquilinum Cover	Sourhope	Bracken Control	1,12	3rd	48	15.82
Frond Length	Cannock	Experiment x Bracken Control & Bracken Control x Fertilizer	1,24	1st	72	97.29
Frond Length	Carneddau 93-94	-	1,4	1st	9	72.79
Frond Length	Carneddau 95-97	-	1,24	1st	54	22.71
Frond Length	Peak	Bracken Control	1,48	1st	108	139.03
Frond Density	Carneddau 98-03	Block & Bracken Control x Spot Spray	1,36	1st	108	12.00
Frond Density	Peak	Block & Bracken Control	1,48	8th	108	62.60
Frond Density	Sourhope	Experiment & Bracken Control	1,12	1st	48	11.42

2.3.2 *Geographical location (locally between and within sites) affects the control of* Pteridium aquilinum *through time.*

There were spatial variations between experiments at both Sourhope and Cannock. At Sourhope, only frond density was significant at this level, with Sourhope 1 having a much greater frond density than Sourhope 2 at the start of the study, although the differences between the experiments reduced through time (Fig. 1).

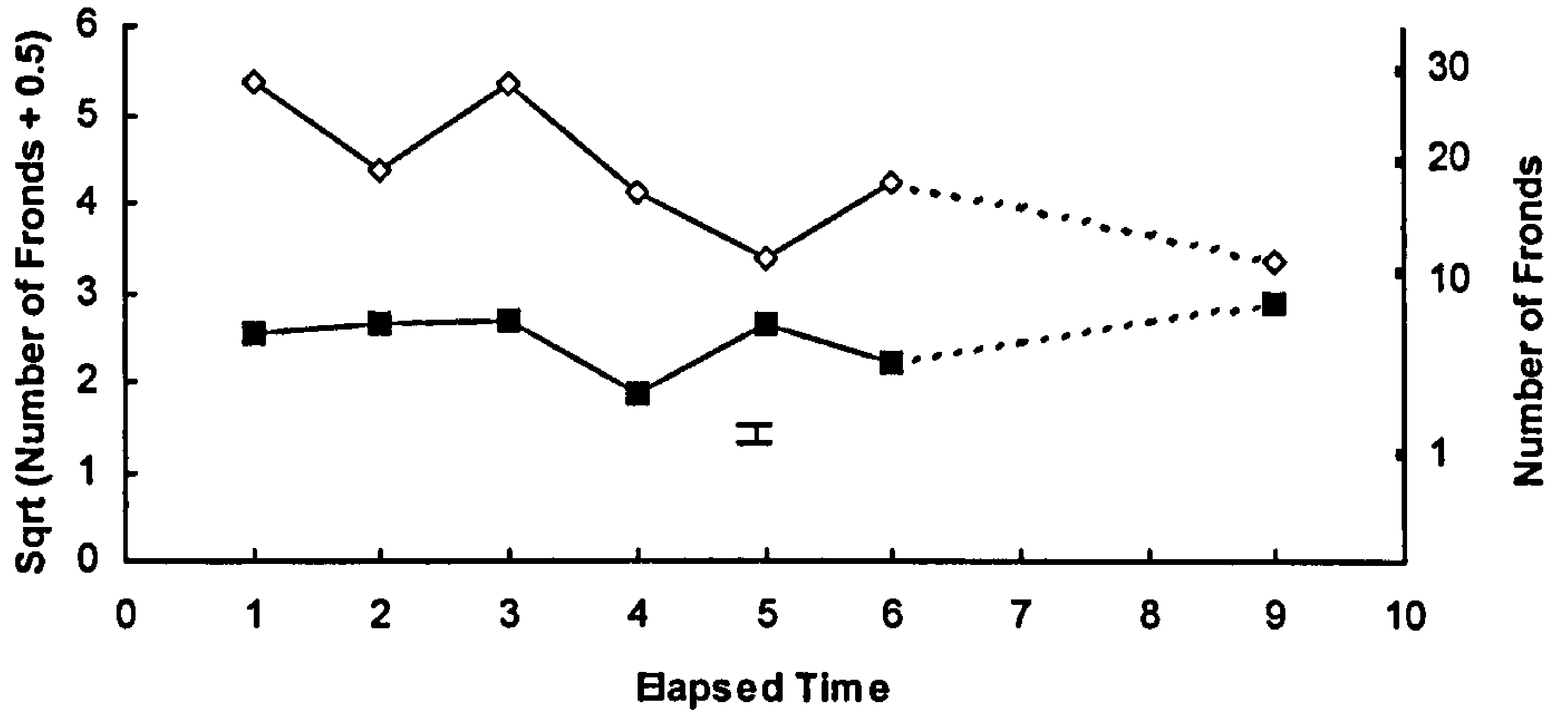
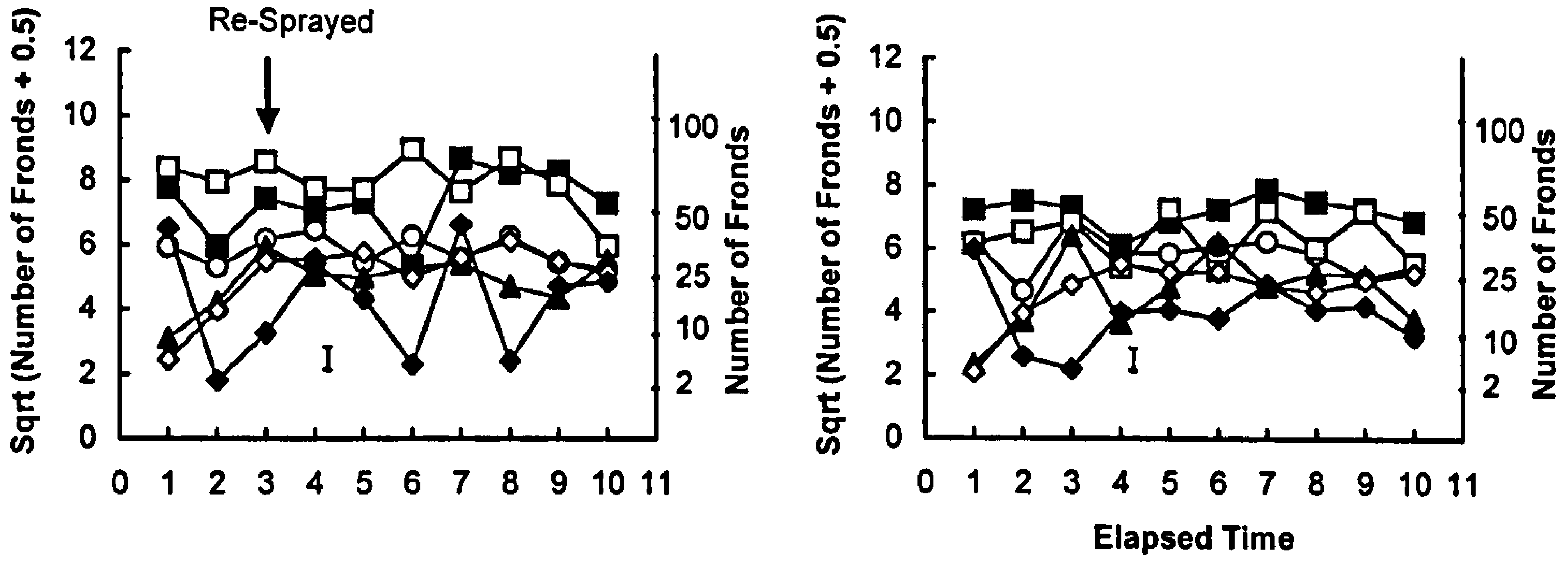


Fig. 1. Experiment effect through time on frond density at Sourhope in August (Sourhope 1= square, Sourhope 2= diampnd); 5th order, $F_{(1,2)}$=103.33 n=24, overall effect $F_{(1,2)}$=69.47 n=216. Elapsed Time=0 is 1993 for Sourhope 1, 1994 for Sourhope 2. Error bars are ± 2S.E.D.

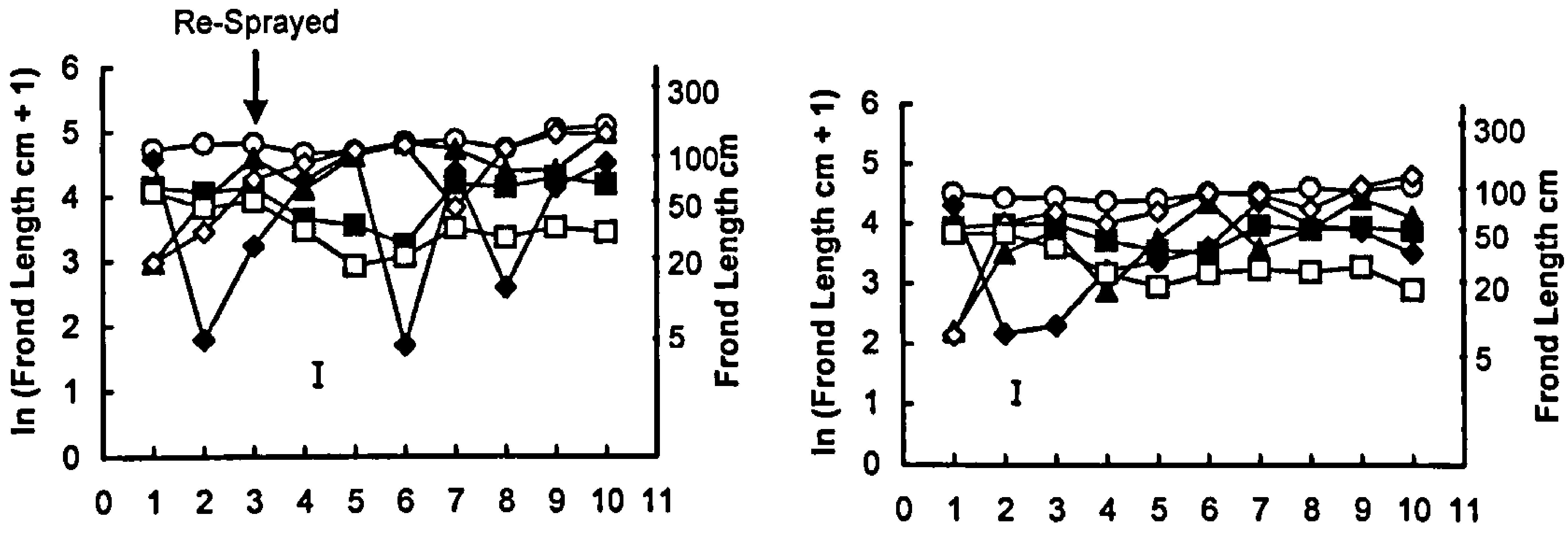
At Cannock there was a significant experiment x bracken control interaction for all bracken response variables (Fig. 2). *P. aquilinum* cover, frond density and length were more or less constant for the untreated controls; the cutting treatments at both experiments had a greater density than the untreated control with the Cut2pa being greater for most of the period at Cannock 1 and Cut1pa at Cannock 2. For frond length Cut1pa reduced length, until years 5 or 6, after which there was recovery to near untreated values whereas there was a continued decline with the Cut2pa treatment. At both experiments the sprayed treatments showed an immediate reduction in cover, length and density, followed by a slow recovery over the 10 years. The CutSpray treatment was initially the most effective at both sites; but at Cannock 1 there were large fluctuations with lows in years 6 and 8.

Significant spatial variations were found between blocks at Carneddau (frond density, $F_{(2,36)}$=6.53) and Peak (frond density, $F_{(2,48)}$=9.19; *P. aquilinum* cover, $F_{(2,48)}$=9.87 at Peak). The blocks are random effects and are reported as indicative, nevertheless if suggests differential *P.aquilinum* responses across the site.

(a) Frond Density; (i) Cannock 1 (ii) Cannock 2



(b) Frond Length; (i) Cannock 1 (ii) Cannock 2



(c) *Pteridium aquilinum* Cover; (i) Cannock 1 (ii) Cannock 2

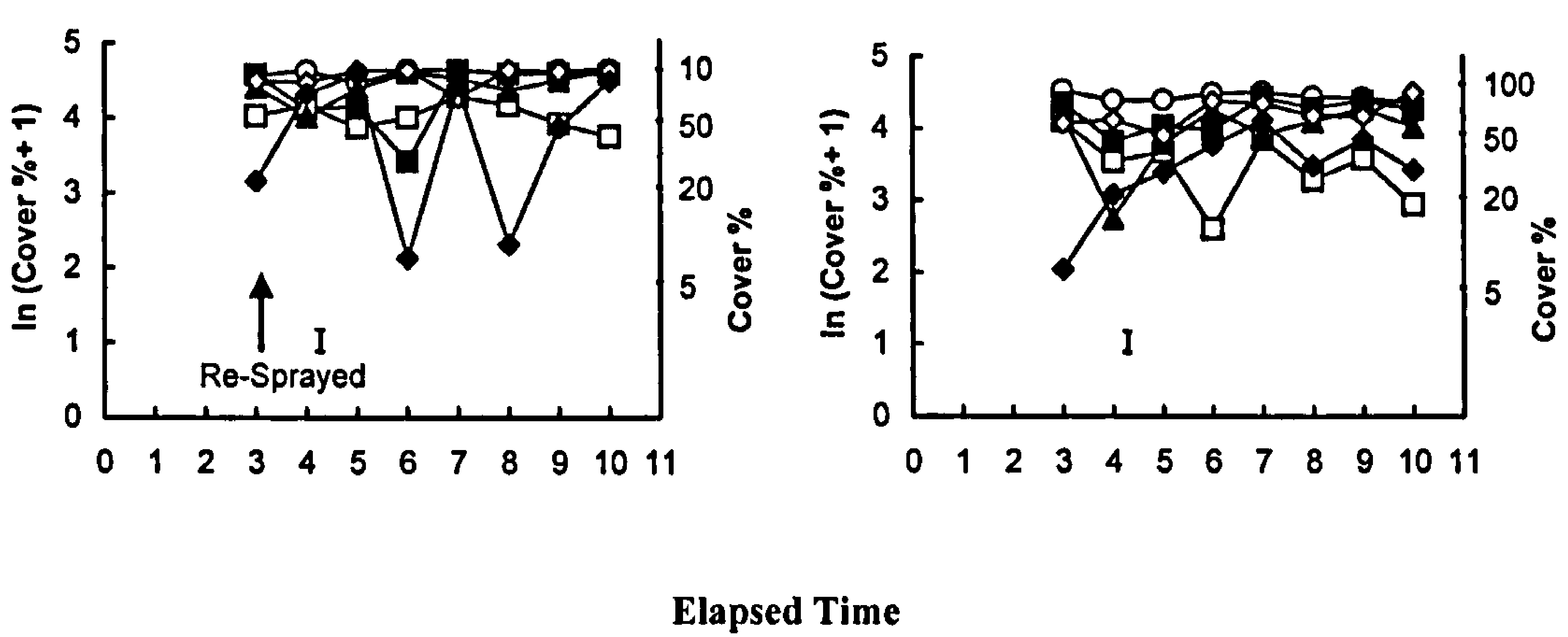


Fig. 2. Experiment x bracken control interactions in August sampling at Cannock (no treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond); (a) frond density (9th order, $F_{(5,10)}$ =11.37 n=6) (b) frond length (3rd order effect, $F_{(5,10)}$=5.47 n=6) (c) *Pteridium aquilinum* cover (2nd order, $F_{(5,10)}$=5.74 n=6). Elapsed Time= 0 is 1993, error bars are ± 2S.E.D.

2.3.3 *Are the bracken control treatments successful at all sites?*

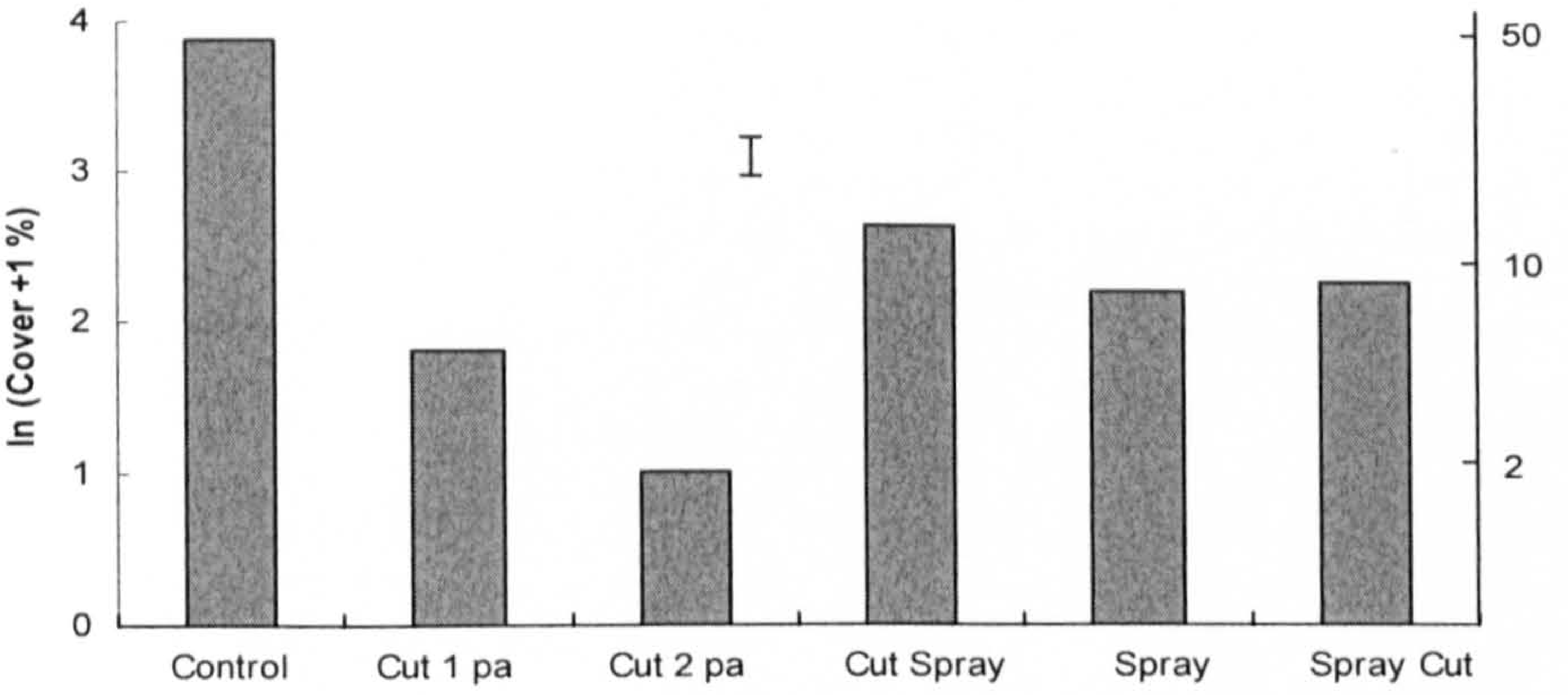
Significant bracken control treatment effects were found for all three *P. aquilinum* response variables at all sites (Fig 3). At the acid grassland sites (Carneddau, Sourhope) and the *Calluna* heath sites (Peak, Cannock) the treatments including asulam were initially superior to cutting-only treatments (Fig. 3) The bracken cover of these spray treatments consistently increased over the 10 years, until they were either converging (Sourhope), or were not significantly different from the untreated controls (Peak and Cannock). At Carneddau there was no significant difference through time, just an overall significant difference between the treatments (Fig. 3a) with Cut2pa being the most effective. The cut treatments showed an increasing impact at Sourhope through time as they maintained a low bracken cover, whereas at Peak an increasing impact was only found in the Cut2pa treatment. At Peak there was clear evidence of significant fluctuations, especially in the cutting treatments. A similar picture was found with two other measures of frond performance at Carneddau, Cannock and Sourhope, with minor differences in the overall rankings of the treatments (Electronic Appendix 1).

At Carneddau spot spraying significantly reduced frond density immediately after application, followed by a steady recovery (Fig. 4a). There were also two significant interactions at this site: (a) seeding x spot spray on frond length, and (b) bracken control x spot spray on cover. Frond length remained approximately constant in the unsprayed spot treatment, but was consistently lower immediately after spot spraying (Fig. 4b). In the spot sprayed treatment where no seeding was applied the frond length remained approximately constant, but where seeding and seeding+fertilizer was applied frond length partly recovered but remained lower than non spot sprayed treatments until year 8, when they started to recover (Fig. 4b). The bracken control x spot spray interaction showed that spot spraying reduced bracken cover significantly in all treatments (Fig. 4c), with the exception of Cut2pa where the reduction was minimal.

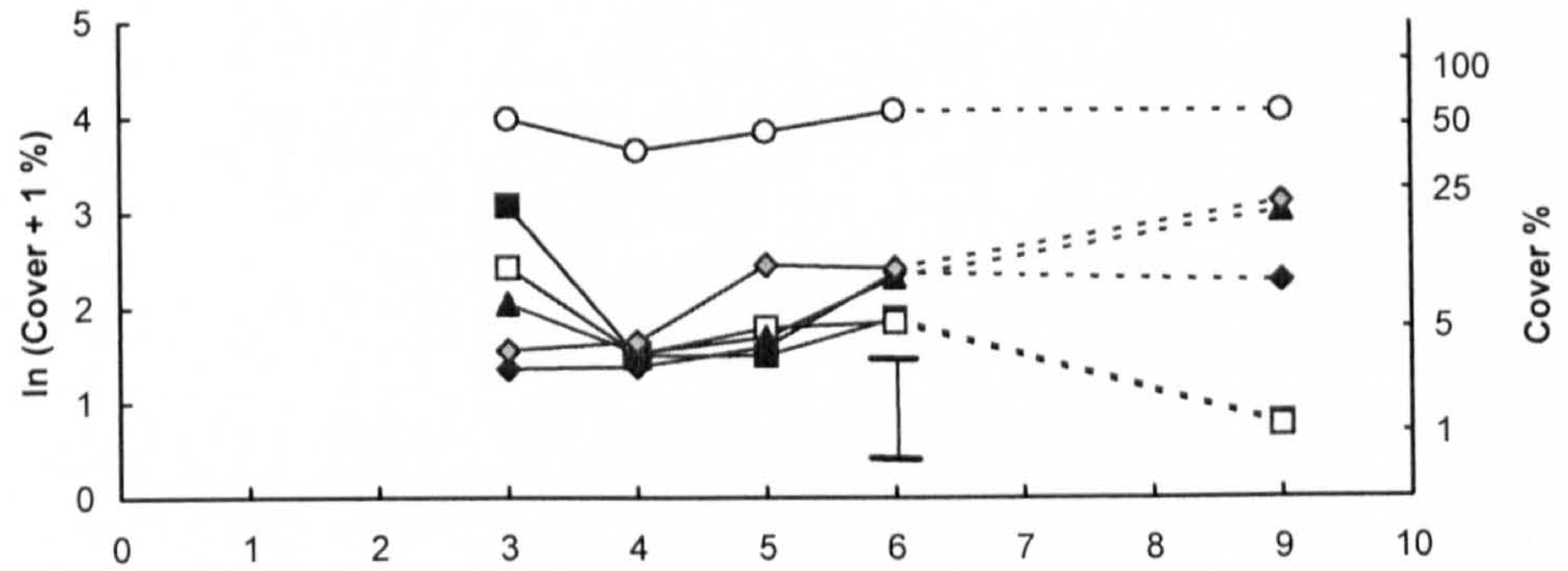
2.3.4 *The treatments applied at the individual site level to restore vegetation influences the performance of* P. aquilinum *through time*

Grass seeding had a significant effect at Sourhope, with frond length declining between years 2 and 4. After year 4 frond length increases, converging with the control in year 6 (Fig. 5). Otherwise there were no other significant effects of the restoration treatments.

(a) Carneddau (1998-2003)



(b) Sourhope



(c) Peak

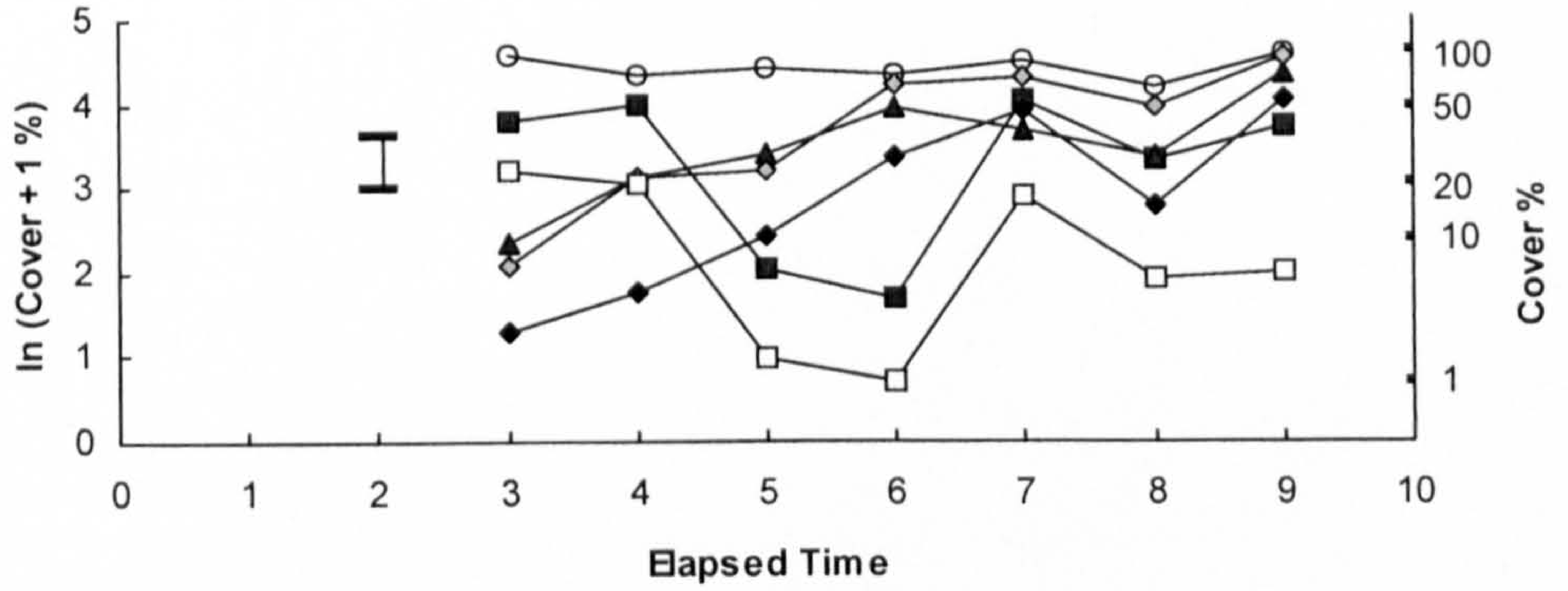
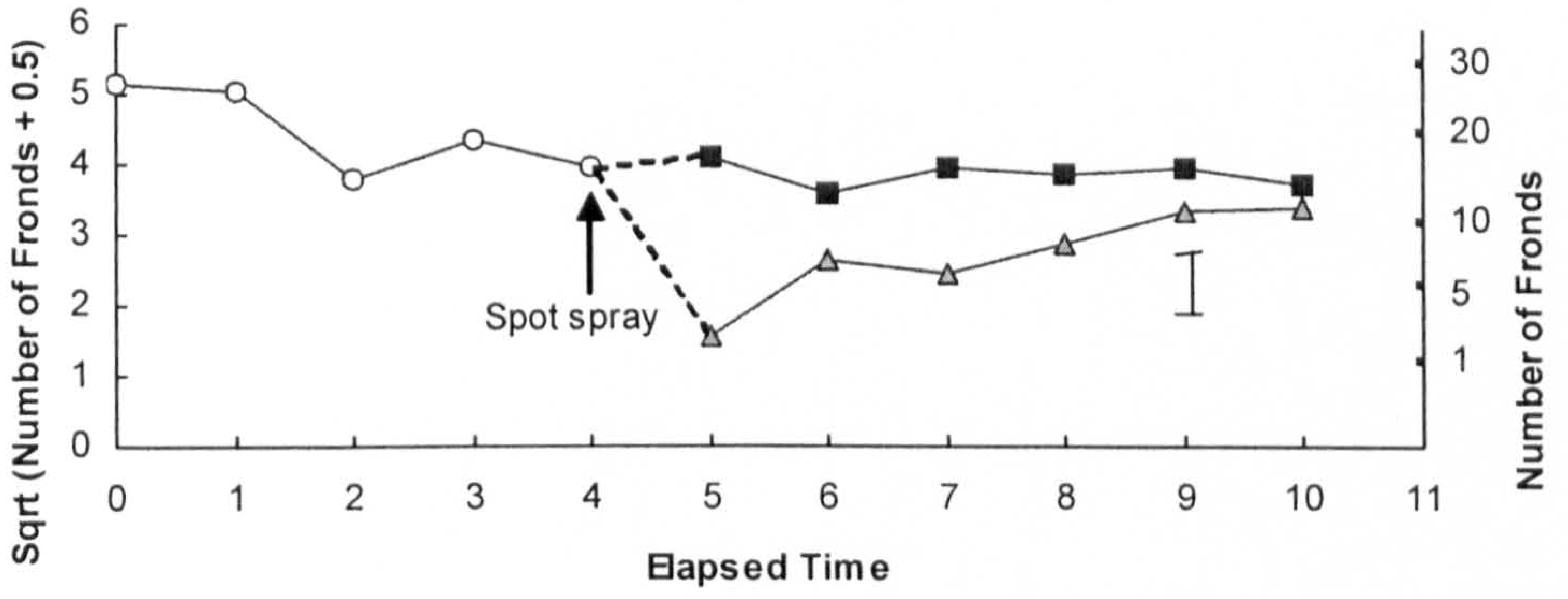
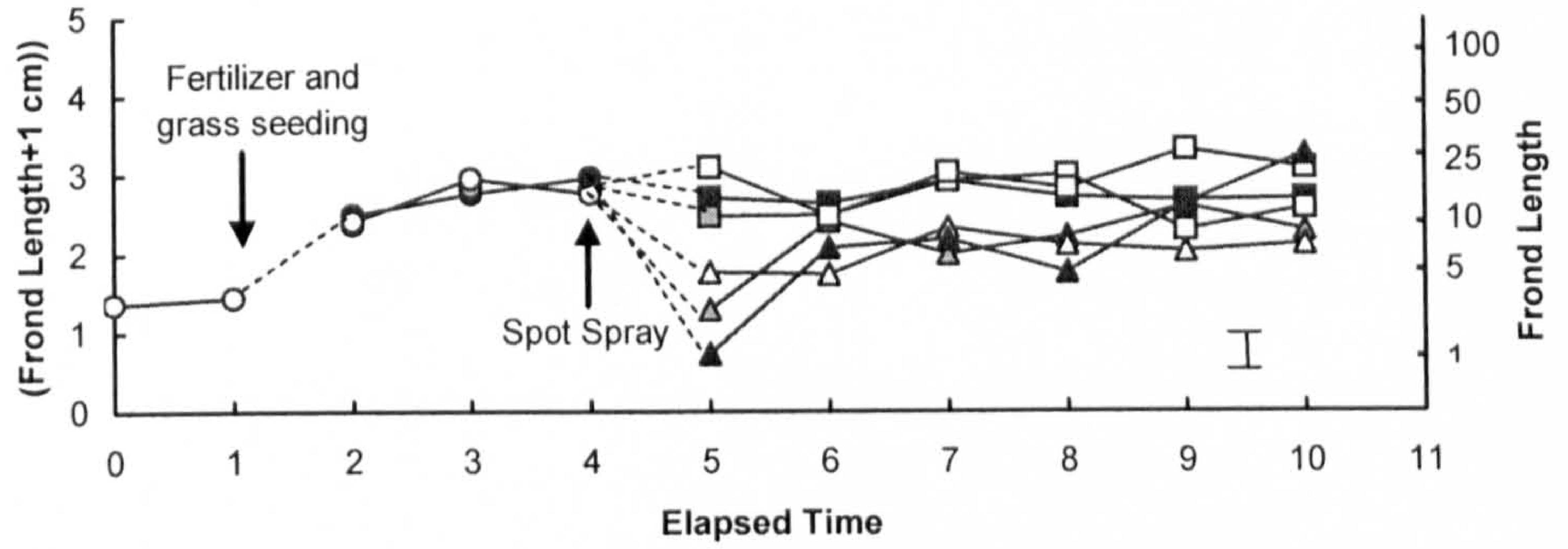


Fig. 3. Bracken control treatment effect on *Pteridium aquilinum* cover in August (no treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond); (a) Carneddau (98-03) (overall effect, $F_{(5,10)}$=50.69 n=18 (Cut2pa n=17)) (b) Sourhope (1st order, $F_{(5,10)}$=8.9 n=8; overall effect, $F_{(5,10)}$=13.24 n=56) (c) Peak (1st order, $F_{(5,10)}$=38.74 n=18). Data for Cannock can be found in Fig.1. Elapsed Time = 0 is 1993 for Carneddau, Peak and Sourhope 1, 1994 for Sourhope 2. Error bars are ± 2S.E.D.

(a) Spot Spray on Frond Density



(b) Restoration Treatment x Spot Spray Interaction on Frond Length



(c) Bracken Control x Spot Spray Interaction on *Pteridium aquilinum* Cover

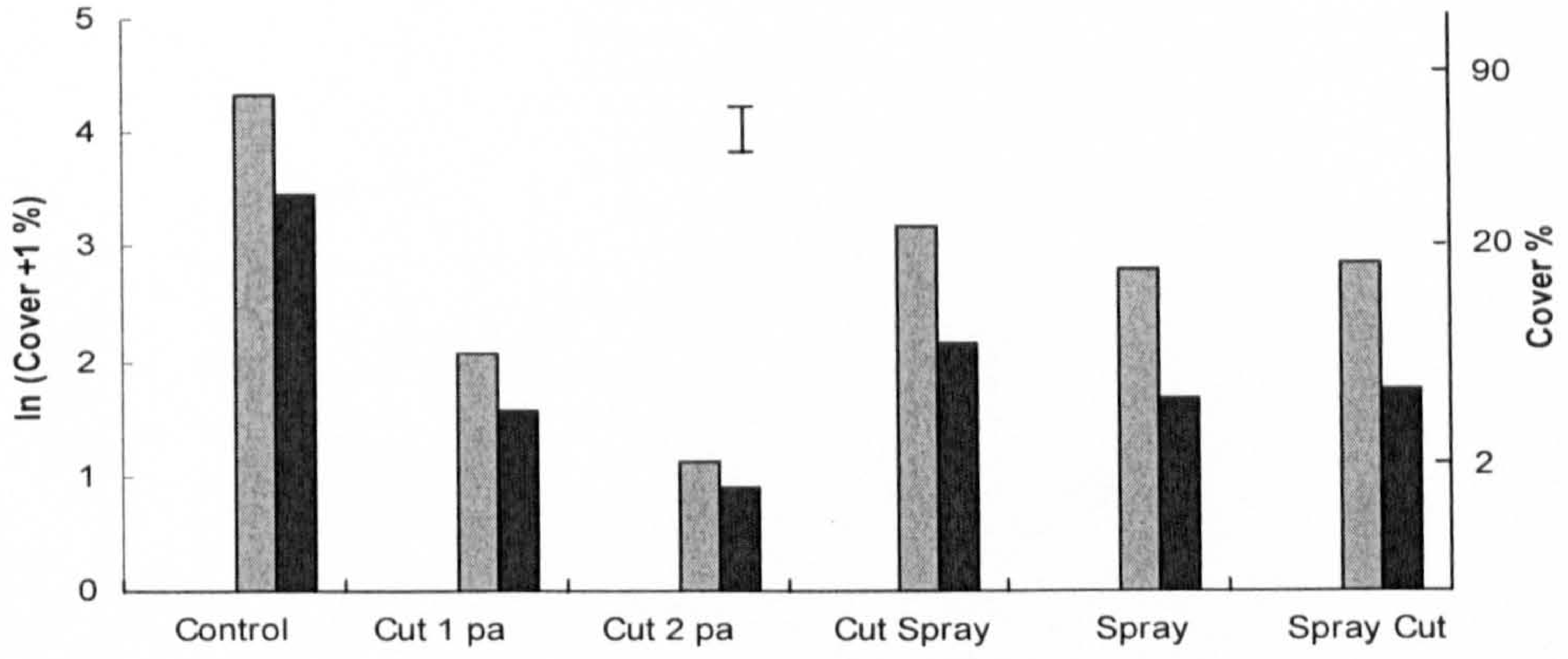


Fig. 4. Effect of spot spraying, restoration and bracken control treatments at Carneddau in August ((a and b) no treatment= square; spot spray= triangle; no restoration treatment= white; fertilizer= black; fertilizer and grass seed= grey; (c) no treatment= grey; spot spray= black) (a) spot spray on frond density (1st order, $F_{(1,36)}=20.27$ n=54) (b) restoration treatment x spot spray interaction on frond length (1st order , $F_{(2,36)}=6.84$ n=18 (Frt_GrS & No SbSbTr n=17) (c) bracken control x spot spray interaction on *Pteridium aquilinum* cover (overall effect, $F_{(5,36)}=3.47$ n=54). Elapsed Time = 0 is 1993. Error bars are ± 2S.E.D.

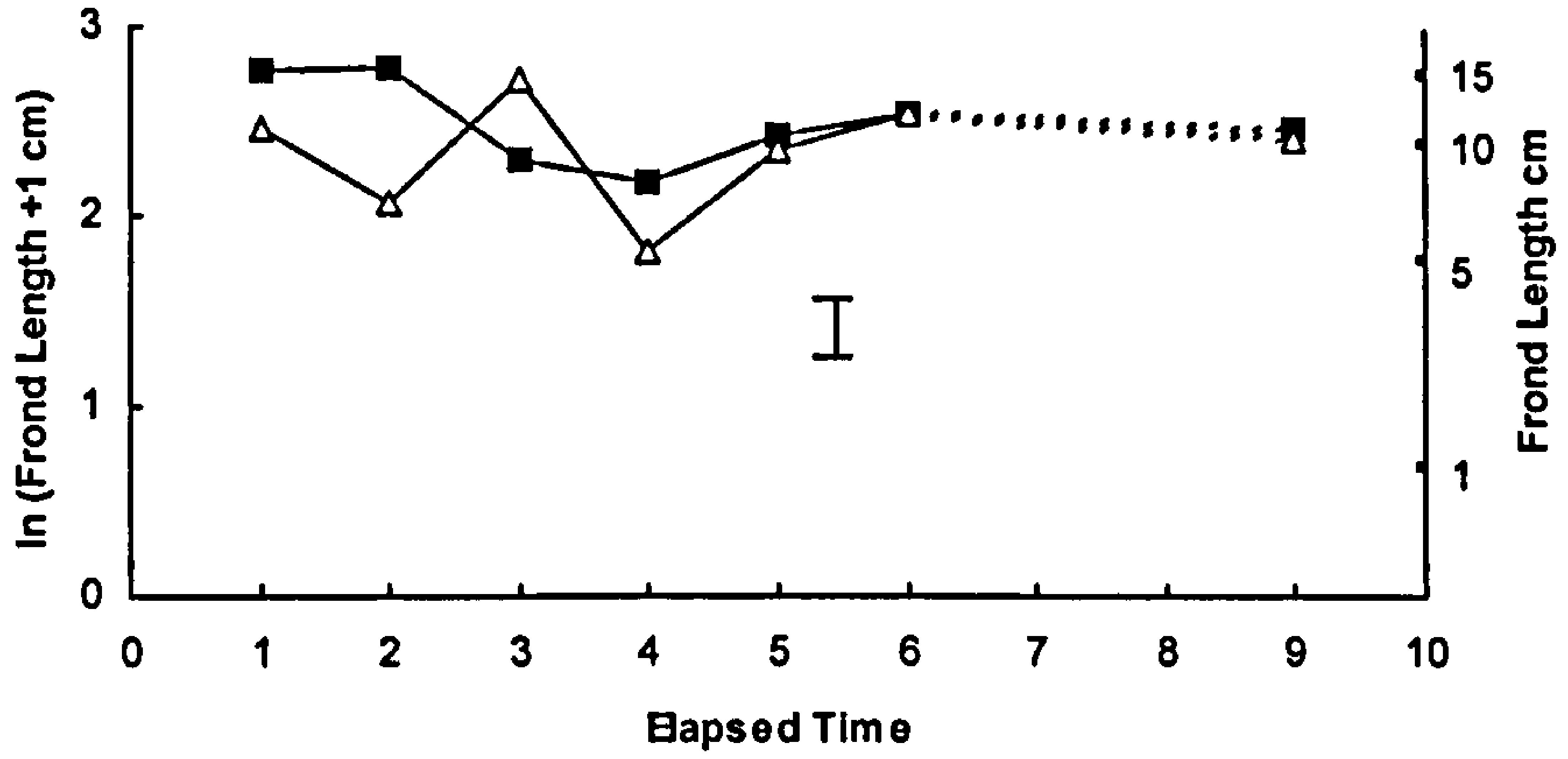


Fig. 5. The effect of grass seeding on frond length at Sourhope in August (No seeding treatment= square; grass seeding= triangle) (6th order, $F_{(1,12)}$=8.95 n=24). Elapsed Time = 0 is 1993 for Sourhope 1 & 1994 for Sourhope 2. Seed treatment applied ET=1. Error bars are ± 2S.E.D.

2.3.5 *Significant differences between June and August*

There were only five additional single-treatment effects found in the June data that were not significant in the August data. Four of the five single-treatment effects were, however, significant in higher order interaction in the August analyses so they are not discussed further here. The exception was a significant effect of fencing at Peak on *P. aquilinum* cover (2nd order effect, $F_{(1,12)}$=24.24, n=54; mean fenced cover is 9.2% compared to a mean unfenced cover of 10.6%, transformed means are 2.32 and 2.45 respectively, ± 2S.E.D=0.17).

2.4 Discussion

2.4.1 *Geographical location (locally between and within sites) affects the control of* Pteridium aquilinum *through time*

An interesting result was that different responses were found between experiments set up on the same site within relatively short distances of each other (< 2.5 km) and on the same vegetation type. At Cannock the bracken treatments produced the same responses at the two sites in both samplings; however at Sourhope the two experiments were markedly different at the start, with frond density being significantly different at the two sites. The Sourhope sites show marked differences in modeled rhizome equilibrium biomass (Pottier *et al.*, 2005). These authors hypothesized that Sourhope 1 was particularly sensitive to microclimatic effects, especially the period of frost-free growth as a result of exposure and shelter, which limits the growing season.

The inter-annual fluctuations noted at Cannock, are almost solely observed in Cannock 1 for the CutSpray treatment. This variation may be due to the patchiness of recovery (Pakeman *et al.*, 2005), in the years with low cover, length and density there was a high percentage quadrats containing 5% or less *P .aquilinum* cover (67, 58 and 42% for ET3, 6 and 8 respectively) compared with other years (25, 0, 0 and 8% for ET4, 5, 7 and 9 respectively). This effect may have been highlighted due to the random nature of the sampling and did not occur in other sprayed treatments as recovery was much more uniform.

These overall results are not too surprising, but this longer term analysis suggests that within-site variability is perhaps less than suggested from analysis of shorter-term data (Le Duc *et al.*, 2000).

2.4.2 *Are the* P. aquilinum *control treatments successful at all sites, and if so which ones?*

Despite local variation, at all sites the continuous cutting treatments, normally Cut2pa, were the most effective at reducing bracken performance in the final year of monitoring (Table 2), with the exception of frond density at the Cannock sites. The cutting treatments generally became most successful at reducing *P. aquilinum* in ET5 or 6 (1998 or 1999) with an increasing impact over time, showing a pattern similar to that described elsewhere (Lowday & Marrs, 1992a; Marrs *et al.*, 1998a, Pakeman *et al.*, 2002). Recovery from the initially successful spray treatments to untreated levels occurred in approximately 10 years, contrasting with a much shorter recovery rate of approximately 6 years found in lowland Britain where the climate is more equitable (Lowday & Marrs, 1992a; Marrs *et al.*, 1998a). It is clear that a single application of asulam to control bracken is not enough and findings here support current good practice guidelines (Anon, 2005). For the heath sites Cut2pa has still not yet reduced frond cover to the same level as the initial CutSpray reduction, at the acid grassland sites the cutting treatments have significantly reduced frond cover below that of the spray treatments in the initial years of the experiment. This might reflect the greater *P. aquilinum* cover, litter cover, litter depth or being initially species poor at the start. It may also reflect other site-specific differences in climatic conditions and other abiotic factors that have not been tested here (see Chapter 1, Table 2 for a summary of estimated initial covers).

Table 2. The most effective treatment for reducing bracken in final year of monitoring for all data presented.

		Site			
Treatment	**Bracken Measure**	**Cannock 1 & 2**	**Carneddau**	**Peak**	**Sourhope 1 & 2**
Experiment x Bracken Control	*P. aquilinum* Cover	Cut2pa			
	Frond Length	Cut2pa			
	Frond Density	CutSpray			
Bracken Control	*P. aquilinum* Cover	Cut2pa	Cut2pa	Cut2pa	Cut1pa/ Cut2pa
	Frond Length	Cut2pa	Cut2pa	Cut2pa	Cut1pa
	Frond Density	CutSpray	Cut2pa	Cut2pa	Cut2pa
Seeding	Frond Length				Seeding
Spot Spraying	Frond Density		Spot Spray		
Seed x Spot Spray	Frond Length		No treatment, Spot Spray		
Bracken Control x Spot Spray	*P. aquilinum* Cover		Cut2pa, Spot Spray		

However, at the Cannock sites the cutting treatments were not the most effective at reducing frond density, the effect of cutting on frond density (i.e. the production of smaller but more numerous fronds) is well known (Lowday & Marrs, 1992a). Possibly due to the high rhizome biomass at this site (Le Duc *et al.*, 2003) and the greatest initial frond cover, if the cutting treatment were to continue the frond density will no doubt decease over time. It was not until the penultimate year of monitoring, ET9, that cutting had the greatest impact on frond density at the Sourhope sites.

The effects of spot spraying with asulam was generally effective in reducing bracken performance, this is in line with manufacturer's recommendations (Anon, 2005; Robinson, 2000). However, a full test of the recently introduced manufacturer's recommended good practice i.e. continued spot spraying without respite (Anon, 2005; Robinson, 2000; The Southern Upland Partnership, 2001) has not been tested here. This practice will be included in revised experimental protocols on two of these experiments from 2004.

2.4.3 *The treatments applied at the individual site level to restore vegetation influences the performance of* P. aquilinum *through time*

In August only one restoration treatment had a significant effect on any of the *P. aquilinum* response variables. There is some evidence to suggest that vegetation can inhibit bracken recovery with frond length initially being reduced in seeded plots at Sourhope, however the evidence is limited as the treatments merge after 3 years and this result is only significant in August monitoring with none of the seeded grasses having a significant increase over time (Cox *et al.*, 2007b). In June only, the exclusion of sheep grazing at Peak had a significant effect on *P. aquilinum* cover. Plots where sheep were fenced out showed a reduction in *P .aquilinum* cover, in August this effect was no longer significant. This contradicts other results which report reduced *P. aquilinum* cover (Pakeman *et al.*, 1997; Williams, 1980) or *P. aquilinum* litter cover (Le Duc *et al.*, 2007a) with moderate grazing

2.4.4 *Issues in the analysis of multi-site data*

In spite of the need for good experimentally-derived information to guide restoration policies there have been surprisingly relatively few attempts to carry out large-scale, long-term, multi-site experiments for the control of pernicious weeds. Most studies either being single-site or short-term. Where multi-site studies have been reported in restoration ecology a mixture of analytical techniques has been used. Pywell *et al.* (2002) used standard ANOVA with repeated measures to assess the factors limiting success when attempting to restore species-rich grassland on arable land in a four-year experiment. Pakeman (2004) preferred a combination of Residual Maximum Likelihood (REML) analysis to test for complex relationships between species response and measured covariables in a 7-year study. In contrast, Marrs *et al.* (2004) used a combination of univariate and multivariate analyses of variance to describe a multi-site experiment on *Molinia caerulea* control. Here, as we used properly-designed classical experiments, we used a variant of the former approach, using standard ANOVA with repeated measures, but extending its usefulness using polynomial contrasts (Gurevitch & Chester, 1986; Le Duc *et al.*, 2007a). The value of this approach is that it is possible to test for treatment effects as in ANOVA, but the temporal trends of these treatment effects can also be identified. This approach becomes more useful with longer datasets. This approach enabled both recovery trajectories to be identified and the detection of peaks and troughs which are almost certainly linked to annual difference in weather factors (Lowday & Marrs, 1992a; Le Duc *et al.*, 2003). This approach has been used successfully to detect change in single sites (Le Duc *et al.*, 2007a).

2.5 *General conclusions*

Despite local variation, all sites reacted in a similar manner to the bracken control treatments. From these data it is clear that long-term control of bracken at all sites and on all measures was best achieved using a continuous cutting treatment, preferably twice per year. Although, this may not be the most cost-effective method as treatment will need to be applied twice a year essentially indefinitely. It is clear that a single application of herbicide is not an effective treatment for long term control, current advice recommends following up with spot spray, yearly, until no new fronds appear (Anon, 2005), but this has not been tested experimentally yet.

Chapter 3

Control of Bracken (*P. aquilinum*): meta-analysis of a multi-site study in the UK

3.1 Introduction

A fundamental limitation in vegetation management and restoration ecology is the ability to predict, with some degree of precision, the likely outcome of a proposed treatment across a range of sites. This is essential to meet the objectives of both policy-makers and those responsible for implementation of practical management schemes. However, it is well known that accurate prediction is difficult when treatments may have to be applied over wide bio-climatic conditions, and where the restoration objectives may vary according to the ecosystem being treated. An obvious solution is to carry out multi-site experiments where the same treatments are applied contemporaneously; however there are relatively few examples of such an approach (Le Duc *et al.*, 2003; Lowday & Marrs, 1992a; Pywell *et al.*, 2002; Pakeman, 2004). This is most problematic when the treatments have to be delivered via an Integrated Land Management Approach (Milligan *et al.*, 2004), where restoration includes the control of invasive species coupled with techniques to restore more appropriate vegetation, and is especially difficult where the invasive weed is problematic, and success is variable.

3.1.1 *The case-study problem*

Pteridium aquilinum (L.) Kuhn is a serious invasive weed of upland and marginal land in many parts of the world (Page, 1995; Pakeman & Marrs, 1992). In the UK, *P. aquilinum* is an especially problematic weed, causing problems in upland heaths and acid grasslands, where it often occurs in dense stands (summarized in Smith & Taylor, 1995). *P. aquilinum* is difficult to control for a range of reasons including, an extensive rhizome system (Le Duc *et al.*, 2003), and a high productivity that produces a dense frond cover and deep litter, which combine to reduce understorey vegetation (Marrs *et al.*, 2000).

The current agricultural and conservation policy in the UK for *P. aquilinum* infestation is delivered through Agri-Environment Schemes (MAFF, 1993, 1996) and Biodiversity Action Plans (Anon, 1995a, b). Essentially, the policy is to reduce *P. aquilinum* infestations where possible and to commonly restore *Calluna vulgaris*-dominated heathland or acid grassland. *P. aquilinum* is considered a mid-successional plant, usually occupying a niche between plagio-climax heath/moor/grassland and woodland (Marrs *et al.*, 2000, Marrs & Watt, 2006), although it can persist for long periods and appears in some cases to represent a highly resilient stable state (Marrs at al., 2000; Suding *et al.*, 2004, Marrs & Watt, 2006).

In the UK *P. aquilinum* occurs across a wide range of conditions and given that succession can occur along many trajectories (Mitchell *et al.*, 2000; Suding *et al.*, 2004), there is potentially a large number of possible outcomes for *P. aquilinum* control/vegetation restoration schemes. In addition, *P. aquilinum* communities are known to have high resilience (Le Duc *et al.*, 2007c) and *P. aquilinum* control often produces variable and conflicting results (Le Duc *et al.*, 2000; Cox *et al.*, 2007a). It is, therefore, important from a national policy perspective to understand the response of *P. aquilinum* to control treatment in a variety of bio-geographical situations.

3.1.2 *Approach to this study*

There are a number of approaches that can be applied to analyze such multi-site studies including univariate analysis of variance (Le Duc *et al.*, 2000; 2003, Cox *et al.*, 2007a, b; Pakeman, 2004; Pywell *et al.*, 2002) and multivariate analysis. Recently there has been an increasing interest in the use of formal meta-analysis in ecological studies, specifically through the development of evidence-based frameworks and systematic review (Pullin & Knight, 2001, 2003, Sutherland *et al.*, 2004, Pullin & Stewart, 2006). Often such meta-analysis has involved the comparison of experiments carried out by different researchers and in different situations with heterogeneity in application methods, for example the review of asulam control of *P. aquilinum* (Stewart *et al.*, 2006). In such analyses it is often difficult to attribute variation in the success of treatments between studies to ecological effect modifiers because of confounding by the different methodologies employed by different researchers at different sites (Stewart *et al.*, 2005, Tyler *et al.*, 2006). However, data from a 10-year study of *P. aquilinum* control, where six replicated experiments were carried out more or less simultaneously, with the same treatments being applied and results collected by the same team of observers (Le Duc *et al.*, 2000; Cox *et al.*, 2007a) does not have these same problems. This dataset provides a unique opportunity to assess the value of meta-analytical approaches in ecological management and assesses the importance of inter-site variability with respect to treatment performance.

Here meta-analytical approaches are used to test the following questions:

1. Does the effectiveness of *P. aquilinum* control treatments vary across sites?
2. Is the best treatment identified in previous research (cutting twice per year) consistent at all sites, and if not why not?

3. Is treatment performance related to *P. aquilinum* rhizome mass, litter cover, litter depth at the various sites?
4. Does successful *P. aquilinum* control influence species richness?

On a more general note we also assess the role of multi-site experiments in applied vegetation management on a quantitative basis.

3.2 Methods

3.2.1 *Experimental sites*

This chapter reports on data from the series of experiments described in Chapter 1, with the addition of a seventh experiment at Cannock Chase (Table 1). Only one bracken control treatment, cutting twice per year, was applied to Cannock 3, with the site specific restoration treatments being; litter burning and *Calluna* seeding.

Table 1. Detailed description of experimental design. Entries for experimental design (split-split-plot randomized block design) represent: number of blocks / number of plots per block / number of sub-plots per plot / number of sub-sub-plots per sub-plot. Square brackets enclose treatment (or treatment start) date. The National Vegetation Classification (NVC, Rodwell, 1991a,b, 1992) descriptions (the codes are explained in the footnote) represent the pre-treated condition; data in brackets being the results obtained when *P. aquilinum* was left out of the calculations. The measured fit was obtained using TABLEFIT version 1.0 (Hill, 1996), and is rated: > 80 very good, > 70 good, > 60 fair, < 60 poor. All experimental treatments were applied in balanced designs with appropriate untreated contrasts, the untreated constrasts are not shown for clarity.

Location	**Cannock Chase**
- Ordnance Survey map reference	SJ 987 178
Experiment:	
- name	Cannock 3
- started	1995
- design	2/2/2/2
- smallest plot	6 x 5 m
- main treatments (*P. aquilinum* control)	Cut twice pa [Jun. 95]
- sub-treatments	Litter burn [Mar. 95]
- sub-sub-treatments	*Calluna* seed (brash) [Dec. 96]
Physical:	
- altitude (m)	175
- aspect (°)	175
- slope (°)	9
Vegetation:	
- NVC class	U2(U2)
- fit	63(62)

NVC classes represented is: U2 *Deschampsia flexuosa* grassland.

3.2.2 *Monitoring*

Monitoring at Cannock 3 was conducted in the same manner as described in Chapter 1.

3.2.3 *Data analysis and presentation*

Mean values for each plot in each block were obtained after appropriate transformation of raw data; frond density using $(Y + 0.5)^{0.5}$, frond length, and cover using $\ln(Y + 1)$. The means were then back-transformed for meta-analysis. Change over time was averaged across years to avoid *post hoc* rationalization regarding the choice of temporal end point. Sub and sub-sub plot treatments were disregarded to prevent any confounding impacts.

The comparative impacts of the applied treatments were analyzed by meta-analysis and meta-regression (Cooper & Hedges, 1994, Scheiner & Gurevich, 2001, Deeks *et al.*, 2001); these analyses were performed on three *P. aquilinum* variables (cover, mean frond density (no m^{-2}) and frond length (cm). Cohen's D effect sizes (Deeks *et al.* 2001) were derived from the treatment and control means, standard deviations and sample sizes. Data were pooled and combined across studies using DerSimonian and Laird random effects meta-analysis based on standardised mean difference (SMD) (DerSimonian & Laird, 1986; Cooper & Hedges, 1994). The random effects model anticipates that the true effect size differs among studies and the aim of the analysis is to quantify such variation in the effect parameters; it is therefore appealing to an ecological question where the true effect is likely to vary between studies (Gurevitch & Hedges, 1999). The standardised mean difference method expresses the size of the treatment effect in each study relative to the variability observed in that study (Deeks *et al.*, 2001).

Questions 1 and 2 (treatment effectiveness across sites, assessing best treatment) were tested by inspection of Forrest plots of the estimated treatment effects from the studies along with their 95% confidence intervals, and by formal tests of homogeneity undertaken prior to each meta-analysis (Thompson & Sharp, 1999). Questions 3 and 4 (testing relationship between treatment performance and explanatory variables including species richness) were tested by examining the associations of treatment effects with *P. aquilinum* rhizome mass, litter cover, litter depth and species richness (rhizome data abstracted from Le Duc *et al.*, 2003) using univariate random effects SMD meta-regression in Stata version 8.2 (Stata Corporation, 2003) using the program Metareg (Sharp, 1998). The association of treatment effect derived from treatment-control comparisons (n=5) with explanatory variables (n=4) and outcome measures (n=3) required 60 regression analyses necessitating the use of bonferroni correction for each outcome measure which were treated as independent metrics (Sankoh *et al.*, 1997).

3.3 Results

The use of Meta-analysis is becoming increasingly prevalent in ecology (Hedges & Olkin 1985, Arnqvist & Wooster, 1995, Osenberg *et al.*,1999, Gurevitch & Hedges, 1999, 2001) but not all ecologists are familiar with the output of such analyses. The results presented in Table 2 summarise the overall impact of different treatments across the six study sites, with the diagonal structure resulting from comparison of all permutations of five treatment comparisons. The pooled effect size (D) is significant when the confidence intervals do not cross zero (Table 2, Figs 1& 2). Effect sizes smaller than 0.2 are considered small by convention (Cohen, 1988) although no actuarial approach to appraising ecological effect sizes exists for D. Thus the majority of comparisons presented illustrate small but statistically significant effects (Table 2). The statistical significance of variation between sites is tested using the *Q* statistic following a chi-squared distribution under the null hypothesis that the true treatment effect is the same for all sites. The majority of the comparisons vary significantly between sites (see below). The forrest plots (Fig.1, Fig 2.) illustrate the effectiveness of each site, the overall pooled impact, and the variation in effect both within and between sites. Further information regarding interpretation of forrest plots is available at http://www.cebc.bham.ac.uk/reviews.htm.

Table 2. Pooled treatment effects based on DerSimonian and Laird SMD meta-analysis of the studies with 95% confidence intervals and tests of homogeneity based on a chi-squared distribution of Q on k-1 degrees of freedom. Significant results ($p<0.05$) are indicated in bold.

(a) Cover (%)

	Cut once per annum	Cut twice per annum	Cut in the first year, sprayed in the second	Sprayed once with herbicide	Sprayed in the first year, cut in the second
Untreated control	**DL 1.585 (0.855-2.315) z = 4.26, p = 0.000** **$H\chi^2$ = 28.71, p = 0.000**	**DL 2.180 (1.529-2.831) z = 6.57, p = 0.000** **$H\chi^2$ = 19.01, p = 0.002**	**DL 1.592 (0.970-2.214) z = 5.01, p = 0.000** **$H\chi^2$ =20.95, p = 0.001**	**DL 1.509 (0.581-2.438) z = 3.19, p = 0.001** **$H\chi^2$ = 44.99, p = 0.000**	DL 0.998 (0.098-1.899) z = 2.17, p = 0.030 **$H\chi^2$ =47.12, p = 0.000**
Cut once per annum		**DL 0.426 (0.170-0.682) z = 3.26, p = 0.001** $H\chi^2$ =3.53, p = 0.618	DL 0.044 (-0.286-0.373) z = 0.26, p = 0.795 $H\chi^2$ =8.28, p = 0.141	DL -0.134 (-0.490-0.222) z = 0.74, p = 0.462 $H\chi^2$ =9.24, p = 0.100	**DL -0.543 (-0.892--0.194) z = 3.05, p = 0.002** $H\chi^2$ =8.58, p = 0.127
Cut twice per annum			DL -0.364 (-0.778-0.049) z = 1.73, p = 0.084 $H\chi^2$ =12.69, p = 0.026	**DL -0.570 (-0.972- -0.168) z = 2.78, p = 0.005** $H\chi^2$ =11.26, p = 0.046	**DL -0.990 (-1.503--0.477) z = 3.78, p = 0.000** **$H\chi^2$ =16.83, p = 0.005**
Cut in the first year, sprayed in the second				DL -0.172 (-0.735-0.390) z = 0.60, p = 0.548 $H\chi^2$ =22.40, p = 0.000	DL -0.535 (-1.119-0.049) z = 1.80, p = 0.072 $H\chi^2$ =23.28, p = 0.000
Sprayed once with herbicide					DL -0.393 (-0.780-0.015) z = 1.89, p = 0.059 $H\chi^2$ =11.36, p = 0.045

(b) Frond length (cm)

	Cut once per annum	Cut twice per annum	Cut in the first year, sprayed in the second	Sprayed once with herbicide	Sprayed in the first year, cut in the second
Untreated control	**DL 2.581 (1.930-3.231) z = 7.78, p = 0.000** **$H\chi^2$ =20.39, p = 0.001**	**DL 3.379 (2.836-3.921) z = 12.20, p = 0.000** $H\chi^2$ =10.87, p = 0.054	**DL 1.545 (0.799-2.291) z = 4.06, p = 0.000** **$H\chi^2$ =36.93, p = 0.000**	**DL 1.460 (0.534-2.386) z = 3.09, p = 0.002** **$H\chi^2$ =56.15, p = 0.000**	**DL 1.389 (0.319-2.458) z = 2.55, p = 0.011** **$H\chi^2$ =74.63, p = 0.000**
Cut once per annum		**DL 0.548 (0.056-1.040) z = 2.19, p = 0.029** **$H\chi^2$ = 21.43, p = 0.001**	**DL -0.514 (-0.865- -0.163) z = 2.87, p = 0.004** $H\chi^2$ =10.96, p = 0.052	**DL -0.611 (-1.140- -0.082) z = 2.27, p = 0.023** **$H\chi^2$ =23.42, p =0.000**	**DL -0.695 (-1.170 - -0.221) z = 2.87, p = 0.004** **$H\chi^2$ =18.73, p = 0.002**
Cut twice per annum			**DL -0.884 (-1.243 - -0.525) z = 4.83, p = 0.000** $H\chi^2$ =10.97, p = 0.052	**DL -1.023 (-1.603 - -0.444) z = 3.46, p = 0.001** **$H\chi^2$ =26.36, p = 0.000**	**DL -1.052 (-1.715 - -0.389) z = 3.11, p = 0.002** **$H\chi^2$ =33.76, p = 0.000**
Cut in the first year, sprayed in the second				DL -0.106 (-0.659 – 0.445) z = 0.38, p = 0.705 **$H\chi^2$ =26.50, p =0.000**	DL -0.138 (-0.707 – 0.429) z = 0.48, p = 0.632 **$H\chi^2$ =27.87, p = 0.000**
Sprayed once with herbicide					DL-0.06 (-0.478 - 0.346) z = 0.32, p =0.752 **$H\chi^2$ =14.54, p =0.012**

(c) Frond density (no m^{-2})

	Cut once per annum	Cut twice per annum	Cut in the first year, sprayed in the second	Sprayed once with herbicide	Sprayed in the first year, cut in the second
Untreated control	DL 0.347 (-0.424-1.119) z = 0.88, p = 0.378 **$H\chi^2$ = 48.47, p = 0.000**	DL 0.615 (-0.323-1.554) z = 1.28, p = 0.199 **$H\chi^2$ = 68.65, p = 0.000**	**DL 1.028 (0.669-1.387) z = 5.61, p = 0.000** $H\chi^2$ =10.16, p = 0.07	**DL 1.279 (0.736-1.823) z = 4.62, p = 0.000** **$H\chi^2$ = 20.89, p = 0.001**	**DL 1.032 (0.474-1.591) z = 3.62, p = 0.000** **$H\chi^2$ =23.26, p = 0.000**
Cut once per annum		DL 0.173 (-0.143-0.489) z = 1.07, p = 0.283 $H\chi^2$ =9.39, p = 0.095	**DL 0.582 (0.013-1.151) z = 2.01, p = 0.045** **$H\chi^2$ =27.72, p = 0.000**	**DL 0.722 (0.240-1.204) z = 2.94, p = 0.003** **$H\chi^2$ =19.07, p = 0.002**	**DL 0.647 (0.334-0.959) z = 4.05, p = 0.000** $H\chi^2$ =8.33, p = 0.139
Cut twice per annum			DL 0.321 (-0.286-0.928) z = 1.04, p = 0.300 **$H\chi^2$ =32.88, p = 0.000**	DL -0.570 (-0.972- -0.168) z = 2.78, p = 0.005 $H\chi^2$ =11.26, p = 0.046	DL -0.990 (-1.503—0.477) z = 3.78, p = 0.000 $H\chi^2$ =16.83, p = 0.005
Cut in the first year, sprayed in the second				DL 0.128 (-0.187-0.443) z = 0.8, p = 0.425 $H\chi^2$ =8.92, p = 0.112	DL 0.023 (-0.415-0.462) z = 0.11, p = 0.915 **$H\chi^2$ =16.96, p = 0.005**
Sprayed once with herbicide					DL -0.125 (-0.523-0.272) z = 0.62, p = 0.537 **$H\chi^2$ =13.58, p = 0.018**

Fig. 1. Forrest plots of individual site effect sizes from the six independent experiments (labeled 1-6) comparing five *P. aquilinum* control treatments (a-e) against untreated controls for three variables, *P. aquilinum* cover (%), mean frond length (cm), and mean frond density (no m^{-2}). Site codes: 1= Cannock 1, 2= Cannock 2, 3= Carneddau, 4=Peak, 5= Sourhope 1, 6=Sourhope6. Control treatment codes: (a) C1=cut once per year; (b) C2=cut twice per year: (c) CS=cut once and sprayed with asulam once; (d) S=sprayed once with asulam; (e) SC= sprayed once and cut once. Solid boxes represent the mean effect size of individual studies with 95% confidence intervals; the open diamond is the pooled effect size generated using standardized mean difference random effects meta analysis.

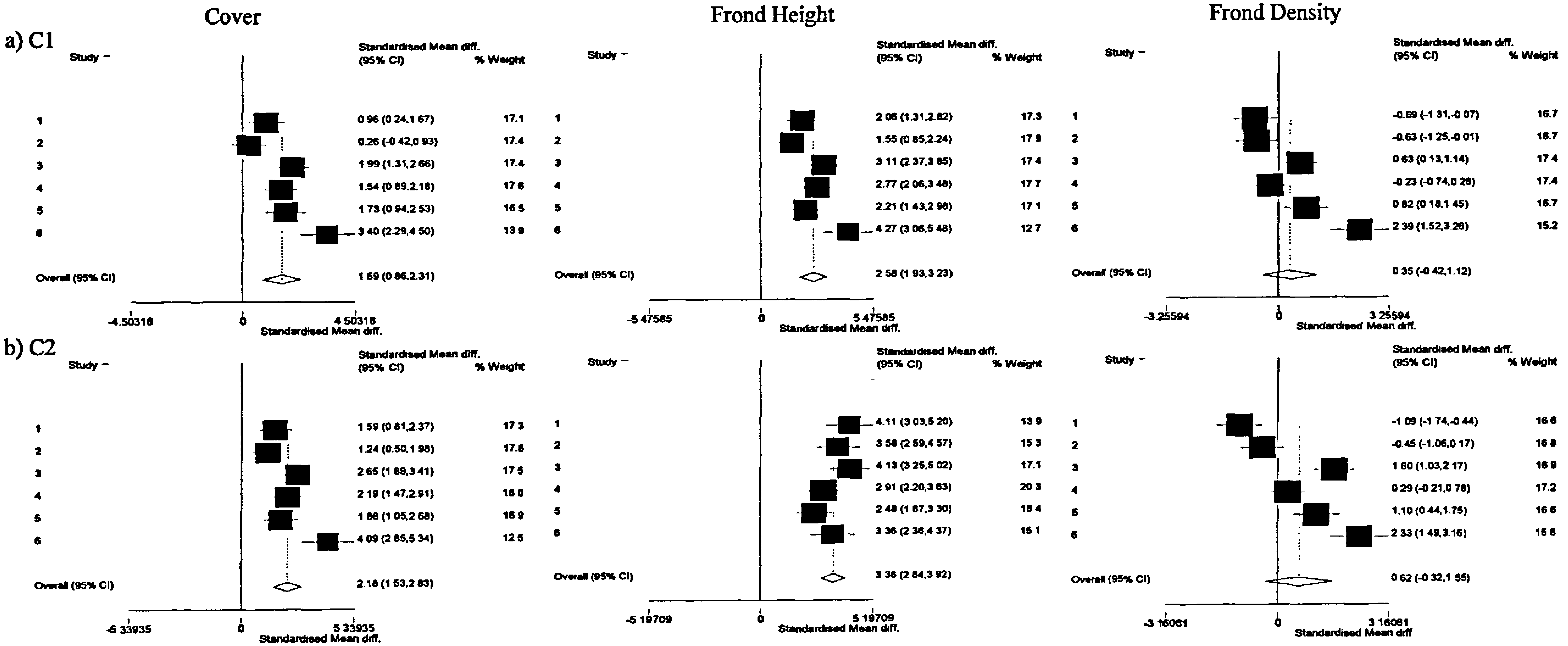


Figure 1 Continued

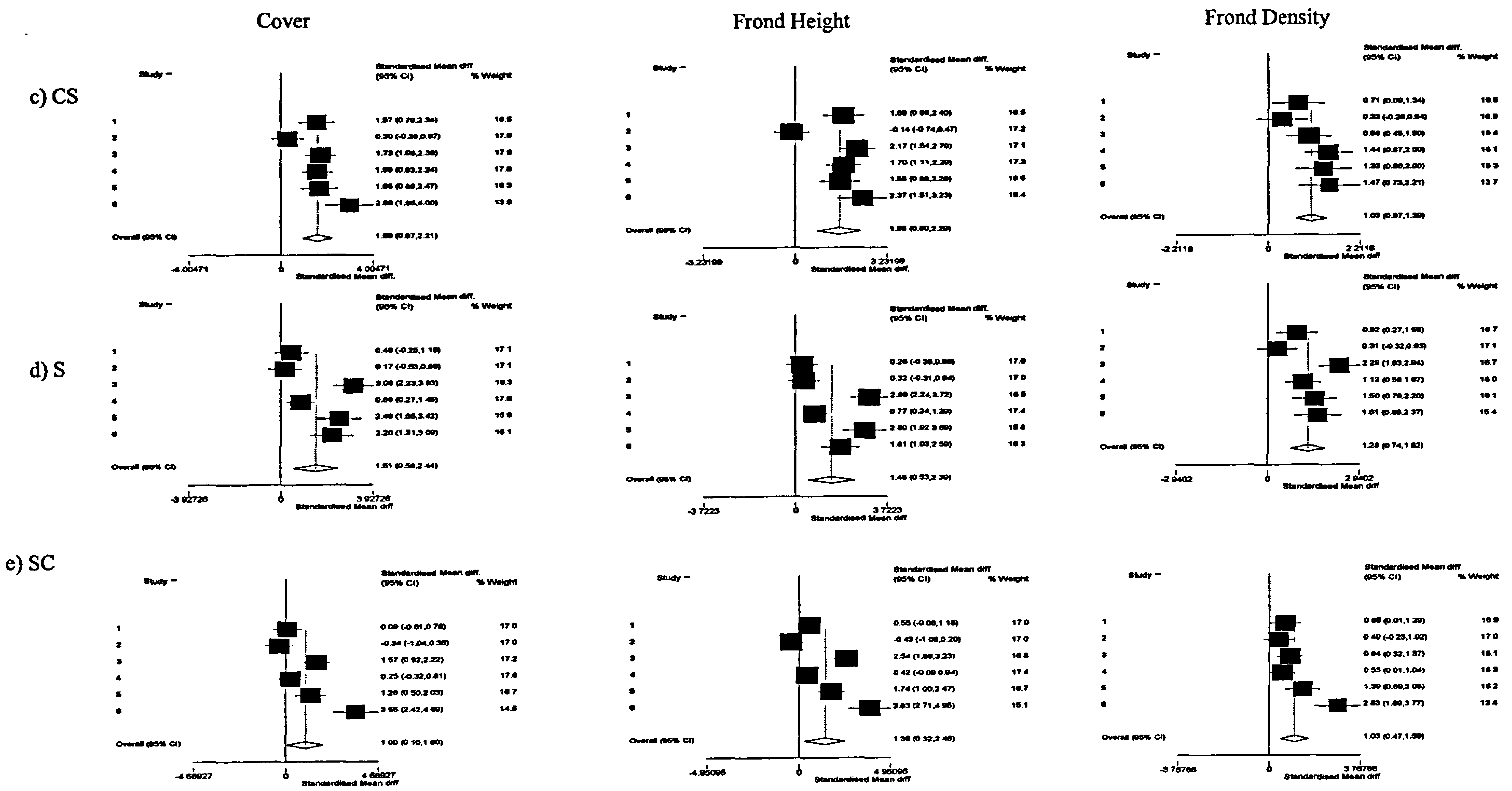


Fig. 2. Forrest plots of individual site effect sizes from the six independent experiments (labeled 1-6) comparing four *P. aquilinum* control treatments (a-d) against the cut twice per year treatment for three variables, *P. aquilinum* cover (%), mean frond length (cm), and mean frond density (no m^{-2}). Site codes: 1= Cannock 1, 2= Cannock 2, 3= Carneddau, 4=Peak, 5= Sourhope 1, 6=Sourhope6. Control treatment codes: (a) C1=cut once per year; (b) CS=cut once and sprayed with asulam once; (c) S=sprayed once with asulam; (d) SC= sprayed once and cut once. Solid boxes represent the mean effect size of individual studies with 95% confidence intervals; the open diamond is the pooled effect size generated using standardized mean difference random effects meta analysis.

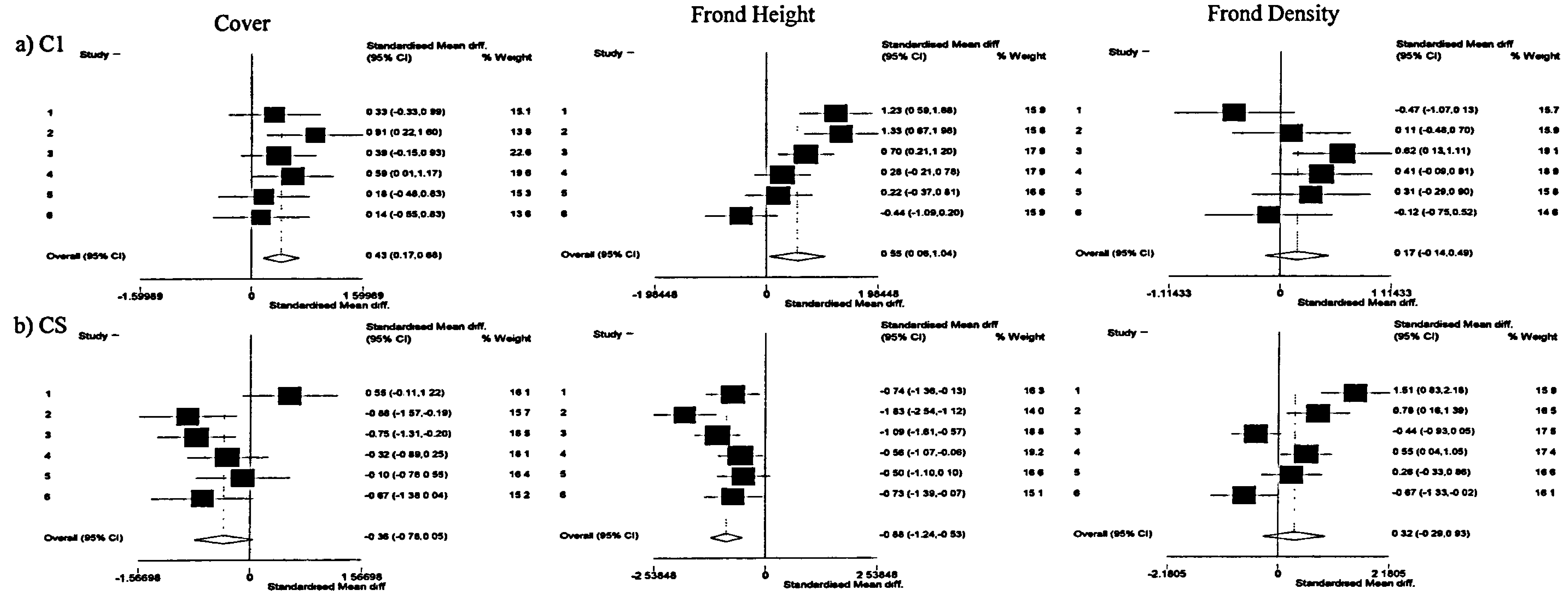
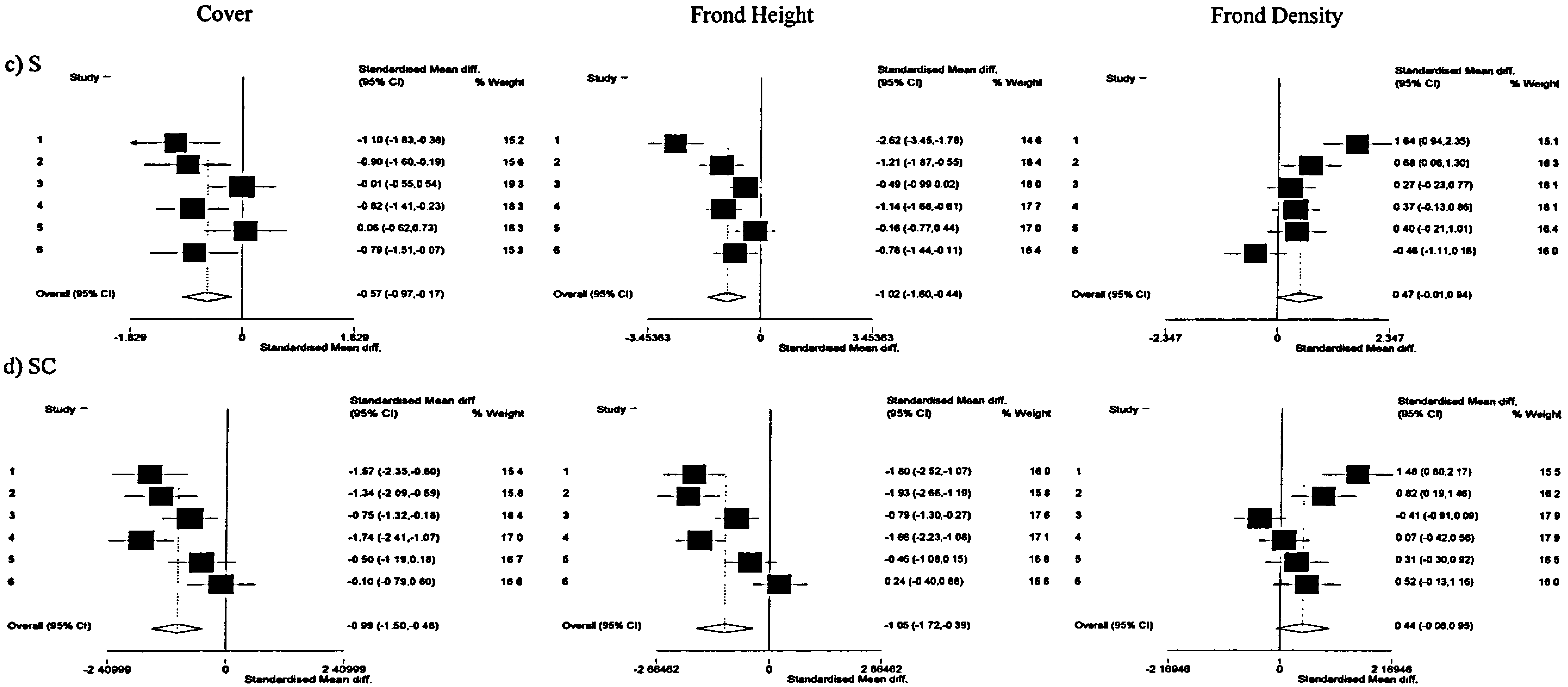


Figure 2 Continued



3.3.1 Question 1: Does the effectiveness of *P. aquilinum* control treatments vary across sites?

There was significant variation ($P<0.05$) between sites for almost all treatments relative to their respective untreated control for all three *P. aquilinum* frond response variables (Table 2, Fig. 1): the two exceptions were (1) the cut twice/yr treatment for frond length and (2) cut and spray for frond density. Cutting twice/yr is the most effective treatment overall for reducing cover and height (biggest significant effect size, Table 2, Fig. 1), but spraying once is more effective in reducing frond density (Table 2, Fig. 1).

There was also significant variation ($P<0.05$) between sites for other treatment comparisons but these varied with the outcome measurement. For cover (Table 2a) there was variation between sites when comparing the cut twice/yr treatment versus spraying and cutting. For frond length, there was significant variation between sites for most treatment comparisons (Table 2b), the exceptions being cutting once or twice/yr versus cutting and spraying. For frond density there was significant site effects for the untreated control versus all treatments except cut and spray (Table 2c). For the other frond density treatment comparisons the picture was variable, with the following being significant: (1) cutting once/yr versus cut and spray and spraying, (2) cutting twice/yr versus cut and spray, spray and cut versus spray and cut and spray.

3.3.2 Question 2: Is the best treatment identified in previous research (cutting twice per year) consistent at all sites, and if not why not?

The effectiveness of cutting twice per year varies significantly ($p<0.05$) between sites in comparison to uncut controls for cover and frond density but not for frond length (Table 2, Figure 2). The relative effectiveness of cutting twice per year does not generally vary significantly ($p<0.05$) except in comparison to sprayed and cut (cover and frond length), sprayed (frond length) and cut and sprayed (frond density) (Table 2, Figure 2). Thus although the effectiveness of cutting varies across sites, it remains the most effective treatment in nearly all cases.

3.3.3 Question 3: Is treatment performance at the various sites related to the effectiveness of the control method?

The effectiveness of *P. aquilinum* control was related to measured rhizome mass only for frond length in the cut twice treatment ($p<0.05$, Table 3a). This reduction in frond length associated with the cut twice treatment produced an increase in effect size of 0.42 per unit increase in rhizome mass (Table 3a) but the result is not significant ($p<0.0025$) when the multiple comparisons are accounted for with Sidak's or Bonferroni adjustment. The relationships of the control treatments with litter cover and depth were varied, with significant negative results found in seven and eight comparisons respectively; although the coefficients were small (Table 3). Adjustment for multiple comparisons reduces the number of significant relationships to one and three for litter cover and depth respectively (Table 3). Where a significant regression coefficient has been found the *P. aquilinum* control treatment has reduced the litter variable relative to the untreated control.

3.3.4 Question 4: Does successful *P. aquilinum* control influence species richness?

The effectiveness of *P. aquilinum* control treatment was significantly related to species richness in 12 out of 15 comparisons (8 of 15 are significant following adjustment for multiple comparisons, Table 3c). Whilst the regression coefficients are low, these are still significant and they indicate that *P. aquilinum* control treatment has increased species richness relative to the untreated control.

Table 3. Meta-regression results. Regression coefficients for statistically significant ($p<0.05$) relationships between effect size and explanatory variables: (a) rhizome mass, (b) litter cover, (c) litter depth, (d) species richness. Non-significant results excluded for clarity. Results that are significant following Sidak's or Bonferroni adjustment ($p<0.0025$) are indicated in bold.

(a) Rhizome mass

Comparison	Outcome measure	Regression coefficient	Z	P
Uncut v cut twice p.a	frond length	0.420	2.45	0.014

(b) Litter cover

Comparison	Outcome measure	Regression coefficient	Z	P
Uncut v cut & sprayed	cover	-0.027	-2.46	0.014
Uncut v sprayed & cut	cover	-0.032	-3.00	0.003
Uncut v sprayed	Frond length	-0.027	-2.46	0.014
Uncut v sprayed & cut	Frond length	-0.036	-2.78	0.005
Uncut v cut once p.a	Frond density	-0.028	-3.47	**0.001**
Uncut v cut twice p.a	Frond density	-0.029	-2.46	0.014
Uncut v sprayed & cut	Frond density	-0.019	-2.83	0.005

(c) Litter depth

Comparison	Outcome measure	Regression coefficient	Z	P
Uncut v cut once p.a	cover	-0.109	-2.08	0.038
Uncut v sprayed	cover	-0.141	-2.53	0.012
Uncut v sprayed & cut	cover	-0.164	-3.14	**0.002**
Uncut v sprayed	Frond length	-0.137	-2.31	0.021
Uncut v sprayed & cut	Frond length	-0.194	-3.27	**0.001**
Uncut v cut once p.a	Frond density	-0.139	-3.22	**0.001**
Uncut v cut twice p.a	Frond density	-0.14	-2.12	0.034
Uncut v sprayed & cut	Frond density	-0.098	-2.94	0.003

(d) Species richness

Comparison	Outcome measure	Regression coefficient	Z	P
Uncut v cut once p.a	cover	0.08	3.92	**<0.001**
Uncut v cut twice p.a	cover	0.069	3.56	**<0.001**
Uncut v cut & sprayed	cover	0.06	2.48	0.013
Uncut v sprayed	cover	0.102	4.06	**<0.001**
Uncut v sprayed & cut	cover	0.106	3.58	**<0.001**
Uncut v cut once p.a	Frond length	0.07	3.83	**<0.001**
Uncut v cut & sprayed	Frond length	0.071	2.91	0.004
Uncut v sprayed	Frond length	0.09	2.82	0.005
Uncut v sprayed & cut	Frond length	0.131	4.64	**<0.001**
Uncut v cut once p.a	Frond density	0.086	2.89	0.004
Uncut v cut twice p.a	Frond density	0.109	4.43	**<0.001**
Uncut v sprayed	Frond density	0.062	4.30	**<0.001**

3.4 Discussion

The results presented here show the usefulness of the meta-analytical approach to investigating the significance of applied ecological restoration treatments in a multi-site study. Often, meta-analysis is used to compare treatment effects derived from different studies (Cooper & Hedges, 1994; Gurevitch & Hedges, 1999) with systematic reviews using meta-analysis to synthesise and summarise research findings to support evidence-based conservation (Stewart *et al.,* 2005, Tyler *et al.,* 2006, Pullin & Stewart, 2006). Formal systematic reviews have being advocated recently in an attempt to avoid the biases associated with previous ecological meta-analyses (Leimu & Koricheva, 2004; 2005). Here, the approach was used to investigate hypotheses within a series of individual experiments on different sites within the UK, which had all been run with common treatments and methodologies. The results allowed cross-site comparisons of applied treatments using a formal statistical approach. There are of course some drawbacks to this approach, one of which is the time frame over which the study effect size is derived. Here, we used a 10-year period, partly because there was 10 years of data available, but also because the results reflected a longer-term impact. As a result shorter-term success of some treatments may have been under-estimated, and this is likely in the treatments where asulam was applied because there is often a good initial effect followed by subsequent regrowth (Marrs *et al.,* 1998a).

The results from the inter-site comparison of all treatments against the untreated controls showed three important results. First, there were significant reductions in at least one *P. aquilinum* performance measure relative to untreated controls for all applied treatments on most sites. Second, there were significant differences in response between sites. Third, different responses were found for some site x treatments comparisons depending on the *P. aquilinum* measure used (frond length, frond density, frond cover). Thus, in answer to our first question, the effectiveness of *P. aquilinum* control varies spatially confirming the predictions of other workers (Pottier *et al.,* 2005).

Comparisons of all treatments at all sites revealed that cutting twice within a year was usually the most effective treatment, but there were a few site x treatment combinations where other treatments were more effective at some sites depending on the measure used. This to some extent is confusing, because where *P. aquilinum* has been cut twice/yr more effective control was obtained most of the time but at the expense of applying 20 treatments. Where other treatments were successful, a fewer number were applied (one or two), with obvious financial implications. Unfortunately, we cannot at this point predict where these treatments are likely to be superior, although the meta-regression gives some indications. Thus, the answer to our second question is that cutting twice within a year is generally the most effective treatment of those tested, but further research is required to assess when this is not the case.

We also investigated the relationship between applied treatments and a range of other *P. aquilinum* variables (rhizome mass, litter cover, litter depth) that have been shown to be important in both *P. aquilinum* control and the subsequent regeneration on semi-natural communities (Paterson *et al.,* 1997, Marrs *et al.,* 1998a). The relationship with the rhizome mass was studied because ultimately the rhizomes are the main part of the *P. aquilinum* control problems (Pottier *et al.,* 2005, Pakeman *et al.,* 1994, Pakeman & Marrs, 1996). Here there was a positive relationship between rhizome mass and the effectiveness of the cut twice/yr treatment, supporting both the hypotheses underlying questions 2 and 3. Litter variables were studied because they represent a barrier to the regeneration of new plant communities (Lowday & Marrs, 1992b, Marrs *et al.,* 2007). Our results supports the hypothesis that most site x treatment combinations reduce the depth and cover of *P. aquilinum* litter, which indicated that the sites showed some reduction in litter and hence should be more amenable to species colonization.

We also showed that there were significant positive effects of *P. aquilinum* control on species richness, which answers question 4. Here the regression coefficients are small, but they are highly significant. This is an important result because it indicates that one of the major outcomes of the *P. aquilinum* control strategy is the development of a plant community with greater plant species diversity than under dense *P. aquilinum* cover. Details of the vegetation development of these experiments has been described by Le Duc *et al.* (2006) and Cox *et al.* (2007a).

A major outcome of this study is the clear need for management experiments to be repeated in different places in order to develop evidence-based policy decisions, especially when such information is to be used to develop national guidelines and funding strategies (Sutherland *et al.,* 2004, Anon, 2005, Pullin & Stewart, 2006). Too often, management conclusions are extrapolated from a single study and our results here shown that there is considerable site variation possibly caused by differences in climatic regime, substrate, past and current management practices, which all influence the starting position before management is applied and the target community desired (Marrs *et al.,* 2000, Marrs & Watt, 2006).

There is also an obvious need to carry out further work to ascertain why *P. aquilinum* is so variable and why in some places it is difficult to control whereas in other places it is apparently less difficult (Pakeman, 2004). This is particularly important for *P. aquilinum* in view of its potential health implications for livestock (Marrs & Watt, 2006), its predicted increase under future climate change scenarios and its potential to increase in area and density as a result of lands use changes resulting from reduced stocking rates encouraged in some Agri-environments schemes (Pottier *et al.,* 2005).

Chapter 4

The effectiveness of the manufactures guidelines for Asulox application at two contrasting upland sites

4.1 Introduction

The control of bracken (*Pteridium aquilinum*) requires a long-term strategy (Lowday & Marrs, 1992a; Marrs *et al.*, 1998a) and when planning to undertake control at least a five year programme should be considered (The Southern Uplands Partnership, 2001). Dense *P. aquilinum* is a problem species for agriculture and conservation, as it is a long-lived robust clonal species (Le Duc *et al.*, 2003) that produces a dense litter layer (Frankland, 1976). It competes effectively with heathland and grassland species, at best reducing their cover but in some cases eliminating them leaving a very depauperate flora (Pakeman & Marrs, 1992). This eventually leads to impacts on seed banks which are also depauperate under bracken (Pakeman & Hay, 1996) leading to potential problems when trying to restore target vegetation post-bracken-control. One of the reasons bracken is so difficult to control is due to its extensive rhizome system (Le Duc *et al.*, 2003).

Asulam [methyl (4-aminobenzenesulphonyl) carbamate] (Asulox, Bayer CropScience) is the most widely used herbicide for *P. aquilinum* control; it is translocated into the rhizome and accumulates in both active and dormant buds, where it effects a lethal action (Veerasekaran *et al.*, 1976, 1977a,b, 1978). It has a relatively narrow spectrum (compared to general herbicides such as glyphosate) affecting mainly other ferns, docks (*Rumex* spp. Horrill *et al.*, 1978, Sheffield *et al*, 2001) and bryophytes (Rowntree *et al.*, 2003). However, asulam can also affect some fine grasses including *Holcus* spp., *Poa* spp. and *Agrostis solonifera* (Cadbury, 1976). Asulam usually produces a very good reduction in fronds the year after spraying, but there is often rapid frond recovery unless follow-up treatments are applied in subsequent years (Robinson, 1986; Lowday & Marrs, 1992a). It is well established that a single application of the herbicide is not sufficient to control bracken (Cox *et al.*, 2007a; Lowday & Marrs, 1992a; Marrs *et al.*, 1998a; Pakeman *et al.*, 1998), with fronds recovering to untreated levels seen in six to seven years (Marrs *et al.*, 1998a; Pakeman & Marrs, 1993). The current manufacturer's guidelines for asulam recommend an initial spray with asulam followed by annual spot spraying until fronds no longer appear in the spring (Anon, 2005; Robinson, 2000; The Southern Uplands Partnership, 2001). Whilst spot-treatment on a single occasion has been shown to reduce frond length, density and cover for up to three years (Cox *et al.*, 2007a), there has been no formal experimental test to support the suggestion that continuous spot-treatment has any additional benefit.

Here we test the efficacy of asulam applied using the manufacturer's recommended guidelines (MRG). We do so within two long-term experiments where bracken control and vegetation restoration treatments have been applied and monitored for 10-years (Le Duc *et al.*, 2000, 2003; Cox *et al.*, 2007a). At one site (Peak) the MRG were applied to three existing bracken control treatments where asulam had been included, and at the second site (Sourhope, Sourhope 1 in Cox *et al.*, 2007a), the MRG was applied as a split-plot treatment to all previously-applied treatments. The success of the bracken control treatments prior to 2003 are discussed in Chapter 2 here we concentrate on the effect of MRG on *P. aquilinum* variables post 2003.

4.2 Methods

4.2.1 *Experimental sites*

Work in this chapter refers to data from just two of the six experiments described in Chapter 1; Peak and Sourhope 1 (referred to as Sourhope throughout this chapter). In 2004 at Peak all plots that had previously been treated with asulam; either a single spray or in combination with a cut were sprayed again using asulam (Asulox, Bayer CropScience), with 4.4 kg ha-1 of active ingredient in 400-litres water ha^{-1} using a standard knapsack. Follow-up spot-spraying took place in the subsequent years using an AccuDos spot-sprayer at 2ml per shot at a ratio of 1:6 Asulox to water. At Sourhope the same spray methodology was applied as a sub-sub-treatment. Each sub-plot was split into two sub-sub-plots whether it had been sprayed with asulam earlier or not.

4.2.2 *Monitoring*

Monitoring continued at both sites using the methodology described in Chapter 1.

4.2.3 *Data analysis and presentation*

Data were transformed using standard procedures (Sokal & Rohlf 1995), number of fronds per quadrat using $(Y + 0.5)^{0.5}$, and individual frond length, and cover estimates using $\ln(Y + 1)$. After transformation the mean frond length per quadrat was calculated. Estimates of values per treatment combination per block were obtained by combining data per quadrat, after transformation, by sub-(sub-) plot.

Individual variables were analyzed for change through time for each site individually. As our objective was to measure the shape of response curves through time, we used repeated-measures ANOVAs with the method of polynomial contrasts (Gurevitch & Chester, 1986). This was carried out by means of PROC GLM in SAS version 8.02 (SAS, 1989). The value of this approach is that it is possible to test for treatment effects as in ANOVA, but the shape of the temporal trends of these treatment effects can also be identified. This approach becomes more useful with longer-term datasets (Le Duc *et al.*, 2007a). For each site we used the appropriate analysis of variance model. The analysis of variance model changed when new treatment combinations were added into an experiment, usually changing the design from a split-plot to a split-split-plot one; thus different segments of the time series were analyzed using different models. Time was denoted as elapsed time (ET), with the start year designated year=0.

Bonferroni correction was used to adjust for the Type I error rate (Cabin & Mitchell, 2000; Sokal & Rohlf, 1995). For August the number of comparisons at all sites was 3. With $\alpha = 0.05$ the critical probability level of 0.0167 was used to assess significance.

We concentrate on results from the late-summer August sampling, the point when *P. aquilinum* reaches maximum frond expansion, with all significant results being described. The early-summer June samples should have provided better comparison between-treatments, but this early sampling proved problematic for two reasons. First, *P. aquilinum* performance was affected by late frosts in some years, and second the staggered sampling times between-experiments would have introduced a considerable bias as sampling is occurring in the most active part of the frond expansion phase (Marrs & Watt, 2006).

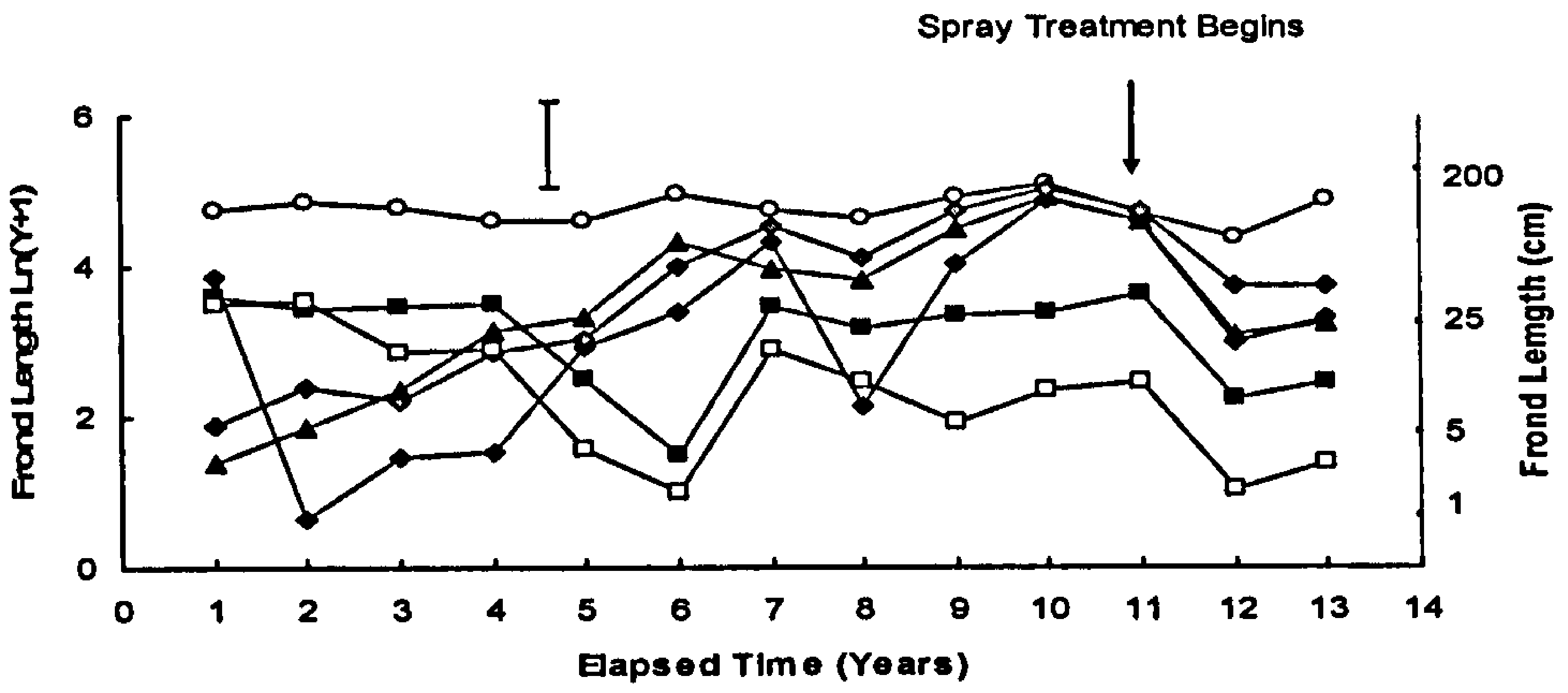
4.3 Results

4.3.1 *Applying the MRG to land previously treated with asulam (Peak)*

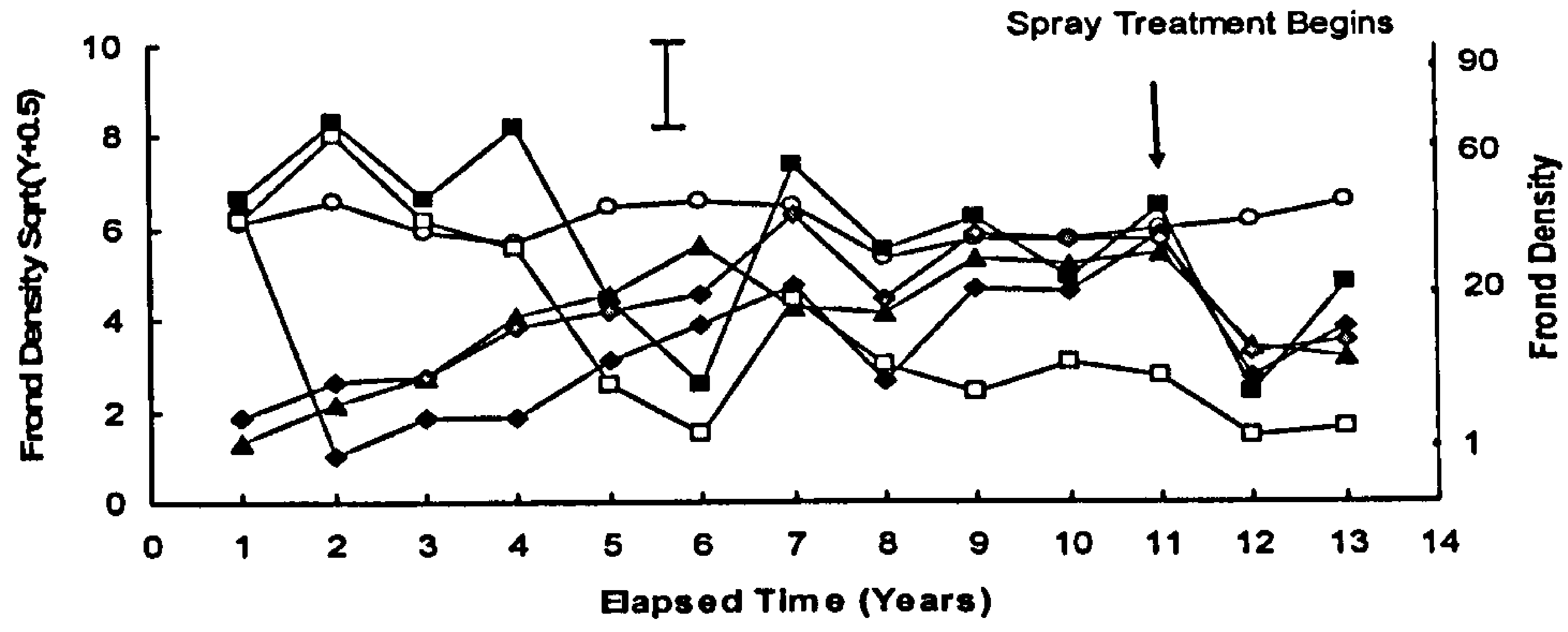
Significant bracken control treatment effects were found for all bracken response variables (Fig.1). In addition an interaction between the bracken control treatments and fencing was found to be significant over time for frond length (Fig. 2). All bracken control treatments show the same pattern for all variables, with a continued decline in the cut treatments observed with a large significant drop between

ET 10 and ET 12. All spray treatments decreased in ET 12 with the introduction of the new spraying regime in ET 10. An increase is seen in all treatments in ET 13, including the untreated control. Cutting twice per year remained the most successful treatment for all variables at this site (Fig. 1).

(a) Frond Length



(b) Frond Density



(c) *Pteridiun aquilinum* cover

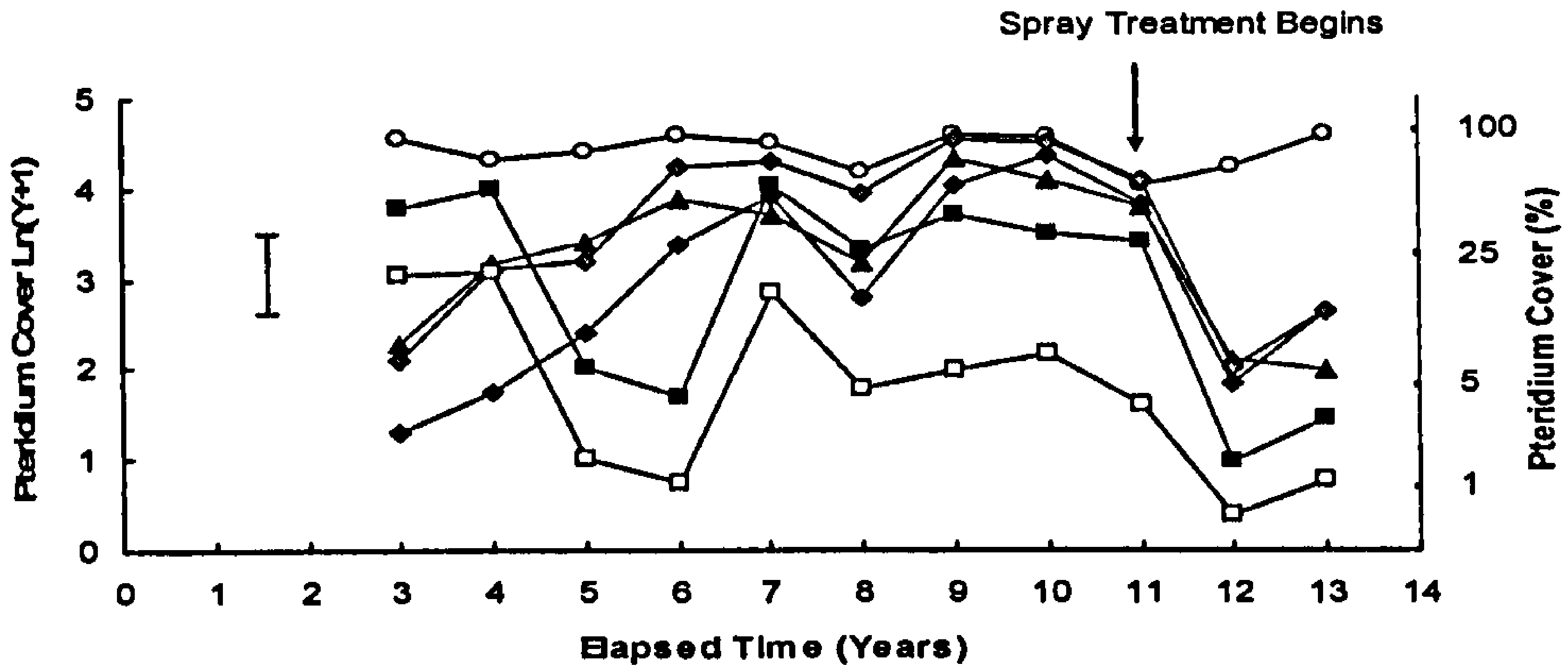
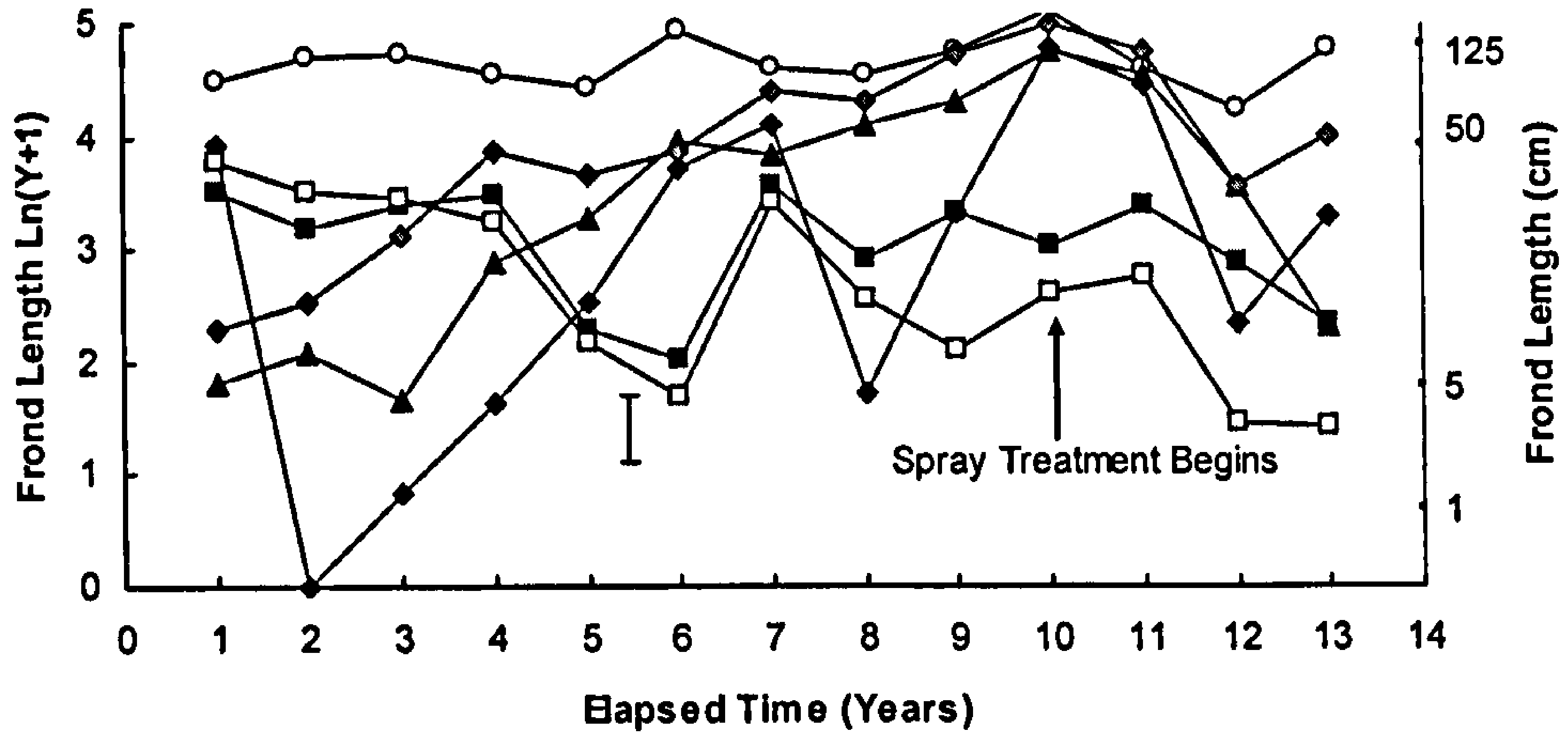


Fig. 1. The effect of bracken control treatments on (a) frond length (1st order effect, $F_{5,10}$=24 n=18); (b) frond density (1st order effect, $F_{5,10}$=26.73 n=18) and (c) cover (1st order effect, $F_{5,10}$=12.65 n=18). No treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond. Error bars are ± 2S.E.D.

The interaction between bracken control treatments and fencing, for the exclusion of sheep, showed an increase in frond length in fenced plots that are cut twice per year between ET 10 and ET13. In the unfenced plots that are grazed a decline in frond length is seen (Fig. 2). A decrease in frond length is seen in sprayed treatments although this decrease is not large enough to be significant in the fenced plots.

(a) No sub-treatment (grazed)



(b) Fencing (ungrazed)

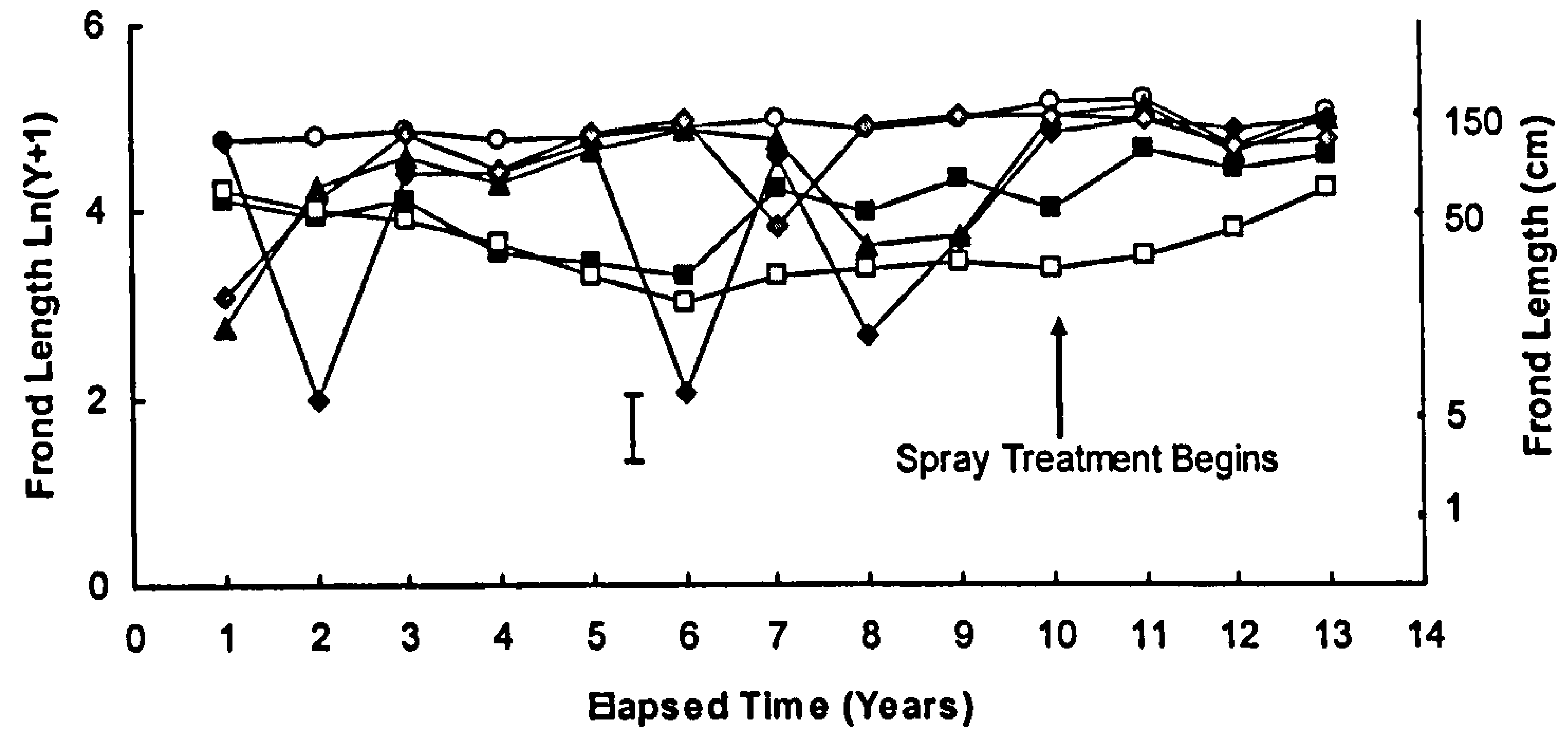


Fig. 2. The effect of bracken control treatments × fencing over time on frond length at Peak (3rd order effect, $F_{5,12}$=7.81 n=9). (a) No sub-treatment and (b) fencing. No treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond. Error bars are ± 2S.E.D.

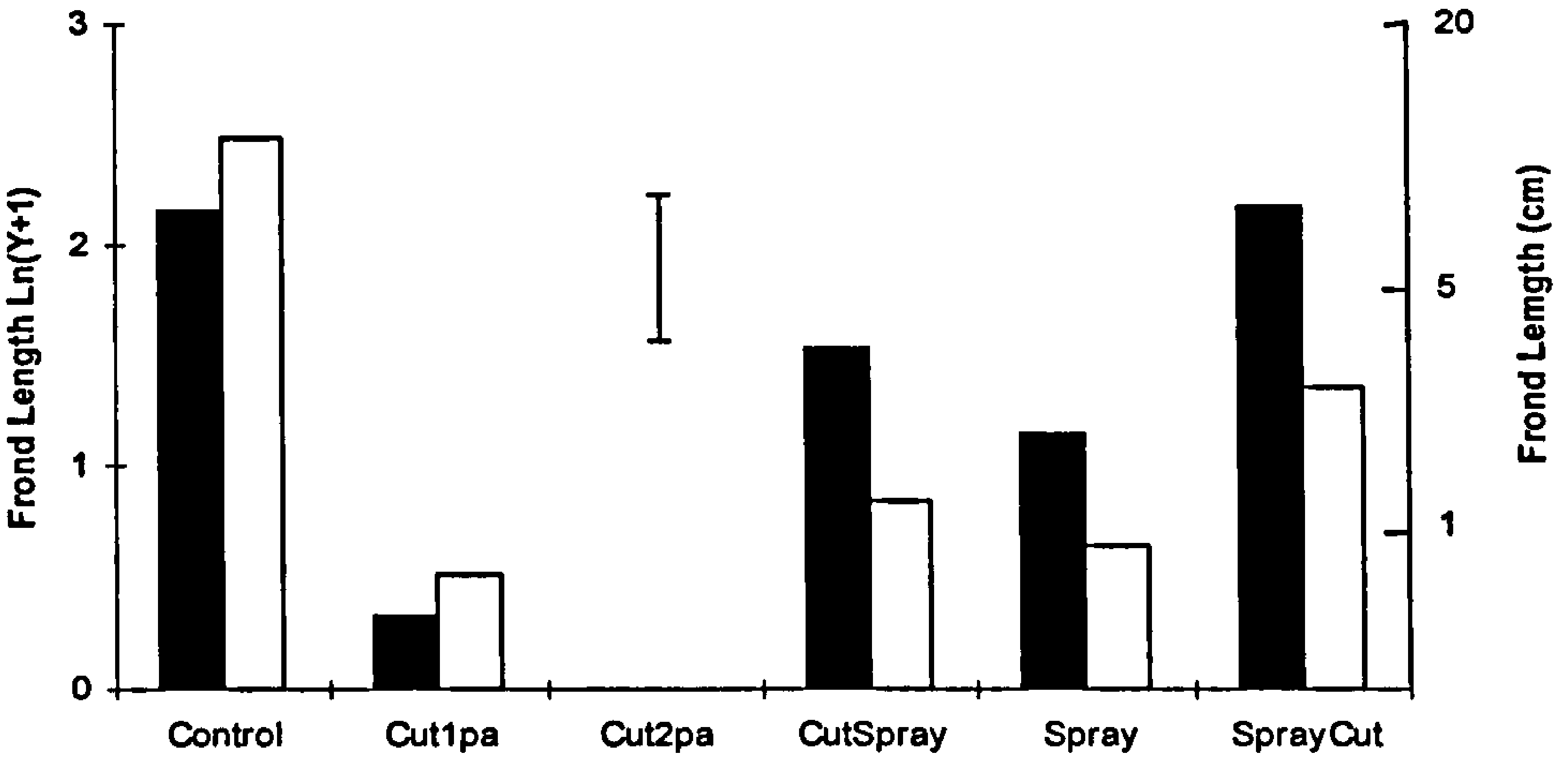
4.3.2 *Applying the MRG to land with 10 years of bracken control (Sourhope)*

Overall interactions between bracken control treatments and the spray-spot-spray sub-treatment were found for all bracken response variables (Fig. 3). Spraying with asulam with one year of follow-up spot-spray treatment significantly decreased frond length in the spray and cut combination treatments (CutSpray and SprayCut) (Fig. 3 a). With good control already established in the cut twice per year plots, no fronds were present in either year. In the untreated control and cut once per year treatment frond length increased under the new spray treatment, however, not significantly.

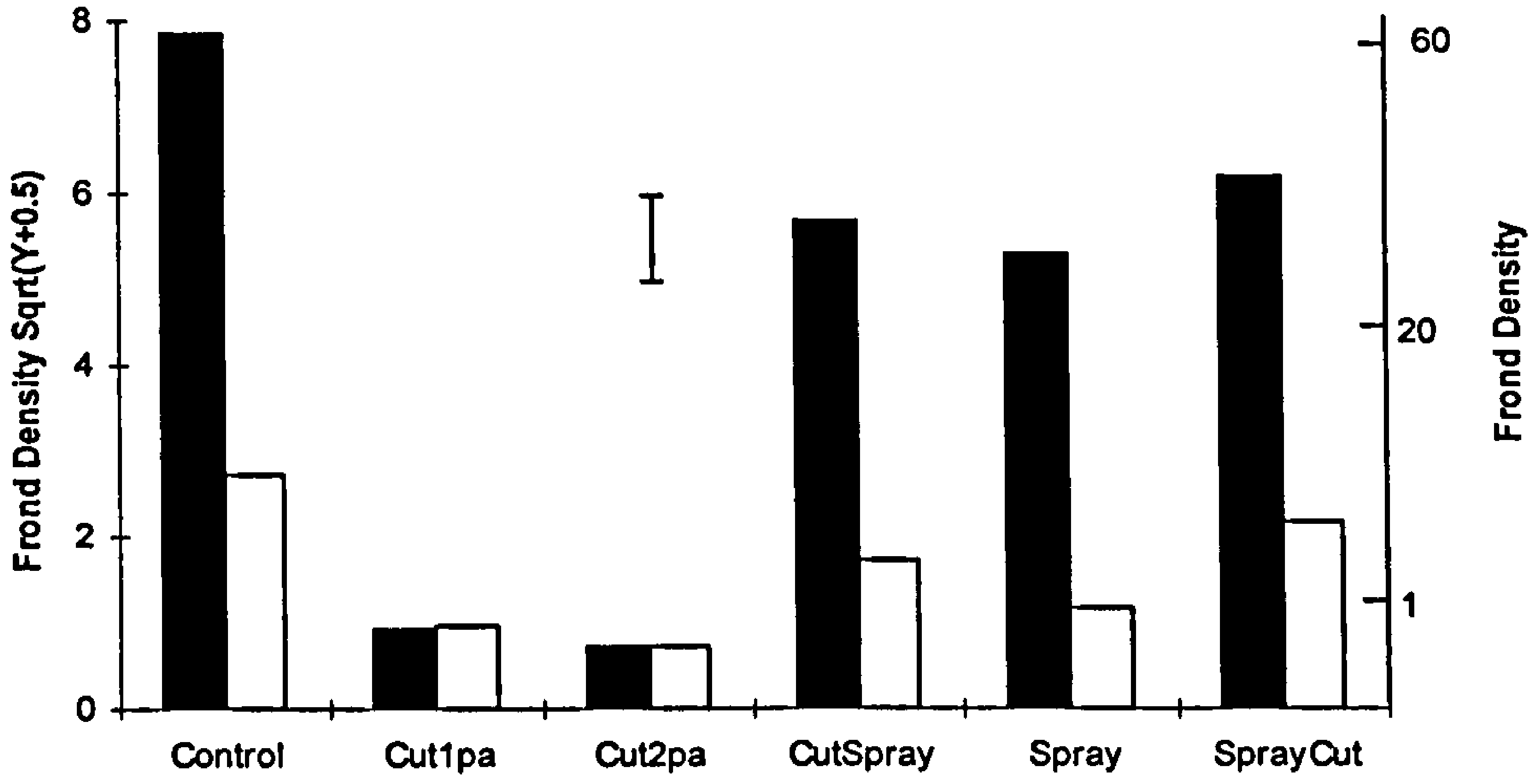
For frond density a significant reduction in the spray, spray and cut combination treatments and the untreated control was seen in the sub-plots were the new spraying regime had been applied (Fig. 3 b). No change was seen in the cut plots with already very low levels of frond density (zero for Cut2pa and <0.5 fronds m^{-2} for Cut1pa). In addition to the overall bracken control treatment effect an effect over time was found for frond density (Fig. 4). All treatments decline from ET 11 to ET 13 (with the exception of Spray in ET 12). By ET 13 the untreated control was not significantly different from the spray and spray and cut combination treatments. The most successful treatments for controlling bracken were the cutting treatments with Cut1pa and Cut2pa both having densities of zero in ET 13.

P. aquilinum cover was significantly reduced in the untreated control and SprayCut treatments; a non significant reduction was also seen in CutSpray plots (Fig. 3 c). A significant increase was seen in Spray plots. With cover in cut plots already being very low, no significant change was seen.

(a) Frond Length



(b) Frond Density



(c) Cover

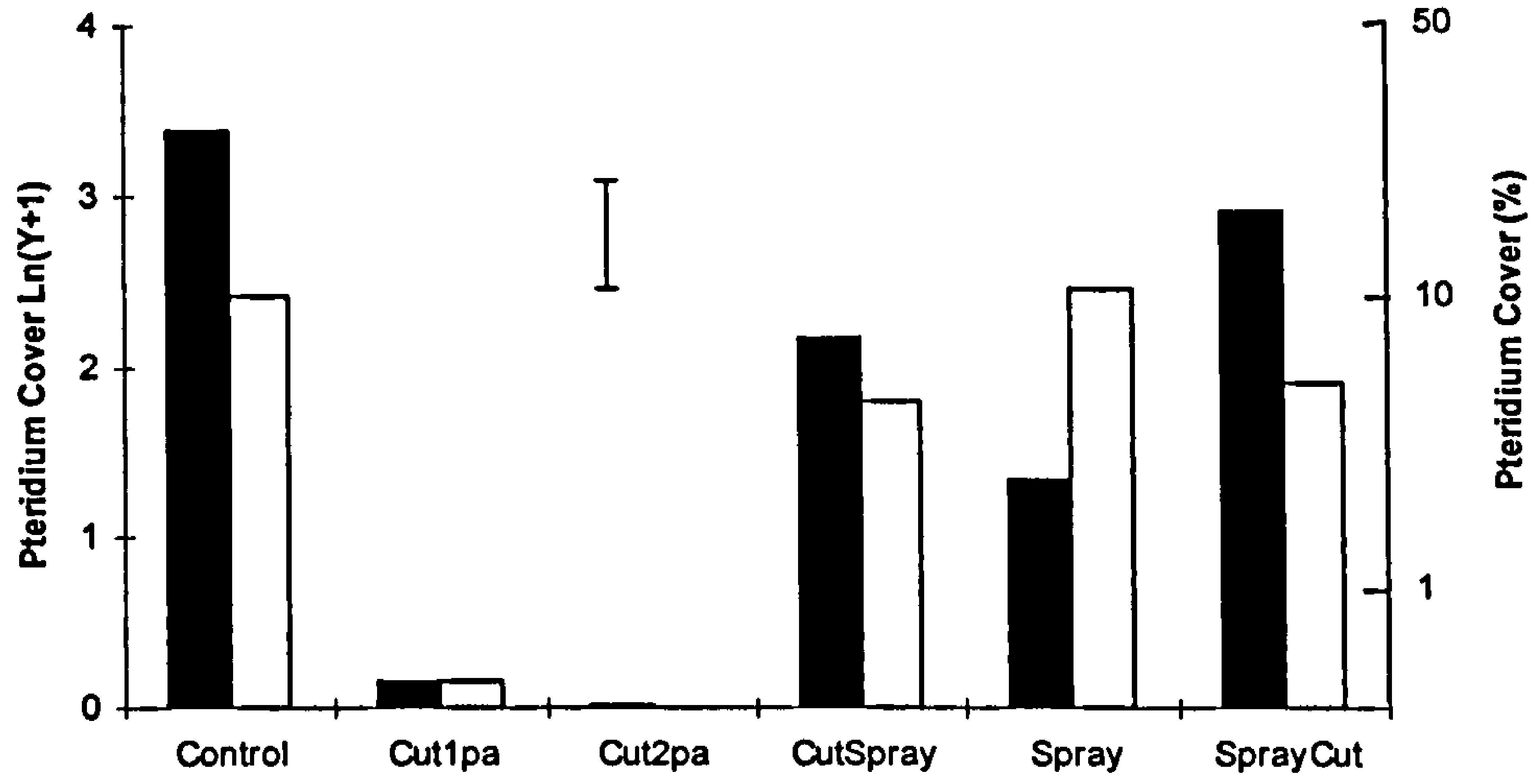


Fig. 3. The effect of bracken control treatments x spray and spot spray at Sourhope on (a) frond length (overall effect, $F_{5,12}$=17.89 n=8); (b) frond density (overall effect, $F_{5,12}$=17.74 n=8) and (c) cover (overall effect, $F_{5,12}$=16.85 n=8). Black= untreated; white= spot-sprayed. Error bars are ± 2S.E.D.

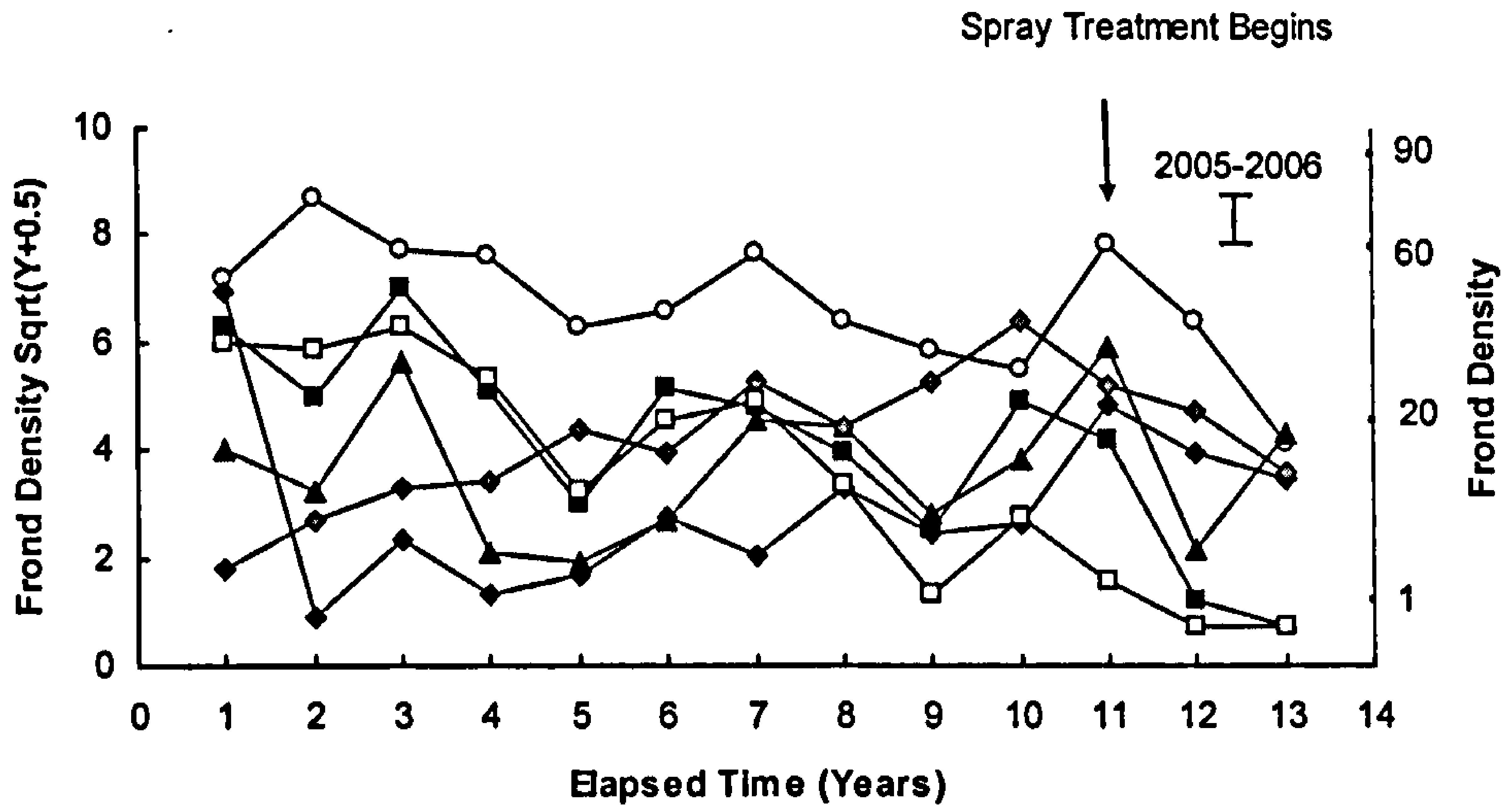


Fig. 4. The effect of bracken control treatments at Sourhope on frond density (1st order effect, $F_{5,10}$=12.95 n=8). White circle= untreated control; white square= cut twice per year; black square= cut trice per year; black triangle= sprayed with asulam; grey diamond= rolled twice per year and black diamond= rolled trice per year. Error bars are ± 2S.E.D.

4.5 Discussion

The effectiveness of the initial re-spray of asulam in 2003 essentially followed the standard pattern of response, i.e. a reduction in the frond variables measured in the year after spraying. At Peak this occurred in all three treatments re-sprayed (CutSpray, Spray and SprayCut). At Sourhope the same response was found for all treatments where bracken showed some recovery from previous treatment (CutSpray, Spray, SprayCut and the untreated control), but a much lesser response where bracken had been reduced by the two cutting treatments. In the cutting treatments at Sourhope the bracken frond performance was relatively poor with very few fronds found in sampled quadrats in 2003, and hence the effect of asulam is lessened as there is no effective target. By the final year of monitoring (2006) cutting twice per year remained the most successful treatment at both sites (Cox *et al.*, 2007a; Chapter 2), and apart from grazing at Peak other restoration treatments had no effect on bracken performance.

Unfortunately, data are only available here for one years response to the continued spot-spraying applied between 2005 and 2006; after the repeat asulam application there is no evidence of a continuing decline. In the final year of monitoring at Peak, after one year of follow-up asulam treatment, there is either a plateau or an increase in all bracken response variables. This may be caused by changes in climate resulting in general annual fluctuations (Le Duc *et al.*, 2000; Marrs *et al.*, 1998a) as a similar response is seen in the untreated and cut plots. At Sourhope, an overall decline after two years of treatment decreased all bracken response variables in all non-cut treatments, with two exceptions; frond length for the untreated control and single spray treatment for *P. aquilinum* cover. Initial patchy control could account for the two variables that increased rather than decrease (Cox *et al.*, 2007a; Pakeman *et al.*, 2005). However, the MRG suggest that this is to be expected and several years spot-spraying is needed to "eradicate" the bracken (Robinson, 2007), perhaps with up to 5-10 years treatment. It is well known that the control of bracken, even with herbicide, is long-term taking at least five years of continuous control (The Southern Uplands Partnership, 2001). Hence, further treatments and ongoing monitoring is needed to investigate this further.

At Peak the fencing to exclude grazing had a significant effect, with a greater more variable response to re-spraying with asulam found in unfenced plots and in fenced areas frond length showed no significant reduction. High levels of grazing are associated with reduced bracken litter (Le Duc *et al.*, 2007a) and can limit bracken regeneration (Pakeman *et al.*, 1997). The presence of deep litter can impede the growth of other vegetation as they struggle to grow under or penetrate the litter (Humphrey & Swaine, 1997). Although this site is only stocked at a low level (ESA prescription) the effect of sheep breaking up litter may have a significant effect on the effectiveness of treatment on frond uptake. However, grazing although beneficial to bracken control can also hinder the generation of the target species for this site, *Calluna*, as sheep are known to eat young seedlings (Putwain *et al.*, 1982). It has been suggest that creation of *Calluna* heath at this site is unrealistic with the development of *Deschampsia flexuosa* dominated acid grassland being far more likely (Le Duc *et al.*, 2007a). No other restoration treatments had any effect.

Interestingly although cutting was the most effective treatments to date and the effects appear cumulative (Cox *et al.*, 2007a), control by cutting appears to reach a point according to the "law of diminishing returns", as it appears cutting becomes increasing difficult as frond length decreases (2.96 cm at Peak with no fronds at Sourhope in the cut twice per year plots by the final year of monitoring). Mechanical cutters will miss the smallest fronds, and eradication is rarely achieved by this method (The Southern Uplands Partnership, 2001). Trying to remove these small fronds with long-handled sickles (gardener's hook) or other handheld implements is labour intensive and suitable for only very small areas (Robinson, 2007). Asulam applied by spot-sprayers should, if applied religiously without respite, be possible and allow even very small fronds to be treated. Robinson (2007) claims that a general spray followed by spot-spraying with asulam every year until fronds are no longer appear will eventually eradicate bracken from the area, although this has not been tested experimentally. Irrespective, monitoring and follow up treatments together with grazing management are essential to maintain control (Anon, 2005).

4.6 Conclusions

As expected re-spraying previously treated bracken with asulam caused a reduction in all bracken response variables at both Peak and Sourhope. Where the bracken has been controlled well by continuous cutting once or twice a year for 13 years, at Sourhope, asulam had very little impact on the few remaining fronds.

Cutting twice per year remains the most successful treatment at both sites, with fronds in the re-sprayed plots at Peak not yet being reduced to the same level as the initial single application of asulam in 1993. A greater reduction in frond length is seen in plots grazing with sheep, suggesting grazing can significantly impact bracken control.

Chapter 5

An assessment of bracken fronds after 10 years of control followed by three years recovery

5.1 Introduction

Bracken (*Pteridium aquilinum*) is a well known invasive species. It is a stronger competitor for water than *Calluna* (Gordon *et al.*, 1999) and if untreated will encroach on neighbouring *Calluna heath* (Pakeman *et al.*, 2002). It has been noted to advance onto lowland grass heath at an average rate of 43 cm per year (Watt 1954) increasing to 87 cm per year on upland *Calluna* heath treated with asulam (Pakeman *et al.*, 2002). Segments of rhizome as small as 9 cm are able to grow (Daniels, 1985).

The problems caused by bracken infestation are many and varied; the quality of grazing is reduced due to the shading out of understorey vegetation (Pakeman & Marrs, 1992), when eaten the frond can cause livestock health problems (Hopkins, 1990) and there is often a considerable reduction in conservation value especially when heath and moorland is invaded (Pakeman & Marrs, 1992). Bracken infestation can cause considerable loss of revenue for farmers in terms of the reduction in available grazing land and through additional expenses such as veterinary fees and control costs (Varvarigos & Lawton, 1991).

Bracken control is carried out for a wide range of reasons including; increasing agricultural production, protecting or enhancing biodiversity, improved recreational access, reinstatement of habitat for game species and forestry planting (Pakeman *et al.*, 2000). The control of bracken is a long-term one (Lowday and Marrs, 1992a; Marrs *et al.*, 1998a) and at least a five year programme should be considered (The Southern Upland Partnership, 2001). Restoration after bracken control can be slow and variable (Le Duc *et al.*, 2000), with abiotic factors such as increased nitrogen deposition and biotic factors such as impoverished seed banks (Bakker & Berendse, 1999) constraining the development of desired post-bracken-control vegetation. Re-invasion in even well controlled bracken is often likely (Pakeman *et al.*, 2005). There are two main strategies that are generally used to control bracken; these are either mechanical control or herbicidal control (Lowday & Marrs, 1992a). In the year after spraying with asulam an initial rapid reduction in bracken response variables is often seen, whereas mechanical control such as cutting once or twice a year has a more gradual effect with increasing impact over time (Le Duc *et al.*, 2000). Recovery to untreated levels, after a single application of asulam, has been found to take six to seven years (Pakeman & Marrs, 1993; Marrs *et al.*, 1998a). Recovery of the bracken after treatment appears to be variable from site to site, and this is probably related to many factors, including local micro-climate, mass of rhizomes present and the competitiveness of the vegetation present (Pakeman *et al.*, 2005). Rapid recovery for bracken cut once per year for six years has been noted by Marrs *et al.* (1998a), whereas cutting twice per year produced a more effective control (Le Duc *et al.*, 2000; Cox *et al.*, 2007a), and a slower recovery (Marrs *et al.*, 1998a).

The objective of this study is to assess the response of bracken fronds to 10 years of control at three contrasting sites followed by three years recovery, with the aim of measuring the rate of recovery in bracken fronds. The success of the control treatments is not discussed here (Cox *et al.*, 2007a; Chapter 2) but the most successful treatments at each site after 10 years of control are summarised in Table 1.

Table 1. The most effective treatment for reducing bracken frond variables in the final year of treatment (ET 10). Cut1pa= cut once per year; Cut2pa= cut twice per year; CutSpray= cut the first year (ET0) then sprayed with asulam in the second (ET2).

		Site		
Treatment	**Bracken Measure**	**Cannock**	**Carneddau**	**Sourhope**
Bracken Control	*P. aquilinum* Cover	Cut2pa	Cut2pa	Cut1pa/ Cut2pa
	Frond Length	Cut2pa	Cut2pa	Cut1pa
	Frond Density	CutSpray	Cut2pa	Cut2pa
Grass Seeding	Frond Length			Grass Seeding
Spot Spraying	Frond Density		Spot Spray	
Seed x Spot Spray	Frond Length		No treatment, Spot Spray	
Bracken Control x Spot Spray	*P. aquilinum* Cover		Cut2pa, Spot Spray	

5.2 Methods

5.2.1 *Experimental sites*

This chapter reports results from three of the six experiments described in Chapter 1; Cannock 1, Carneddau and Sourhope 2. Sites are referred to hereafter as Cannock, Carneddau and Sourhope.

5.2.2 *Treatments*

All treatments, control and restoration were stopped in 2003 and the regeneration post-bracken control observed.

5.2.3 *Monitoring*

All experiments continued to be monitored using the same methodology described in Chapter 1.

5.2.5 *Data analysis and presentation*

Data were transformed using standard procedures (Sokal & Rohlf, 1995), number of fronds per quadrat using $(Y + 0.5)^{0.5}$, and individual frond length, and cover estimates using $\ln(Y + 1)$. After transformation the mean frond length per quadrat was calculated. Estimates of values per treatment combination per block were obtained by combining data per quadrat after transformation by sub- (sub-) plot.

Individual variables were analyzed for change through time for each site individually. As our objective was to measure the shape of response curves through time, we used repeated-measures ANOVAs with the method of polynomial contrasts (Gurevitch & Chester, 1986). This was carried out by means of PROC GLM in SAS version 8.02 (SAS, 1989). The value of this approach is that it is possible to test for treatment effects as in ANOVA, but the shape of the temporal trends of these treatment effects can also be identified. This approach becomes more useful with longer-term datasets (Le Duc *et al.*, 2007a). For each site we used the appropriate analysis of variance model. The analysis of variance model changed when new treatment combinations were added into an experiment, usually changing the design from a split-plot to a split-split-plot one; thus different segments of the time series were analyzed using different models. Time was denoted as elapsed time (ET), with the start year designated year=0.

Bonferroni correction was used to adjust for the Type I error rate (Cabin & Mitchell, 2000; Sokal & Rohlf, 1995). For August, the number of comparisons at all sites was 3. With $\alpha = 0.05$ the critical probability level of 0.0167 was used to assess significance.

Here we concentrate on results from the late-summer August sampling when *P. aquilinum* has reached maximum frond expansion, with all significant results being described as a comparison to previous analysis (Cox *et al.*, 2007a).

5.3 Results

The aim of this study was to measure the rates of bracken recovery after release from treatment over a three year period at three contrasting sites. This was achieved by considering three *P. aquilinum* frond variables (mean frond length, frond density and cover).

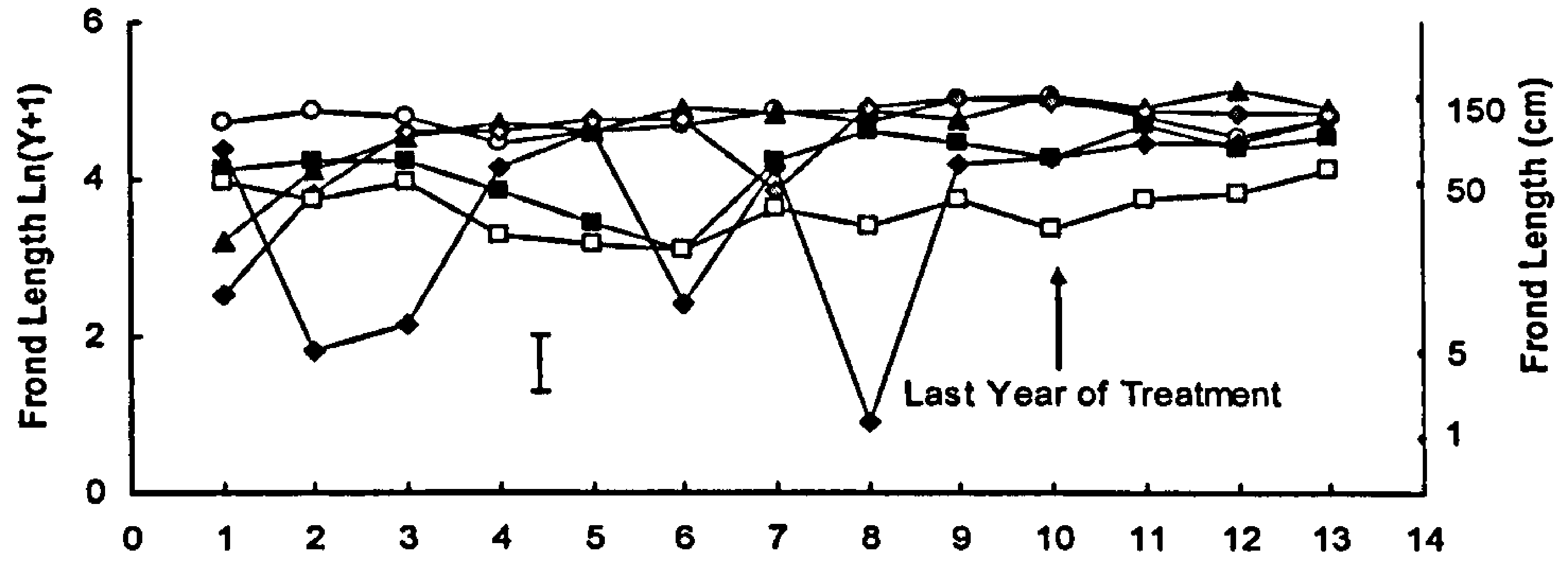
5.3.1 *The heathland site (Cannock)*

The interaction between bracken control treatments and restoration treatments was significant at Cannock for frond length (Fig.1). The main effects were caused by treatments designed to control bracken, the interacting effects of the three vegetation restoration treatments (untreated, fertilizer addition, surface disturbance) produced different effects in different years (e.g. ET 6 and 8 in the CutSpray treatment). In the final year of bracken control treatment (ET 10), the Cut2pa treatment was the most successful at reducing frond length, however, there was a general increase towards the untreated values after treatment stops. In ET 13, after three years of recovery, Cut2pa plots still have the lowest frond length although this is no longer a significant difference from the untreated plots.

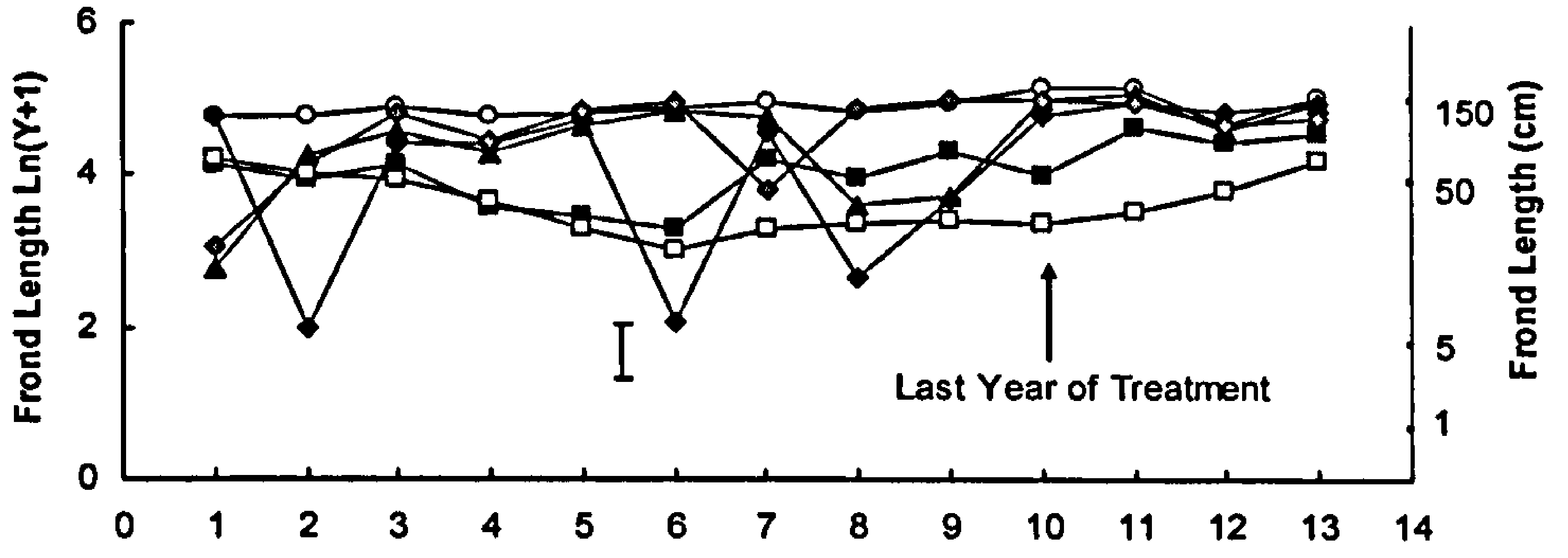
Similarly, there were significant effects of the bracken control treatments on frond density and frond cover. The Cut1pa and Cut2pa treatments were least effective at reducing frond density, indeed densities were often increased (Fig.2 a), and all other control other treatments showed no significant difference from the untreated control. Frond density was reduced in cut treatments between ET 8 and ET 11, however, once treatment stops this trend is reversed and density again increases significantly.

P. aquilinum cover (Fig. 2 b) showed a general decline in cut twice per year plots until ca. ET 8 but there was an increase between years 10 and 13 for most treatments, with no significant difference between the untreated controls and most bracken control treatments in year ET. The exception was plots that were sprayed in ET0 and then cut in the following year. Here frond cover is significantly lower than the untreated control in ET 13 and ET 11, although no significant difference was observed in any other year.

(a) No Sub-treatment



(b) Fertilizer



(c) Fertilizer and harrowing

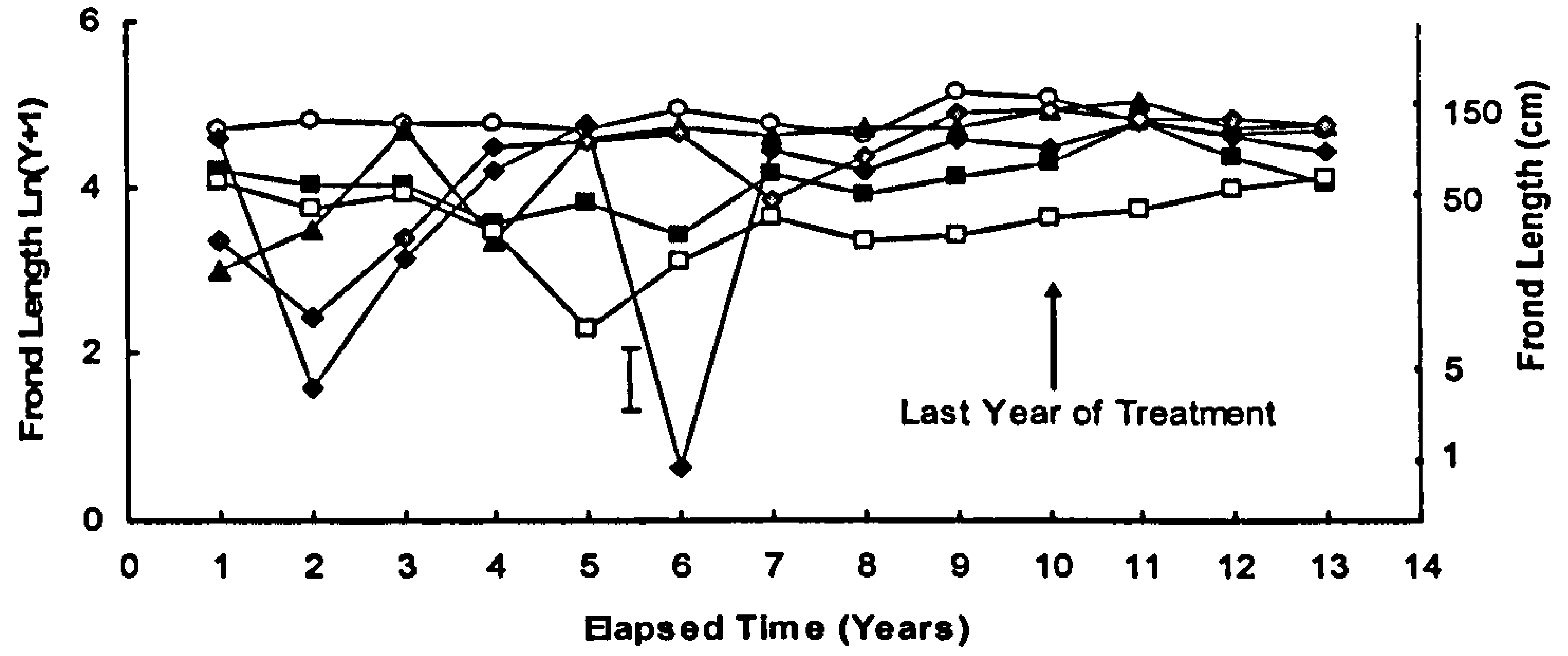
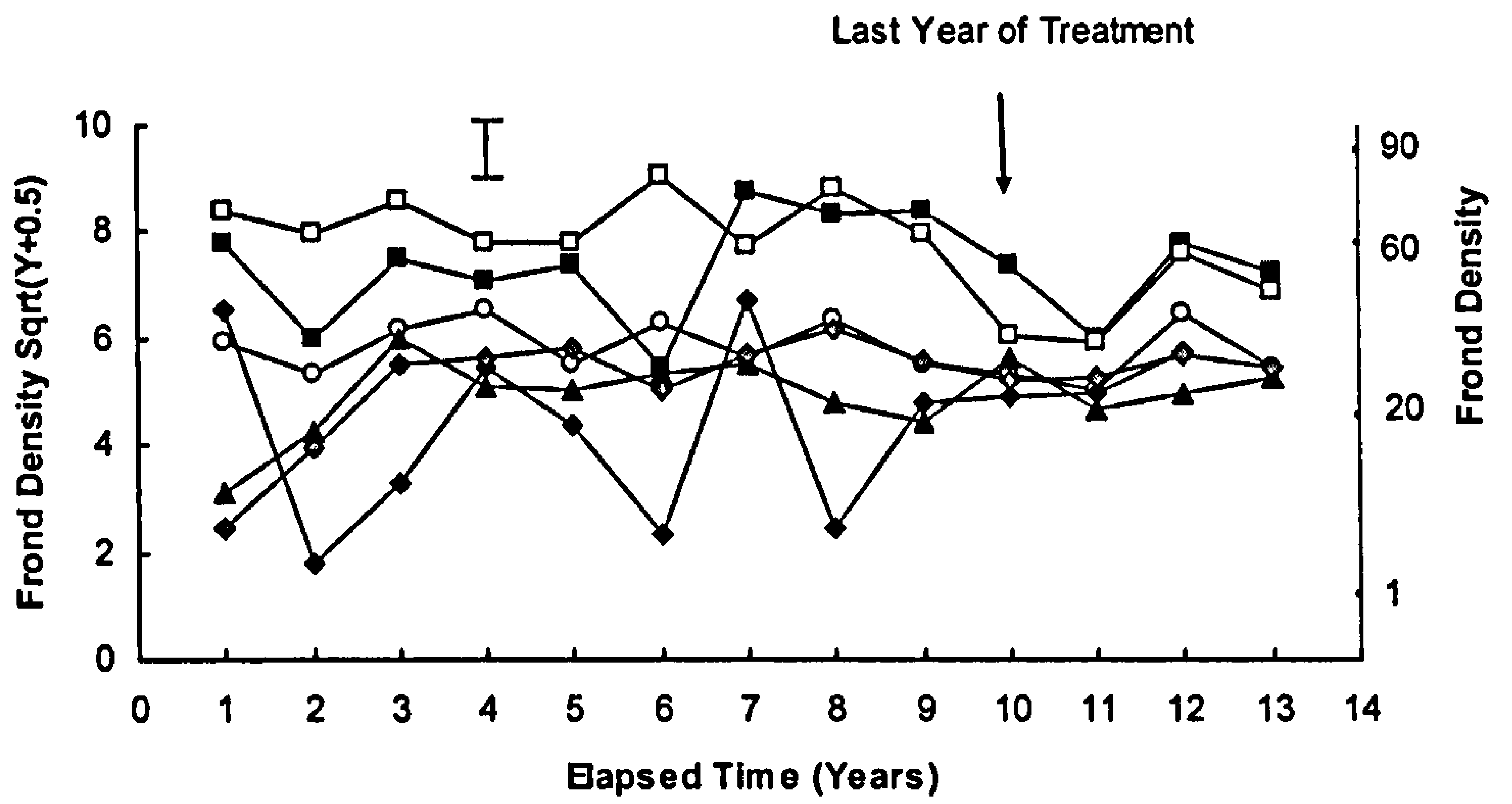


Fig. 1. The effect of bracken control treatments on frond length at Cannock (a) no sub-treatment; b) fertilizer and (c) fertilizer and harrowing (7th order effect, $F_{10,12}$=4.31 n=2). No treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond. Error bars are ± 2S.E.D.

(a) Frond density



(b) *Pteridium aquilinum* cover

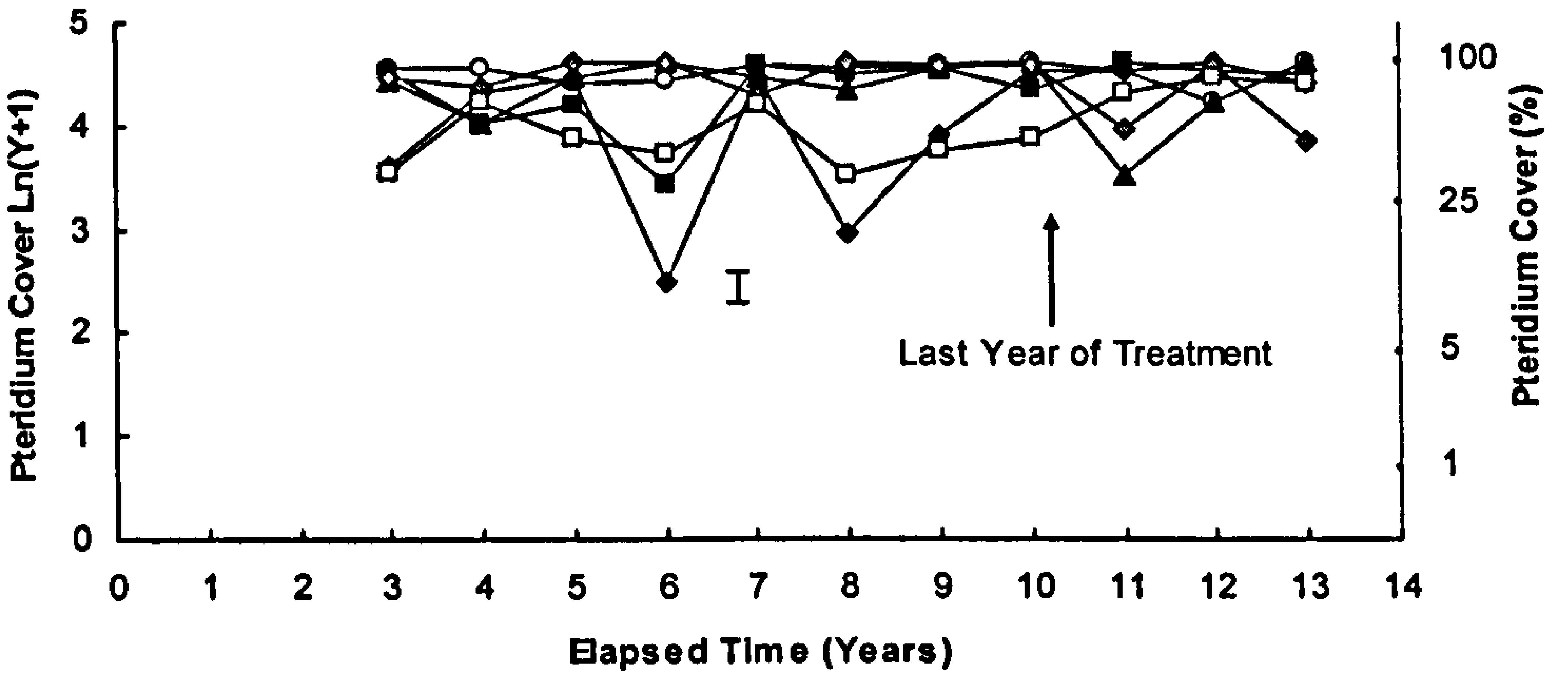
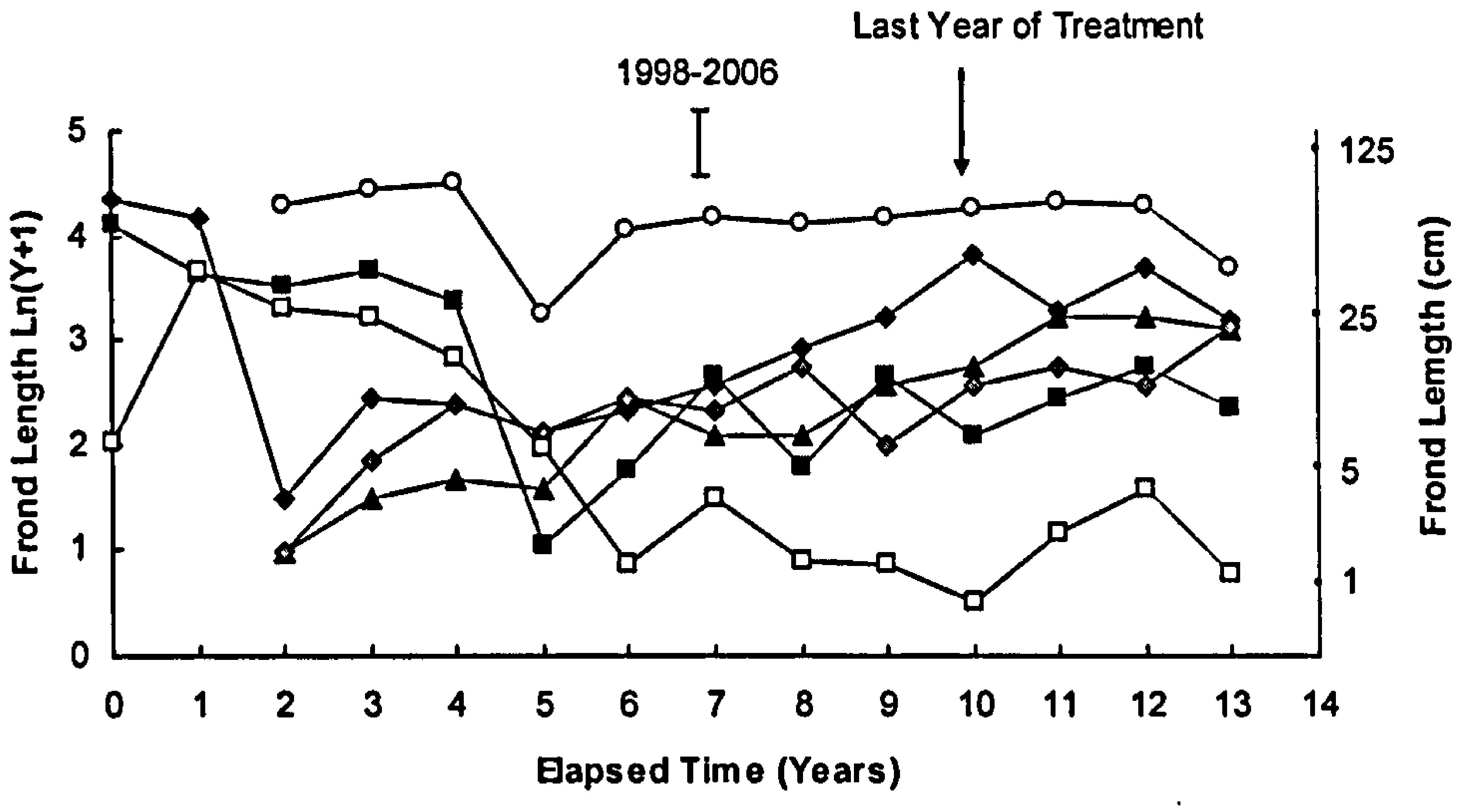


Fig. 2. The effect of bracken control treatments at Cannock on; (a) frond density (1st order effect, $F_{5,5}$=12.64 n=6) and (b) *P. aquilinum* cover (4th order effect, $F_{5,5}$=11.13 n=6). No treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond. Error bars are ± 2S.E.D.

5.3.2 *The acid grassland sites (Carneddau & Sourhope)*

At both the acid grassland site, Carneddau and Sourhope, significant bracken control treatment effects were seen for frond length (Fig. 3). Both sites show the same trend, with cutting twice per year being the most successful treatment in the last year of treatment (ET 10). When control ceases there was a steady increase towards untreated levels over the next three years. At both the sites, the cutting treatments remain significantly below the untreated plots. There is a dip in ET 13 for Cut2pa at Carneddau but this decline is also seen in other treatments, including the control, and at other sites (Sourhope, Fig.3 b).

(a) Carneddau



(b) Sourhope

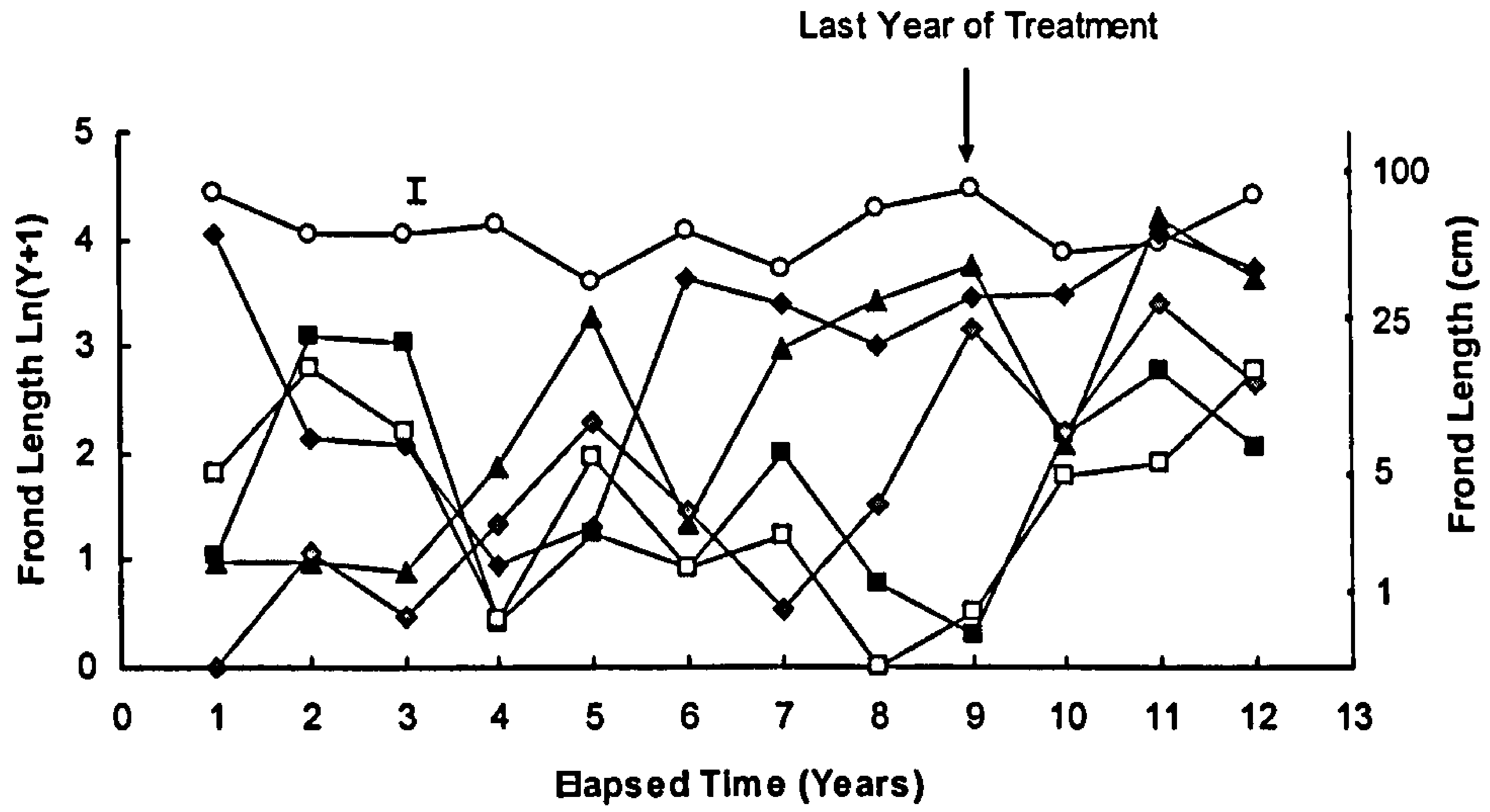


Fig.3. The effect of bracken control treatments on frond length (a) at Carneddau (6th order effect, $F_{5,5}$=10.42 n=18); (b) at Sourhope (2nd order effect, $F_{5,5}$=63.9 n=4). No treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond. Error bars are ± 2S.E.D.

At Carneddau, a significant overall bracken control treatment × spot-spray (sub-sub-treatment) interaction (Fig. 4 a) was found for frond density in addition to the significant main treatment interaction over time (Fig. 4 b). The bracken control treatment × spot-spray interaction shows that on average spot-spraying in 1998 reduced frond density in all treatments. The significant bracken control treatment effect showed a reduction in frond density in all treated plots compared to the untreated control, with the cutting treatments having the greatest effect. By the final year of monitoring (ET 13) cutting twice per year had the lowest frond density, with some increase seen in ET 11 and 12 once treatment had stopped, although a dip is seen in ET 13. This dip appears to be a general trend in all treatments in this year.

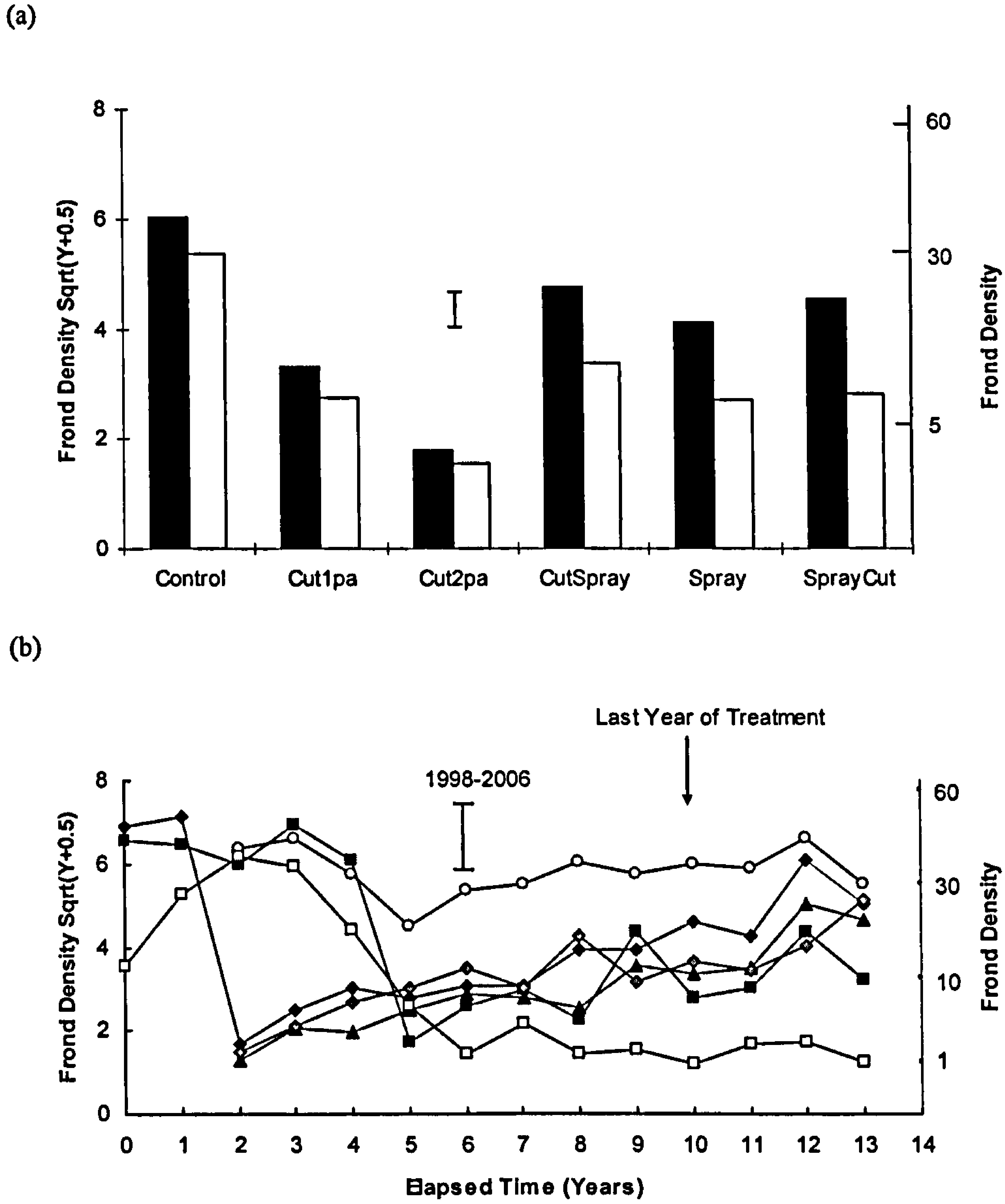


Fig.4. The effects of bracken control treatments on frond density at Carneddau; (a) overall interaction between main treatment and sub-sub-treatment (overall effect, $F_{5,36}$=3.63 n=81). Black bar= no sub-sub-treatment. (b) Main treatment effect (1^{st} order effect, $F_{5,10}$=5.21 n=18). No treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond. Error bars are ± 2S.E.D.

The significant bracken control effect on frond density was also found at Sourhope (Fig. 5) with an increase in cutting treatments since treatment stopped in ET 9, although all treatments still have significantly lower frond density than the untreated control in the final year of monitoring (ET 12).

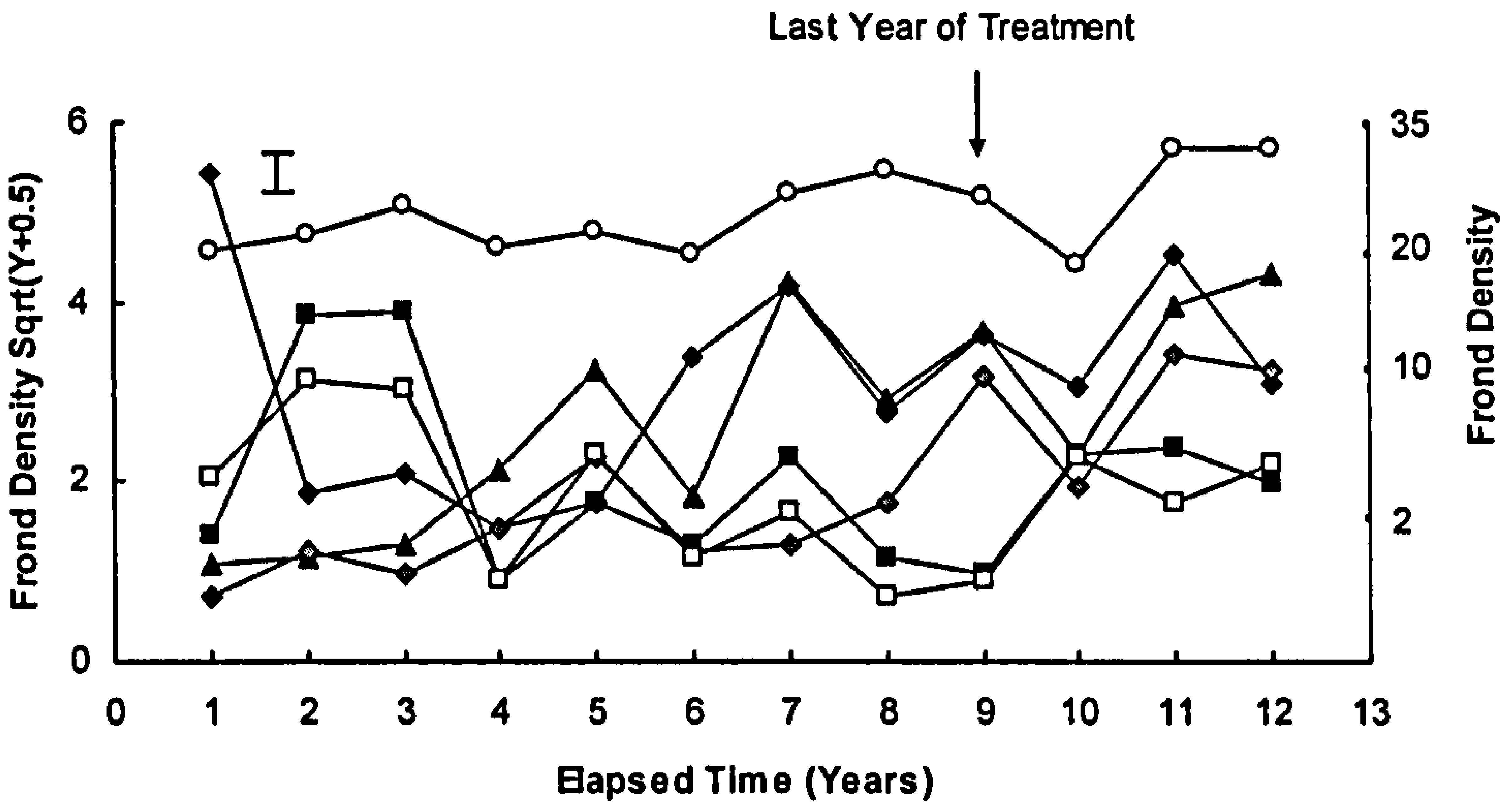
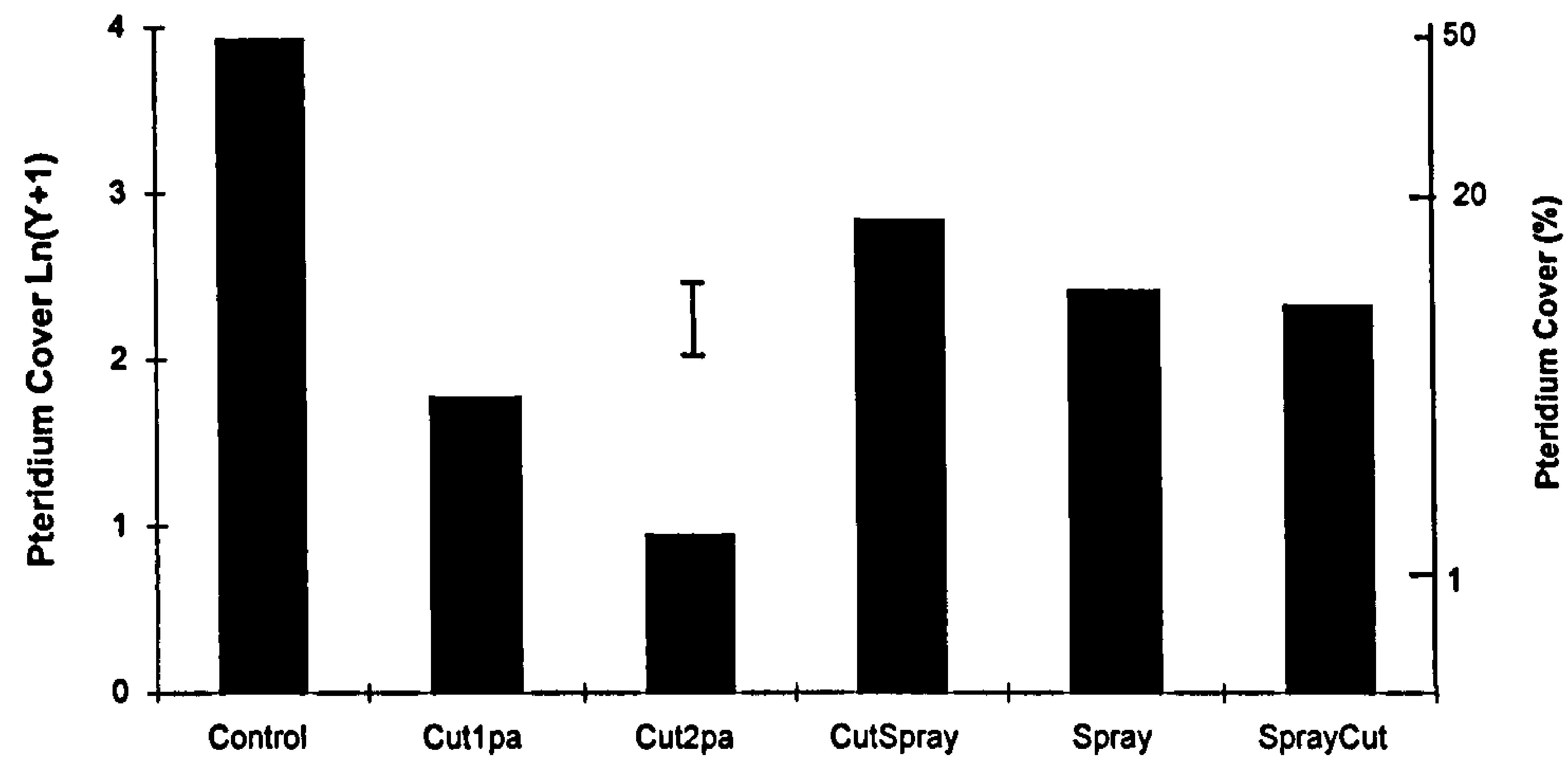


Fig. 5. The effects of bracken control treatments on frond density at Sourhope; 1st order effect, $F_{5,5}$=16.39 n=4. No treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond. Error bars are ± 2S.E.D.

At Carneddau, only an overall effect was found on *P. aquilinum* cover (Fig. 6 a), which showed a reduction in all bracken control treatments, with cutting twice per year being the most successful. At Sourhope, an increase in cover in both cutting treatments from ET 9 can be seen (Fig. 6 b) although *P. aquilinum* cover is still significantly lower in these plots compared to the untreated control in the final year of monitoring (ET 12).

(a) Carneddau



(b) Sourhope

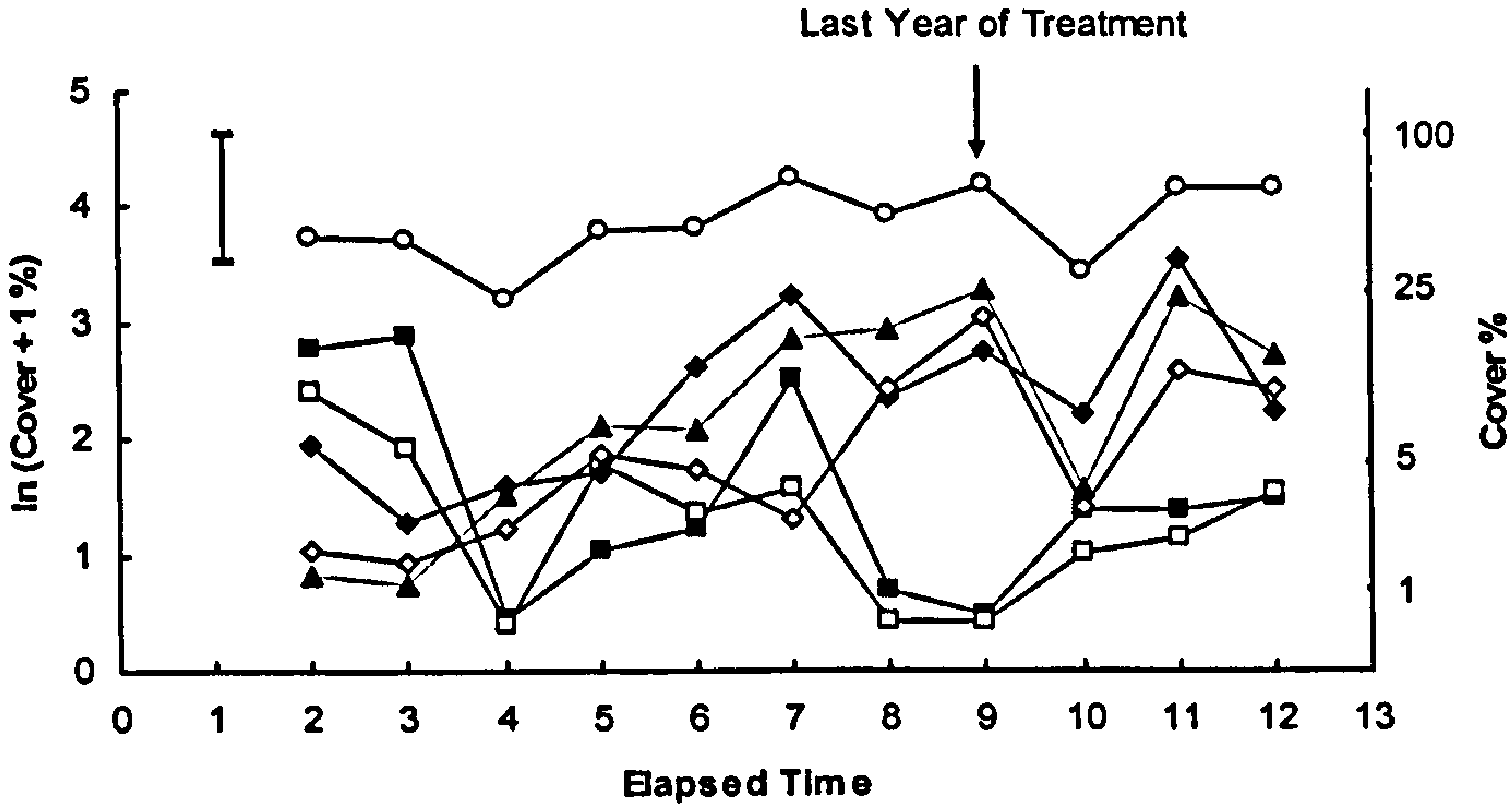


Fig. 6. The effects of bracken control treatments on *P.aquilinum* cover at; (a) Carneddau (overall effect, $F_{5,10}$=41.07 n=162) and (b) Sourhope (1st order effect, $F_{5,5}$=12.51 n=4). No treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond. Error bars are ± 2S.E.D.

5.4 Discussion

The sites tested reflected a range of vegetation types where bracken has invaded and are typical of the range of situations where bracken is controlled in the UK. At all sites long-term experiments testing five bracken control treatments have been compared. In addition at each site, there were site-independent vegetation restoration treatments. After 9 or 10 years these combined treatments have provided vegetation with variably suppressed bracken (Cox *et al.*, 2007a; Chapter 2). The variability in the degree of bracken control may reflect the initial site conditions with Cannock having the greatest rhizome biomass resulting in the largest *P. aquilinum* cover, bracken litter cover and depth. In the final year of treatment cutting either once or twice per year was the most successful at reducing frond variables at all sites. The only exception is frond density at Cannock where cut in the first year followed by spray with asulam in the second is best.

Here we investigated the response after the bracken was released from the control treatments.

5.4.1 *Recovery from 10 years of continuous cutting*

The recovery rate of bracken frond variables from the cutting treatments appears to be directly related to the degree of control (Marrs *et al.*, 1998a). Rapid recovery is seen at Cannock after the cutting treatments have stopped (Table 2), suggesting that cutting, even twice a year for 10 years did not effectively control the bracken. Out of the three bracken response variables, only frond length had been significantly reduced by the final year of bracken control treatments (2003). The initial reduction in frond variables is much better at the acid grassland sites (Carneddau and Sourhope) which have a much lower untreated mean cover and length. At Cannock *P. aquilinum* cover was only reduced to 47 % in comparison to 1% at the acid grassland sites and untreated means of 50 and 47% at Carneddau and Sourhope respectively.

The effect of cutting on frond density is well known (Lowday & Marrs, 1992a) with relatively slow reductions in frond measures, especially for frond density, which often shows an initial increase followed by a decline. This decline did not occur at Cannock until after seven years of continuous cutting and did not decline to below that of the untreated control or spray treatments at any point; this poor control might explain the rapid recovery after release. In comparison, frond density at Carneddau and Sourhope reached a peak in the third year of treatment before declining rapidly.

At Carneddau and Sourhope, after three years of recovery, all frond variables remained significantly lower in both the cutting treatments. A rapid recovery from a small base was seen at Sourhope, and a slower recovery is seen at Carneddau (Table 2). If frond length continues to recover at the same rate at Sourhope (1.12 cm year^{-1}) it will take five years from the last year of treatment to reach the same length as untreated fronds. At Carneddau this would take 44 years at a rate of 0.09 cm year^{-1}. The much slower recovery seen at Carneddau reflects results found by Marrs *et al.* (1998a) where a very slow recovery for frond biomass in plots cut twice per year for six years was observed. Frond recovery may be slower at Carneddau due to the much higher levels of grazing at this site compared to Sourhope.

Moderate grazing has been reported to reduce *P. aquilinum* cover (Pakeman *et al.*, 1997; Williams, 1980).

Table 2. The difference between Cover (%), frond length (cm) and frond density (fronds m^{-2}) in cut twice per year (Cut2pa) plots after 10 years of continuous treatment and with three years of recovery, compared to the mean untreated control plots. Back-transformed means are presented with transformed means in parenthesis ± SE.

Site	**Variable**	**Mean Control**	**Last Year of Treatment (Et 10)**	**Last Year of Sampling (Et 13)**	**Trend**
Cannock	Cover (%)	**90.54** (4.52± 0.34)	**47.34** (3.88± 0.56)	**84.05** (4.44± 0.41)	Increase
	Length (cm)	**123.03** (4.82± 0.38)	**30.69** (3.46± 0.57)	**62.83** (4.16± 0.40)	Increase
	Density (fronds m^{-2})	**33.30** (5.81± 0.70)	**36.08** (6.05± 0.99)	**46.67** (6.87± 1.17)	Increase
Carneddau	Cover (%)	**50.08** (3.93± 0.65)	**1.43** (0.89± 1.01)	**0.83** (0.61± 1.03)	Decrease
	Length (cm)	**60.84** (4.12± 0.59)	**0.66** (0.51± 1.09)	**1.14** (0.76± 1.21)	Increase
	Density (fronds m^{-2})	**33.52** (5.83± 0.76)	**0.96** (1.21± 1.12)	**0.99** (1.22± 1.14)	Increase
Sourhope	Cover (%)	**46.49** (5.00± 0.68)	**0.54** (0.43± 0.93)	**3.74** (1.56± 0.58)	Increase
	Length (cm)	**58.80** (4.09± 0.53)	**0.67** (0.51± 1.01)	**14.96** (2.77± 1.18)	Increase
	Density (fronds m^{-2})	**46.49** (3.86± 0.58)	**0.28** (0.88± 0.59)	**4.28** (2.18± 0.83)	Increase

5.4.2 *Recovery after spraying with asulam in 1993 or 1994 and combination treatments*

The varying rate of *P. aquilinum* recovery after asulam treatment may be due to small differences in initial treatment success (Williams, 1980). After a single application of asulam Marrs *et al.* (1998a) found recovery took roughly six years, with Pakeman & Marrs (1993) suggesting seven years. At Cannock it took around 10 years for recovery and 13 years plus at Carneddau and Sourhope.

Varying recovery rates for bracken control by cutting or by asulam may be due to the degree of bracken control. Although vegetation type may be a factor, *Calluna* heath was the target vegetation for Cannock, whereas Carneddau and Sourhope are acid grassland sites with higher species richness, lower *P. aquilinum* cover, smaller litter depth, litter cover and rhizome mass. Impoverished seed banks are known to hinder restoration of heath and grassland (Bakker & Berendse, 1999), with seed for grassland species tends to be relatively short-lived in comparison to heath land species (Bossuyt & Hermy, 2003). Thus age of the stand and existing understorey vegetation would also influence control and recovery.

Inter-regional variation could also be due to broad climate differences (Le Duc *et al.*, 2000) or other untested biotic factors.

Pakeman *et al.* (2005) observed two trajectories for recovery after asulam treatment relating to grazing pressure; (1) the dominance of *Vaccinium myrtillus* where grazing is low and *V.myrtillus* is already present under the bracken or (2) a mix of mosses dominated by *Campylopus introflexus* and grasses especially *Deschampsia flexuosa* and *Rumex acetosella*. Both Carneddau and Sourhope are grazed by sheep, with the levels of grazing at Carneddau being high enough to cause habitat degradation to the surrounding *Vaccinium* heath (Brittion *et al.*, 2005).

5.5 Conclusions

The rate of recovery is dependent of the initial degree of control, which presumably reflects the starting rhizome biomass of the bracken, which produces a frond density and *P. aquilinum* cover significantly higher or comparable to the untreated control at Cannock in the final year of monitoring. A very quick recovery from well-controlled bracken is seen at Sourhope, while a much slower recovery from equally well-controlled bracken is seen at Carneddau. The difference in recovery rates may be due to grazing pressure which is considerably higher at Carneddau, broad climatic variation or untested biotic factors.

Chapter 6

The effectiveness of bruising as a method for bracken control

6.1 Introduction

There are two main strategies that are generally used to control *Pteridium aquilinum*; these are either mechanical control or herbicidal control (Lowday & Marrs, 1992a). Mechanical control is normally by cutting. Fronds are cut during early summer, before and up to the point of maximum frond expansion, with the aim of withdrawing the maximum amount of carbohydrates and nutrients from the rhizome reserves (Hunter, 1953; Williams & Foley, 1976). When this strategy is used it is advisable to cut the fronds before the new assimilates start being translocated from the fronds to the rhizomes in large amounts (late July/early August in Britain) (Williams & Foley, 1976). Cutting can be carried out one, two or three times annually (Braid, 1959; Williams, 1980). This strategy also has important benefits in that it breaks up and fragments the litter layer, hence assisting other species to colonize (Lowday & Marrs, 1992b).

For herbicidal control, asulam [methyl (4-aminobenzenesulphonyl) carbamate] is the most widely used herbicide; it is translocated into the rhizome and accumulates in both active and dormant buds, where it effects a lethal action (Veerasekaran *et al.*, 1976, 1977a,b, 1978). Asulam frequently produces a very good reduction in fronds in the year after spraying, but there is often rapid frond recovery unless other treatments are applied in subsequent years (Lowday & Marrs, 1992a; Robinson, 1986). Herbicide action has a limited impact of bracken litter (Marrs *et al.*, 2007) and is unlikely to have a direct effect on the amount of rhizome carbohydrate reserves in the short term, and herbicides which attack frond buds on the rhizome are most successful. Current advice for good control is either cutting twice per year, essentially indefinitely (Marrs *et al.*, 1998a), or asulam applied once by sprayer and followed up by spot spraying without respite until there are no fronds appearing in spring (Anon, 2005; Robinson, 2007).

Recently, however, there has been a resurgence of interest in the use of bruising as an alternative for mechanical control. Bruising is a generic term and includes crushing and rolling the bracken; the technique is an old one, but it fell out of favour in the middle of the 20th Century with the development of mechanically driven cutters (Braid, 1948). Although bruising bracken is considered a less effective control method in comparison to cutting (Anon, 2005), because of the reduced damage to the litter layer, it is especially suitable for difficult terrain which might damage a cutter (Marrs & Watt, 2006).

The resurgence in interest in the use of bracken bruisers is a result of maker's claims that they are more effective than cutting. However, there is no experimental evidence to assess the effectiveness of bruising relative to the more commonly-used techniques of cutting or asulam use. The purpose of this study is, therefore, to compare the effectiveness of bruising against the current good practice guidelines of cutting or herbicide application. We aim to test the following hypotheses;

Is bruising an effective method of bracken control?

Assuming it is an effective control method, is it as good as or better than cutting twice per year or the manufacturer of asulams recommended guidelines of an initial spray plus continued application without respite?

Here, we attempt to assess effectiveness holistically, comparing the effects of bracken control treatments on the bracken canopy, the bracken rhizomes and litter mass, the composition of the understory vegetation and soil chemistry. Unfortunately, this paper only reports the first two years of this study; a longer period will be needed to test these hypotheses fully.

6.2 Methods

6.2.1 *The Experiment*

The experiment is located at Bamford Edge in the Peak District National Park (SK213 841, Longitude 1°41'W Latitude 53°41'N). Eighteen plots (20m × 20m separated by 2m buffers) were mapped using GPS (Leica Geosystems GS20) in November 2004; and plot corners were marked. The experimental design used was a randomized blocks design with three replicate blocks each containing six plots which were pre-selected randomly for application of one of six bracken control treatments, these were: (1) an untreated control (U); (2) cut twice per year (C2); (3) cut thrice per year (C3); (4) rolled twice per year (R2); (5) rolled thrice per year (R3); and (6) asulam applied by spraying in 2005 followed up by spot spraying of emergent fronds without respite until fronds are no longer present (S).

6.2.2 *Application Bracken Control Treatments*

Cutting was applied using petrol motor strimmers by Terra-firma Environmental Services Ltd. Bruising was done the same day using a bruiser supplied by Peter Gotham, Bracken Bruisers Ltd trailed by a four-wheel-drive ATV. Unfortunately because of various logistical problems it was only possible to apply two mechanical treatments in 2005, the cut thrice per year and the bruised thrice per year are therefore equivalent to their respective twice per year treatments in year 1. The first application of these treatments in 2005 was on the 28th July and the second on 22nd August. A full set of treatments were applied in 2006, the first on the 7th July, the second on 18th August and the third on the 4th September.

Asulam was applied by knapsack sprayer in early September 2005 at an application rate of 4.4 kg ai /ha (11 litres Asulox/ha). Follow-up spot-spraying was applied in 2006 with an AccuDos spot-sprayer at 2ml per shot at a ratio of 1:6 Asulox to water.

6.2.3 *Monitoring and Data Analysis*

6.2.3.1 Vegetation and Bracken Response

Vegetation and bracken response monitoring was based on the methods of Le Duc *et al.* (2000). In June five pre-selected random co-ordinates on 1m grids within each plot were selected, two sets of measurements were then made. 1m × 1m quadrats were used to estimate the cover (%) of all plant species present, non-living ground cover and average bracken litter depth. A smaller 0.5m × 0.5m quadrat was then placed concentrically inside the large one. All bracken fronds were cut at ground level, counted and frond length measured.

In August, three randomly pre-selected co-ordinates per plot were selected and bracken frond measurements were made using the same methodology as June; *P. aquilinum* cover was also assessed.

Data were transformed using standard procedures (Sokal & Rohlf, 1995); number of fronds per quadrat using $(Y + 0.5)^{0.5}$, and individual frond length and cover estimates using $\ln(Y + 1)$. After transformation the mean frond length per quadrat was calculated. Estimates of values per treatment combination per block were obtained by combining data per quadrat after transformation.

Individual variables were also analyzed for change through time. As our objective was to measure the shape of response curves through time, we used repeated measures ANOVAs with the method of polynomial contrasts (Gurevitch & Chester, 1986). The value of this approach is that it is possible to test for treatment effects as in ANOVA, but the temporal trends of these treatment effects can also be identified. This approach becomes more useful with longer-term datasets. Time was denoted as elapsed time (ET), with the start year designated year=0 (2005). This was carried out using PROC GLM in SAS version 8.02 (SAS, 1999).

Bonferroni correction was used to adjust for the Type I error rate (Cabin & Mitchell, 2000; Sokal & Rohlf, 1995). For the June sampling there was a large number of comparisons (44) as all species identified were analyzed. With $\alpha = 0.05$ a critical probability level of 0.0011 was used to assess significance. For August the number of comparisons was 3, with $\alpha = 0.05$ the critical probability level of 0.0167 was used to assess significance. The order number, referring to the shape of the polynomial curve, is either overall or through time (1st order). Results are presented in the text as; the *F*-test statistic, significance for that order and n. As only significant results after Bonferroni correction are discussed here, they are conservative.

6.2.3.2 Rhizome and Litter Mass

One rhizome sampling pit ($0.5m^2$) was dug in each plot in January 2005, 2006 and 2007, i.e. in the over winter phase when changes in carbohydrate flux and hence dry weight should be at a minimum (Williams & Foley, 1976), following methods in Le Duc *et al.* (2003). All pits were dug to a depth where the rhizomes no longer appeared (20-50cm). Rhizomes were collected, washed to remove soil, dried at 85°C and weighed to give a total dry mass (kgm^{-2}). Thereafter, the samples were sorted into roots, long-shoots (storage rhizomes) and short-shoots (frond bearing rhizomes) as described by Watt (1940) and reweighed.

Bracken litter mass was assessed at two points: a baseline winter sample and immediately before cutting/bruising application in June of each year. At each sampling point five $0.25m^2$ quadrats were located at pre-selected random co-ordinates within each plot. The following samples were taken in order (1) upright, senesced fronds were cut at ground level, (2) the compacted bracken litter and other vegetation litter were cut at ground level. The compacted litter sample was separated into bracken litter and other vegetation litter in the laboratory (Marrs *et al.*, 2007). All samples collected were dried at 85°C and weighed, and converted to $g\ m^{-2}$.

Data were transformed using standard procedures (Sokal & Rohlf, 1995), using ln(Y + 1). Estimates of values per treatment combination per block were obtained by combining data per quadrat after transformation. To test for spatial variation and the impact of any treatment over time, individual variables were analyzed using repeated measures ANOVAs with the method of polynomial contrasts as described above.

6.2.3.3 Soil Chemistry

Soil samples were collected in April of each year. In each plot, five 0.5 m^2 quadrats were located at randomly pre-selected co-ordinates. Two cores (7cm deep, 6cm in diameter) were taken for each set of samples and bulked. Fresh pH was measured in 1:2 slurry of soils to deionised water. Fresh soil (5 g) from each sample was shaken for 30 minutes in 30 ml 2M potassium chloride before and after incubation at 20°C for 30 days to estimate the amount of available inorganic nitrogen (Allen, 1989). Ammonium-nitrogen was estimated using colorimetry (Allen, 1989). The remainder of the soil samples were air dried and sieved through a 2 mm sieve; at each stage of the process the soil sample was weighed. Organic matter present was estimated by loss-on-ignition (Allen 1989). Estimates of exchangeable calcium and potassium were extracted from 4g sub-samples in 100ml of 1M ammonium acetate. For extractable P, a 2.5 g sub-sample was extracted in 50 ml Olsen's reagent and P was measured using the molybdate-blue method (Allen, 1989).

Data were transformed using standard procedures (Sokal & Rohlf, 1995), using ln(Y + 1). Estimates of values per treatment combination per block were obtained by combining data per quadrat after transformation. To test for spatial variation and the impact of any treatment over time individual variables were analyzed using repeated measures ANOVAs with the method of polynomial contrasts as described above.

6.3 Results

6.3.1 *The effect of bracken control treatments on bracken*

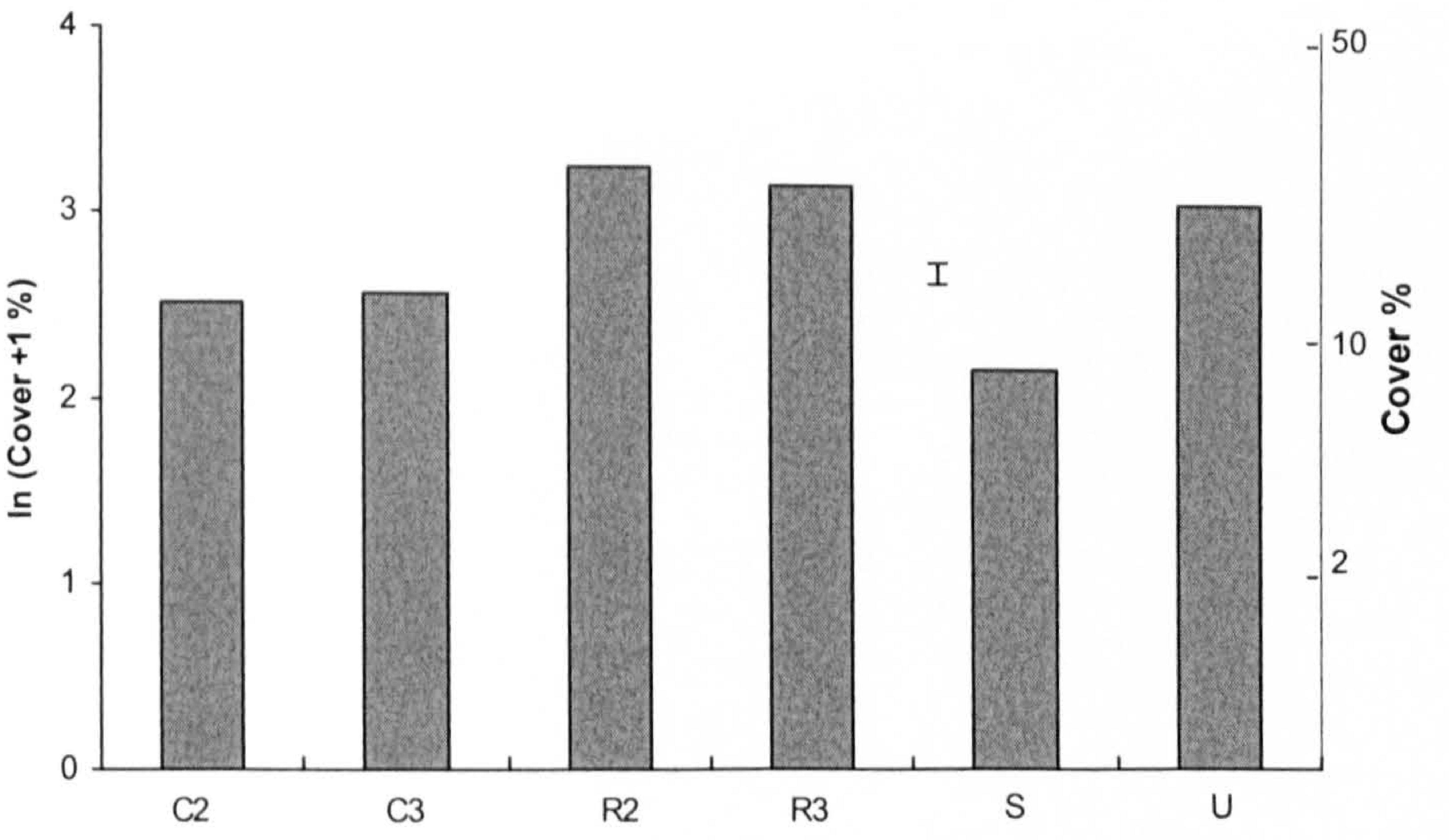
Three bracken response variables (cover, density and mean frond length) were measured twice a year, in June and when the frond is fully expanded in August.

In June, only *P. aquilinum* cover was affected by the bracken control treatments, with a significant impact overall (overall effect, $F_{5,10}$=10.0 n=36), and a significant effect through time ($F_{5,10}$=10.24 n=18). Overall, cover was reduced most in sprayed treatments compared to the cutting treatments with no difference between C2 and C3 (Fig. 1a). The rolling treatments increased cover compared to the untreated control. Over time, spraying showed the greatest decline between 2005 and 2006 (Fig. 1b), the two cutting treatments also reduced *P. aquilinum* cover but was less effective. The control and rolling twice per year remained the same but cover was significantly increased in 2006 compared to 2005 in plots that were rolled three times per year.

In August all bracken response variables were affected overall by the bracken control treatments: cover ($F_{5,10}$=5.34 n=36); frond density ($F_{5,10}$=7.15 n=36) and frond length ($F_{5,10}$=720.26 n=36). All variables were reduced the most by the cutting treatments (Fig.2) and to a lesser extent spraying reduced cover and length. There were no significant differences between the rolling treatments and the untreated plots for any of the measured bracken response variables.

As well as the overall effect, *P. aquilinum* cover ($F_{5,10}$=5.34 n=18) also showed significant differences through time for some treatments . There was no difference between 2005 and 2006 for the rolling treatments and untreated plots; the sprayed plots show a significant reduction and the cut treatments both show an increase between 2005 and 2006, although both remain significantly lower than all other treatments (Fig. 3).

(a)



(b)

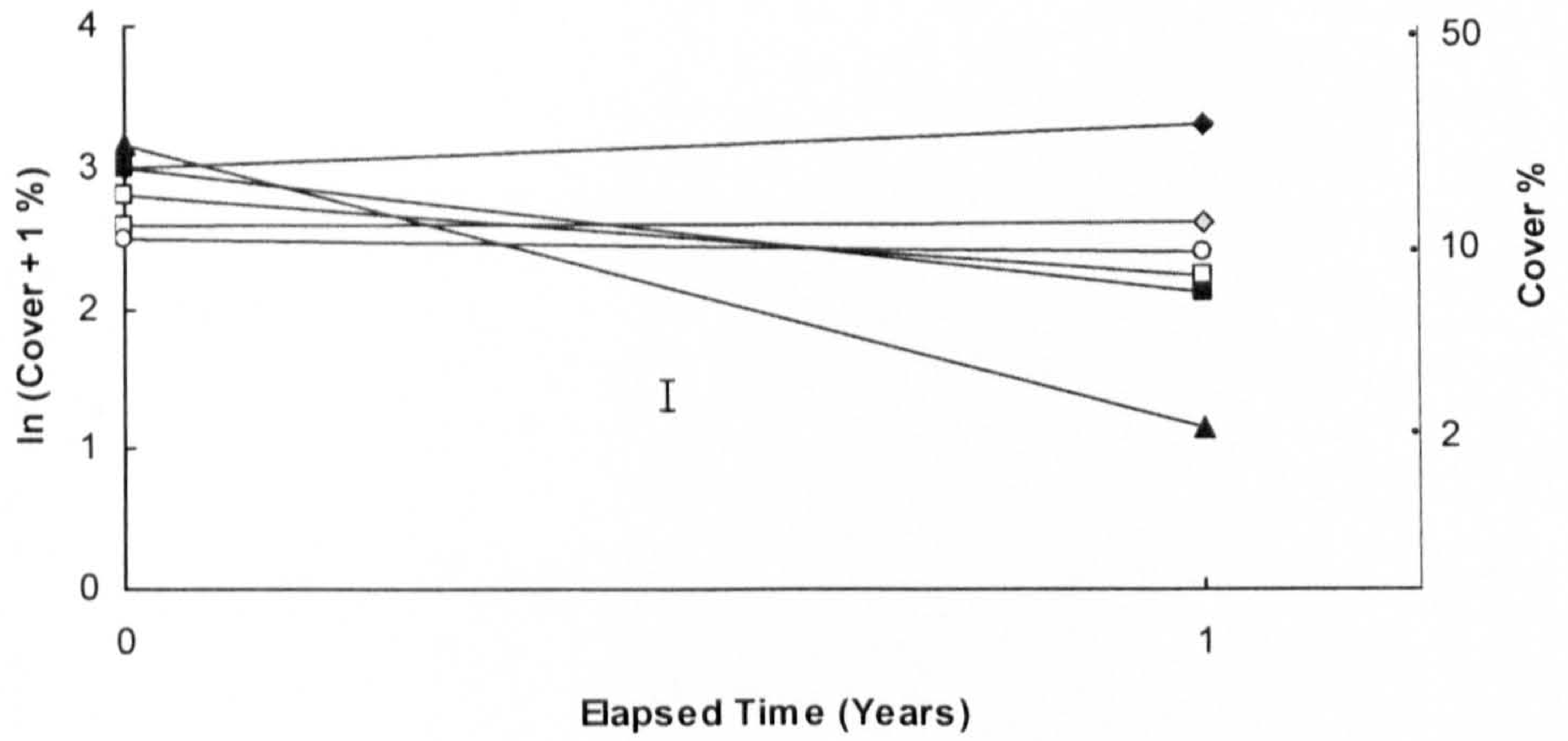
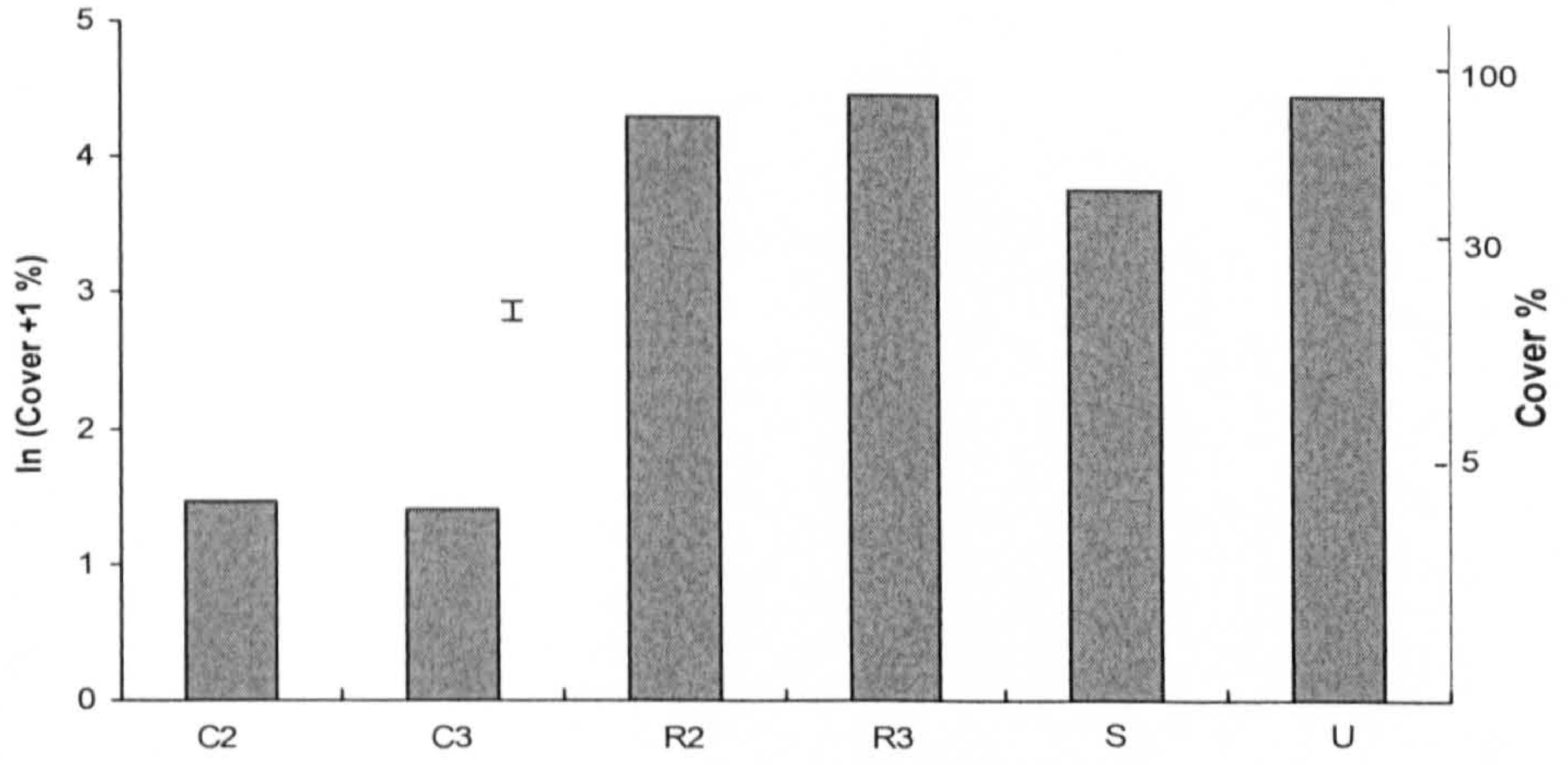
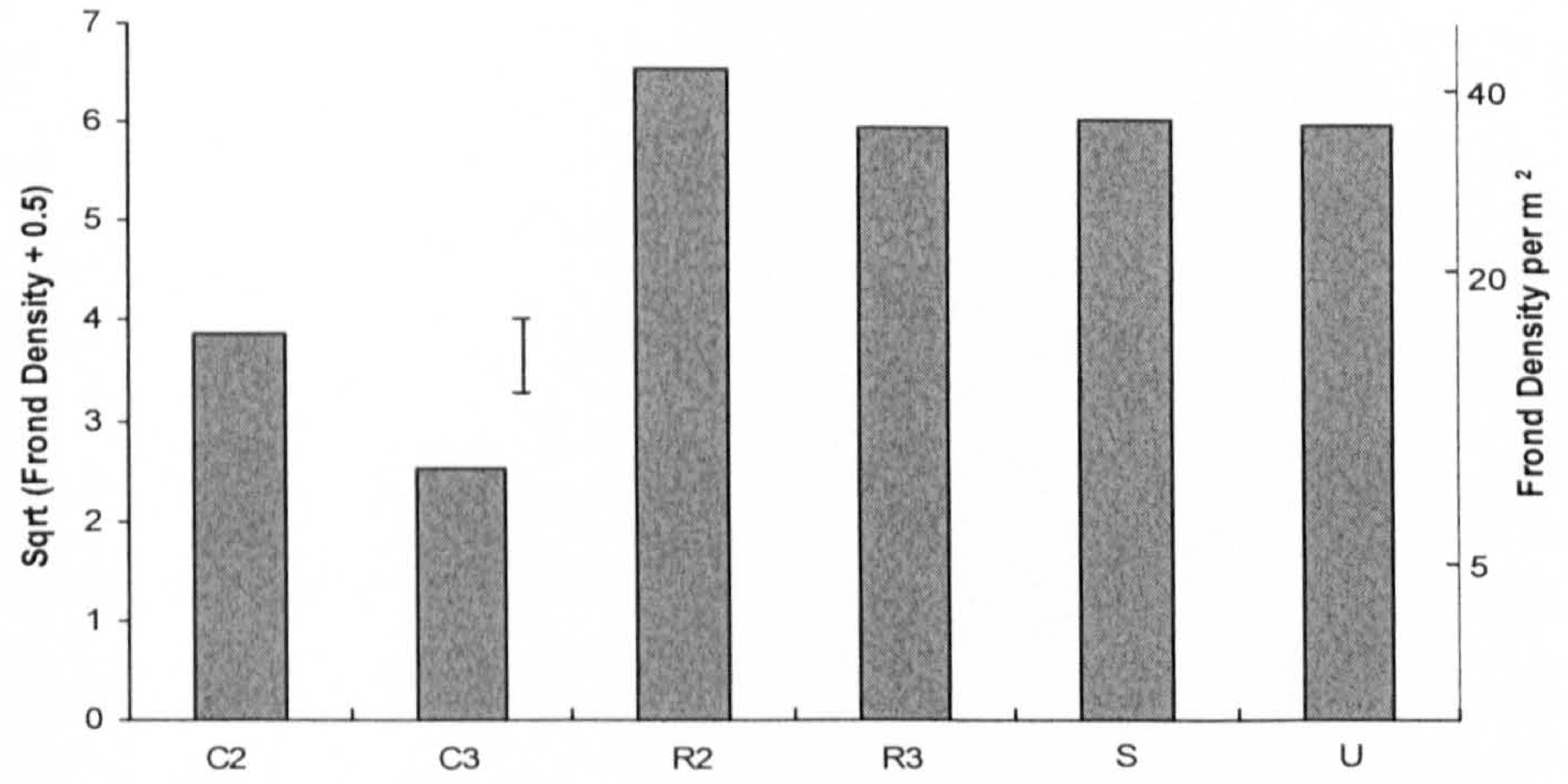


Fig. 1. The effect of bracken control treatments on *P. aquilinum* cover in June: (a) overall effect ($F_{5,10}$=10.0 n=36) and (b) through time (1st order effect, $F_{5,10}$=10.24 n=18). White circle= untreated control; white square= cut twice per year; black square= cut thrice per year; black triangle= sprayed with asulam; grey diamond= rolled twice per year and black diamond= rolled trice per year. Error bars are ± 2S.E.D.

(a) *P. aquilinum* Cover



(b) Frond Density



(c) Frond Length

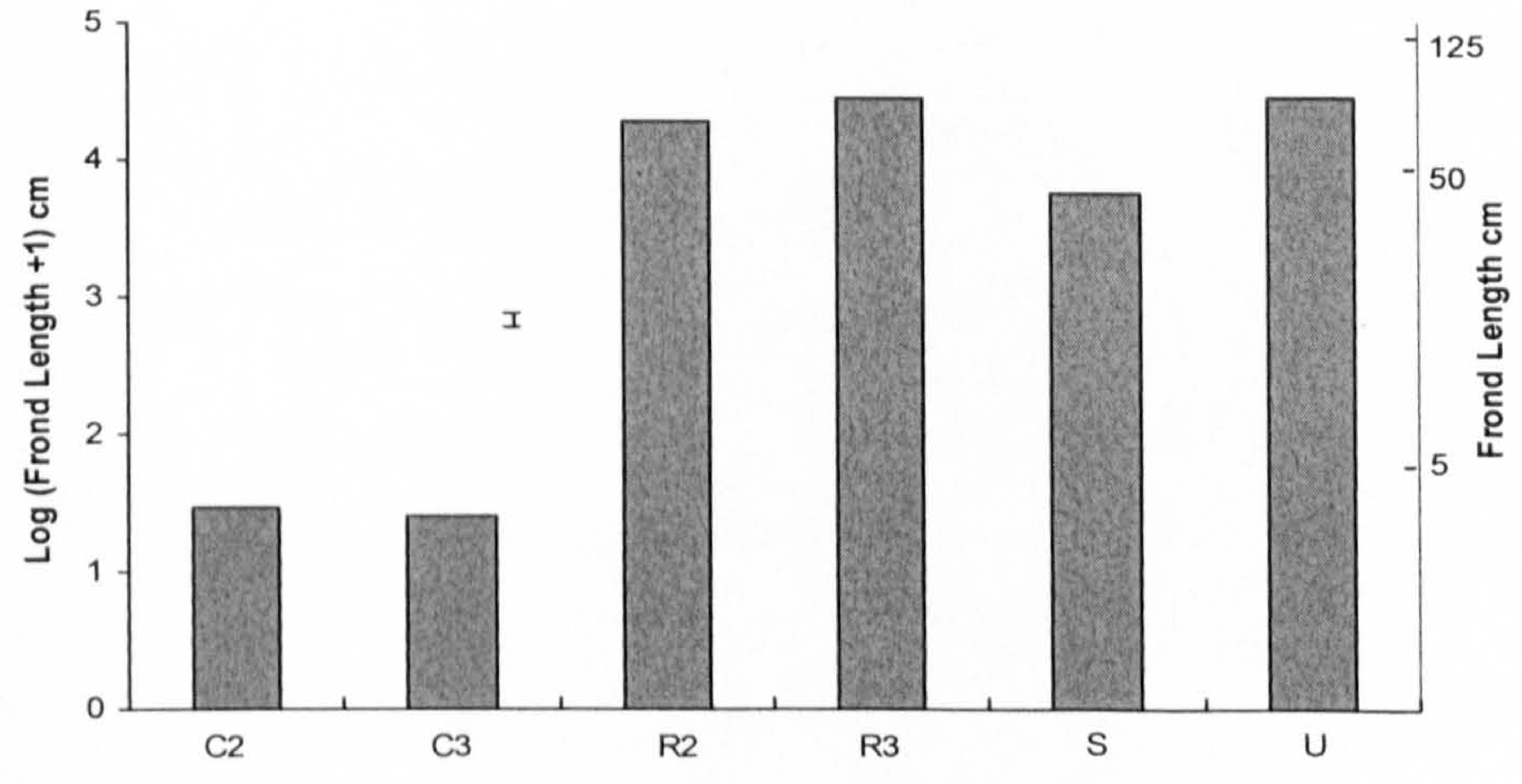


Fig. 2. The overall effect of bracken control treatments in August on; (a) *P. aquilinum* cover ($F_{5,10}$=5.34); (b)frond density ($F_{5,10}$=7.15) and (c) frond length ($F_{5,10}$=720.26). n=36, error bars are ± 2S.E.D.

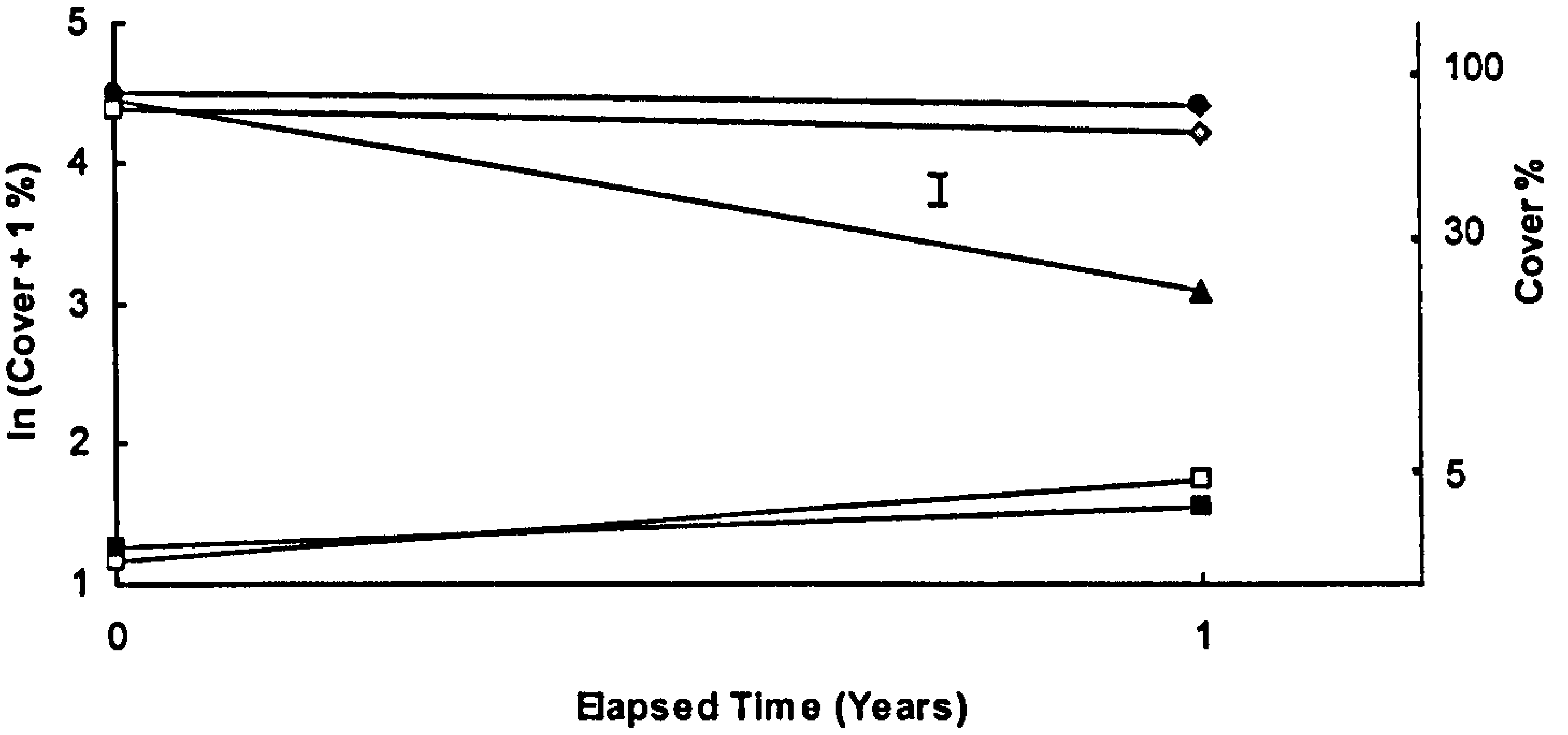


Fig. 3. The effect of bracken control treatments over time on *P. aquilinum* cover in August; 1st order effect, $F_{5,10}$=5.34 n=18. White circle= untreated control; white square= cut twice per year; black square= cut thrice per year; black triangle= sprayed with asulam; grey diamond= rolled twice per year and black diamond= rolled trice per year. Error bars are ± 2S.E.D.

6.3.2 *The effect of treatment on species composition of understory vegetation*

The species found in the understory at this site are all typical of acid heathland (Table 1). The most abundant species were *Deschampsia flexuosa* and *P. aquilinum*, but a large percentage of the total cover was attributed to bracken litter. There were no significant differences caused by bracken control treatment for any of the understory species (other than *P. aquilinum)* recorded, and this included all non-living cover variables (e.g. bracken litter).

6.3.3 *The effect on rhizome mass*

No rhizome fraction or the ratio, between frond bearing and storage rhizomes, varied significantly with any bracken control treatment (Table 2 a). Nor did rhizome mass significantly vary over time (Table 2 b).

Table 1. Cover (%) of higher plants, ferns and bryophytes. Data are Geometric means for cover. + = <0.01%.

Species	Vegetation
(a) Higher Plants and Ferns	
Agrostis capillaris	1.54
Agrostis vinealis	0.23
Carex spp.	0.02
Carex caryophyllea	0.04
Carex pilulifera	+
Chamerion angustifolium	+
Deschampsia flexuosa	25.80
Festuca ovina	0.47
Festuca rubra	0.59
Fraxinus excelsior	+
Galium saxatile	+
Holcus lanatus	0.04
Luzula campestris	0.03
Luzula multiflora	0.02
Potentilla erecta	0.06
Pteridium aquilinum	20.08
Rumex acetosella	+
Vaccinium mrytillus	0.27
Veronica officinalis	+
(b) Bryophytes	
Dicranum scoparium	0.23
Hypnum compressiforme	0.02
Hypnum jutlandicum	0.47
Lophocolea bidentata	+
Pleurozium schreberi	0.21
Polytrichum formosum	0.11
Pseudoscleropodium purum	0.82
Ptilidium ciliare	+
Rhytidiadelphus squarrosus	1.55

Table 2. The mean total dry mass of rhizomes for (a) each treatment (n=3) and (b) each rhizome section (n=18) in kgm^{-2} ± standard error, n=3.

(a)

Sampling	Total Dry Mass Fraction (kgm^{-2})					
Year	U	R2	R3	C2	C3	SS
ET0 (2005)	2.22±0.79	2.28±0.85	2.03±0.73	1.83±0.76	1.72±0.76	2.61±0.40
ET1 (2006)	2.57±1.14	2.26±0.51	2.24±0.42	1.66±0.79	1.74±0.83	1.64±0.76
ET2 (2007)	1.85±0.86	1.73±0.75	2.95±0.60	2.20±0.51	2.13±0.76	1.70±0.64

(b)

Sampling Year	Dry Mass Fraction (kgm^{-2})			
	Frond Bearing	Storage	Total	Ratio (=Frond Bearing/Storage)
ET0 (2005)	0.36±0.43	1.57±0.66	2.11±0.75	0.17±0.25
ET1 (2006)	0.36±0.39	1.55±0.74	2.02±0.84	0.18±0.21
ET2 (2007)	0.35±0.39	1.61±0.67	2.09±0.78	0.17±0.18

6.3.4 *The effect of treatment on litter mass*

Of the two sets of litter mass assessed, only one variable in January was found to be significantly affected by the bracken control treatments. Dry weight of senescent fronds decreased in all treatments in the second year of sampling (Fig. 4), with reductions in mass from 191 gm^{-2} in ET0 to $10gm^{-2}$ in untreated plots in ET1. A reduction to zero was found in both the cut plots.

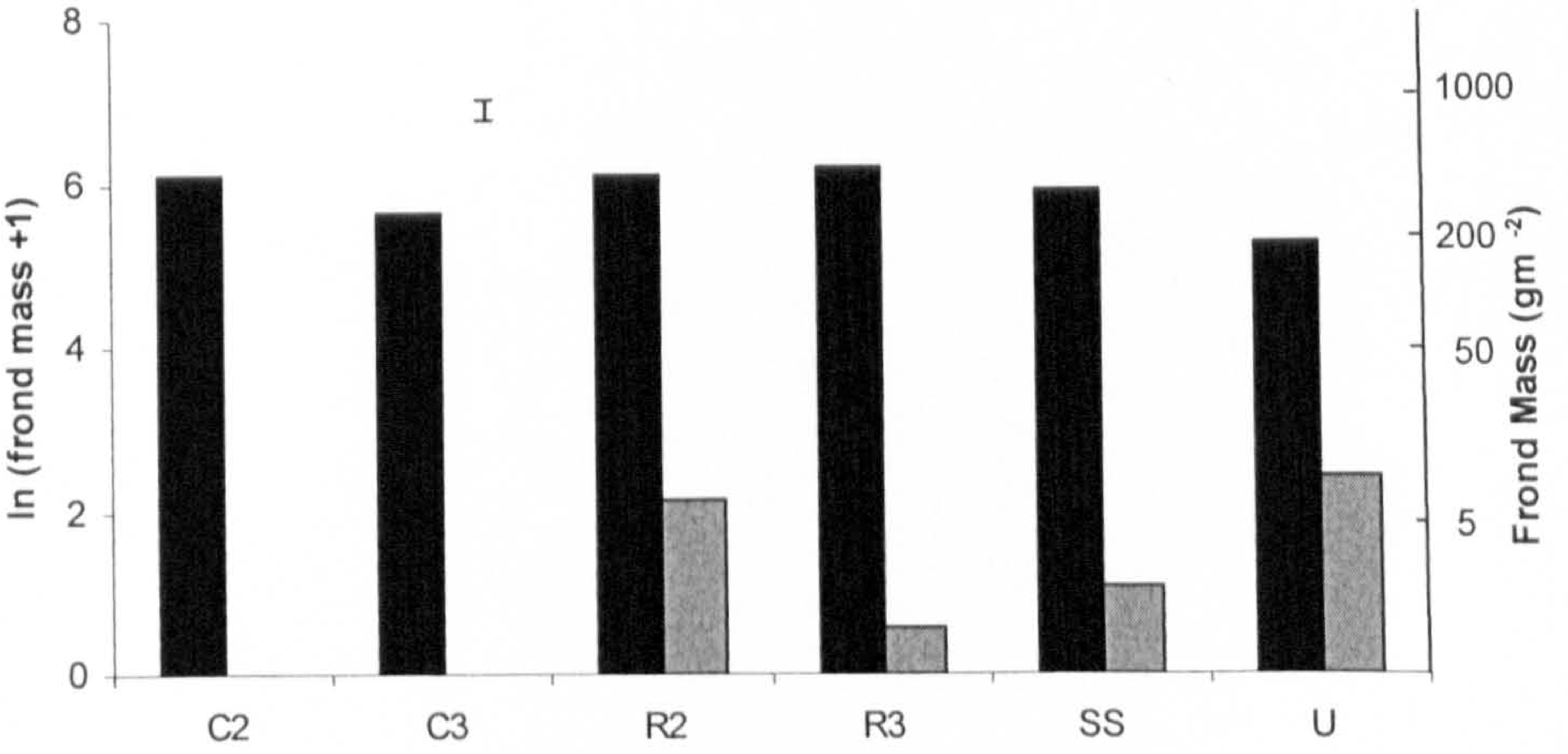


Fig. 4. The effect of bracken control treatments over time on senescent frond dry mass in January (gm^{-2}); 1st order effect, $F5_{,10}=5.26$ n=3. Black bars= ET1 (2005); grey bars= Et2 (2006). Error bars are ± 2S.E.D.

6.3.5 *The effect of treatment on soil chemistry*

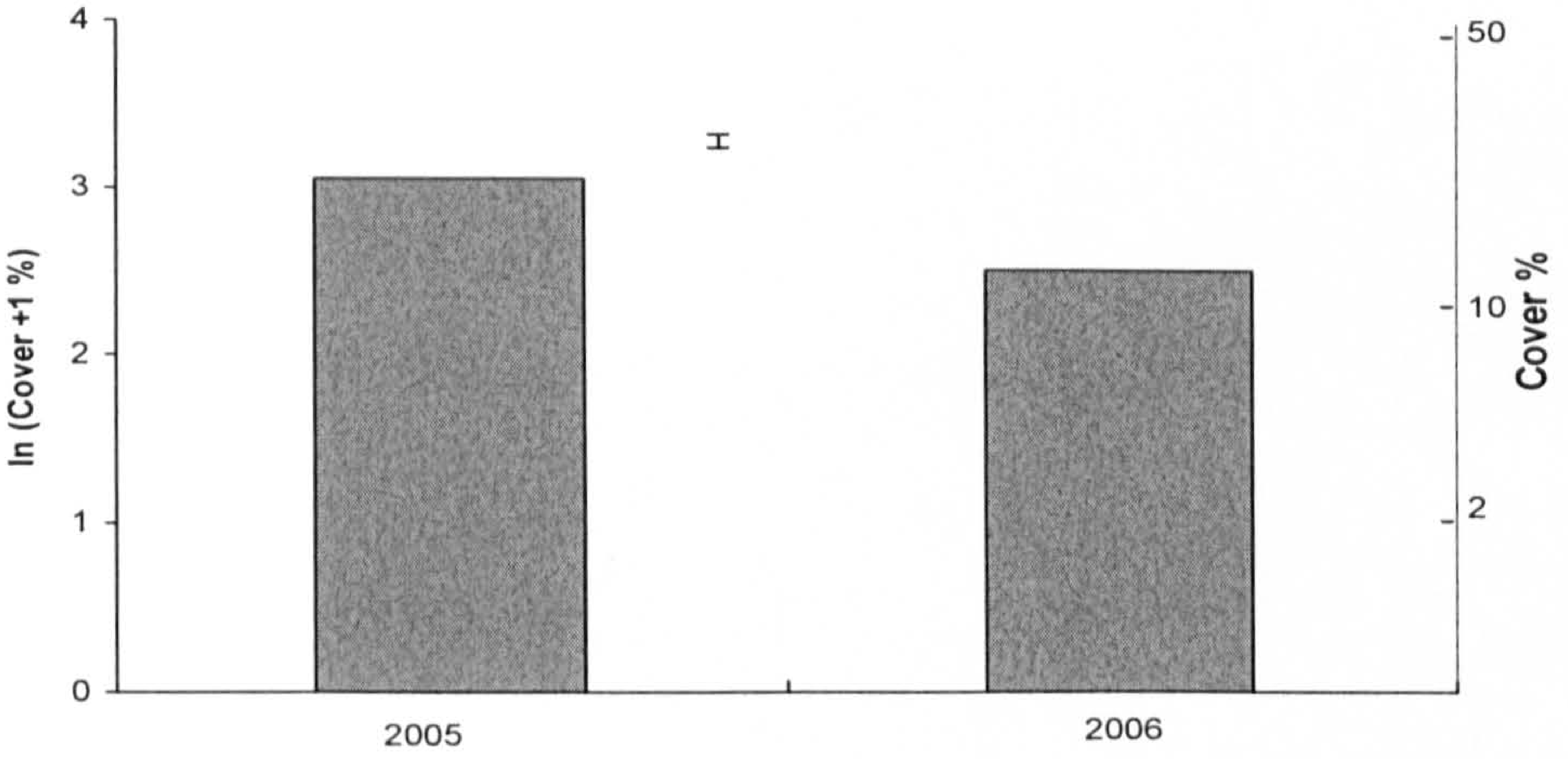
The soil was acidic (pH range = 4.1-4.8, site arithmetic mean ± SE = 4.38 ±0.18 n=36) with a loss-on-ignition of ca. 30% (range= 15.6-62.8%, site arithmetic mean ± SE = 30.0% ±0.55 n=36 . The concentration of extractable P (range =6.7 - 172.4 µg P g^{-1}), ammonium- N (range 3 -505 µg N gg^{-1}. and nitrate-n (negligible) are all low (Allen, 1989). The concentration of exchangeable calcium and potassium are also classified as are low to medium (Allen, 1989); ranges =9.3 - 19.1 µg Ca g^{-1}) and 9.4 - 12.6 µg K g^{-1})

With only one year of treatment it is, perhaps, not surprising that the treatments had no impact on any of the soil chemistry variables tested. There was some variability between blocks for LOI% ($F_{2,9}$=15.32 n=18 with block C having the highest LOI in both years but significantly increasing in ET1 (from 34% in ET0 to 47% in ET1).

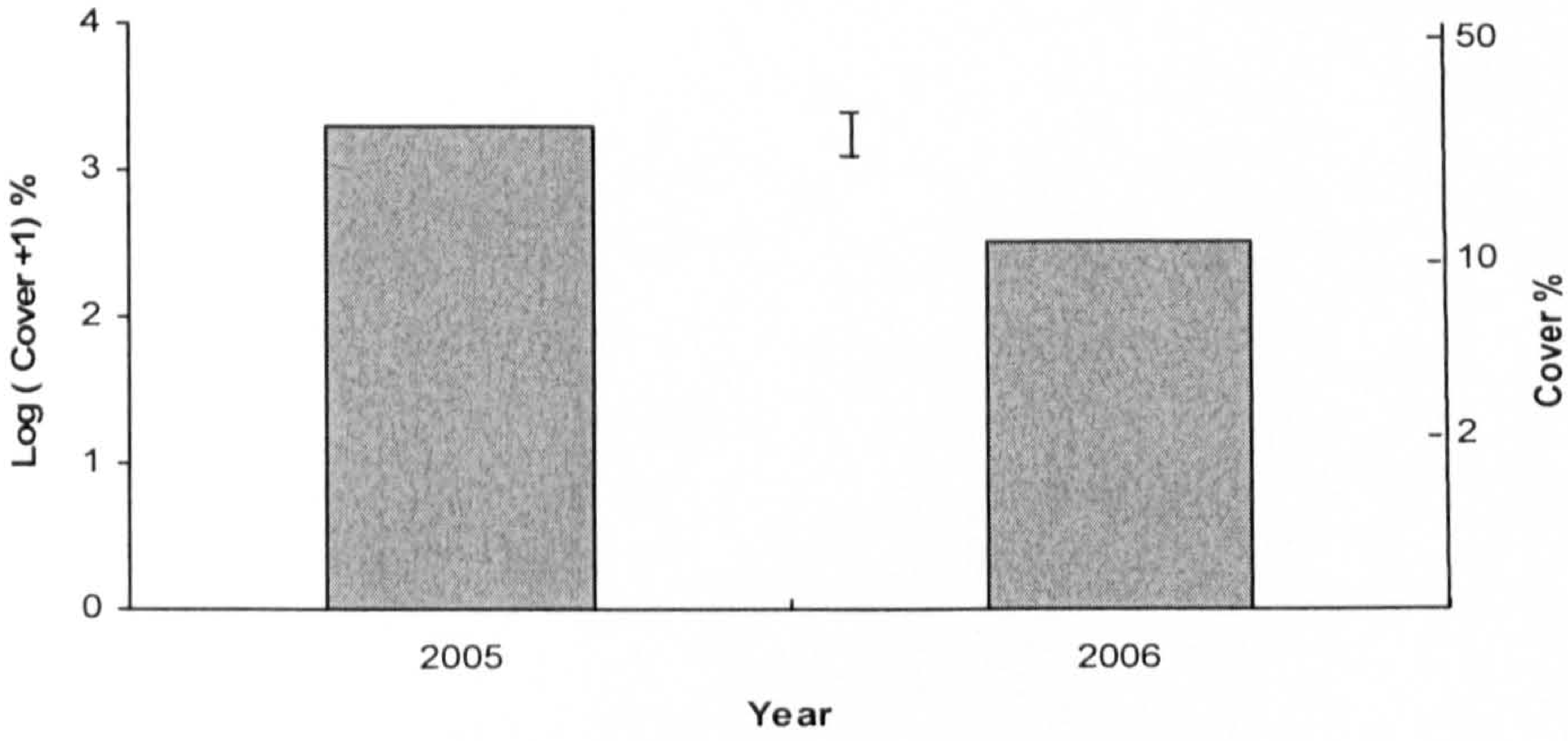
6.3.6 *Effects independent of treatment*

Significant changes were detected between the years that were independent of any bracken control treatment effect; these were found for the cover of *P.aquilinum, D. flexuosa* and *Dicranum scoparium*, litter mass and some soil chemistry variables. In June, three species were decreased significantly between 2005 and 2006 (Fig. 5); *P. aquilinum* cover (1st order effect, $F_{1,10}$=57.29 n=18); *D. flexuosa* ($F_{1,10}$=24.73 n=18) and *D. scoparium* ($F_{1,10}$=22.55 n=18). Bracken control treatments had no significant effects on *D. flexuosa* or *D. scoparium,* although these treatments did have an effect on *P. aquilinum* cover. In August, frond length significantly decreased from 2005 to 2006 ($F_{1,10}$=12.25 n=18), although the bracken control treatments were also found to significantly affect frond length.

(a) *P. aquilinum*



(b) *Deschampsia flexuosa*



(c) *Dicranum scoparium*

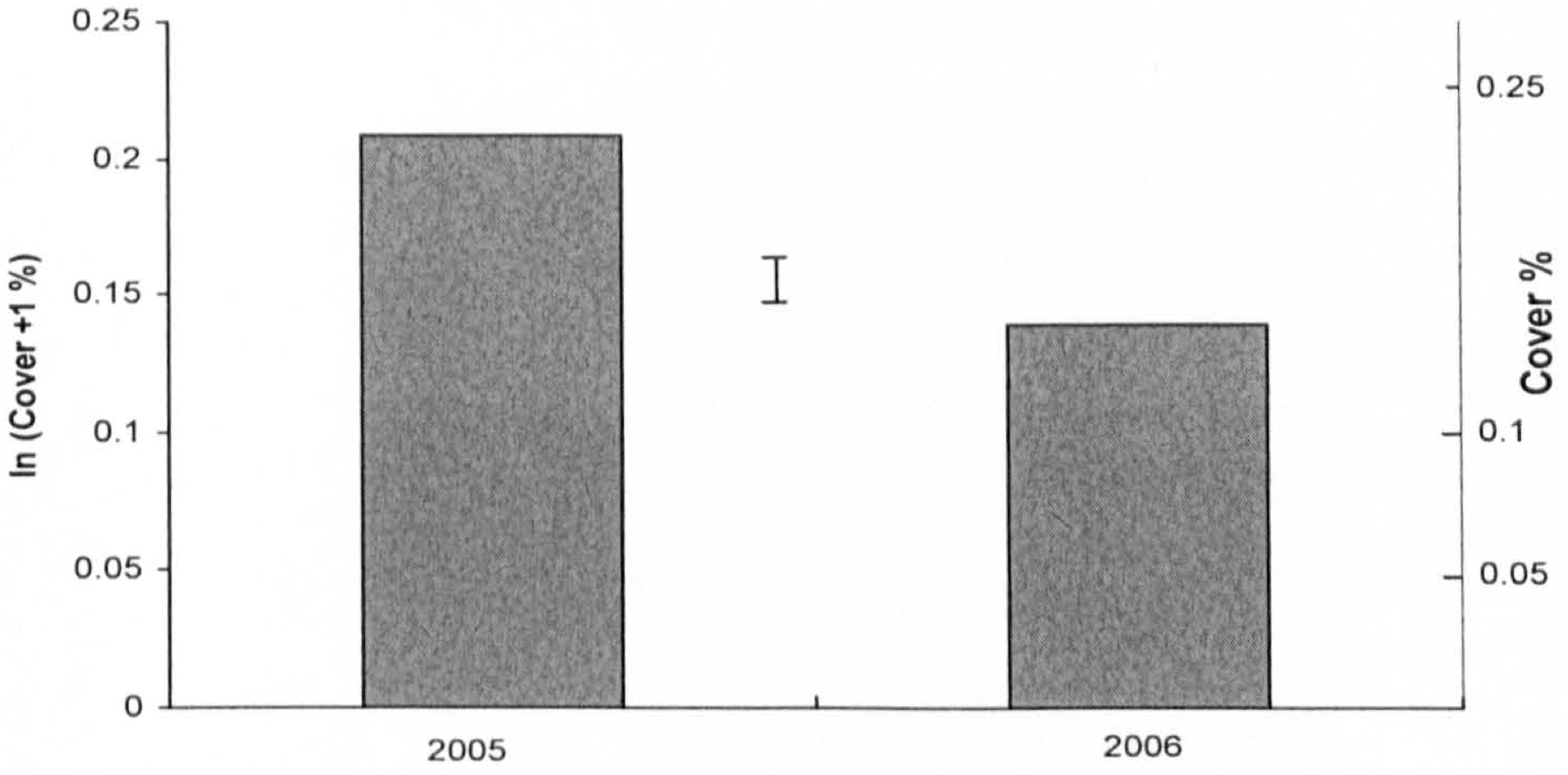


Fig. 5. Significant difference of species cover in June trough time; (a) *P. aquilinum* cover ($F_{1,10}$=57.29); (b) *Deschampsia flexuosa* cover ($F_{1,10}$=24.73) and (c) *Dicranum scoparium* (1st order effect, $F_{1,10}$=22.55). All 1st order effects, n=18, error bars are ± 2S.E.D.

In January, a significant reduction in senescent frond mass over time was found ($F_{(1,5)}$=153.82 n=18), however, frond mass was also significantly effected by treatment (Fig.4). In June, bracken litter was found to significantly decrease over time ($F_{(1,5)}$=16.30 n=18) impendent of any treatment effects. The mean bracken litter mass falling from 573 gm^{-2} in ET0 to 265 gm^{-2} in ET1.

Significant variation through time was found for ammonium, calcium and potassium with all increasing from ET0 to ET1 (Table 3).

Table 3. The mean mass of extractable ammonium (-N) and exchangeable Calcium and Potassium (µgg^{-1}) for each year. Back transformed means ± standard error in parenthesis.

Element	ET0 (2005)	ET1 (2006)
Ammonium (µgg^{-1})	80.33 (4.40 ±1.14)	164.94 (5.11±0.75)
Calcium (µgg^{-1})	9.32 (2.33 ±0.58)	19.12 (3.00 ±0.48)
Potassium (µgg^{-1})	9.42 (2.34±0.52)	12.59 (2.61 ±0.37)

6.4 Discussion

6.4.1 *Is bruising an effective method of bracken control?*

Not surprisingly, there were no significant effects on understorey species at this early stage of the experiment. Marrs & Lowday (1992) found it took 2-3 years of bracken control treatments for heath vegetation to re-colonise and even then it was predominantly where the species had been seeded. In addition it has been reported that control treatments alone may have little effect in creating the desired species community (Pakeman *et al.*, 1997). Jacquemart *et al.* (2003) found although cutting as a control treatment reduced the problem species (*Molinia*) it had little impact on vegetation composition.

As the bracken control treatments are to be applied every year, it might be expected that the significant effects of the bruising treatments will increase over time, as has been reported for cutting (Le Duc *et al.*, 2000). The treatments also had little effect on the other factors (rhizomes, litter mass and soil chemistry) measured, with the only significant treatment effect occurring in senescent frond mass in January.

The total mass of rhizomes ranged from 2.95 kgm^{-2} to 1.64. An average of 1.85kgm^{-2} of rhizome was found at a neighbouring site by Le Duc *et al.* (2003) and 1.18 kgm^{-2} was found in untreated *Calluna* heath by Marrs *et al.* (1993). Although ratios of frond bearing rhizomes to the total dry mass are much lower than those presented by Le Duc *et al.* (2003), low frond bearing to total rhizome mass ratio has been reported in invading fronts and previously controlled bracken (Le Duc *et al.*, 2003). This site has already had some degree of bracken control as a result of being aerial sprayed with asulam in the early 1990's (Marrs & Frost, 1996). Marrs *et al.* (1993) suggest that rhizome biomass should be reduced to <0.2-0.3 kg m^{-2} in order to keep frond production low (<0.1 kgm^{-2} of frond biomass). A figure that may be obtained in bruising treatments and would be expected in cut treatments in time as impact on bracken response variables is initially slow but increases with time (Cox *et al.*, 2007a). In plots with the greatest total rhizome mass this would require a reduction of 75 to 90 %.

The results, after only one year of treatment, suggest that bruising is less effective than cutting as a mechanical control (Anon, 2005). All bracken response variables in August and *P. aquilinum* cover in June increased in the rolled three times per year plots compared to the untreated control, rather than the desired decrease. Although this increase was only significant for *P. aquilinum* cover in June (25 and 26% for R2 and R3 compared to 19% for U in ET 1). All other treatments in June, showed a significant decline both overall and through time. The increase in *P. aquilinum* cover in August may be due to the fronds now lying flat to the ground in comparison to the upright fronds in untreated plots.

One grass, *D. flexuosa* and one bryophyte, *D. scoparium* decreased significantly over time. This suggests factors other than the bracken control treatments are influencing species composition. Both species are desirable in terms of developing heathland, so an increase rather than a decrease would be favoured. As the land is stocked at low level (one sheep per 0.5 ha) the decrease in *D. flexuosa* might be brought about by an increase in sheep grazing. This is possibly due to an increase in available access for sheep, as they are reluctant to barge through bracken stands to reach grass (Robinson, 2007) and will preferentially grazing in open areas (Pakeman *et al.*, 2000). The response of *D. flexuosa* to reduced sheep grazing is well known (Rawes, 1983; Anderson & Radford, 1994; Pakeman, 2004) and it is noted that the species is often preferentially grazed (Duffey *et al.*, 1974). *D. scoparium* has been found by Hulme *et al.* (2002) to be associated with high levels of grazing (2.1 sheep ha^{-1}). It also increased with grazing with on overall steady increase at Peak (Chapter 8). This study is not long enough to see any distinct patterns such as the synchronous peaks of *A. vinealis* at Sourhope (Chapter 8) which could be attributed to fluctuations in weather and climate.

Other variables found to vary with time, independent of any treatment, include ammonium, calcium and potassium which all increased over time. Long-term experiments have also found potassium and calcium not to be affected by bracken control (Marrs *et al.*, 2007). It is suggested this could be due to the transfer of some nutrients from bracken to the developing vegetation during the control process (Marrs *et al.*, 2007). Previous studies of soil nutrients have also reported very variable results (Mitchell *et al.*, 1997). Extractable ammonium tends to be low increasing with succession (Mitchell *et al.*, 1997) with higher frond biomass being found on soils with higher nitrogen contents (Watrud *et al.*, 2003) thus an increase, as observed at this experiment, would be going against the desired trend.

6.5 Conclusions

After only one year of bracken control, cutting and spraying treatments all reduce *P. aquilinum* cover in June and in August, with cutting thrice per year being the most effective. However the bruised plots showed an increase in cover in comparison to the untreated controls. Expected declines in rhizome mass (Paterson *et al.*, 1997; Le Duc *et al.*, 2003) and litter mass (Marrs *et al.*, 2007) were not seen in the cut and sprayed treatments at this early stage. It could be assumed that bruising would act with the same accumulative impact as cutting (Cox *et al.*, 2007a) but continued annual treatment is required to do this.

Chapter 7

Does bruising 'bleed the rhizomes dry'? An assessment of the physiological effect of bruising on bracken fronds

7.1 Introduction

There are two main strategies that are generally used to control *Pteridium aquilinum*; these are either mechanical control or herbicidal control (Lowday & Marrs, 1992a). Mechanical control is normally by cutting. However, there has recently been a resurgence of interest in the use of bruisers as an alternative to cutters. Bruising is a generic term and includes crushing and rolling the bracken; the technique is an old one, but it fell out of favour in the middle of the 20th Century with the development of mechanically driven cutters (Braid, 1948). Although bruising bracken is considered a less effective control method in comparison to cutting (Anon, 2005), because of the reduced damage to the litter layer, it is especially suitable for difficult terrain which might damage a cutter (Marrs & Watt, 2006). The resurgence in interest in the use of bracken bruisers is a result of maker's claims that they are more effective than cutting.

Bruisers are rollers or bars that are driven over the bracken, at best cutting the fronds, but more usually breaking them (Fig. 1).

Fig. 1. Bracken being bruised by a bruiser trailed on an ATV.

The aim of mechanical bracken control is to prevent fronds translocating carbohydrate to the storage rhizomes thus replenishing reserves (Williams & Foley, 1976). This is done by cutting or damaging fronds when they are in the expansion phase, and dry weight and carbohydrates in the rhizome are at an annual low (Williams & Foley, 1976), normally mid-June to late-July in the UK (Anon, 2005; Southern Uplands Partnership, 2001). Cutting will do this by severing the frond from the rhizome. Bruised fronds; however, remain attached although damaged, with observations having shown that fronds remain green. There is a belief among some practitioners that this practice allows the fronds to remain alive and "bleed the rhizome of resources – water, carbohydrate and nutrients" (e.g. http://www.brackenbruiser.co.uk/, accessed 4/4/07). This remains untested. We investigated how bruising affects the bracken frond immediately after application by conducting some structural and physiological experiments.

Two hypotheses were tested;

(1) Do the fronds remain alive after bruising, and if so, is performance comparable to untreated fronds?

(2) Is there any impact on the rhizomes as an effect of control due to bruising (i.e. are the rhizomes being "bled the rhizome of resources – water, carbohydrate and nutrients")?

In order to test hypothesis 1; Do the fronds remain alive after bruising, and if so, is performance comparable to untreated fronds?, a series of three experiments were set up to assess the level of performance in damaged fronds by analysing photosynthesis and transpiration rates. Experiment 1 assessed the photosynthesis and transpiration rates of cut, bruised and untreated fronds three weeks after treatment in 2005. Experiment 2, in 2005, assessed whether or not the extent of damage caused by the bruiser would affect the photosynthesis or transpiration rate, and ultimately the survival of the frond. Experiment 3 took place in 2006 over a seven week period to assess the long-term effect of damage caused. Details of the dates and locations of these three experiments are in Table 1. Sections of bruised stems were also observed under the light and scanning electron microscope.

Table 1. The date and location of the three experiments to investigate photosynthesis and transpiration rates after bruising.

Date	Experiment	Location
23rd August 2005	Experiment 1	Block C of experiment at Bamford Edge (SK 213 841)
12th – 16th August 2005	Experiment 2	Ashton Street, University of Liverpool (SJ 395 385).
7th July – 25th August 2006	Experiment 3	Randomly selected co-ordinates in bruised and control plots on the experiment at Bamford Edge.

In order to test the second hypothesis; is there any impact on the rhizomes as an effect of control due to bruising? A series of rhizome pits were dug before any treatment had been applied to the site in January 2005 and repeated in 2006 and 2007.

7.2 Methods and Data Analysis

7.2.1 *The Experimental Site*

The experiment was set up in winter 2004 at Bamford Edge in the Peak District National Park (SK213 841, Longitude 1°41'W Latitude 53°41'N). Eighteen plots (20m x 20m separated by 2m buffers) were mapped using GPS (Leica Geosystems GS20) and plot corners were marked. The experimental design used was a randomized blocks design with three replicate blocks each containing six plots that were pre-selected randomly for application of one of six bracken control treatments. These were: (1) an untreated control (U); (2) cut twice per year (C2); (3) cut thrice per year (C3); (4) rolled twice per year (R2); (5) rolled thrice per year (R3); and (6) asulam applied by spraying in 2005 followed up by spot spraying of emergent fronds without respite until fronds are no longer present (S).

7.2.2 *Bracken treatment application*

Cutting was applied using petrol motor strimmers by Terra-firma Environmental Services Ltd. Bruising was done the same day using a bruiser supplied by Peter Gotham, Bracken Bruisers Ltd trailed by a four-wheel-drive ATV. Unfortunately, because of various logistical problems it was only possible to apply two mechanical treatments in 2005. The cut thrice per year and the bruised thrice per year are therefore equivalent to their respective twice per year treatments in year 1. The first application of these treatments in 2005 was on the 28th July and the second on 22nd August. A full set of treatments were applied in 2006, the first on the 7th July, the second on 18th August and the third on the 4th September.

Asulam was applied by knapsack sprayer in early September 2005 at an application rate of 4.4 kg ai /ha (11 litres Asulox/ha). Follow-up spot-spraying was applied with an AccuDos spot-sprayer at 2ml per shot at a ratio of 1:6 Asulox to water.

7.2.3 *Photosynthesis and Transpiration Rate Monitoring*

Photosynthesis and transpiration rate were measured using a LCA-4 IRGA Leaf Chamber Analyser (LCA-4, 1993). An individual pinnule in a PLC-4 type leaf chamber, and CO_2 uptake and H_2O transpired and other parameters measured. For each set of readings taken sunlight (Lux) was measured. Due to the serrated shape of bracken leaves they did not fill the chamber, accordingly the sampled area of each pinnule was excised and the leaf area calculated using WinFOLIA scanner-based software. To account for the variable leaf areas both photosynthesis and transpiration rate had to be recalculated using the formulas; $A=U_s \times \Delta C$ and $E=U_s \times \Delta W$ respectively. Where U_s is the molar flow per unit leaf area, ΔC is the difference in CO_2 across the leaf chamber and ΔW is the difference in water concentration (LCA-4, 1993).

Pinnae from the upper layer of the frond (i.e. the latest pair of pinnae to fully expand) were selected in each case. This ensured the pinnae had maximum exposure to the available sunlight, despite evidence that stomatal conductance shows no significant difference between the upper and lower pinnae (Roberts *et al.*, 1980; 1984).

7.2.3.1 Experiment 1

This experiment compared the photosynthesis and transpiration rates of bruised, cut and untreated fronds three weeks after treatment. Fronds were sampled from three $0.5m^2$ quadrats located randomly in each of the six plots within one of the blocks (Block A) on the experiment at Bamford Edge (Table 1). As only two applications of the bracken control treatments had occurred in ET1 it meant there were two replicate plots randomly allocated to each treatment. In order to allow for variation over time and the time required for the leaf chamber to stabilise, three readings were taken on each leaf (two per quadrat) 30 seconds apart (30, 60 and 90 seconds).

7.2.3.2 Experiment 2

This experiment was designed to assess the effect of varying levels of damage over time (up to 96 hours). It was conducted on a small bracken patch on Ashton Street at the University of Liverpool (Table1). In each of three replicate blocks, six fronds were selected randomly and a cutting treatment applied with a razor blade in a series of patterns (Fig. 2). Measurements of leaf chamber temperature (Tch), leaf chamber volume gas flow rate at Tch and ambient pressure (V) were also made. Recordings were taken before damage (0 hours) then at 24, 48 and 96 hours after damage had been inflicted. Readings at 72 hours were planned, but not taken as heavy rain made recording impossible.

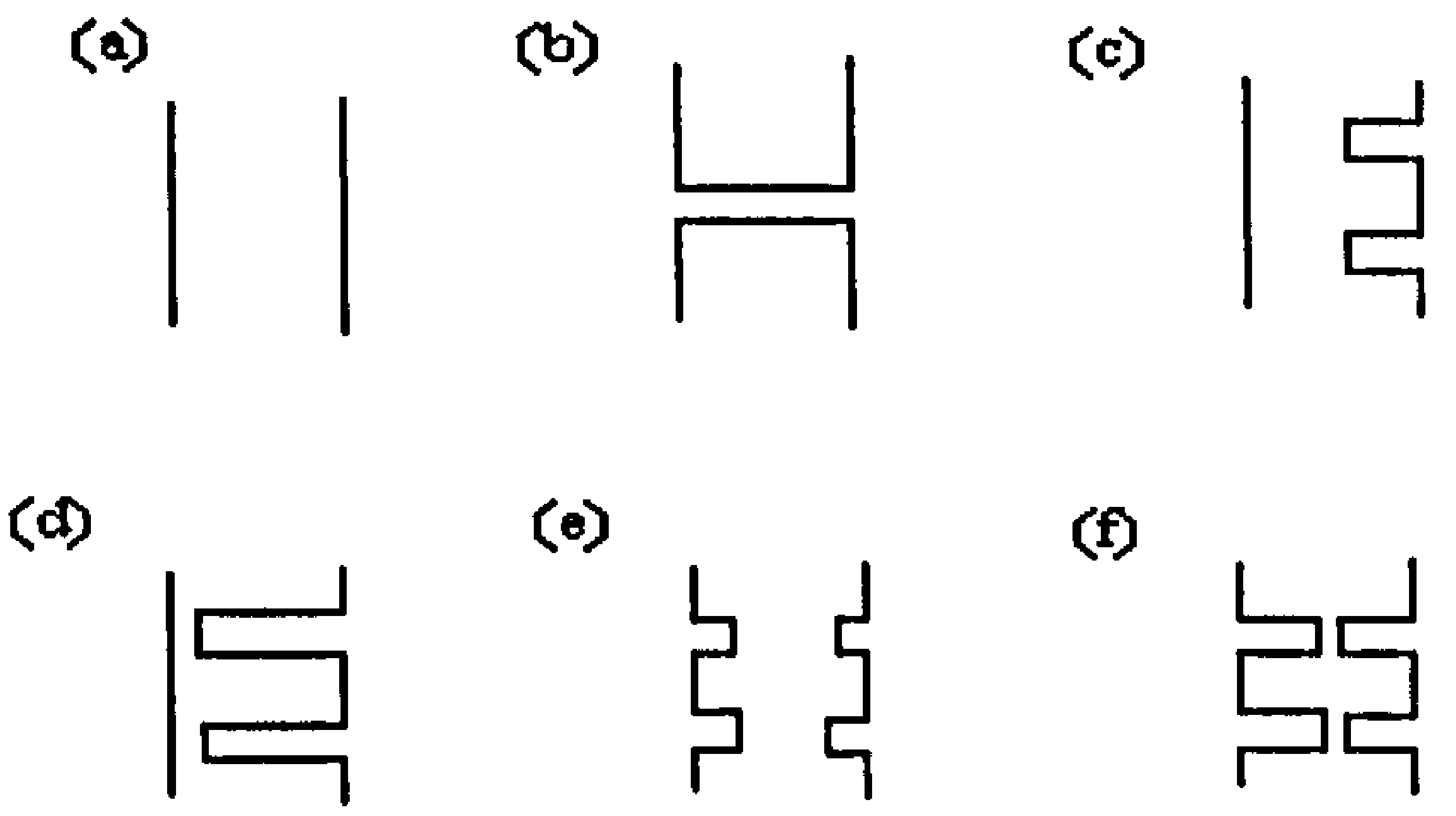


Fig. 2. The six treatments applied to fronds (a) Treatment a (T a); Untreated frond (b) Treatment b (T b); Cut (c) Treatment c (T c); Rachis cut in two places (d) Treatment d (T d); Cut until almost severed in two places (e) Treatment e (T e); Outside layer cut along circumference in two places (f) Treatment f (T f); Circumference cut, in two places, to leave a few fibres in the centre.

Data for Experiment 2 were transformed using $Y'=1/(Y+0.1)$. Individual response variables (transpiration and photosynthesis) were analysed for change through time and for change between fronds. The analysis of variance procedure was carried out in SAS version 8.02 (SAS, 1989)

7.2.3.3 Experiment 3

Conducted in 2006, this experiment started just before the first bruising treatment was applied to the experiment (Table 1). Readings were taken from fronds within five randomly selected 1m^2 quadrats in the bruised twice per year and the control plots of each block. In order to allow for variation over time and the time required for the leaf chamber to stabilise, three readings were taken on each leaf 30 seconds apart (30, 60 and 90 seconds). Monitoring took place every week for seven weeks (7th July to 25th August). Readings at week six were planned but prevented by rain.

Data for Experiment 3 were transformed using $Y'=1/(Y+0.1)$. Using R (version 2.3.1), linear mixed effects-models fitted in REML, were tested against a null-model for both the rate of photosynthesis and transpiration. An ANOVA was then performed to test for any significant difference between the models, re-run with a Maximum Likelihood test. In addition general linear models were used to test the effect of time, time^2 and time^3 against null models for both the rate of photosynthesis and transpiration. We follow Crawley's (2005) methodology for testing treatment effects and time as a repeated measure.

7.2.4 *Observations of Damaged Fronds using Scanning Electron Microscopy*

20 varying lengths of bruised and undamaged fronds were cut and dehydrated using a simple freeze dehydration method (Veltkamp *et al.*, 1994).The sections were placed in absolute ethanol at -18°C for 2 hours, then placed in a 4°C chamber overnight before being returned to -18°C absolute ethanol and stored at 4°C until critical point drying.

The specimens were dried from absolute ethanol in CO_2 using a Polaron E300 critical point drier, glued to stubs and coated with 60% gold-palladium. Suitable sections were then viewed using a Philips 501B scanning electron microscope.

7.2.5 *Rhizome Monitoring*

One rhizome sampling pit ($0.5m^2$) was dug in each plot in January 2005, 2006 and 2007, i.e. in the over winter phase when changes in carbohydrate flux and hence dry weight should be at a minimum (Williams & Foley, 1976), following methods in Le Duc *et al.* (2003). All pits were dug to a depth where the rhizomes no longer appeared (20-50cm). Rhizomes were collected, washed to remove soil, dried at 85°C and weighed to give a total dry mass (kgm^{-2}). Thereafter, the samples were sorted into roots, long-shoots (storage rhizomes) and short-shoots (frond bearing rhizomes) as described by Watt (1940) and reweighed.

7.3 Results

7.3.1 *Do the fronds remain alive after bruising? If so, is performance comparable to untreated fronds?*

7.3.1.1 Experiment 1

Results show that the rate of photosynthesis in fronds that had been bruised three weeks earlier was unaffected in comparison to untreated fronds (Fig. 3a), with a non-significant reduction from 7.99 μmol m^{-2} s^{-1} in untreated living fronds to 7.15 μmol m^{-2} s^{-1} in bruised fronds. The mean photosynthesis rate for cut fronds was calculated as –0.04 μmol m^{-2} s^{-1}. The transpiration rate was significantly reduced, from 1.80 mol m^{-2} s^{-1} to 1.31 mol m^{-2} s^{-1} in bruised fronds (Fig. 3b).

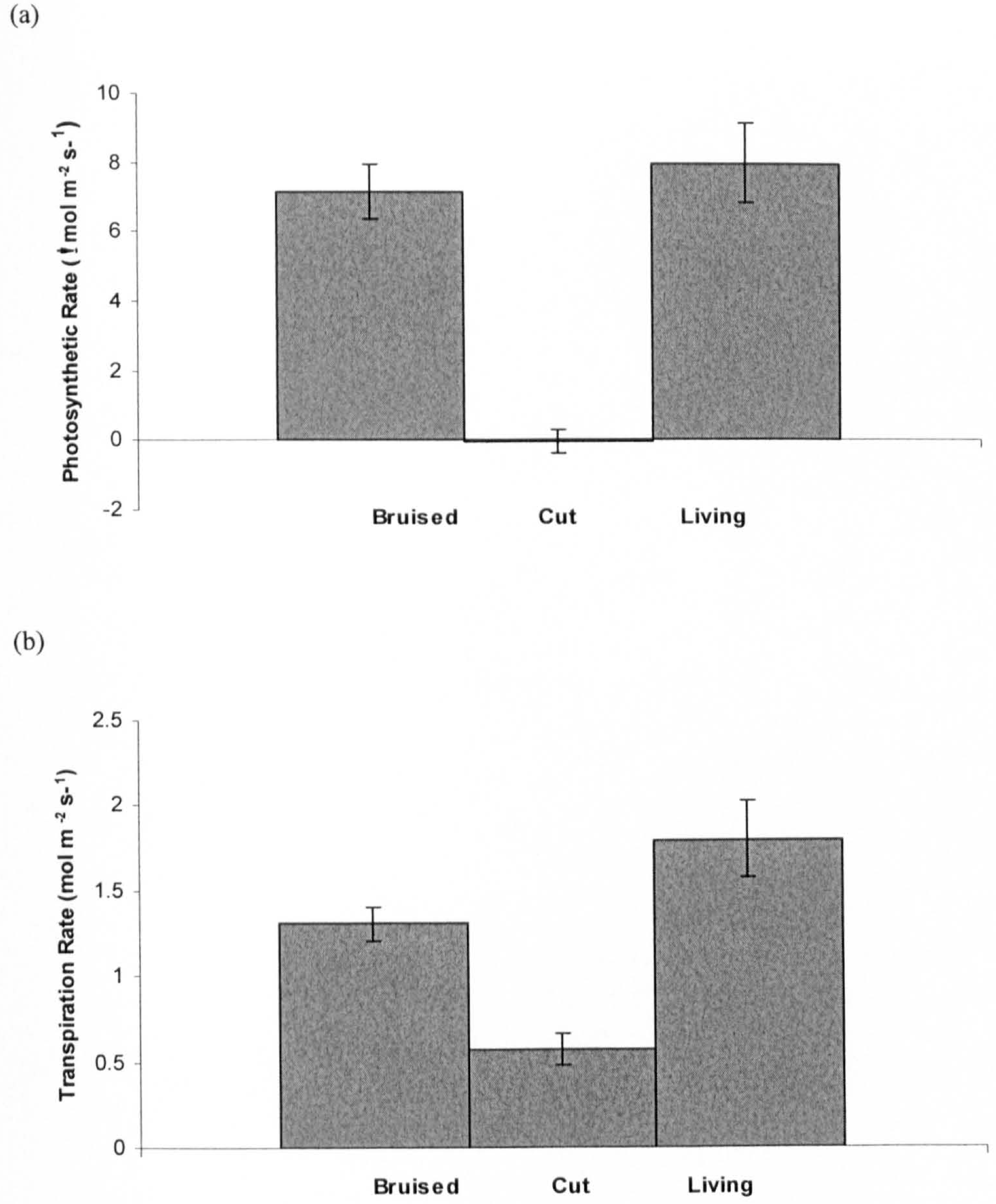


Fig. 3. The arithmetic mean (n=12) (a) photosynthesis and; (b) transpiration rate of fronds cut and bruised three weeks prior. Error bars are ± standard error.

7.3.1.2 Experiment 2

The rate of photosynthesis and the rate of transpiration were both significantly different between fronds over time, $F_{5,10}$=4.4 and $F_{5,10}$=9.59, respectively (Fig. 4). With Treatment b (cut fronds) having the lowest photosynthesis and transpiration rates.

There was also an overall difference in the transpiration rate (Fig. 5) with the cut fronds (Tb) having a significantly lower rate of transpiration, 0.107 mol m^{-2} s^{-1} compared with 0.234 mol m^{-2} s^{-1} for the untreated control (Ta).

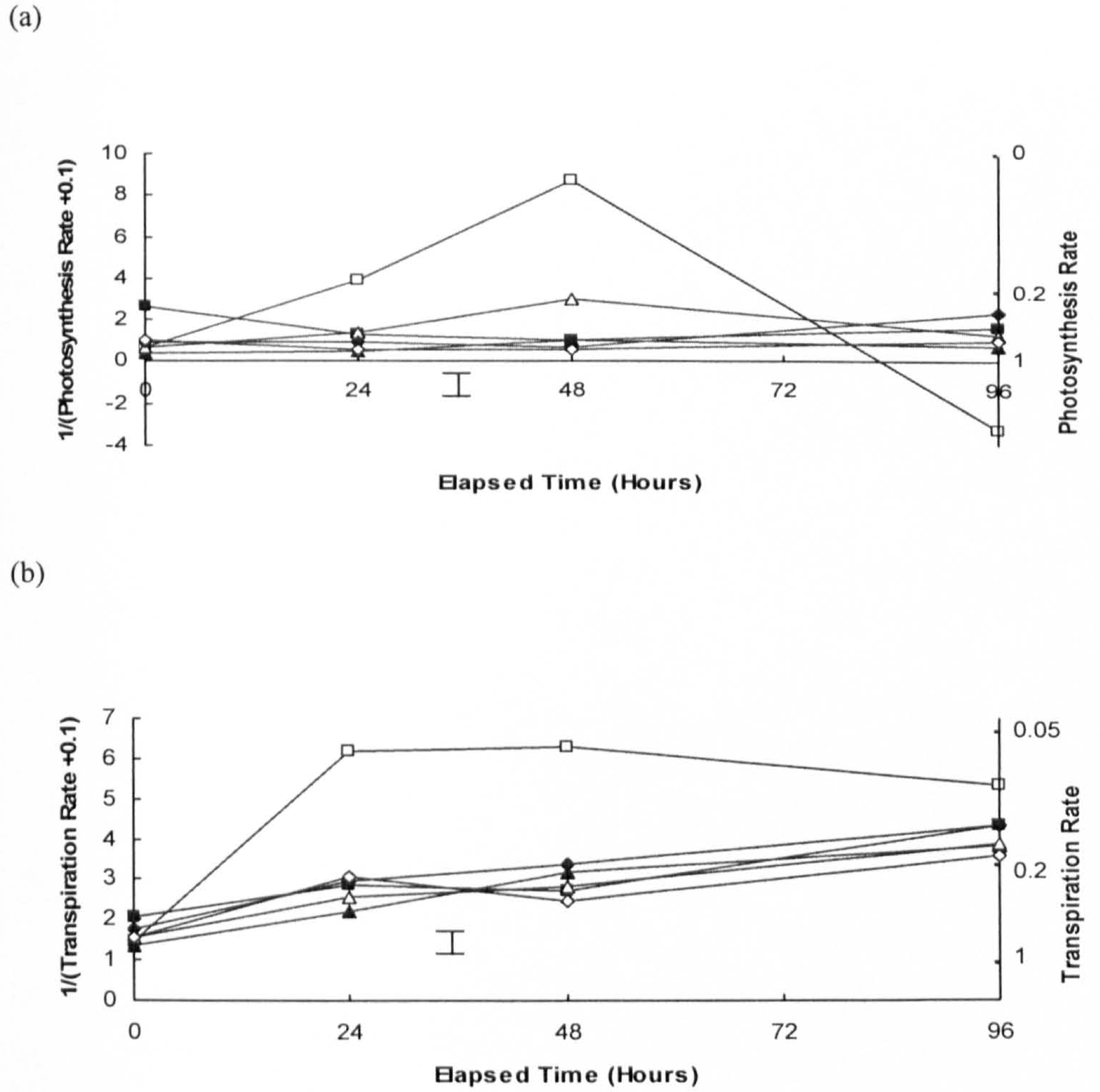


Fig. 4. The (a) photosynthesis rate (n=9) and; (b) the transpiration rate of treated fronds (n=9). Treatment a= Black Square;.Treatment b= White Square; Treatment c= Black Triangle; Treatment d= White Triangle; Treatment e= Black Diamond; and Treatment f=White Diamond.. Error bars are ± 2S.E.D.

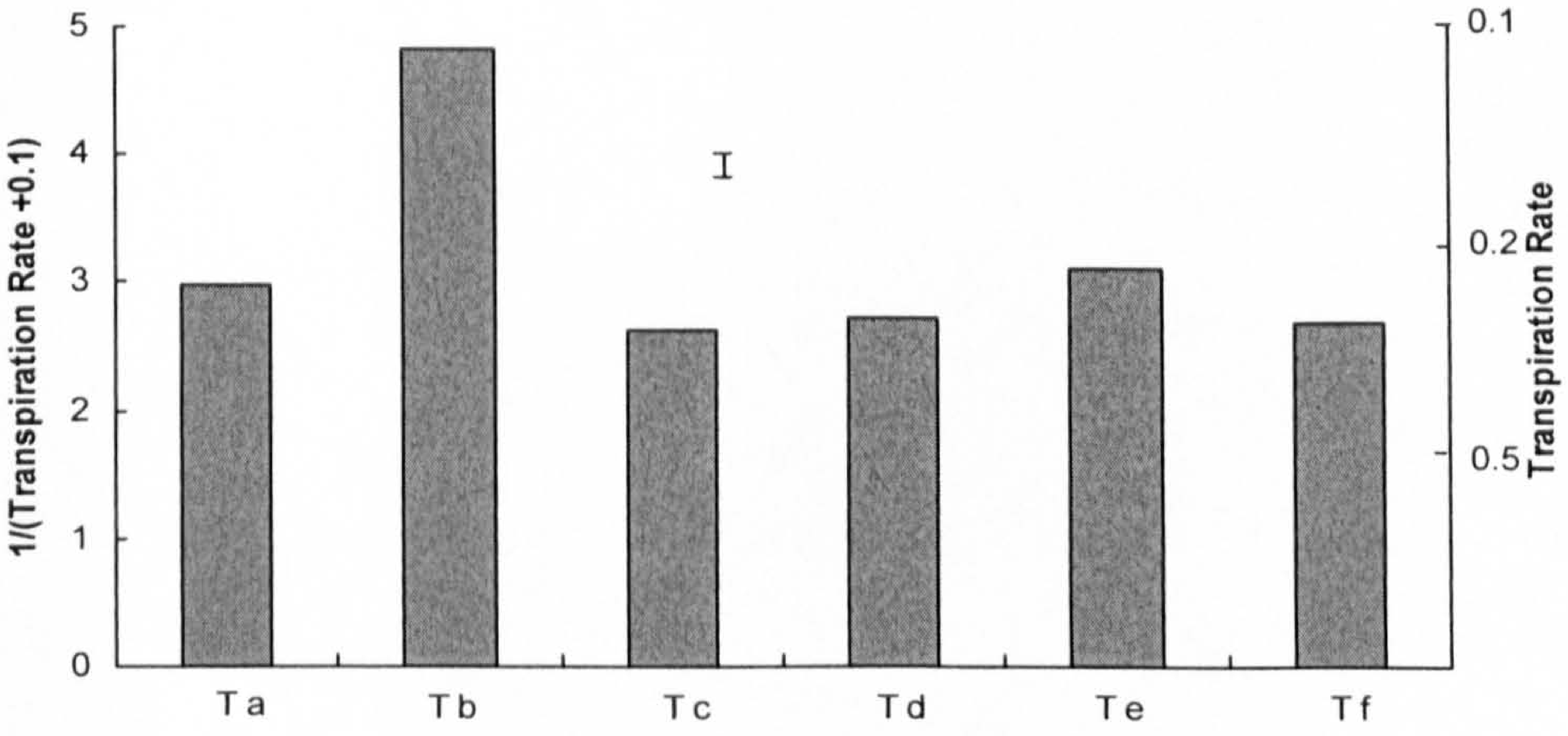


Fig. 5. The mean transpiration rate for treated fronds over 96 hours ($F_{(5,10)}=7.39$ n=144). Ta- Tf reflects the treatments described in Fig. 2. Error bars are ± 2S.E.D.

Transpiration rate was also found to significantly differ between blocks and between monitoring times. A number of factors could have caused the differences in transpiration rate that were not taken into consideration, such as sunlight (Fig. 6).

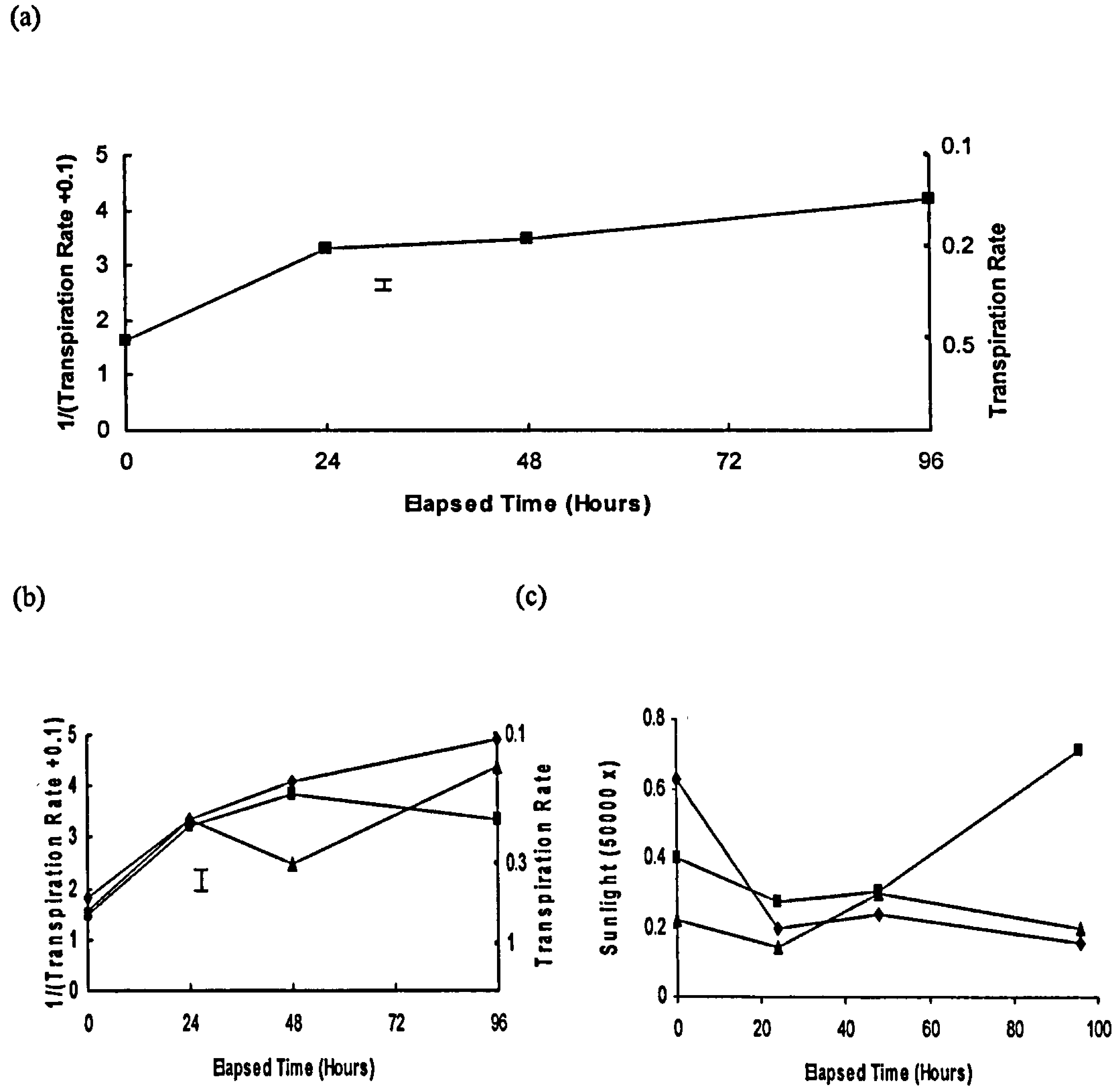


Fig. 6. The transpiration rate of (a) overall mean through time ($F_{1,10}$=39.17 n=54); (b) mean of each block through time ($F_{2,10}$=5.87 n=18) and; (c) the mean sunlight readings (n=12). Square=Block A; Diamond= Block B and; Triangle =; Block C. Error bars are ± 2S.E.D.

7.3.1.3 Experiment 3

To test for treatment effects, the bracken control treatments (bruising and untreated control), were analysed as fixed effects and time as a random effect. The model including treatment was not significantly different from a null model, P=0.2349. Time was tested using repeated measures and again there was no significant temporal response (P>0.05 for all terms, Table 2).

Table 2. The P values for treatment and time tested as a repeated measure (P=0.05*).

	Photosynthesis Rate	Transpiration Rate
Bruised		
Time	0.95	0.68
Time 2	0.75	0.47
Time 3	0.10	0.62
Untreated Control		
Time	0.39	0.75
Time 2	0.08	0.17
Time 3	0.08	0.44

7.3.2 *Observations of Damaged Fronds*

Of the 20 sections, three of the undamaged controls and five of the bruised stems were observed using the SEM. In the bruised fronds, xylem vessels were continually found to be intact despite damage to the hardened outer layers and soft internal tissue (Fig. 7).

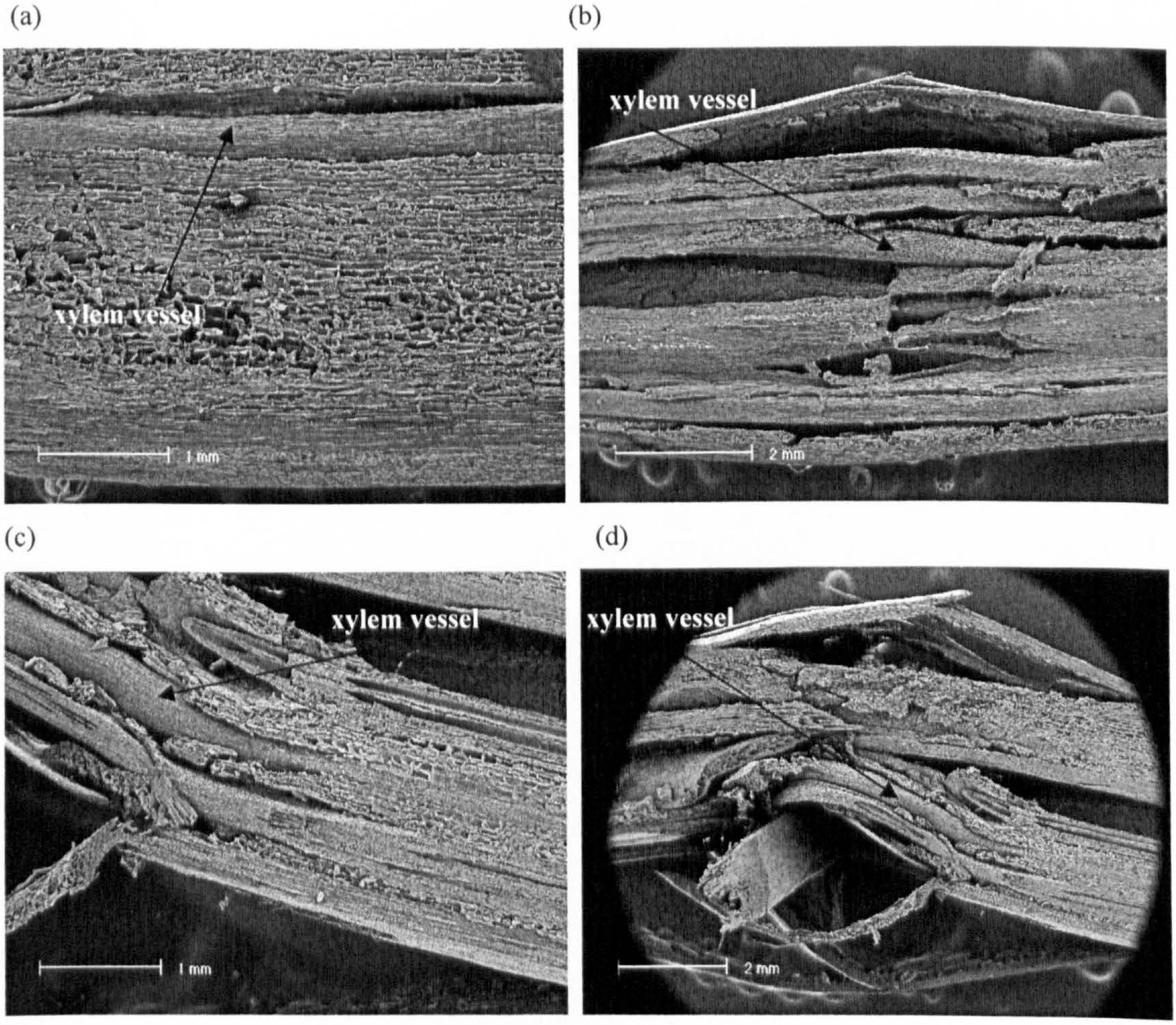


Fig. 7. (a) An undamaged stem with intact xylem vessel and supportive tissue. (b), (c) & (d) sections of stem from three different bruised fronds showing damaged external and soft tissue layers but intact xylem vessels.

This suggests that the fronds transport mechanisms may still be functional even after extensive damage, supporting the results found in Experiment 2 and Experiment 3 were various degrees of damage to the frond stem had little impact on photosynthesis rates and transpiration rates and fronds remained active for weeks after being damaged.

7.3.3 *Is there any impact on the rhizomes as an effect of control due to bruising?*

There was no significant difference between the dry weight of total rhizome mass, storage rhizomes, frond bearing rhizomes or the ratio of frond bearing to storage rhizomes in any of the three years tested, for any treatment (Table 3).

Table 3. The mean total dry mass of rhizomes for (a) each treatment (n=3) and (b) each rhizome section (n=18) in kgm^{-2} ± standard error, n=3.

(a)

Sampling Year	Dry Mass Fraction (kgm^{-2})			
	Frond Bearing	Storage	Total	Ratio (=Frond Bearing/Storage)
ET0 (2005)	0.36±0.43	1.57±0.66	2.11±0.75	0.17±0.25
ET1 (2006)	0.36±0.39	1.55±0.74	2.02±0.84	0.18±0.21
ET2 (2007)	0.35±0.39	1.61±0.67	2.09±0.78	0.17±0.18

(b)

Sampling Year	Total Dry Mass Fraction (kgm^{-2})					
	U	R2	R3	C2	C3	SS
ET0 (2005)	2.22±0.79	2.28±0.85	2.03±0.73	1.83±0.76	1.72±0.76	2.61±0.40
ET1 (2006)	2.57±1.14	2.26±0.51	2.24±0.42	1.66±0.79	1.74±0.83	1.64±0.76
ET2 (2007)	1.85±0.86	1.73±0.75	2.95±0.60	2.20±0.51	2.13±0.76	1.70±0.64

7.4 Discussion

7.4.1 *Do the fronds remain alive after bruising, if so, is performance comparable to untreated fronds?*

Bruised fronds remained alive and green for up to seven weeks after the initial bruising treatment, with no significant difference between the photosynthesis and transpiration rates in bruised and untreated fronds. In Experiment 2 the significant differences reflected the fronds cut completely (Fig. 4), with other treatments, representing lesser damaged fronds, being comparable to the untreated controls. This suggests that increasing the amount of damage caused by the bruiser, such as increasing the weight, will have little effect, at least in the short term, on frond survival. Even in severely damaged fronds, key structures such as the xylem vessels remaining intact, despite extensive damage to other tissues (Fig.7). Although the phloem vessels have not been identified in this study it is possible that the fronds are still translocating carbohydrates to the rhizome to the same degree as the untreated controls as they are producing carbohydrate an equivalent rate. However, it is also possible that the damage cause by the bruiser is causing less efficient transport from the frond the rhizome, thus an accumulative effect will be seen in future years if bruising is continued.

The variation seen through time for this experiment may relate to factors other than management, with conductance limited by light (Roberts *et al.*, 1984), time of day and hence sunlight may have been significant (Fig. 6). Other untested variables such as; soil moisture and atmospheric humidity (Roberts *et al.*, 1984) may also have affected photosynthesis.

7.4.2 *Is there any impact on the rhizomes as an effect of control due to bruising?*

None of the bracken control treatments had any impact on the rhizomes. Paterson *et al.* (1997) found cutting twice per year reduced rhizome biomass after just one year of treatment, although only significantly in three out of six treatments. Mechanical control aims to withdraw the maximum amount of carbohydrates and nutrients from the rhizome reserves (Hunter, 1953; Williams & Foley, 1976). When a cutting strategy is used it is advisable to cut the fronds when dry weight and carbohydrates in the rhizome are at an annual low (Williams & Foley, 1976). Normally mid-June to late-July in the UK (Anon, 2005; Southern Uplands Partnership, 2001), before the new assimilates start being translocated from the fronds to the rhizomes in large amounts in late July/early August (Williams & Foley, 1976). As each year the rhizome is weakened by being cut before the fronds become net importers of carbohydrate (Lowday & Marrs, 1992a) the effect becomes accumulative. This could also be the case for bruised bracken but a steady increase, rather than decrease, in total rhizome biomass is seen for bruising and cutting three times a year (Table 3b). This suggests that the rhizomes are not being 'bled of resources', at least over this time period. The fact that fronds also photosynthesise and transpire at comparable rates to the untreated controls for at least seven weeks after bruising suggests that the fronds may still act as net exporters of carbohydrate to the rhizome, and yearly bruising will need to be carried out for longer to see any effect.

The reduction in frond bearing rhizomes or the lowering of the ratio of frond bearing to storage rhizomes would be expected with the application of asulam (Veerasekaran *et al.*, 1978) as the herbicide acts by eradicating buds. However, Williams & Foley (1975) and Paterson *et al.* (1997) found asulam had no effect on the storage rhizome mass in the two years after treatment. This suggests that the few fronds emerging in the years following treatment are either producing enough carbohydrate to regenerate the rhizome system or a significant reduction will be seen in future years (Le Duc *et al.*, 2003) with continued treatment.

Variation from year-to-year seen by others (Le Duc *et al.*, 2003; Marrs *et al.*, 1998c; Pakeman & Marrs, 1994; Paterson *et al.*, 1997) is not reflected here. Le Duc *et al.* (2003) hypothesised that a dry summer followed by two wet summers was the cause of this variation as soil aeration is a limiting factor for bracken (Poel, 1961). This may be the case here with 2004 being a wet summer (meteorological data for Sheffield, 10km from the site, May-September rainfall average is 8.3% above England's 1971-2000 average) followed by a dry summer in 2005 (5% below average) meaning the decline in rhizome mass caused by treatment could be counteracted by a better growing season.

7.5 Conclusions and Future Work

After only one year of bracken control, cutting and spraying treatments all reduced *P. aquilinum* cover in June and in August, with cutting thrice per year being the most effective. However the bruised plots showed an increase in cover in comparison to the untreated controls. Expected declines in rhizome mass (Paterson *et al.*, 1997; Le Duc *et al.*, 2003) and litter mass (Marrs *et al.*, 2007) were not seen in the cut and sprayed treatments at this early stage. It could be assumed that bruising would act with the same accumulative impact as cutting (Cox *et al.*, 2007) but continued annual treatment and monitoring will be need to test this.

The aim of both cutting and bruising is to disrupt the resource flux between rhizomes and fronds. In intact bracken there are three stages (derived from Williams & Foley 1976; Marrs & Watt 2006):

Stage 1: Rhizomes are the source; fronds are the sink, the rhizomes resources are used to fuel frond growth.

Stage 2: Intermediate point: fronds become self-sustaining in terms of carbon through photosynthesis; nutrients may still be translocated from rhizome.

Stage 3: Fronds are the source, and rhizomes the sink. As season progresses fronds do not grow further and presumably carbohydrates translocated back to the rhizomes.

The aim of cutting and bruising is to maximise the resource withdrawal in Stage 1. Cutting does this by physical removal of tissue, removal of apical dominance and a further removal of resources from the rhizomes as new fronds are produced in a repeat of Stage 1.

Our results suggest that bruising is less effective because the physiological processes (photosynthesis and transpiration) remain at a similar rate to untreated stands. As there is no evidence that the carbohydrates leak from the damaged fronds, and they do not grow any further, it is reasonable to suggest that they export the resources back to the rhizome. The lack of new fronds being produced after bruising suggests their production is prevented either by the continuation of hormone transport, or shading by the bruised fronds which carpet the ground.

This study must, however, only be viewed as preliminary. The entire experiment needs to be carried out over a much longer time period, Moreover, future studies should incorporate tracers (radioactive or stable isotopes) to study carbohydrates flux between compartments through time in intact bracken (both amounts and rates); and how these fluxes are impacted by management (cutting, bruising and herbicide application). This information is essential in order to develop more effective models of the bracken plant and its control.

Chapter 8

Factors affecting the restoration of heathland and acid grassland on *Pteridium aquilinum*-infested land across the UK: a multi site study

8.1 Introduction

There is an increasing need for restoration ecology to assist in the development of national strategies, for example in the implementation of agri-environments schemes developed by the European Union (MAFF, 1993, 1996) and Biodiversity Action Plans set to meet conservation objectives (Anon, 1995a, b). Policy-makers require practical management strategies that are cost-effective and deliverable in a wide range of situations. Inevitably, this will require some form of multi-site experiment to ensure that there is: (a) a broad geographical coverage, and (b) a reasonable coverage of the types of restoration problem likely to be encountered. Surprisingly, there have been relatively few attempts to carry out such large-scale, multi-site experiments in ecological restoration especially over the longer-term; most studies have been either single-site or of short duration (< 8 years) (e.g. Pywell *et al.*, 2002; Pakeman, 2004; Marrs *et al.*, 2004).

The difficulty in providing general advice to policy makers becomes more complex when the restoration aims are to control a single invasive weed which invades a range of community types and establish new understorey vegetation as the required target vegetation will vary in different situations. One example of this problem is *Pteridium aquilinum* (L.) Kuhn (bracken) (nomenclature; Stace (1997), for higher plants; Hill *et al.*, (1991, 1992, 1994) for bryophytes; Coppins (2002) for lichens) control in the United Kingdom, where the policy aim is to reduce *P.aquilinum* infestations and restore either heathland or grassland vegetation. Dense *P.aquilinum* is a problem species for conservation in most situations, as it is a long-lived robust clonal species (Le Duc *et al.*, 2003) producing a dense litter layer that prevents the establishment of other species (Frankland, 1976) and competes effectively with heathland and grassland species, resulting in a reduction in diversity of plant species (Pakeman & Marrs, 1992).

Thus, ecological restoration of dense *P.aquilinum* patches requires at least two treatment strategies: control of the *P.aquilinum*, and restoration of suitable target vegetation. Under experimental conditions, and in practice, *P.aquilinum* control is often highly variable and gives conflicting results (Le Duc *et al.*, 2000) and vegetation development during bracken control is often slow and unpredictable, especially in upland areas of the UK (Marrs *et al.*, 1998a). This variability in the success may be due either to regional effects (climate, geology), or to localized effects interacting with the management applied.

Localized effects might be ascribed to (1) local microclimate or soil conditions, (2) local standing vegetation, (2) its derived seed rain, (4) recruitment from the soil propagule bank, and (5) potential seed rain derived from the surrounding landscape.

In order to develop a national policy for bracken control and restoration of alternative vegetation, a series of experiments was set up at four regional locations throughout the UK; at two of these locations replicated experiments were set up to assess local scale effects. The experiments assessed the efficacy of five treatments (cutting once or twice per year, a combination of cutting or asulam spraying in year one followed by asulam spraying or cutting in year two and asulam in year one only) designed to control *P.aquilinum* relative to an untreated comparison in a range of contrasting ecological situations (Le Duc *et al.*, 2007a; Cox *et al.*, 2007a). Accordingly, these control treatments were combined with site-specific treatments designed to restore appropriate heathland or grassland vegetation, as thought appropriate to the site. Thus, the experiments were a compromise to assessing the success bracken control at the national scale and local scale control/restoration practices.

We hypothesized that: (1) Local differences between sites would affect community change; (2) Treatments applied to control *P.aquilinum* (same at all sites) would influence community change; and, (3) Treatments applied at the individual site level to restore vegetation influences community change towards the target vegetation. The experiments started in 1993 or 1994 and were monitored for 9 or 10 years.

8.2 Methods

This chapter discusses the results of species data from the six experiments described in Chapter 1.

8.2.1 *Data analysis and presentation*

Data were transformed using standard procedures (Sokal & Rohlf, 1995), species richness using $(Y + 0.5)^{0.5}$, and species cover using $\ln(Y + 1)$. Estimates of values per treatment combination per block were obtained by combining data per quadrat, after transformation, by sub- (sub-) plot.

Individual response variables (species cover, species richness and measured abiotic factors) were analyzed for change through time for each site separately. Some taxa (eg *Cladonia* spp. *Betula* spp., *Carex* spp. and *Festuca* spp.) were grouped into aggregate taxa, denoted spp. As our objective was to measure the response of species through time, repeated-measures ANOVAs with the method of polynomial contrasts were used (Gurevitch & Chester, 1986). The value of this approach is that it is possible to test for treatment effects as in ANOVA, but the shape of the temporal trends of these treatment effects can also be identified. This approach becomes more useful with longer-term datasets. Results are presented in the text as; the order number (referring to the shape of the polynomial curve, 1st order being linear, and subsequent orders being the equivalent polynomial (i.e. 2nd order = quadratic), the F-test statistic and n. As only significant results after Bonferroni correction are discussed here, they are conservative.

Time was denoted as elapsed time, with the start year designated year=0. Analysis was carried out using PROC GLM (SAS, 1989). For each site we used the appropriate analysis of variance model; however for Cannock and Sourhope we initially analyzed both experiments together, with experiment included as the first level in a split-split-split plot design. Where a significant difference was indicated but that species was absent from one experiment, the analysis was repeated for the single experiment where the species was present.

The analysis of variance model changed when new treatment combinations were added into an experiment, changing the design from a split-plot to a split-split-plot one; thus different segments of the time series were analyzed using different models. At Sourhope there was an additional problem in 2001, data could not be collected because of the Foot and Mouth epidemic in Britain. At this site the experiments were also started in different years, and accordingly the loss of the 2001 data resulted in the absence of two years information.

Bonferroni correction was used to adjust for the Type I error rate (Sokal & Rohlf, 1995; Cabin & Mitchell, 2000). For the June sampling there were 85, 131, 110 and 144 analyses at Cannock, Carneddau, Peak and Sourhope respectively. With $\alpha = 0.05$ the critical probability levels of 0.0006, 0.0004, 0.0005 and 0.0004 were used to assess significance. A common problem with this type of data is that many species datasets contain a large number of zero entries. Here, only species which were present in at least 20% of all recorded quadrats are presented. Data for other species where a significant response was found are available from the corresponding author.

A very large number of significant results were derived, even after Bonferroni correction. In order to simplify the presentation and interpretation of the results a three level approach to data presentation and analysis audit has been used. Level 1 is the raw data held in the web database; www.appliedvegetationdynamics.co.uk, Level 2 includes all the significant results in graphical form along with tables of all significant results from the repeated measures ANOVA using polynomial contrasts held in Electronic Appendix 2, and Level 3 are the data presented here, which includes just the lowest significant order found in the polynomial contrast analysis.

8.3 Results

8.3.1 *Effects through time*

Significant variation in time was found for 10 species across all four sites (Table 1). Three main response patterns for time effects were detected (Table 1); Type 1, are species starting from zero or a very low level, increasing to reach a peak before falling again; Type 2, are species increasing steadily over time and Type 3 are species declining over time.

Table 1. Species with significant variation through time not associated with any treatment. Type 1, are species starting from zero or a very low level, increasing to reach a peak before falling again; Type 2, are species increasing steadily over time, and Type 3 are species declining over time. After Bonferroni correction P= 0.0006, 0.0004, 0.0005 and 0.0004 for Cannock, Carneddau, Peak and Sourhope respectively.

Species	Site	Pattern Type	Order of Effect	Df	F Value
Deschampsia flexuosa	Peak	3	2nd	1,10	106
Festuca ovina	Carneddau 98-03	3	4th	1,10	615
Festuca rubra	Carneddau 98-03	2	2nd	1,10	242
Galium saxatile	Carneddau 94-97	1	1st	1,10	136
Galium saxatile	Peak	2	3rd	1,10	249
Pleurozium schreberi	Carneddau 98-03	2	3rd	1,10	57.9
Rhydtidiadelphus squarrosus	Carneddau 94-97	1	1st	1,10	31.8
Rhydtidiadelphus squarrosus	Carneddau 98-03	1	4th	1,10	123
Rumex acetosella	Cannock	2	6th	1,10	3077
Species Richness	Carneddau 98-03	2	1st	1,10	29.85

Species richness showed a Type 1 response at the acid grassland site Carneddau with a significant decline starting in 1998 (ET=5) after an initial increase. Declining from 10.5 species m^{-2} in 1998 to 9 species m^{-2} in 2003 (1st order, $F_{(1,10)}=29.85$ n=216). For individual species different responses were detected at different sites and in different time periods on the same sites e.g. *Galium saxatile* at the Carneddau acid grassland site (1st order, $F_{(1,10)}=136$ n= 162) and the Peak heath site (3rd order, $F_{(1,10)}=239$ n= 216). Although *G.saxatile* had similar % cover at both sites (ranging from 0.7 to 10.0 %) and a dip in year 7 (2000) the two sites showed different response patterns. At Peak an overall increase through time was observed, perhaps influenced by this species' significant response to bracken control treatments. At Carneddau, *G.saxatile* cover increased to reach a peak in year 4 (1997) before declining; no other significant effects were observed.

8.3.2 Hypothesis 1: Local differences between sites would affect community change

8.3.2.1 *Between-experiment spatial effects*

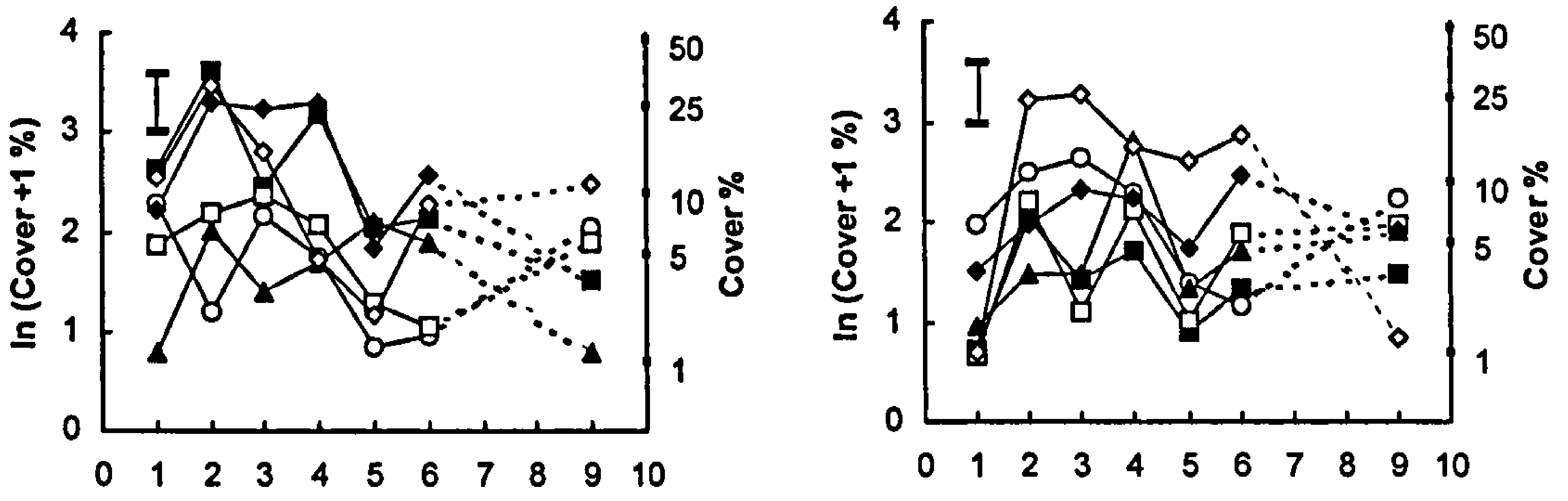
Two types of responses were detected. The first included species that were present at one experiment but not the other, these species normally appeared in small quantities in a limited number of years. At Cannock these were: *F.ovina, Dicranum bonjeanii* and *Quercus* spp. present only at Cannock 1; *Pinus sylvestris* and *Vaccinium vitis-idaea* present only at Cannock 2, and at Sourhope: *Dactylis glomerata* and *Helictotrichon pratense* were found only at Sourhope 2. Only *V.vitis-idaea* appears in more than 20% of quadrats. The second were species that were present on both experiments but there was a significant difference in cover between experiments. *R. acetosella* (6th order, $F_{1,2}=3207$ n=36) with greater cover at Cannock 1 compared to Cannock 2 and *Agrostis vinealis* with a greater cover at Sourhope 1 (1st order, $F_{1,2}=13741$ n=24). Superimposed on the site responses for *A. vinealis* at Sourhope was an obvious cyclic effect for at least 6 years, as there was no data between years 7-9 so no inference can be drawn for this period.

8.3.2.2 *Significant experiment × bracken control × restoration treatment interactions*

D.flexuosa (2nd order, $F_{(5,12)}=12$ n=2) at Sourhope displayed a complex series of responses (Fig. 1), with a differential cover between the experiments, being greater at Sourhope 1 (1-25%) compared to Sourhope 2 (0.5-5%). At Sourhope 1 (Fig. 1i & ii), where no seeding was applied *D. flexuosa* cover was lowest in the Spray plots. This was followed by a recovery period until declining again after year

6. In the seeded treatment SprayCut follows a similar pattern with the increase in *D. flexuosa* cover being greater but again declining after year 6. At Sourhope 2 (Fig. 1iii & iv), *D. flexuosa* was greater in the CutSpray treatment regardless of whether or not seed was applied.

(i) Sourhope 1, no treatment (ii) Sourhope 1, grass seeding



(iii) Sourhope 2, no treatment (iv) Sourhope 2, grass seeding

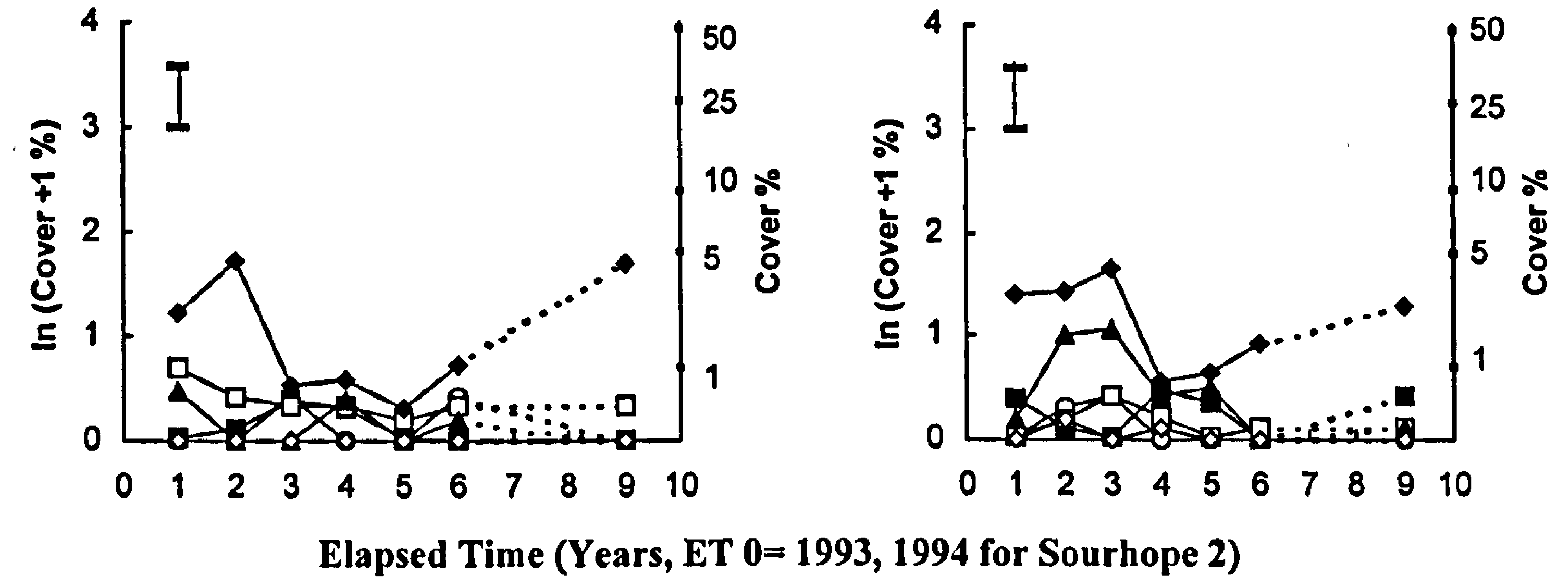


Fig. 1. Effects of space (experiment), bracken control and restoration treatments on species *Deschampsia flexuosa* at Sourhope (2^{nd} order, $F_{(5,12)}=12$ n=2) (i) Sourhope 1, no restoration treatment (ii) Sourhope 1, grass seeding (iii) Sourhope 2, no restoration treatment (iv) Sourhope 2, grass seeding. No treatment= white circle; Cut1pa= black square; Cut2pa= white square; Spray= black triangle; CutSpray= black diamond; SprayCut= grey diamond. Error bars are ± 2S.E.D (standard error of the difference between two means (Sokal & Rohlf 1995)).. Gaps in the temporal data are presented as a dashed line.

8.3.3 Hypothesis 2: Treatments applied to control *P.aquilinum* (same at all sites) influences community change

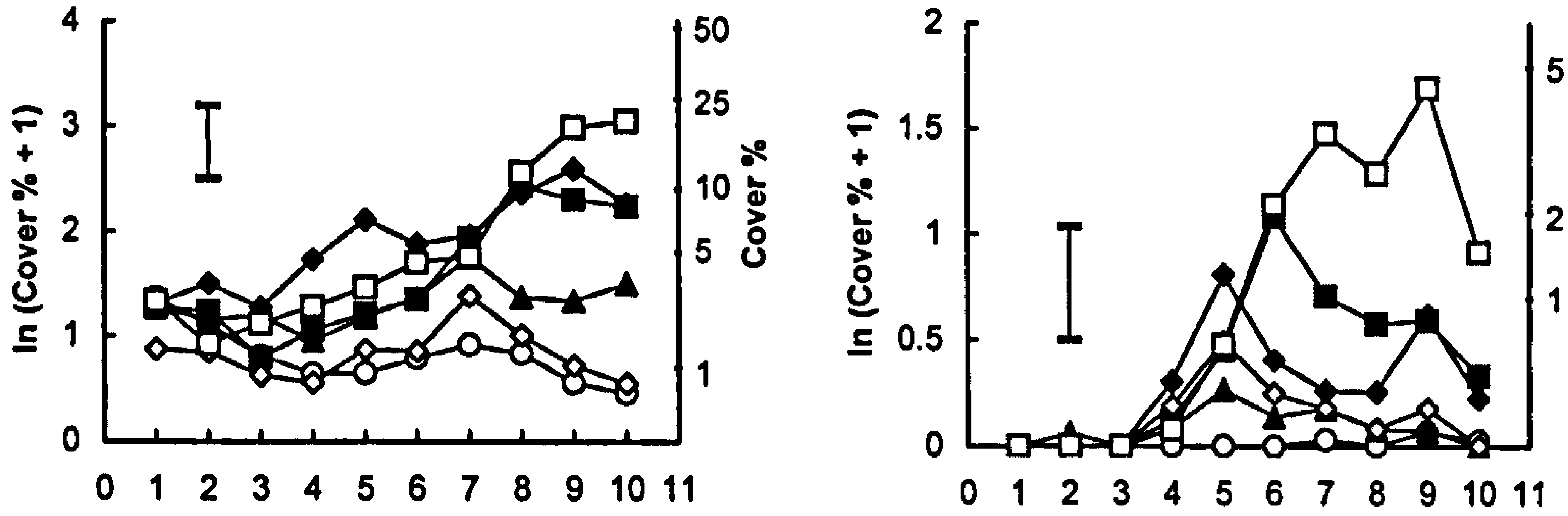
Of the 470 species tested across the four sites, bracken control treatments on their own increased only three species; two higher plants and one bryophyte, at the heath sites. No positive effects were found at the acid grassland sites (summarized, Table 2). All bracken control treatments increased *D. flexusoa* cover (1st order, $F_{(5,10)}$= 17.31 n=12, Fig.2a), *Campylopus introflexus* (1st order, $F_{(5,10)}$= 12.1 n=12, Fig. 2b) at Cannock and *G.saxatile* (5th order, $F_{(1,12)}$=13.6 n=18, Fig. 2c) at Peak in comparison to the untreated plots. A steady increase in cover over time resulted in the Cut2pa plots having the greatest cover for all three species by the final year of sampling. Maxima of 20% (*D.flexuosa*) and 24% (*G.saxatile*) were reached in the final year, with *C.introflexus* reaching 4.5% in the penultimate year. The increase in *D.flexuosa* occurred from an initially small cover (1.25%) despite having the greatest cover of any species, after *P.aquilinum* and litter, in the untreated plots at Cannock 1. A similar pattern was seen for *G.saxatile* at Peak with a 0.5% cover in untreated plots. The increase in already common species could be replacing the previously dominant bracken litter which fell from 65 and 85% in untreated plots to 19 and 1% in cut twice per year plots at Cannock and Peak, respectively.

Table 2. A summary of the significant species responses to the multi-site bracken control treatments. Experiment in the Significant Effect column refers to a significant difference between Sourhope 1 and Sourhope 2.

Site	**Species**	**Species Response**	**Treatments which increased species cover**	**Significant Effect**
Cannock	*Deschampsia flexuosa*	Increased	Cutting twice per year	Bracken Control
Cannock	*Campylopus introflexus*	Increased	Cutting twice per year	Bracken Control
Peak	*Galium saxatile*	Increased	Cutting twice per year	Bracken Control
Sourhope	*Deschampsia flexuosa*	Complex	-	Experiment × Bracken Control × Grass Seeding
Carneddau	*Pseudoscleropodium purum*	Decreased	-	Bracken Control

Pseudoscleropodium purum (overall effect, $F_{(5,10)}$=14.09 n=108,) at Carneddau was most abundant in the untreated plots. This species had comparatively low cover, reaching a maximum of 0.4%.

All bracken control treatments at Peak increased species richness in a linear model (1st order, $F_{(5,10)}$=27.01 n=18) compared to the untreated plots, and by 2003 the cutting treatments were the most successful.



(a) *Deschampsia flexuosa* at Cannock

(b) *Campylopus introflexus* at Cannock

(c) *Galium saxatile* at Peak

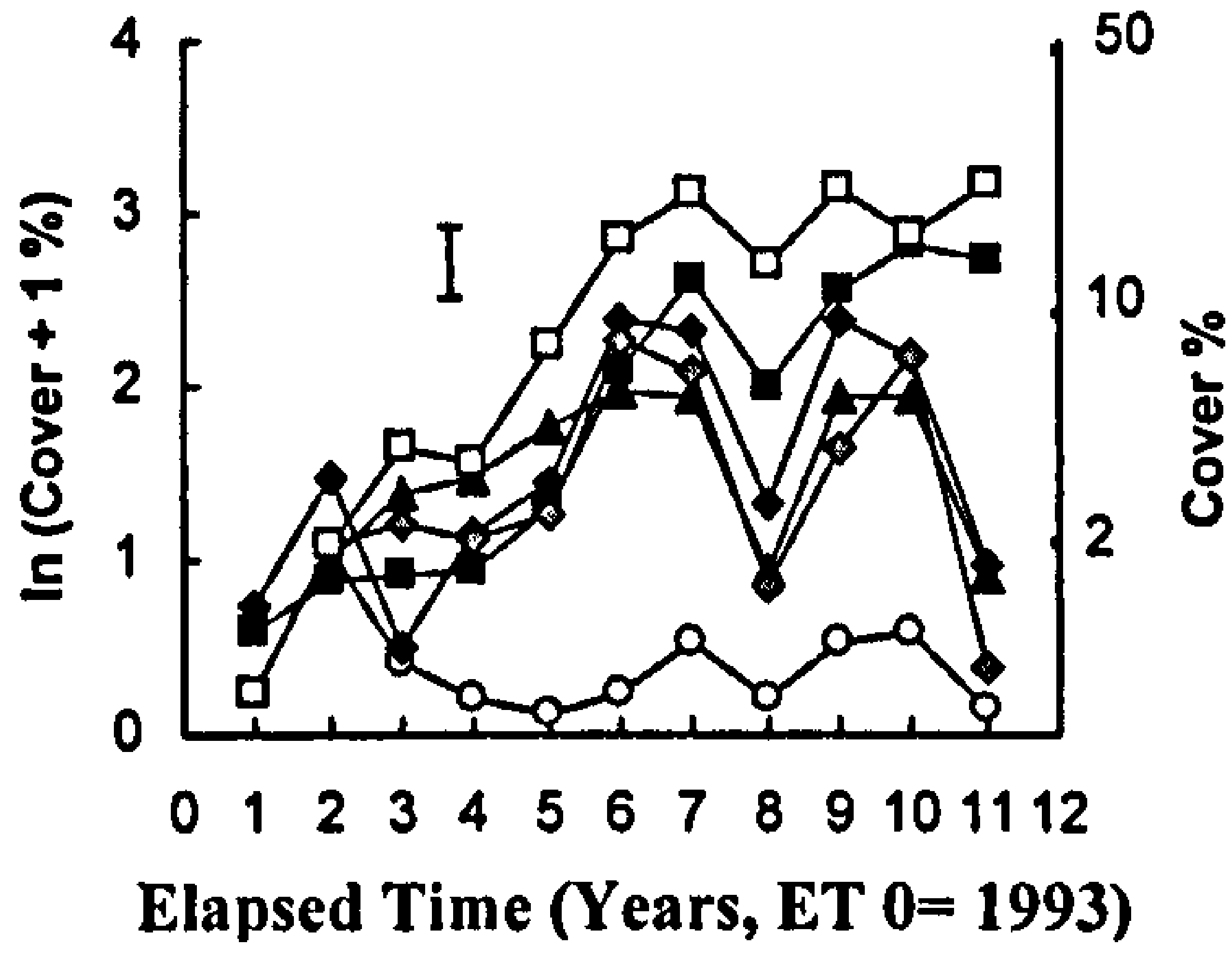


Fig. 2. Effect of bracken control treatments on (a) *Deschampsia flexuosa* at Cannock (1st order, $F_{(5,10)}$= 17.31 n=12), (b) *Campylopus introflexus* at Cannock (1st order, $F_{(5,10)}$= 12.1 n=12), (c) *Galium saxatile* at Peak (5th order, $F_{(1,12)}$=13.6 n=18). No treatment= white circle; Cut1pa= black square; Cut2pa= white square; Spray= black triangle; CutSpray= black diamond; SprayCut= grey diamond. Error bars are ± 2S.E.D (standard error of the difference between two means (Sokal & Rohlf 1995)).

8.3.4 Hypothesis 3: Treatments applied at the individual site level to restore vegetation influences community change towards the target vegetation

8.3.4.1 *Grazing at the Peak* Calluna *heath*

Two species showed an overall effect of grazing (Table 3). *D.flexuosa* (overall effect, $F_{(1,12)}$=32.5 n=540) had a greater cover in the fenced treatment. In contrast, *F.ovina* (overall effect, $F_{(1,12)}$=33.2 n=540) and species richness (overall effect, $F_{(1,12)}$=40.8 n=540) were greater in the unfenced treatment. Three species (*F.ovina* (3rd order effect, $F_{(1,12)}$=26.5 n=54), *F.rubra* (1st order effect, $F_{(1,12)}$=23.2 n=54), *Hypnum jutlandicum* (1st order effect, $F_{(1,12)}$=25.1 n=54) showed a significant time × fencing interaction, increasing in the unfenced treatment.

Table 3. Fencing at the Peak heath site; back-transformed mean percent cover values, df= 1,12.

Species	Unfenced	Fenced	Order of Effect	F Value
Deschampsia flexuosa	7.17%	17.21%	Overall	32.5
Festuca ovina	1.23%	0.29%	Overall	33.2
			3rd	26.5
Festuca rubra	1.38%	0.58%	1st	23.2
Hypnum jutlandicum	1.28%	0.47%	1st	25.1

8.3.4.2 *Fertilizer/disturbance at the Cannock* Calluna *heath*

Fertilizer addition produced a lower *Calluna vulgaris* cover at Cannock 2 (4th order, $F_{2,24}$=10.5 n=12) either no treatment or surface disturbance + fertilizer until year 9 when it increased inline with the other two treatments (Fig. 3). Although found at both sites *C.vulgaris* was consistently greater at Cannock 2 (Fig. 3), restoration treatments were significant only at this site.

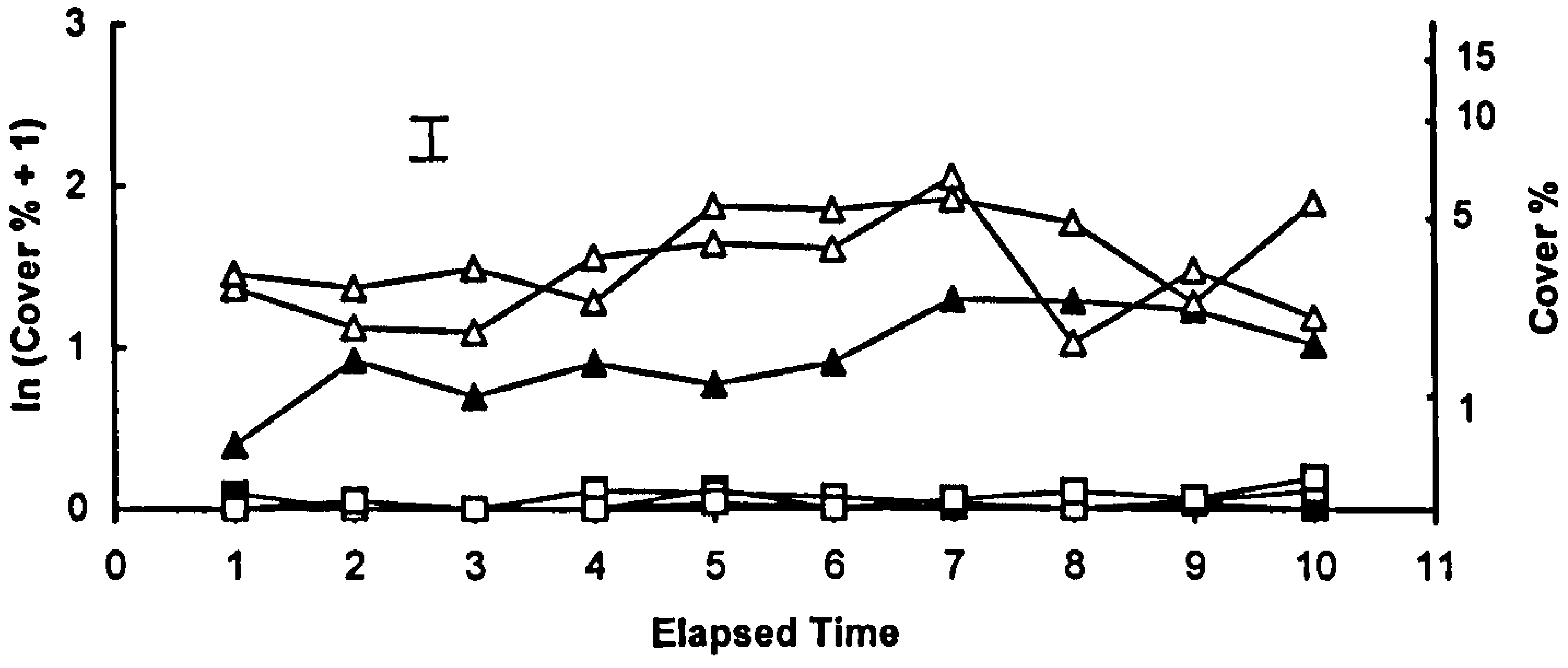


Fig. 3. Significant effect of space (experiment) × restoration treatment through time on *Calluna vulgaris* cover at Cannock (Cannock 1 = square; Cannock 2 = triangle; no treatment= white; fertilizer= black; fertilizer and surface disturbance= grey); 4th order, $F_{(2,24)}$ = 10.5 n=12. Elapsed Time=0 is 1993. Error bars are ± 2S.E.D (standard error of the difference between two means (Sokal & Rohlf 1995)).

8.3.4.3 *Seeding at the Peak* Calluna *heath site*

At Peak *Calluna* brash addition increased *C.vulgaris* cover to 0.19% (overall effect, $F_{(2,48)}$=9.63 n=360), whereas *Calluna* seeding had very little impact when compared to untreated plots, both with a cover of 0.07%.

8.3.4.4 *Grass seeding at the acid grassland sites*

There were no significant effects of seeding or any of its interactions on any species at Carneddau or Sourhope, this included the sown species.

8.3.4.5 *Effects of spot spraying at the Carneddau acid grassland*

F.ovina showed an increase in cover in sprayed plots, (overall effect; 12% compared to 8%; $F_{1,36}$=29.24 n=54).

8.4 Discussion

This series of long-term experiments allowed us to test a series of treatments deigned to control an invasive species (*P.aquilinum*) and restore different target communities. The results assist in developing national implementation policies.

8.4.1 Hypothesis 1: Local differences between sites would affect community change

There were a considerable number of spatial effects detected, between experiments on the same site and as a result of spatial effects in interaction with applied treatments. This result might appear an obvious one, in that it confirms that local spatial effects control restoration processes. Results were, however, complex and contradictory. For example, at Sourhope two experiments located < 2.5 km from each other showed; (1) Complex significant results, including synchronous peaks of *A.vinealis* in the different experiments, which were started in different years, suggesting that weather was the main driver for this species, although this remains to be confirmed experimentally. (2) *D.flexuosa* responds differently to the same treatments at the two Sourhope sites. Observations at the Peak heathland in March 2005 illustrate the importance of local spatial effects. All of the mature tree specimens (*Betula pubescens, Sorbus acuparia* and *Quercus petraea*) in the experimental area were in the un-grazed plots of Block A, and all were approximately 10 years old (M.G. Le Duc & H.A. McAllister, personal communication). This suggests that recruitment occurred as the *P.aquilinum* vegetation was initially controlled and this particular block was nearest to the seed sources (Tong *et al.*, 2006) or had better access to dispersal vectors. There is also potential for similar colonization at other sites with *Betula* stands common in the vicinity of Cannock, Sourhope (Ghorbani, 2005). However, natural colonization can take many years where bracken had been controlled (Marrs & Lowday, 1992). With bracken litter acting as a potential trap for *C.vulgaris* (Ghorbani, 2005) and, potentially, other seeds.

Taken collectively, these spatial effects suggest that it is almost impossible to develop a "one-size-fits-all" national policy that will guarantee the development of a predicted target vegetation community, because community development involves so many uncontrollable factors, for example, the regional and local seed pool, dispersal of seed on to a given site, which will depend on micro-climatic factors, the site propagule bank and the site conditions when the seeds arrive or begin to germinate (Harper, 1977). *C.vulgaris* was found to be common in the seed bank at both Cannock sites (Ghorbani, 2005). Although less potential is seen for development of target species from existent seed banks at Sourhope and Carneddau in addition the heavily grazed dense sward at Carneddau limiting colonization (Ghorbani, 2005).

8.4.2 Hypothesis 2: Treatments applied to control *P.aquilinum* (same at all sites) influences community change

Relatively few effects of the bracken control treatments were found on the cover of other plant species, and where they were detected, it was only at single sites. At the acid grassland sites (Carneddau and Sourhope) no species were found to increase significantly. At the *Calluna* heath sites (Cannock and Peak) no target species were significantly increased although two common higher plants and one bryophyte did increase their cover. Experiments aimed at restoring oligotrophic heathland in the Netherlands found mixed results, after 25 years of cutting there had been an increase in target species but the community still resembled the original one, typical of eutrophic conditions (Bakker *et al.*, 2002). Jacquemart *et al.* (2003) also cutting as a control treatment reduced the problem species (*Molinia*) it had little impact on vegetation composition. With added problems when trying to regenerate *Calluna* heath including; evidence that *Calluna* establishment from seed can be hindered by competition (Allison & Ausden, 2004), as it is able to establish and grow well on arable soil in the absence of other species (Lawson *et al.*, 2004); and the establishment of *Calluna* from seed may also be hindered by the presence of bracken litter. Experiments conducted on old *Pinus* plantation land found the removal of the litter and humus layers increased *Calluna* establishment (Allison & Ausden, 2006).

The increase of *D.flexuosa*, *G.saxatile* and *C.introflexus* by treatment particularly in cutting twice per year compares to the greatest reduction in *P.aquilinum* cover by the later years of sampling. The increase of *C.introflexus* at Cannock where the desired habitat is *Calluna* heath could have mixed effects. Carpets of *C.introflexus* were shown to have a negative effect on seed germination but a positive effect on seedling performance once germination had occurred (Equihua & Usher, 1993).

Whilst it is accepted that it is unreasonable to expect different species to respond to the same main treatments at every site, it is important to remember that the sites were replicated on relatively similar vegetation (heathland and acid grassland). It must be concluded that bracken control treatments, on their own, have relatively little influence on the subsequent long-term development of vegetation

8.4.3 Hypothesis 3: Treatments applied at the individual site level to restore vegetation influences community change towards the target vegetation

At Peak, the response of *D.flexuosa* to grazing was predictable. The reduction of *D.flexuosa* with sheep grazing is well known (Rawes, 1983; Anderson & Radford, 1994; Pakeman, 2004) and it is noted that the species is often preferentially grazed (Duffey *et al.*, 1974).

It is clear that seeding worked best at Peak (with *C.vulgaris* when applied as brash and seeded *A.castellana* increasing) and produced less satisfactory results elsewhere, even though the treatment combinations were designed to produce site-specific targets. The selection of sites was designed to provide a range of bracken control scenarios across the UK, and they can broadly represent high bracken infestation on acid grassland sites and heathland sites. At the grassland sites, there was a depauperate understory flora, rather than no existing flora, at the start of the experiment and the results suggest that in such situations it is unnecessary to add additional species or spend a great deal of effort in vegetation restoration; natural colonization processes will be sufficient to establish acid grassland. For sites like Peak and Cannock where the original target vegetation was *Calluna* heath and restoration treatments were designed to target this, both Marrs *et al.* (1998b) and Le Duc *et al.* (2007a) conclude that grass heath vegetation is the most likely outcome on sites. Increased soil nutrients may be a factor here as *C. vulgaris* tends to be found on infertile soils (Gimingham, 1992), although fertilizer addition has been prescribed for heathland restoration elsewhere in the uplands (Anon, 1988). High frond biomass is also associated with increased levels of nitrogen (Watrud *et al.*, 2003)

8.5 Conclusions

The isolated use of bracken control treatments has relatively little influence on the subsequent long-term development of target vegetation, with a few already abundant species increasing their cover. Thus the development of target vegetation requires a combination of control and restoration treatments that take into consideration the aspects of that site. This may include management for more than one factor, for example, soil condition and the present seed bank (De Graaf *et al.*, 1998).

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Chapter 9

The creation of alternate stable states

9.1 Introduction

A fundamental issue in vegetation management and restoration ecology is the ability to be able to predict with some degree of precision the likely outcome of proposed treatments. This is essential to meet the objectives of both policy-makers and those responsible for implementation within wide-scale practical management schemes. However, it is well known that accurate prediction is difficult when treatments may have to be applied over wide bio-climatic conditions, and where the restoration objectives may vary according to the ecosystem being treated. An obvious solution is to carry out multi-site experiments where the same treatments are applied contemporaneously; although, there are relatively few examples of such an approach (Le Duc *et al.*, 2003; Lowday & Marrs, 1992a, b; Pywell *et al.*, 2002; Pakeman, 2004). This is most problematic when the management treatments have to delivered via an Integrated Land Management Approach (Milligan *et al.*, 2004), where restoration includes the control of invasive species coupled with techniques to restore more appropriate vegetation.

From a theoretical perspective the aims of ecological restoration, where one community is transformed to another, is to overcome the resistance and resilience of the treated community and move it towards a new community with sufficient resistance and resilience to prevent a return to the original state, essentially to create an alternative stable state (ASS), or basin of attraction (Beisner *et al.*, 2003). This can be done in two ways; by altering either the state variables of the system (e.g. species composition), or its ecosystem parameters (e.g. removal of grazing by fencing), the aim being to force the existing ecosystem to follow a trajectory towards an ASS. If the resilience (Beisner *et al.*, 2003; Mitchell *et al.*, 2000) of the existing system is low, the perturbation may be enough to allow the successional trajectory to reach a new set of state variables, and thus an ASS. However, where the starting state has high resilience, the original community could re-establish rapidly (Marrs & Le Duc, 2000), thus wasting restoration effort.

Where ecosystem parameters are changed then we would expect any effect to be a permanent one. However, where state variables are altered they can be described as two types (see Bender *et al.*, 1984); (1) a "one-off" treatment would be classified as a "pulse-treatment", and (2) a treatment that is applied continuously is described as a "press-treatment". Where a "pulse" treatment has been applied and a new stable ecosystem is formed then we would expect it to be an ASS. However, where a "press treatment" is applied then it is creating a continuing pressure to maintain the new system, and under those circumstances it is not known whether that new state is stable without the continued application of treatment. Testing whether or not such an AS is an ASS can be done by stopping the press treatment and assessing whether the AS produced is stable and remains or whether it returns to its original state.

There have been few attempts to assess whether ecological restoration treatments have succeeded in detecting whether alternative stable states or alternative states have been formed and none that have used multi-site experiments to cover a wide range of a national restoration problem. Here we attempt to provide a national view of attempts to produce ASS or AS in an UK case-study. A series of seven replicated experiments were available, testing the same methods to control a pernicious weed (*Pteridium aquilinum*) followed by site-specific treatments to restore heathland or acid grassland.

9.1.1 *The case-study problem*

P. aquilinum is a serious invasive weed of upland and marginal land in many parts of the world (Page, 1995; Pakeman & Marrs, 1992). In the UK, *P. aquilinum* is an especially problematic weed, causing problems in upland heaths and acid grasslands, where it often occurs in dense stands (summarized in Smith & Taylor, 1995). *P. aquilinum* is difficult to control for a range of reasons including, an extensive rhizome system (Le Duc *et al.*, 2003), and high productivity that produces dense frond cover and deep litter, which combine to reduce understorey vegetation (Marrs *et al.*, 2000). The current agricultural and conservation policy in the UK for *P. aquilinum* infestation is delivered through Agri-Environment Schemes (MAFF, 1993, 1996) and Biodiversity Action Plans (Anon, 1995a, b). *P. aquilinum* is considered a mid-successional plant, usually occupying a niche between plagio-climax heath/moor/grassland and woodland (Marrs *et al.*, 2000, Marrs & Watt, 2006), although it can persist for long periods and appears in some cases to represent a highly resilient stable state (Marrs at al., 2000; Suding *et al.*, 2004, Marrs & Watt, 2006). Essentially, the policy is to reverse succession by reducing *P. aquilinum* infestations where possible and restore either *Calluna vulgaris*-dominated heathland or acid grassland.

In the UK *P. aquilinum* occurs across a wide range of conditions and given that succession can occur along many trajectories (Mitchell *et al.*, 2000; Suding *et al.*, 2004), there is potentially a large number of possible outcomes for bracken control/vegetation restoration schemes. In addition, *P. aquilinum* communities are known to have high resilience (Le Duc *et al.*, 2007c) and control often produces variable and conflicting results (Cox *et al.*, 2007a; Le Duc *et al.*, 2000). It is, therefore, important from a policy perspective to identify whether an AS or ASS can be achieved under a range of management conditions.

9.1.2 *Approach to this study*

There are a number of approaches that can be applied to analyze such data including univariate analysis of variance (Marrs *et al.*, 1998a, b; Le Duc *et al.*, 2000, 2003, 2007a, Cox *et al.*, 2007a, b; Chapters 2, 8) and formal meta-analysis (Chapter 3). However, these approaches do not allow the effects of applied treatment on the overall vegetation community to be assessed in the same analysis or allow a comparison with target vegetation types. Here, we build on the single-site multivariate study of plant community change (Le Duc *et al.*, 2007c). We have extended this study through the use of multivariate analysis of variance to analyze a series of seven randomized-block experiments, each with a common series of weed control treatments applied as main treatments. Within each experiment site-specific vegetation management treatments (vegetation restoration/bracken follow-up treatments) were applied as sub- and sub-sub-treatments. We hypothesized that the different bracken control treatments would result in different trajectories and varying rates of success, and we hoped to answer the following questions:

(1) What is the range of variation covered by sites and how does this relate to potential target communities?

(2) What is the effect of bracken control treatments on their own at the individual sites?

(3) What is the modifying effect of the restoration/follow-up on the bracken control responses at each site?

The first two questions were answered by inspection of a multivariate analysis of variance and relating the resulting analysis to potential target communities derived from the British National Vegetation Classification Scheme (Rodwell, 1991a, b, 1992). The third question was assessed by comparing two multivariate analyses of variance (with and without the vegetation restoration/bracken follow-up treatments) using a Procrustes Rotation Analysis; this procedure identified both the species and treatments where the vegetation restoration/bracken follow-up treatments had greatest effect.

It was hoped that this approach would allow the results of seven experiments to be compared within a national framework and identify the treatments that produced AS and ASS (i.e. effective treatments) and those where resilience of the starting *P. aquilinum* community was too high (i.e. ineffective treatments).

9.2 Methods

9.2.1 *Experimental sites*

This chapter reports on data from the series of experiments described in Chapter 1, with the addition of a seventh experiment at Cannock Chase (Table 1). Only one bracken control treatment, cutting twice per year, was applied to Cannock 3, with the site specific restoration treatments being; litter burning and *Calluna* seeding.

Table 1. Detailed description of experimental design. Entries for experimental design (split-split-plot randomized block design) represent: number of blocks / number of plots per block / number of sub-plots per plot / number of sub-sub-plots per sub-plot. Square brackets enclose treatment (or treatment start) date. The National Vegetation Classification (NVC, Rodwell, 1991a,b, 1992) descriptions (the codes are explained in the footnote) represent the pre-treated condition; data in brackets being the results obtained when *P. aquilinum* was left out of the calculations. The measured fit was obtained using TABLEFIT version 1.0 (Hill, 1996), and is rated: > 80 very good, > 70 good, > 60 fair, < 60 poor. All experimental treatments were applied in balanced designs with appropriate untreated contrasts, the untreated constrasts are not shown for clarity.

Location	**Cannock Chase**
- Ordnance Survey map reference	SJ 987 178
Experiment:	
- name	Cannock 3
- started	1995
- design	2/2/2/2
- smallest plot	6 x 5 m
- main treatments (*P. aquilinum* control)	Cut twice pa [Jun. 95]
- sub-treatments	Litter burn [Mar. 95]
- sub-sub-treatments	*Calluna* seed (brash) [Dec. 96]
Physical:	
- altitude (m)	175
- aspect (°)	175
- slope (°)	9
Vegetation:	
- NVC class	U2(U2)
- fit	63(62)

NVC classes represented is: **U2** *Deschampsia flexuosa* grassland.

The bracken control treatments applied in this study at main-plot level reflect a combination of "pulse" and "press" treatments (Bender *et al.*, 19984; Table 2). The treatments involving asulam were pulse-treatments and the annually applied cutting treatments are press ones. The restoration treatments are mainly pulse treatments applied to change ecosystem state variables; the exception was fencing treatment at Peak, which is a pulse treatment and aimed to change the ecosystem parameters (Table 2).

Table 2. Experimental treatments tested, type of changes induced (*sensu* Beisner *et al.*, 2004), and the type of perturbations produced (*sensu* Bender *et al.*, 1984). Additionally, all treatments included experimental 'controls' where no treatment was applied.

Treatment		**Induced Change**		**Perturbation Type**	
Type	**Description**	**State variable**	**Parametric**	**Pulse**	**Press**
Bracken control	Cut once per year	√			√
	Cut twice per year	√			√
	Herbicide	√		√	
	Herbicide + single cut	√		√√	
	Single cut + herbicide	√		√√	
Follow up	Spot spray	√		√	
Restoration	Sheep grazing	√			√
	Stock-proof fencing		√		√
	Calluna Brash	√		√	
	Calluna Litter	√		√	
	Grass seed	√		√	
	Fertilize	√		√	
	Fertilize and grass seed	√		√	
	Fertilize and harrowing	√		√	

9.2.2 *Monitoring*

Monitoring at Cannock 3 was conducted in the same manner as described in Chapter 1.

9.2.3 *Data analysis*

Multivariate analysis of variance using the constrained ordination method described by ter Braak & Šmilauer (1998) was used to describe changes in the entire community dataset. All calculations were performed on transformed data ($\log_e x+1$), replicate data within sub-(sub)-plots were averaged. The resultant dataset had 3234 samples and 223 species, which was reduced to 132 species by removing those species that occurred only once. Data were weighted to account for the number of sub-samples making up each data-point. Analyses were performed using the VEGAN package (Oksanen, 2005) implemented in the R-environment (Venables *et al.*, 2005). Initially, a Detrended Correspondence Analysis (DCA) was performed; the eigenvalues were 0.5430, 0.2202, 0.1776 and 0.1686, and the gradient lengths were 5.0, 3.1 3.9 and 2.9 for the first four axes. The gradient lengths supported the use of the unimodal, Canonical Correspondence Analysis (CCA), model (ter Braak & Šmilauer, 1998).

The significance of each factor and interaction was determined using separate CCA runs. In each run the factors and their interactions were included as environmental variables. Significance was assessed using Monte Carlo permutation tests of the residuals with 999 permutations, permutations were restricted within the appropriate level of the experiment. The model used was a split-split- plot design with experiment at the top level, followed by bracken control treatment, and time.

In order to identify the effects of the main-plot, bracken control treatments, which were constant between sites, from the site-specific vegetation restoration/follow-up control treatments applied at sub- and sub-subplot treatments, the multivariate analysis of variance was performed twice. Analysis 1 included all plots (i.e. all treatments applied to sub-(sub)-plots were included); Analysis 2 repeated this analysis but the effects of the sub- and sub-sub-plot treatments removed as covariables. Analysis 2 reflects the effects of the main bracken control treatments on their own with no subsidiary treatment effect, whereas Analysis 1 includes the effects of the restoration/follow-up treatments. In both analyses (Table 3) almost all treatment combinations were significant. As the highest order interaction (experiment × bracken control treatment × time) was significant in both analyses, these models were used for all subsequent investigations. This significance of these interactions were re-tested with 9,999 permutations as recommended by Legendre and Legendre (1998); both were highly significant (*PF=0.40,* $P<0.00001$). In order to relate the vegetation types detected in this study with the wider

British vegetation, a selection of upland vegetation communities (National Vegetation Classification (NVC) communities; Rodwell, 1991a, b, 1992), that could be considered target communities from a restoration perspective were plotted as passive samples within these ordinations. The NVC communities could of cause only be plotted approximately as only those species that had been found in this study could be used.

Table 3. Results of the multivariate analysis of variance using restricted permutation tests (999 permutations) of a multi-site experiment carried out to test the effects of bracken control treatments and enhance moorland/grassland vegetation over 10-years. The analysis has been performed on the entire dataset and with vegetation restoration and follow-up treatments removed as a covariable.

		No effect of vegetation restoration/follow-up treatments		Including effects of vegetation restoration/follow-up treatments	
	Analysis action	Sub & Sub-sub- treatments removed as covariables		All data included	
Source	df	λ	PF	λ	PF
Total	3234				
Experiment (E)	6	0.2343	4.49***	0.2315	***
Error (I)	8				
Bracken control Main Treatments (MT)	5	0.0845	0.32***	0.8549	0.32***
E*MT	30	1.3022	0.95***	1.3562	0.98***
Error (II)	46				
Time (T)	9	0.1137	0.22***	0.1151	0.22***
E*T	54	1.2456	0.47***	1.2991	0.49***
MT*T	45	0.1200	0.05ns	0.1204	0.05ns
E*MT*T	270	1.9224	0.39***	1.9751	0.40***
Error (III)	2761				

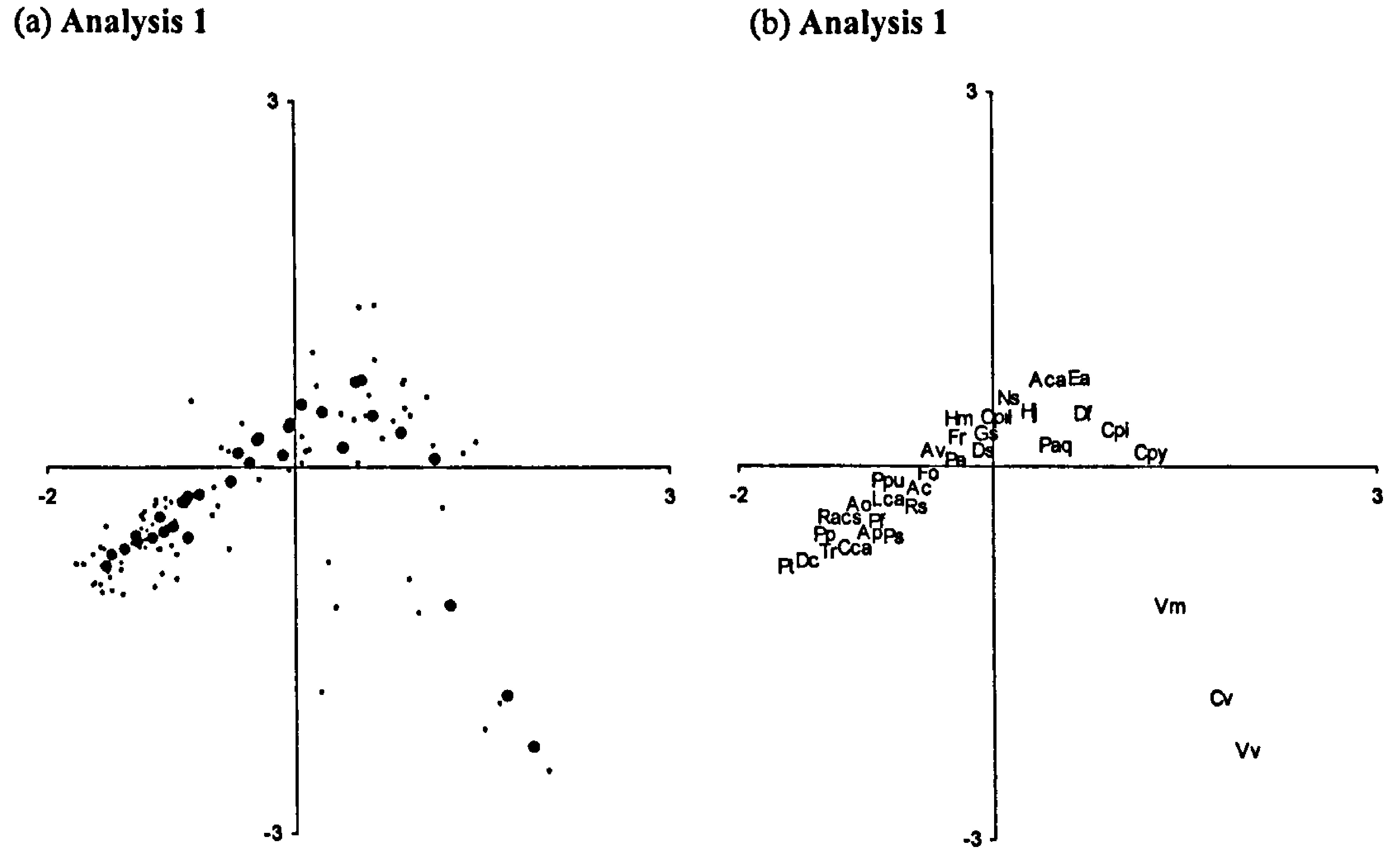
In order to answer the first question, the outputs from both analyses were examined. The dispersion of the different sites in species ordination space was examined using bivariate standard-deviational (SD) ellipses for axes 1 and 2 (Milligan *et al.*, 2004). To answer question two, the effects of bracken control treatments on their own was examined by assessing the treatment interaction trajectories in time through species space and various distance measures made using Euclidean geometry (maximum distance moved, time to maximum distance, distance moved after maximum time period). To answer the final question, the modifying effects of the restoration/follow-up treatments (sub-(sub-)-plot treatments), the CCA ordinations of the experiment × bracken control treatment × time interaction produced from Analysis 1 and 2 (both species and treatments) were compared using Procrustes rotation. This analysis was performed after scaling to unit variance and the significant assessed using a permutation test with 999 permutations (Oksanen, 2005). The residuals from the Procrustes analyses were then used to: (1) identify the species that were most affected by the restoration/follow-up treatments (upper and lower quartiles), and (2) the site × bracken treatment interactions that were most affected. The latter was done by calculating mean values for the main-plot treatments at each experiment followed by analysis of variance. Two analyses were done; the first included the six experiments with a common design, and the second analyzed the data from Cannock 3. Repeated-measures ANOVAs with polynomial contrasts (Gurevitch and Chester, 1986; Le Duc *et al.*, 2007a) was used, implemented in PROC GLM in SAS version 8.02 (SAS, 1989)

9.3 Results

9.3.1 *What is the range of variation covered by the experimental sites?*

The species ordination from Analysis 1 (including all experimental treatment combinations) showed a species gradient from the bottom left to the top right quadrant (Fig. 1a, b). Species typical of fertile acid-grassland (e.g. *Trifolium repens*) were in the bottom left, those associated with acid grasslands were plotted around the centre, *P. aquilinum* was located close to the centroid but in the top right quadrant, and the heathland target species (eg. *C. vulgaris*, *Vaccinium myrtillus*, *V.vitis-idea*) are in the lower right quadrant with other less abundant species (e.g. *Molina caerulea*). The corresponding biplot for Analysis 2, where the effects of restoration/follow-up treatments were removed as covariables was very similar to that of Analysis 1 except that it was plotted in a different rotation (Fig. 1c, d), with the species gradients from the upper left quadrant to the lower right.

The vegetation at each of the sites reflected the vegetation in the surrounding landscape, and to some extent the target vegetation set for restoration (Fig. 2). Cannock 2 and 3, where a *Calluna*-dominated heath was the target, were clearly associated with heathland species, and the grassland sites (Sourhope and Carneddau) were associated with the grassland end of the vegetation gradient. However, Cannock 1 and Peak, where heathland vegetation was also the target, were intermediate between grassland and heathland reflecting a more mixed composition. The NVC vegetation types reflected this progression of vegetation types from upland grasslands through to heathland and woodland (Fig. 3).



(a) Analysis 1

(b) Analysis 1

(c) Analysis 2

(d) Analysis 2

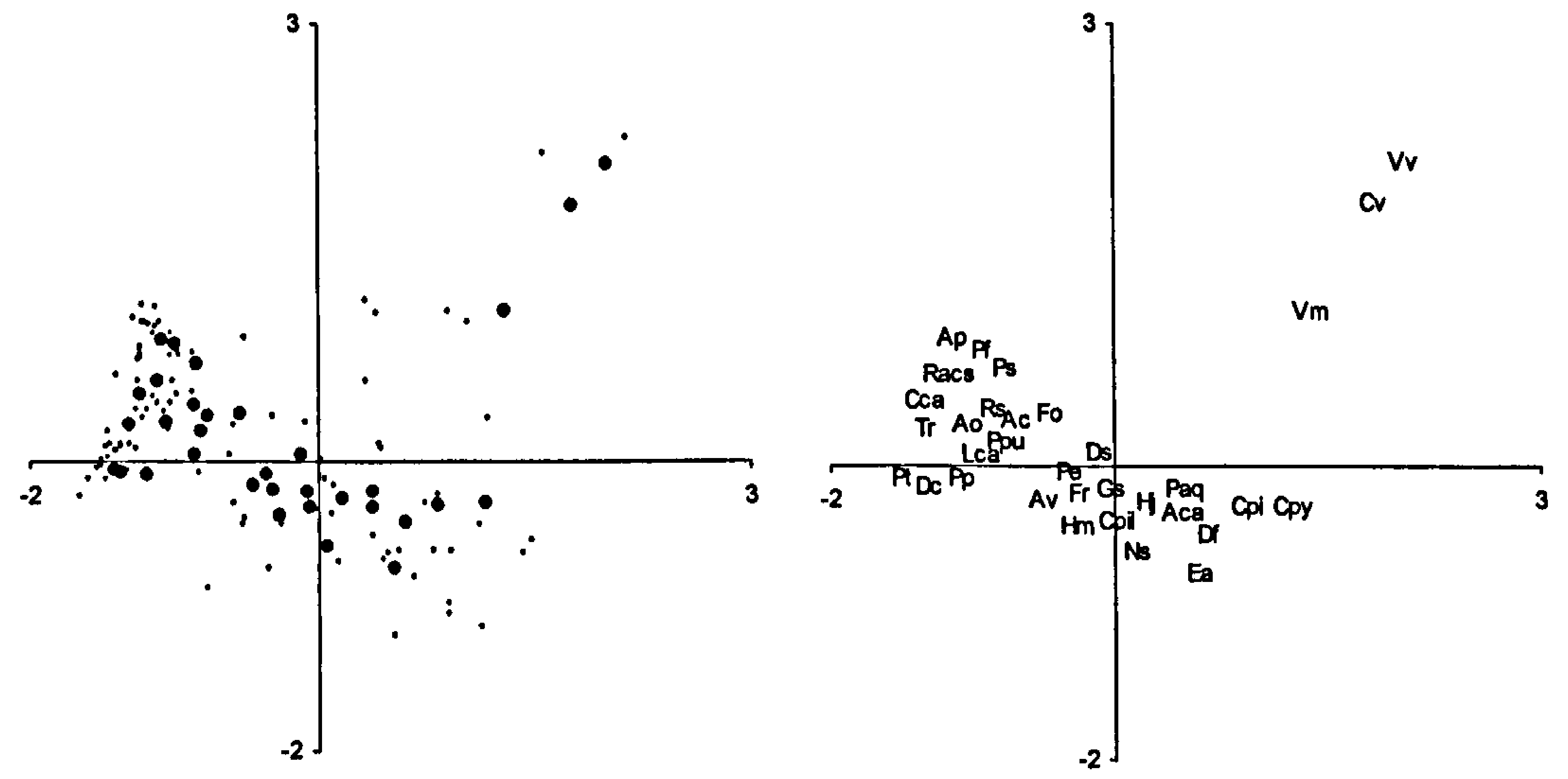


Fig. 1. CCA species plots for two ordinations; Analysis 1 (a, b) of all treatments and Analysis 2 (c, d) with restoration/ follow-up treatments removed as co-variables. For clarity all species are plotted (a, c) with the most abundant 25% of species identified as large black dots, these abundant species are coded in b and d. Sepcies codes: Ac, *Agrostis capillaris,* Aca, *Agrostis canina,* Ao, *Anthoxanthum odoratum.* Ap, *Aira praecox,* Av, *Agrostis vinealis,* Cca, *Carex caryophyllea,* Cpi, *Campylopus introflexus,* Cpil, *Carex pilulifera,* Cpy, *Campylopus pyriformis,* Cv, *Calluna vulgaris,* Dc, *Deschampsia cespitosa,* Df, *Deschampsia flexuosa,* Ds, *Dicranum scoparium,* Ea, *Chamerion angustifolium,* Fo, *Festuca ovina,* Fr, *Festuca rubra,* Gs, *Galium saxatile,* Hj, *Hypnum jutlandicum,* Hm, *Holcus mollis,* Lca, *Luzula campestris,* Ns, *Nardus stricta,* Paq, *Pteridium aquilinum,* Pe, *Potentilla erecta,* Pf, *Polytrichum formosum,* Pp, *Poa pratensis,* Ppu, *Pseudoscleropodium purum,* Ps, *Pleurozium schreberi,* Pt, *Poa trivialis,* Racs, *Rumex acetosa,* Rs, *Rhytidiadelphus squarrosus,* Tr, *Trifolium repens,* Vm, *Vaccinium myrtillus,* Vv, *Vaccinium vitis-idaea.*

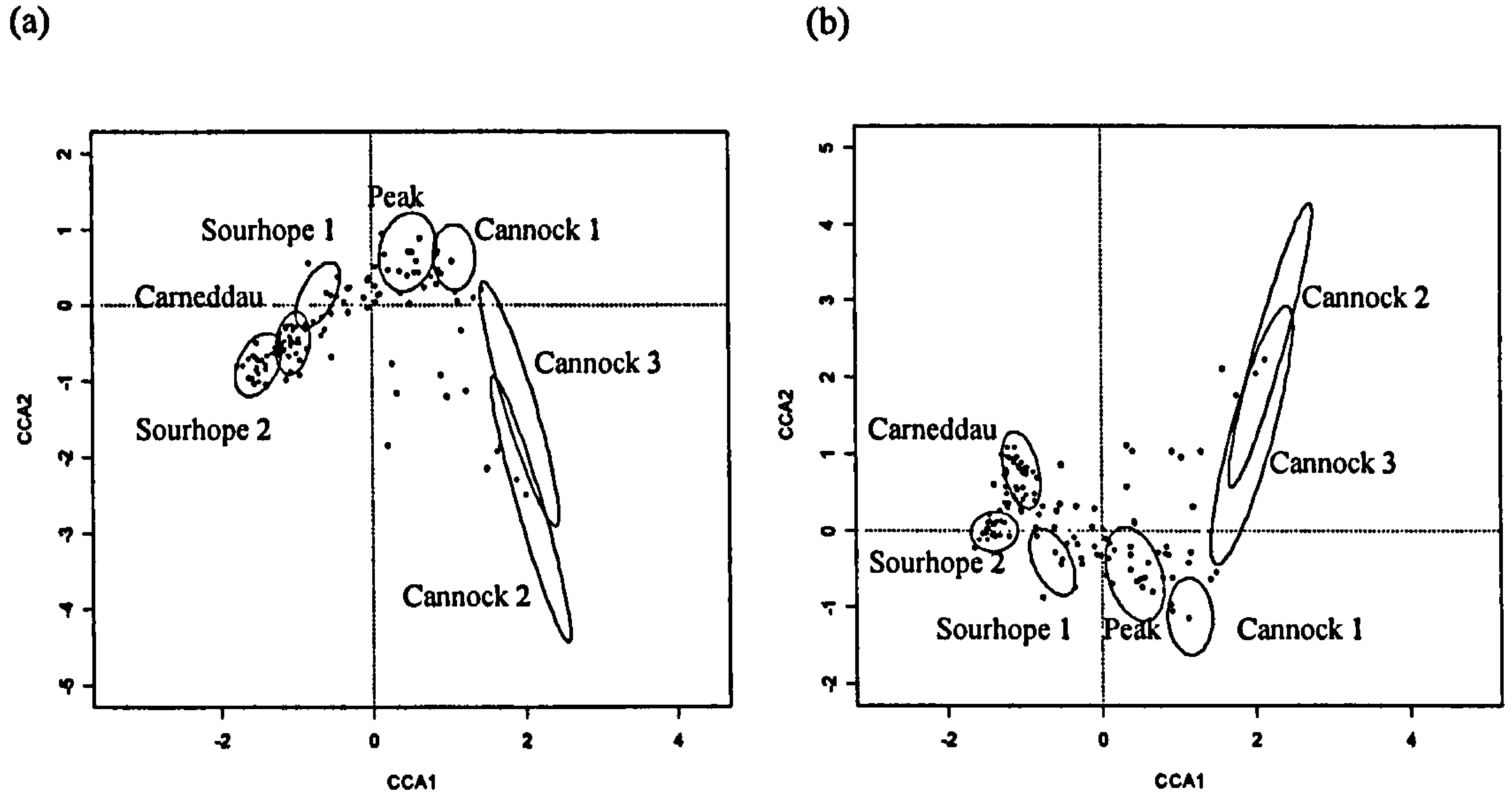


Fig. 2. The dispersion of the seven experimental sites in species ordination space described using bivariate standard-deviational ellipses. Dots represent the same species as in Fig. 1 a & c: (a) Analysis 1 including all treatments, and; (b) Analysis 2 with restoration/ follow-up treatments removed as co-variables.

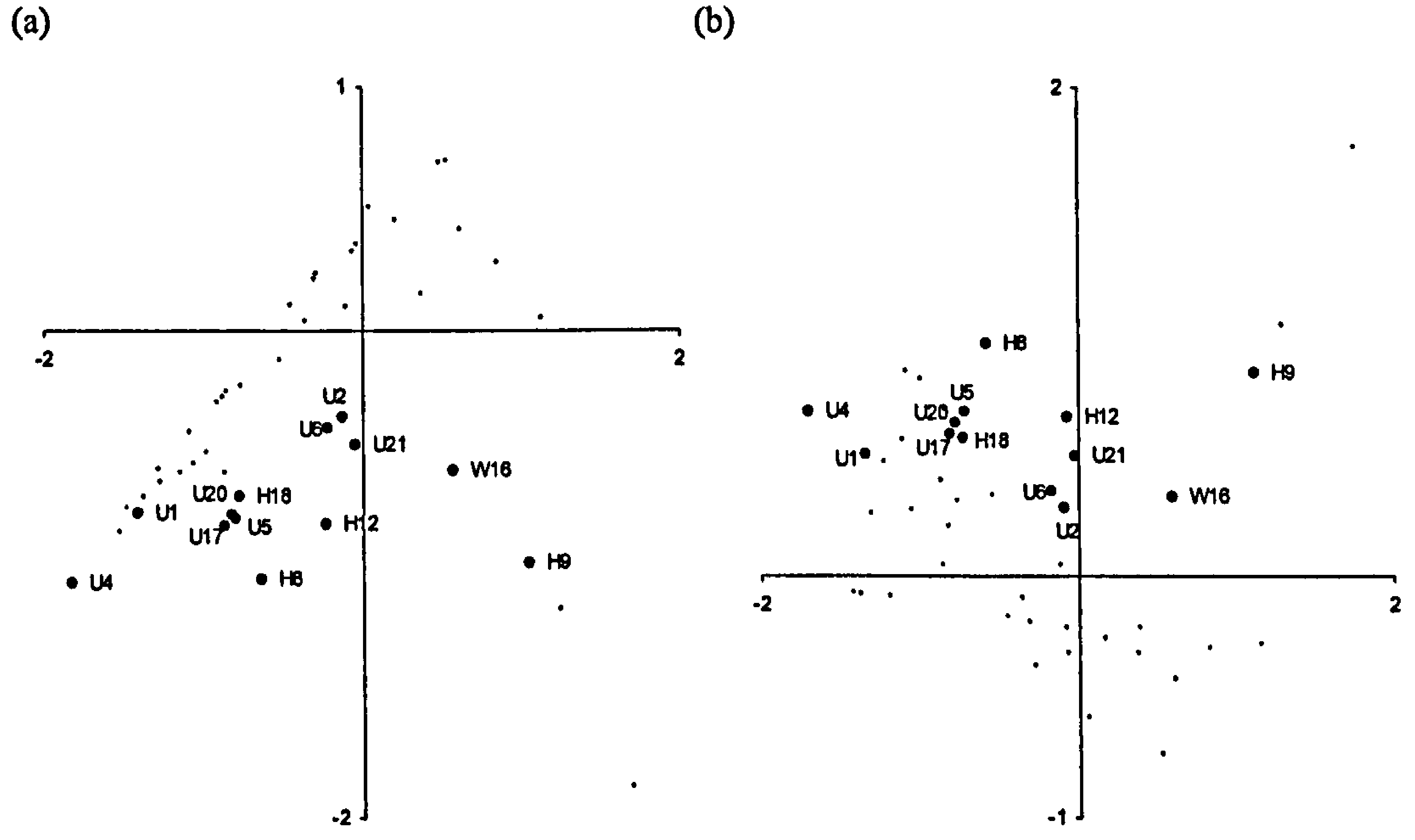


Fig. 3. The distribution of selected upland British National Vegetation Classification communities plotted in species space (Fig. 1): (a) Analysis 1 with all treatments and (b) Analysis 2 with restoration/ follow-up treatments removed as co-variables. The most abundant 25% of species are presented as small dots (as Fig. 1 b,d). NVC communities are: H8, *Calluna vulgaris- Ulex gallii* heath; H9, *Calluna vulgaris- Deschampsia flexuosa* heath; H12, *Calluna vulgaris- Vaccinium myrtillus* heath; H18, *Vaccinium myrtillus- Deschampsia flexuosa* heath; U1, *Festuca ovina- Agrostis capillaris- Rumex acetosella* grassland; U2, *Deschampsia flexuosa* grassland; U4, *Festuca ovina- Agrostis capillaris- Galium saxatile* grassland; U5, *Nardus stricta- Galium saxatile* grassland; U6, *Juncus squarrosus- Festuca ovina* grassland; U17, *Luzula sylvatica- Geum rivale* tall herb community; U20, *Pteridium aquilinum- Galium saxatile* community; U21, *Cryptogramma crispa- Deschampsia flexuosa* community; W16, *Quercus* spp.- *Betula* spp.- *Deschampsia flexuosa* woodland.

9.3.2 *What is the effect of the bracken control treatments on their own at individual sites?*

The effects of treatment induce trajectories through species ordination space, this study generated a potential 38 trajectories for each analysis. All trajectories were inspected and whilst only a few from Analysis 2 (with restoration/follow-up treatments removed) are presented here as examples, summary data were derived (Table 4).

Table 4. The minimum, maximum distance from the start point, the year in which they occurred and end point distance from the Elapsed Time= 0 start point for each treatment at each site, calculated using Euclidian geometry. Two patterns were obsereved in the trajecories (see discussion in text): Pattern type 1 is a circular pattern, moving away from the start position but over the experimental period returning close to the start; Pattern Type 2 is a clear directional movement away from the start position, often with considerable resonating inter-annual fluctuations.

		Pattern Type	Minimum Distance	Year	Maximum Distance	Year	Distance at End
Cannock 1	Control	First	0.14	1997	0.70	1999	0.39
	Cut1pa	First	0.25	2001	0.78	2000	0.44
	Cut2pa	First	0.10	2002	0.52	1999	0.17
	CutSpray	First	0.23	2002	0.59	1999	0.25
	Spray	First	0.44	1996	1.20	2003	1.20
	SprayCut	First	0.02	1994	0.55	1999	0.23
Cannock 2	Control	First	0.06	2002	7.36	1995	0.16
	Cut1pa	First	0.04	1994	4.27	1996	0.77
	Cut2pa	First	0.03	1994	3.59	1996	0.42
	CutSpray	First	0.04	1994	11.16	2000	2.30
	Spray	First	0.60	2003	10.70	1994	0.60
	SprayCut	First	0.24	2001	9.23	1994	0.95
Cannock 3	Control	First	0.67	1997	4.88	1999	2.51
	Cut2pa	Second	0.67	1996	10.03	2000	8.21
Carneddau	Control	Second	0.03	1997	1.27	2000	0.39
	Cut1pa	Second	0.39	1997	2.22	1998	1.09
	Cut2pa	Second	0.37	1997	1.70	2002	0.82
	CutSpray	Second	0.47	2001	1.73	1998	0.49
	Spray	Second	0.34	2001	2.31	1994	0.44
	SprayCut	Second	0.42	2003	2.02	1998	0.42
Peak	Control	First	0.16	2003	2.03	1994	0.16
	Cut1pa	Second	0.52	1997	1.73	1994	0.61
	Cut2pa	Second	0.57	1995	2.02	1994	1.43
	CutSpray	Second	0.38	2003	1.81	1994	0.38
	Spray	Second	0.25	2003	1.37	1994	0.25
	SprayCut	Second	0.09	2003	1.03	1994	0.09
Sourhope 1	Control	First	0.27	1995	2.01	1999	0.33
	Cut1pa	First	0.30	1995	3.06	2000	1.04
	Cut2pa	First	0.20	1997	3.21	2000	0.99
	CutSpray	First	0.18	1997	2.96	2000	0.61
	Spray	First	0.48	1998	4.03	2000	1.05
	SprayCut	First	0.17	1998	2.28	2000	0.35
Sourhope 2	Control	First	0.06	2003	0.33	1995	0.06
	Cut1pa	First	0.02	1998	0.36	2003	0.36
	Cut2pa	First	0.03	1998	0.32	2003	0.32
	CutSpray	First	0.01	2002	0.17	2000	0.11
	Spray	First	0.02	2002	0.30	2000	0.07
	SprayCut	First	0.01	2002	0.58	1999	0.03

Two major trajectories were observed, the first common in untreated plots was a circular pattern, moving away from the start position but over the experimental period returning close to the start (Fig. 4). The second pattern type is where there a clear directional movement, away from the start position and remaining in a new position, even though there were considerable resonating inter-annual fluctuations, i.e. similar to the Carneddau untreated controls (Fig. 5a).

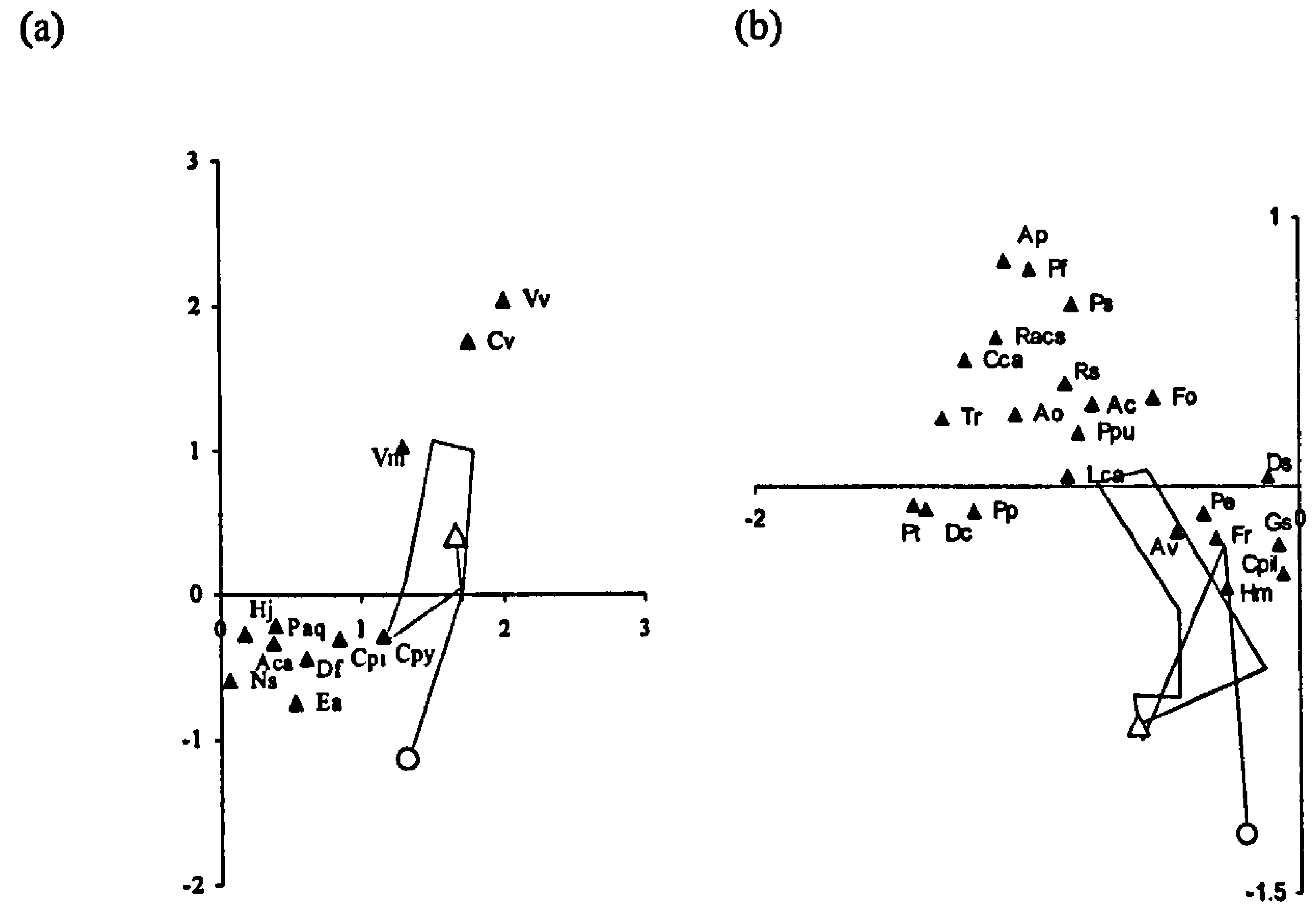


Fig. 4. Example trajectories of untreated control treatments at: (a) Cannock 3, (b) Sourhope 1 illustrating circular movement and high resilience. Circles; start points, ET= 0; Triangles; end points in 2003 ET=10, except for Cannock 3 ET= 8. Species represented are the most abundant 25% within the plotted section of the species biplot (Fig. 1). See Fig. 1 for species names.

A Type 1 trajectory was detected in six of the seven untreated plots, the exception being Carneddau where a resonating Type 2 pattern was found (Fig. 5a). The Type 1 circular trajectory can be seen at acid grassland sites (Sourhope) as well as the heath sites (Cannock) for all bracken control treatments and at the more mixed Peak site for the untreated control only (Fig. 6). A Type 1 trajectory implies a starting ecosystem with high resistance in a stable equilibrium or high resilience, or both (Suding, 2004). Type 2 was found for all treatments at the acid grassland Carnneddau site with the control moving least far from the start and Cut1pa moving the furthest. Similar patterns were also observed at Peak with Cut2pa, moving furthest from the start point and SprayCut moving the least. Examples of these patterns are presented in Figs. 5 & 6.

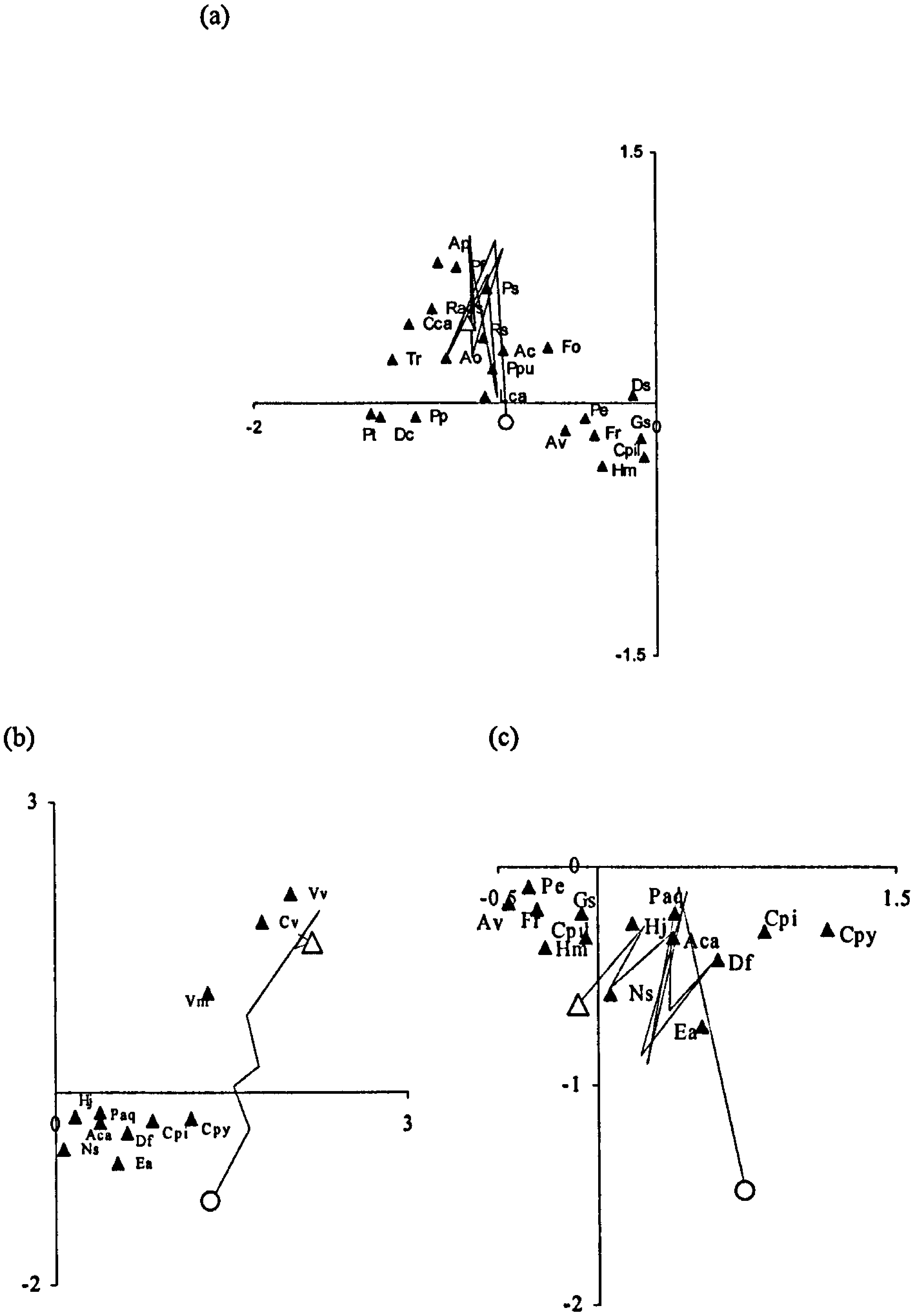


Fig. 5. Example trajectories of treatments that show movement towards alternate stable states: (a) Carneddau, Control; (b) Cannock 3, Cut2pa; (c) Peak, Cut2pa. Circles; start points, ET= 0; Triangles; end points in 2003 ET=10, except for Cannock 3 ET= 8. Species represented are the most abundant 25% within the plotted section of the species biplot (Fig. 1). See Fig. 1 for species names.

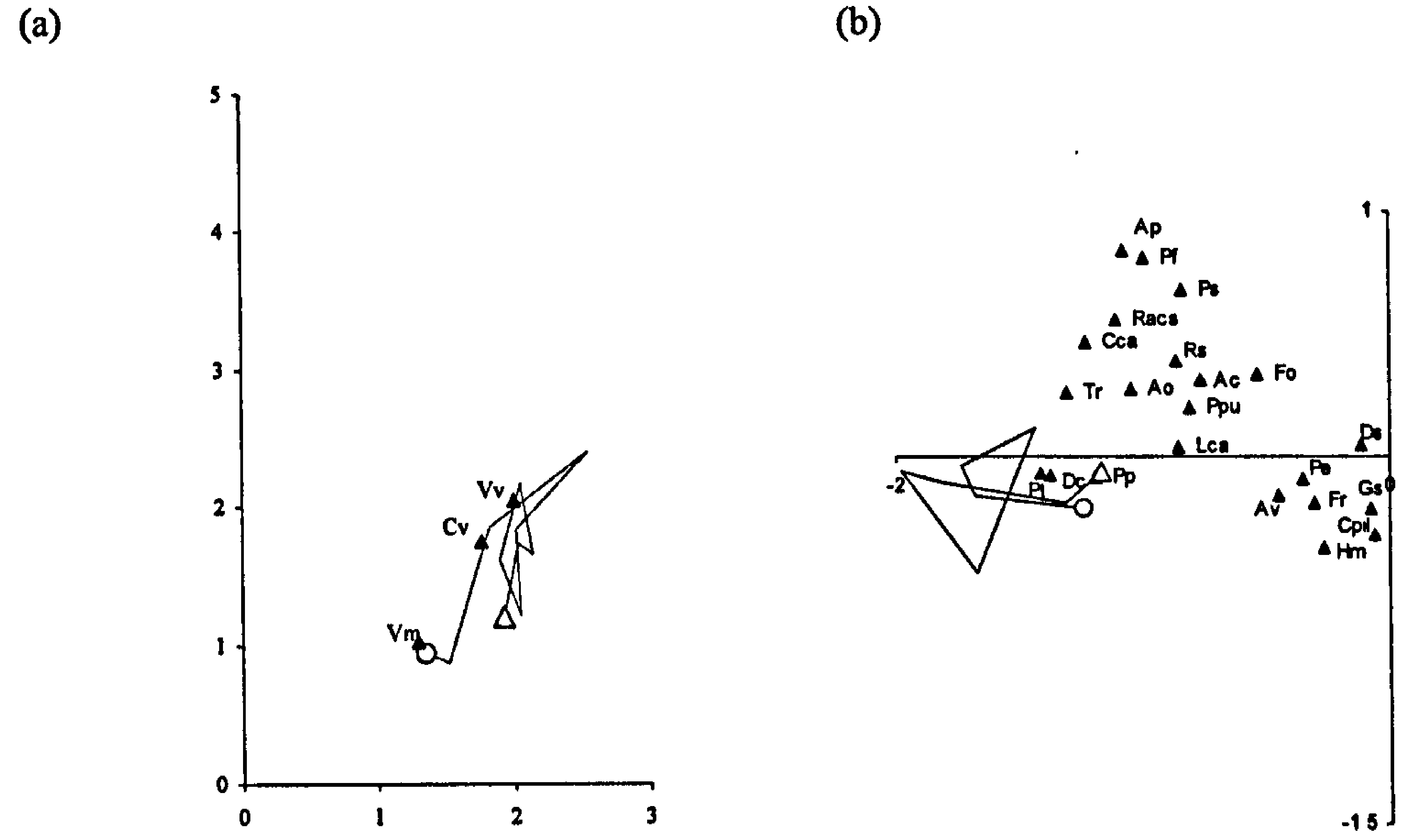


Fig. 6. Example trajectories of treatments that show considerable resilience: (a) Cannock 2, Cut 2pa; (b) Sourhope 2, SprayCut. Circles; start points, ET= 0; Triangles; end points in 2003 ET=10. Species represented are the most abundant 25% within the plotted section of the species biplot (Fig. 1). See Fig. 1 for species names.

The pattern types and derived data (Table 4) are a guide as to the length and the shape of the trajectory, but they do not take into account the direction in which the treatments are causing the trajectory to move. At Carneddau, were the Type 2 trajectory was observed, the trajectory started in the lower left quadrant with species like *Agrostis vinealis* and *Potentilla erecta* moving into the upper left quadrant towards species such as *Rumex acetosa* and *Carex caryophyllea*. At Peak the Type 2 trajectory moved towards acid grassland species, close to the centroid of the biplot. The cut twice per year treatment moved distinctly more to the left towards species such as *Nardus stricta* and *Holcus mollis* (Fig.5). The Type 2 trajectory was also observed in a more linear form at Cannock 3 for the cut twice per year treatment; here the trajectory moves from grassland species in the lower right quadrant towards the target heathland species in the upper right (Fig. 5).

9.3.3 *What is the modifying effect of the restoration/follow-up on bracken control responses at each site?*

The symmetric Procrustes rotation analyses for the six site analysis (excluding Cannock 3) produced a correlation of 0.967 and 0.941 for sites and species ordinations respectively, and both were significant (P< 0.0010, based on 999 permutations), indicating little variation between the two analyses.

The residuals from the species analysis were used to rank species (Electronic Appendix 3); those in the lower quartile (i.e. species showing the least deviance between the two analyses) contained many of the most abundant species, including *P. aquilinum*, *Deschampsia flexuosa* and *Potenilla erecta*. The upper quartile, those with the greatest deviance because of the effects of restoration/follow up treatments tended to be species of low cover (maximum mean cover found pooled over the site = 0.06% for *Poa trivalis*) and of low frequency, and found mainly at one site, usually Sourhope 2.

The repeated-measures ANOVAs with polynomial contrasts of the residuals for the six sites was significant at all levels: i.e. for the overall mean effect through time and time in interaction with site, main bracken control treatments and site × main treatment. The overall mean effect through time (Fig. 7a.) shows an increase in deviance between the two analyses through time with a resonating pattern appearing after four years. This indicates that the restoration/ follow-up treatments are having a greater impact through time. The overall mean effect was significant at 1st, 2nd, 3rd and 6th orders, with the 1st order being most significant.

The effects of site showed that the restoration/follow-up treatments had least effect at Cannock 2, intermediate effects at Cannock 1, Carenddau, Peak and Sourhope 1 and the greatest effect at Sourhope 2 (Fig. 7b). There was very little effect of the bracken control treatments on residuals at most sites but there were significant effects at (1) Cannock 1 where the untreated control had the least effect, all other treatments had a larger residual, with little difference between them, and (2) Sourhope 2 where the untreated control had one of the greatest effects; at this site the treatment order was: spraying then cutting, untreated control, spraying, cutting twice yearly, cutting once yearly, cutting then spraying. The significant effects identified for the time × site × bracken control treatment interaction were mainly associated with the Sourhope 2 site (Fig. 7c). The untreated control increases steadily through time, with all other treatments either remaining static or showing a marginal decline. At, the start spraying followed by cutting has the largest residuals, with cutting followed by spraying having the least effect; after year 4 there was little change as a result of bracken control treatment.

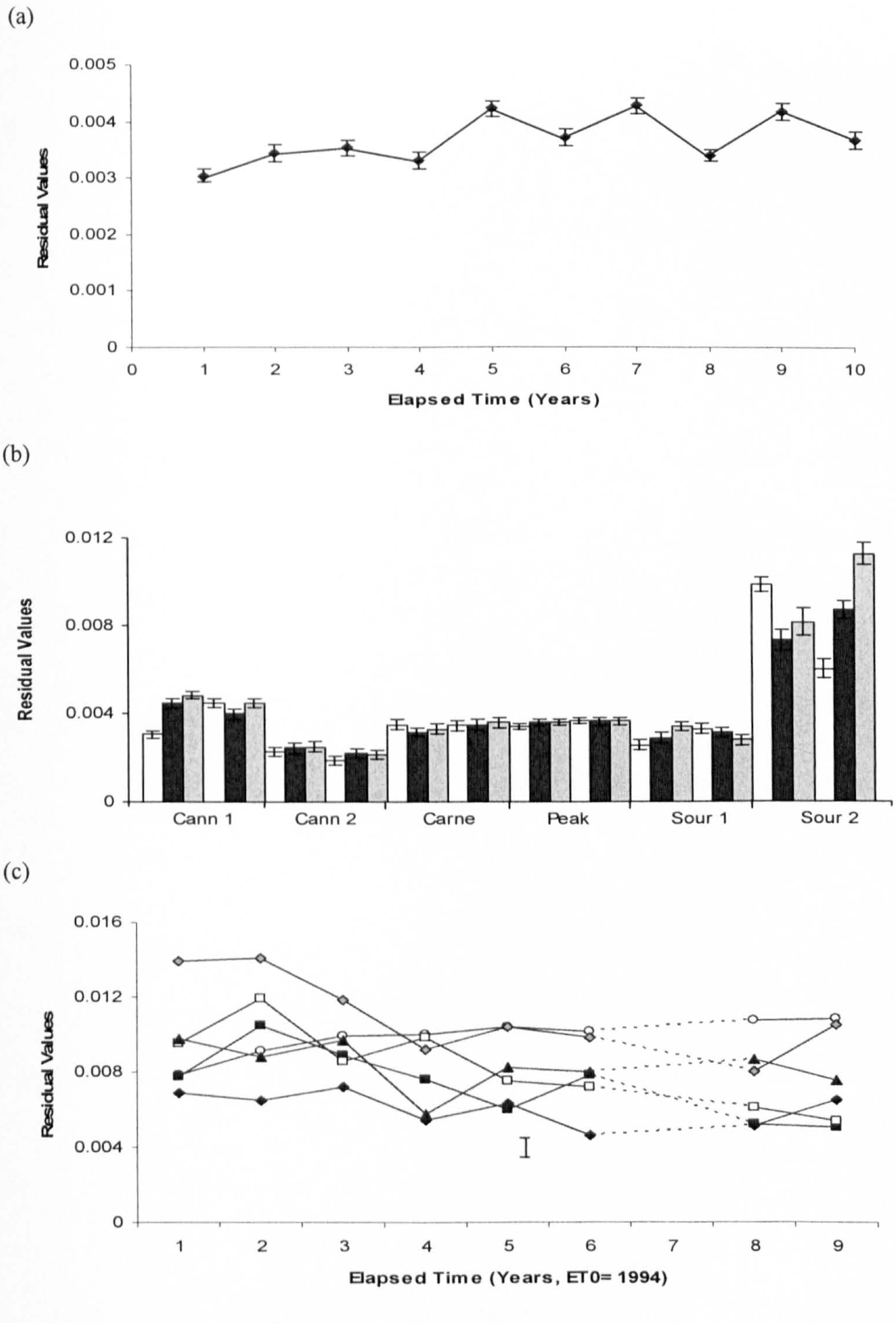


Fig. 7. Significant results from a repeated measures analysis of variance with polynomial contrasts of the residuals produced from the Procrustes rotation analysis comparing Analysis 1 (including all treatments) with Analysis 2 (restoration/ follow-up treatments removed as co-variables) (a) The overall mean effect of time for all six sites. The 1st order relationship was significant ($F_{(1,40)}$=151.22***) (b) The overall site x bracken control treatment interaction. The 1st order relationship was significant ($F_{(25,40)}$=3.04***) (treatments are presented, from left to right, in the order; Control, Cut 1pa, Cut2pa, CutSpray, Spray and SprayCut for each site). For a and b standard error bars are presented. (c) The overall site x bracken control treatment x time interaction for Sourhope 2. The 1st order relationship was significant (1st Order, $F_{(25,40)}$=5.58***n=4) and error bars are ± 2S.E.D. (no treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond.

The ANOVA for Cannock 3 produced two significant results, an overall mean through time and the effect of cutting twice per year. There was an increase in mean residual through time until year 7 followed by a slight reduction. The overall mean for main treatments was also marginally significant: cutting twice per year had greater residuals than the controls (the mean residual values ± SE for cut twice per year and the untreated control are; 0.0034±0.0001, 0.0032±0.0003 respectively, $F_{(1,2)}$=18.52*).

9.4 Discussion

The analysis presented here is novel in several respects. The method allowed, in the same analysis, the effects of bracken control treatments applied to a range of sites covering a range of problem situation within the uplands of the UK to be assessed in terms of the changes in overall vegetation community composition over a relatively long time period. There were significant challenges in the analysis of these data, the sites were chosen to provide a representative coverage of upland vegetation types, the same bracken control treatments were applied to all sites (or a subset of them, Cannock 3), but different vegetation restoration/bracken follow up treatments were applied at the individual site level to reflect local conditions and requirements (Le Duc *et al.*, 2003). This analysis was effectively a multivariate meta-analysis, but the analysis had to be restricted to comparing only the effects of bracken control treatments. This was done by two multivariate analyses of variance of the entire dataset. Analysis 1 included all the data, but this could not be used to assess sub-treatment effects, so the main analysis reported, Analysis 2, included the bracken control treatments on their own, with all sub-treatment effects, i.e. all the restoration/follow-up treatments, removed as a covariable. This analysis showed that all treatment combinations were significant, and the results were used to answer two questions:

(1) What is the range of variation covered by sites and how does this relate to potential target communities?

(2) What is the effect of bracken control main-treatments on their own, at the individual sites?

The analysis went further by comparing this restricted analysis with the full analysis to answer a third question:

(3) What is the modifying effect of the restoration/follow-up on the bracken control responses at each site?

This question was answered relatively crudely by comparing the two constrained ordinations using Procrustes rotation analysis. This analysis merely identified those species and main treatments where the inclusion of the sub-treatments significantly modified the response of the bracken control treatments. These results are, therefore, indicative and further analysis of each individual site, where the interactions between the bracken control treatments and the restoration treatments can be assessed. Le Duc *et al.* (2007c), for example, have shown, that different interactions produce different trajectories, and produce AS, some of which were postulated to be ASS.

Here, we are studying a much simplified model system, as we have only considered a very small subset of potential number of state variables within the test ecosystem, viz vegetation composition through time in response to management. A complete assessment of the biotype would include a measure of the ecosystem function (eg. nutrient cycling) and the component fauna (Mitchell *et al.*, 2000).

9.4.1 *What is the range of variation covered by sites and how does this relate to potential target communities?*

Both species ordinations showed a species gradient from acid grassland through to heathland, this is unsurprising since the sites were selected to cover this gradient. The gradient was correlated with the relative positions of typical NVC vegetation types (upland grassland, heathland and upland woodland; Rodwell, 1991a,b, 1992), suggesting that the vegetation communities being produced through the experimental management is heading the desired direction. What is interesting though, was the relative positions of the sites in the overall vegetation space; the Sourhope and Carneddau sites were expected to develop into acid grassland, and the Cannock ones were expected to develop into heathland, and these sites were at the expected extremes of the gradient. However, the Peak site was also expected to develop into heathland but it occupied an intermediate position between grassland and heathland. There was also considerable variability between the duplicate experiments at Cannock and Souhope, with significant differences between the partner experiments; Cannock 2 (and 3) being positioned nearer the heathland end than Cannock 1, and Sourhope 2 being positioned nearer the grassland end than Sourhope 1. The vegetation at each of the sites reflected the vegetation in the surrounding landscape (e.g. Tong *et al.*, 2006), and to some extent the target vegetation set for restoration

9.4.2 *What is the effect of bracken control treatments on their own, at the individual sites?*

This analysis compared the trajectories of the bracken control treatments on their own without any influence of the restoration/follow up treatments, the latter were removed because different restoration/follow up treatments were applied at the different sites. Within the species ordination all bracken control treatments at all sites showed some movement away from the start position. The resultant trajectories were classified into two types based on trajectory movement. Type 1 showed a more or less circular pattern, where there was return to near the original position suggesting high resilience of the original stable state, or hysteresis, a movement away from the original point but not returning to the same exact point and taking a different route to get there (Beisner *et al.*, 2003). The latter could potentially push the ecosystem into configurations that are more difficult to rectify in the long term than the starting state, as well as potentially moving away from the target vegetation. For example, Marrs & Lowday (1992) found heathland to be invaded with *Carex arenaria* and *Calamagrostis epigejos* after bracken control, essentially clearing one weed to replace it with another. The Type 2 trajectory showed movement away from the original position, but thereafter fluctuation around a position some distance from the start point, suggesting that an AS had been achieved.

Type 1 trajectories were found for all treatments at 4 out of the 7 sites (Cannock 1, 2, Sourhope 1, 2), and for the untreated controls at Cannock 3 and Peak. This suggests that at these sites the vegetation is very resilient and bracken control treatment on its own does not produce an AS. Type 2 trajectories were found at Cannock 3 (cutting twice per year), Carneddau (all treatments) and Peak (all treatments except the untreated control), suggesting at that at these sites there was a potential for the bracken control treatments on their own to develop an AS. Interestingly, there was very little evidence for a differential effect between those treatments classified as "press" or "pulse" at any site. This confirms results from analysis of single species responses (Cox *et al.*, 2007b, Chapter 8), where positive significant effects were found for only three species (*Galium saxatile, Deschampsia flexuosa* and *Campylopus introflexus*) across two sites. These results of course apply only to the developing vegetation under the controlled bracken, the effects of the "press" treatments (especially cutting twice per year) are usually more effective than pulse ones, for controlling bracken, though not exclusively (Cox *et al.*, 2007a; Chapters 2 and 3).

9.4.2.1 Direction of alternate states

For the most part trajectories moved towards the desired vegetation, the exception being the Peak site. Trajectories for the treatments at Peak tend to move at this scale of analysis towards *D. flexuosa* and *P. aquilinum* dominated state, not towards the target heath species. Le Duc *et al.*, (2007c) concluded that acid grassland rather than *Calluna* heath is the only possible ASS at this site, probably being *Deschampsia* based.

9.4.2.2 Why the resonating pattern?

The stochasticity seen in many of the Type 2 trajectories are almost certainly caused by parameters that were omitted from the model, specifically climatic fluctuations between years. This effect has been demonstrated using the cover values of individual species, for example, *Agrostis vinealis* at Sourhope showed an obvious cyclic effect for at least six years suggesting that external factors (probably climate) were important (Cox *et al.* 2007b, Chapter 8). Other environmental factors, vegetation heterogeneity, soil conditions etc. may all cause fluctuations and need to be considered in further studies (Beisner *et al.*, 2003).

9.4.3 *What is the modifying effect of the restoration/follow-up on the bracken control responses at each site?*

In this part of the analysis the aim was to test how effective the restoration/follow-up treatments were in influencing the effects of the bracken control treatments applied at each site. The effects of site-based individual restoration/follow-up treatments, and their interactions with bracken control treatments, are not considered here.

In the six site comparison, the site-specific restoration/follow-up treatments produced an ordination significantly different from the one where they were excluded. This approach was useful as it indicated that the inclusion of the restoration/follow-up treatments indicated:

1. Common species were relatively unaffected, this is surprising as some of these are included as seed inoculums and these species might have been expected to increase in the sub-treatments.

2. Species that were relatively uncommon and present at single sites tended to be at a greater cover where the restoration/follow-up treatments were applied.
3. The effects of the restoration/follow-up treatments appeared to increase through time.
4. There were significant differences in impact of restoration/follow-up treatments between different sites, and this probably reflected a combination of (a) the sites, and (b) the fact that some treatments have more impact than others. The greatest effect seemed to occur on grassland rather than heathland.

For Cannock 3 the same increase in effect through time was found, and cutting twice per year had a greater effect than the untreated plots.

9.5 General conclusions

All bracken control treatments appeared enough to change the species composition of the vegetation. Two types of trajectory were identified, the first showing a movement a circular type movement that implies high resilience and a return to the original state or one close by. The second showed a movement away from the original state and fluctuations around a new point some distance away. Here, it is possible that the treatments have overcome the resistance and the resilience of the original *Pteridium*-dominated state, and the potential for creation of an ASS. This second type of trajectory appeared to be confined to specific sites (Cannock 3, Carneddau, Peak) and also appeared not to be dependent on whether the treatments applied were of the "pulse" or "press" form (Bender *et al.*, 1984). The clearest example of a the creation of an ASS was in the cut twice per year treatment at Cannock 3, where the trajectory moved towards heathland and there was very little evidence of fluctuations, however, the cutting twice per year treatment is of the "press" type and to test its stability the cutting treatments would need to be stopped. At the other sites (Cannock 1 & 2, Sourhope 1 & 2) there was a return to the original or near-original state.

The effect of the site-specific restoration/follow up treatments in modifying the effect of the bracken control treatments appeared to have little or no impact on the creation of AS or ASS at five of the seven sites, although an increasing impact over time is seen. The effects of these additional treatments need to be assessed further at the individual site level.

Chapter 10

General Discussion

10. General Discussion

This project has encompassed a range of studies on bracken control methods, its recovery from long-term treatment and the subsequent regeneration of desired target habitats. Dense *P. aquilinum* infestation is known to cause revenue loss for farmers (Varvarigos & Lawton, 1991) along with biodiversity and conservation loss (Pakeman & Marrs, 1992). In the UK the aims of restoration policies are often to restore heath and acid grassland, and this is driven either by Biodiversity Action Plans to meet conservation needs (Anon, 1995a, b) or in agriculture by agri-environment schemes developed to meet EU requirements (MAFF, 1993, 1996). One of the major issues highlighted in *P. aquilinum* control is the high variability in success rates (Le Duc *et al.* 2000, 2003), and a cost-effective control strategy has proved elusive. In order to develop effective management strategies to tackle this problem, there is a need to assess treatment effectiveness at a range of contrasting situations. Moreover, as bracken control is known to take a long time (Marrs *et al.*, 1998a,b,c), experiments must, therefore, cover a long period. Thus, to develop effective bracken control and vegetation restoration strategies at the national scale, there is a need for long-term fully replicated experiments carried out in various bio-climatic regions. This need has been recognized as a general requirement in restoration ecology (Hayes & Holl, 2003, Pywell *et al.*, 2002) as most experiments in this field are either single site or relatively short term (Pywell *et al.*, 2002; Pakeman, 2004; Marrs *et al.*, 2004). In this thesis long-term, multi-site bracken control experiments were analyzed to assess efficacy of various control treatments and subsequent re-vegetation, in addition methods of bracken control previously untested in formal experiments were studied.

The aims of this project were;

- To assess the effectiveness of bracken control treatments on *P. aquilinum* on long-term experiments at different sites throughout the UK.
- To assess the effects of bracken control treatments on *P. aquilinum* using formal meta-analysis.
- To assess the efficacy of the current manufacture's recommended guidelines for asulam at two contrasting long-term experiments over a three year period.

- To assess bracken fronds on three contrasting sites after 10 years of control followed by three years recovery.
- To assess the effectiveness of bruising as a method for bracken control.
- To answer the question; does bruising 'bleed the rhizomes dry'? By assessing the physiological effect of bruising on bracken fronds.
- To assess the effectiveness of bracken control treatments and treatments designed to restore vegetation in the restoration heathland and acid grassland on *P. aquilinum* – infested land on long-term, multi-site experiments across the UK.
- To find out whether or not different bracken control treatments would result in different trajectories and varying rates of success for the restoration of heathland and acid grassland.

The results and conclusions drawn from the research undertaken are now discussed in turn.

10.1. The effectiveness of bracken control treatments on P. aquilinum across a range of multi-site long-term experiments through out the UK (Chapter 2)

Despite local variation between sites with similar vegetation, all sites reacted in a similar manner to the bracken control treatments. From these data it is clear that long-term control of bracken at all sites and on all bracken frond measurements was best achieved using a continuous cutting treatment, preferably twice per year. However, this may not be the most cost-effective method as treatment will need to be applied twice a year essentially indefinitely. It is clear that a single application of herbicide is not an effective treatment for long term control, current advice recommends following up with spot spray, yearly, until no new fronds appear (Anon, 2005). This method was tested experimentally in Chapter 4.

10.1.1 *The assessment of the effects of bracken control treatments on P. aquilinum using formal meta-analysis (Chapter 3)*

The results from the inter-site comparison of all treatments against the untreated controls showed three important results. First, there were significant reductions in at least one *P. aquilinum* performance measure relative to untreated controls for all applied treatments on most sites. Second, there were significant differences in response between sites. Third, different responses were found for some site × treatments comparisons depending on the *P. aquilinum* measure used (frond length, frond density, frond cover). Thus, the effectiveness of *P. aquilinum* control varies spatially confirming the predictions of other workers (Pottier *et al.*, 2005). As with results from Chapter 2, comparisons of all treatments at all sites revealed that cutting twice within a year was usually the most effective treatment, but there were a few site x treatment combinations where other treatments were more effective at some sites depending on the performance measure used.

These results show the usefulness of the meta-analytical approach to investigating the significance of applied ecological restoration treatments in a multi-site study. Formal systematic reviews have being advocated recently in an attempt to avoid the bias's associated with previous ecological meta-analyses (Leimu & Koricheva, 2004; 2005).

10.1.2 *The efficacy of the current manufacture's recommended guidelines for asulam on two long-term experiments (Chapter 4)*

As expected re-spraying bracken previously treated with asulam caused a reduction in all bracken response variables at both sites tested (Peak and Sourhope). However, the response detected depended on degree of success of the previous treatment. For example, where bracken had been controlled well by continuous cutting once or twice a year for 13 years, at Sourhope, asulam had very little impact on the few remaining fronds. Significant impacts were found where the treatments had been less successful.

Cutting twice per year remained the most successful treatment at both sites, with fronds in the sprayed plots at Peak not yet being reduced to the same level as a single application of asulam in ET 0. A greater reduction in frond length is seen in plots grazing with sheep, suggesting grazing can significantly affect bracken control.

10.1.3 *The recovery of bracken fronds on three different sites after 10 years of control followed by years recovery (Chapter 5)*

The rate of recovery after release from treatment is dependent of the initial degree of control. At the *Calluna* heath site Cannock frond density and *P. aquilinum* cover being significantly higher or comparable to the untreated in the final year of monitoring. Thus, recovery to untreated levels occurred within three years. At Sourhope and Carneddau the bracken control treatments were much more effective. After three years of recovery, frond length, density and cover remained significantly lower in both the cutting treatments (cutting once per year and cutting twice per year) at Carneddau and Sourhope. Rapid recovery in cut treatments after 10 years of control was seen at Sourhope, a slower recovery is seen at Carneddau. The difference in recovery rates may be due to grazing pressure which is considerably higher at Carneddau, broad climatic variation or untested biotic factors. For *P. aquilinum* treated with asulam in 1993 or 1994 it took around 10 years for recovery at Cannock and 13 years plus at Carneddau and Sourhope. Marrs *et al.* (1998a) found recovery took roughly six years, with Pakeman & Marrs (1993) suggesting seven years.

10.2 The effectiveness of bruising as a method for bracken control (Chapters 6 & 7)

After only one year of bracken control, cutting and spraying treatments all reduce *P. aquilinum* cover in June and in August, with cutting thrice per year being the most effective. However the bruised plots showed an increase in cover compared to the untreated controls. Expected declines in rhizome mass (Paterson *et al.*, 1997; Le Duc *et al.*, 2003) and litter mass (Marrs *et al.*, 2007) were not seen in the cut and sprayed treatments at this early stage. It could be assumed that bruising would act with the same accumulative impact as cutting (Cox *et al.*, 2007a) but continued annual treatment and monitoring will be need to test this.

In order to test the hypothesis; that bruising bracken meant the fronds remained alive and 'bled the rhizomes of nutrients', photosynthesis and transpiration rates of bruised frond were compared to undamaged fronds. There was no evidence to suggest that bruising significantly harmed the fronds, with no significant reduction in either photosynthesis found in fronds bruised in the field or artificially cut. This suggests that the fronds are continuing to function normally, even though they have been flattened. The hypothesis behind bruising is related to the disruption of carbohydrate fluxes between rhizome and frond. In early spring the developing fronds are dependent on carbohydrate flux from the rhizomes; once approximately 60% developed they become self-sufficient and photosynthesise enough for growth and eventual export back to replenish the rhizomes (William & Foley, 1976). Bruising (like cutting) aims to break this cycle, so that carbohydrate is withdrawn but not returned. The additional benefit of bruising is that the frond remains alive and continues to make an additional drain on the rhizome stores (and water) with no return. Our results suggest that this is not the case as the fronds continue to operate at more or less the same rates as untreated fronds. Indeed, maintenance of the intact frond canopy after bruising may prejudice long-term control because presumably the fronds also continue to produce hormones which maintain apical dominance results in fewer new fronds emerging. If this is so, and it remains to be verified experimentally, this could actually prolong the persistence of bracken.

Irrespective, our results shown that bruising bracken twice or three times per year, after two years of treatment, did not reduce frond performance, and with the fronds photosynthesising and transpiring at similar rates to untreated fronds for up to seven weeks after treatment. Clearly, we did not expect to see major effects in two years and to assess the impacts on the fronds or rhizomes will require prolonged annual treatments for many years.

10.3. To assess the effectiveness of bracken control treatments and treatments designed to restore vegetation in the restoration heathland and acid grassland on *P. aquilinum* – infested land on long-term, multi-site experiments across the UK (Chapter 8)

In order to determine the effect of bracken control treatments and treatments designed to restore vegetation on species community change we hypothesized that:

(1) Geographical location (locally between sites) affects community change through time. Analysis showed there were a considerable number of spatial effects detected, between experiments on the same site and as a result of spatial effects in interaction with applied treatments. This result might appear an obvious one, in that it confirms that local spatial effects control restoration processes.

(2) Treatments applied to control *P. aquilinum* (same at all sites) influenced community change through time. However, the isolated use of bracken control treatments has relatively little influence on the subsequent long-term development of target vegetation, with a few already abundant species increasing their cover and no multi-site trends were observed. At the acid grassland sites (Carneddau and Sourhope) no species were found to increase significantly due to the effects of bracken control treatments. At the *Calluna* heath sites (Cannock and Peak) target species were not significantly increased although two common higher plants (*G. saxtile* and *D. flexuosa*) and one bryophyte (*C. introflexus*) did increase their cover. Thus the development of target vegetation requires a combination of control and restoration treatments that take into consideration the aspects of that site. This may include management for more than one factor, for example, soil condition and the present seed bank (De Graaf *et al.*, 1998).

(3) Treatments applied at the individual site level to restore vegetation influences community change towards the target vegetation through time. Three types of restoration treatment were investigated across the suite of experiments: (1) the restriction of sheep grazing at Peak, (2) seeding at Sourhope, Carneddau and Peak, and (3) litter disturbance by harrowing and fertilizer addition at Cannock. At Peak, the response to grazing was predictable with the increase in *A. capillaris*, *F. ovina*, *F. rubra* and some mosses. The reduction of *D. flexuosa,* as seen at Peak, by reduced sheep grazing is well known (Rawes, 1983; Anderson & Radford, 1994; Pakeman, 2004) and it is noted that the species is often preferentially grazed (Duffy *et al.*, 1974). It is clear that seeding worked best at Peak (with *C. vulgaris* when applied as brash and seeded *A. castellana* increasing) and produced less satisfactory results elsewhere, even though the treatment combinations were designed to produce site-specific targets. Litter disturbance by harrowing and fertilizer addition at Cannock had no impact on community change.

10.3.1. *Success rates and successional trajectories when restoring heathland and acid grassland on dense bracken (Chapter 9)*

Although cutting twice per year has often been found to be the most successful treatment for controlling bracken (Lowday & Marrs, 1992a; Marrs *et al.*, 1998a; Cox *et al.*, 2007a), the success of one bracken control treatment relative to another could not be identified, from the trajectories, in terms of creating alternative state (AS) or an alternative stable state (ASS). All sites show movement away from the start position but at some sites even the of "press-type" treatments in the form of cutting once or twice per year do not appear to be successful at overcoming the original states resilience. This occurs at both heathland (Cannock 1 & 2) sites and acid grassland sites (Sourhope 1 & 2). Alternatively, all of the bracken control treatments applied at the acid grassland Carneddau site and the heathland Peak site, even those considered "pulse" treatments (spraying with herbicide and the spraying and cutting combinations), appear to be enough to overcome the site's resilience and create new alternative states. None of the new states appear stable as a lot of stochasticity is seen, although this maybe due to the simplified model used. The application of site-specific treatments designed to restore semi-natural habit appear to have little or no impact on the creation of AS or ASS at any site.

10.4. Limitations of this work

The analysis of long-term data in Chapters 2, 3 & 8 may have resulted in the shorter-term success of some treatments being under-estimated, and this is likely in the treatments where asulam was applied because there is often a good initial effect followed by subsequent re-growth (Marrs *et al.*, 1998a). In at least three areas, results are based on 3 years of experimental and survey work. This is a major criticism but the results are reported with the caveat that further research is needed to verify the longer-term nature of this work, and to assess longer-term effectiveness.

10.5. Relevance to current weed control and restoration management

The results of this study have shown the success of various bracken control treatments and the impact of weed control treatments on subsequent restoration. In addition, the results from site-specific restoration treatments as well as previously untested but commonly used methodologies for bracken control have been analysed. These results can be used by policy makers to improve current advice for weed control and restoration practice.

This work suggests;

1. The control of bracken is a long-term endeavour. A single application of asulam, even in conjunction with a cut, is not adequate for long-term control. After ten years of control cutting twice per year was the most successful treatment.
3. Recovery from ten years of continuous cutting depends on the level of bracken control; it may take as little as two years, although where previous control has been good then there recovery takes longer than 6 years. Moderate grazing may help control the rate of recovery.
4. Follow-up, spot spraying asulam appears to be initially successful, although more than three years of treatment is still required.
5. Initially, bruising does not appear to be as effective at controlling bracken as cutting although again treatment of more than two years is necessary.
6. Restoration treatment success can be very variable and local site conditions should be taken into consideration.

10. 6. Future Research

10.6.1 *Long-term multi-site experiments*

This research has highlighted the variability in the success of bracken control (Chapter 2, 3 & 4) and the consequences for recovery rates (Chapter 4) and regeneration of desired communities (Chapter 8) at the national- and-local scale on sites with similar vegetation. Thus, there is an obvious need to carry out further work to ascertain why *P. aquilinum* is so variable and why in some places it is difficult to control whereas in other places it is apparently less difficult (Pakeman 2004). This is particularly important for *P. aquilinum* in view of its potential health implications for livestock (Marrs & Watt 2006), its predicted increase under future climate change scenarios and its potential to increase in area and density as a result of lands use changes resulting from reduced stocking rates encouraged in some Agri-environments schemes (Pottier *et al.,* 2005).

The need for long-term as well as multi-site experiments has been highlighted by the inconclusive results from experiments to test the efficacy of bruising as a bracken control treatment set up in 2004 and the addition of new asulam application trails on existing experiments again started in 2004. Ideally these experiments (Chapters 4, 5, 6 & 7) would be continued for at least another three years so a total of five years data could be analysed.

10.6.2 *Bracken and nutrients*

The soil chemistry analysis in Chapter 6 found nutrients including, N, K and Ca not to differ due to bracken control treatments despite significant decreases in *P. aquilinum* in some treatments. It is suggested this could be due to the transfer of some nutrients from bracken to the developing vegetation during the control process (Marrs *et al.*, 2007). *P. aquilinum* rhizomes have been found to be effective absorbers of P and Mg (Smith & Lockwood, 1990) the control of *P. aquilinum* could involve the leaching of P and N into near by water sources (Marrs *et al.*, 2007). Thus the control of *P. aquilinum* could potentially result in the conflict between achieving conservation and biodiversity objectives and increasing environmental costs in terms of polluting aquatic systems and long-term site degradation due to nutrient loss, described by Marrs *et al.* (2007). This theory has yet to be tested over a range of sites covering areas where large scale bracken control is likely to take place. There has also been no large scale survey of the rhizomes in terms of nutrient cycling with research concentrating on litter turn over (Marrs *et al.*, 2007).

10.6.3 *Bruising as a method for bracken control*

Chapter 7 found that the photosynthesis and transpiration rate in bruised fronds remained comparable to that of untreated fronds. Through observing sections of bruised fronds under the scanning electron microscope it was found the xylem vessel remains intact in even severely damaged fronds. However, the phloem vessels were never observed. Clarification of whether or not the frond is fully-functioning and carbohydrate is being translocated from the rhizome is still required. As there is no evidence that the carbohydrates leak from the damaged fronds, and they do not grow any further, it is reasonable to suggest that they export the resources back to the rhizome. The lack of new fronds being produced after bruising suggests their production is prevented either by the continuation of hormone transport, or shading by the bruised fronds which carpet the ground.

This study must, however, only be viewed as preliminary. The entire experiment needs to be carried out over a much longer time period, Moreover, future studies should incorporate tracers (radioactive or stable isotopes) to study carbohydrates flux between compartments through time in intact bracken (both amounts and rates); and how these fluxes are impacted by management (cutting, bruising and herbicide application). This information is essential in order to develop more effective models of the bracken plant and its control.

10.6.4 *Restoration management*

Chapter 8 highlighted the lack of effect the addition of seed had at both of the acidic grassland site. Seed banks under dense bracken tend to be poor (Mitchell *et al.*, 1998; Pakeman & Hay, 1996). Impoverished seed banks are known to hinder restoration of heath and grassland (Bakker & Berendse, 1999), with seed for grassland species tends to be relatively short-lived in comparison to heath land species (Bossuyt & Hermy, 2003). Thus the addition of seed for target species seems logical. Further investigation into why grass seeding did not have a significant impact on restoration success could help refine restoration management practises and increase the success rate of restoration.

10.6.5 *Alternative policy objectives*

Although restoration policy in the UK is aimed at reversing succession by controlling *P. aquilinum* a mid-successional species, and creating grassland or heath (Anon, 1995a, b; MAFF, 1995, 1996). Data in this thesis suggests that the creation of woodland may be a viable option. The need to target resource to the most cost effect areas has been highlighted by Mitchell *et al.* (1997). Further investigation into the natural colonisation of trees at Peak (Chapter 8) could be beneficial in terms of developing alternative policy objectives.

10.7. Concluding remarks

A fundamental limitation in vegetation management and restoration ecology is the ability to predict, with some degree of precision the likely outcome of a proposed treatment across a range of sites. This work has shown the value of long-term, multi-site experiments in weed control and restoration management. In addition it has increased our understanding of bracken control and the subsequent regeneration of desired vegetation communities. These results have been related to practical conservation with the aim of helping to target resources for long-term bracken control and the restoration of heath and grassland.

Reference List

Allen,S.E. (1989) *Chemical analysis of ecological materials.* Blackwells, Oxford.

Allison,M. & Ausden,M. (2004) Successful use of topsoil removal and soil amelioration to create heathland vegetation. *Biological Conservation*, **120**, 221-228.

Allison,M. & Ausden,M. (2006) Effects of removing the litter and humic layers on heathland establishment following plantation removal. *Biological Conservation*, **127**, 177-182.

Alonso-Amelot,M.E., Castillo,U., Smith,B.L. & Lauren,D.R. (1996) Bracken ptaquiloside in milk. *Nature*, **382**, 587.

Anderson,P. & Radford,E. (1994) Changes in Vegetation Following Reduction in Grazing Pressure on the National-Trust Kinder Estate, Peak District, Derbyshire, England. *Biological Conservation*, **69**, 55-63.

Anon. (1988) *Heathland restoration: A handbook of techniques.* British Gas Plc., Southampton.

Anon. (1995a) Biodiversity UK Steering Group Report, Vol II. Action Plans. London, HMSO.

Anon. (1995b) Biodiversity UK Steering Group Report, Vol I. Meeting the Rio Challenge. London, HMSO.

Anon. (2005) Bracken control, vegetation restoration and land management. Rural Development Service Technical Advice, Note 23. RDS, Defra, London.

Arnquist,G. & Wooster,D. (1995) Metaanalysis – synthesizing research findings in ecology and evolution. *Trends in Ecology & Evolution*, **10**, 236-240.

Bakker,J.P. & Berendse,F. (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology & Evolution*, **14**, 63-68.

Bakker,J.P., Elzinga,J.A. & de Vries,Y. (2002) Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient-poor soils. *Applied Vegetation Science*, **5**, 107-120.

Barr,C.J., Bunce,R.G., Clarke,R.T., Fuller,R.M., Furse,M.T., Gillespie,M.K., Groom,G.B., Hallam,C.J., Hornung,M., Howard,D.C., & Ness,M.J. (1993) Countryside survey 1990: main report. Countryside 1990 series: Volume 2. Department of the Environment, London.

Beisner,B.E., Haydon,D.T. & Cuddington,K. (2003) Alternative states in ecology. *Frontiers in Ecology*, **1**, 376-386.

Bender,E.A., Case,T.J. & Gilpin,M.E. (1984) Perturbation Experiments in Community Ecology - Theory and Practice. *Ecology*, 65, 1-13.

Block,W.M., Franklin,A.B., Ward,J.P.Jr., Ganey,J.L. & White,G.C. (2001) Design and Implementation of Monitoring Studies to Evaluate the Success of Ecological Restoration on Wildlife. *Restoration Ecology*, 9, 293-303.

Blumenthal,D.M., Jordan,N.R. & Svenson,E.L. (2003) Weed control as a rationale for restoration: The example of tallgrass prairie. *Conservation Ecology*, 7.

Bossuyt,B. & Hermy,M. (2003) The potential of soil seedbanks in the ecological restoration of grassland and heathland communities. *Belgian Journal of Botany*, 136, 23-34.

Braid,K.W. (1948) Bracken control - artificial and natural. *Journal of the British Grass Society*, 3, 181-189.

Braid,K.W. (1959) *Bracken: a review of the literature.* Commonwealth Agricultural Bureaux, Hurley, Berkshire.

Britton,A.J., Pearce,I.S.K. & Jones,B. (2005) Impacts of grazing on montane heath vegetation in Wales and implications for the restoration of montane areas. *Biological Conservation*, 125, 515-524.

Broome,A.C. (2007) Management of butterfly habitat in north west Scotland: the effects of five years of cattle grazing. *Aspects of Applied Biology*, 82, 199-212.

Cabin,R.J. & Mitchell,R.J. (2000) To Bonferroni or not to Bonferroni: when and how are the questions. *Bulletin of the Ecological Society of America*, 81, 246-248.

Cadbury,C.J. (1976) Botanical implications of bracken control. *Botanical Journal of the Linnean Society*, 73, 285-294.

Caporn,S.J.M., Brooks,A.L., Press,M.C. & Lee,J.A. (1999) Effects of long-term exposure to elevated CO2 and increased nutrient supply on bracken (Pteridium aquilinum). *Functional Ecology*, 13, 107-115.

Cohen,J. (1988) *Power analysis for the behavioural sciences.* Lawrence Erlbaum Associates, New Jersey, USA.

Cooper-Driver,G.A. (1976) Chemotaxonomy and phytochemical ecology of bracken. *Botanical Journal of the Linnean Society*, 73, 35-46.

Cooper,H. & Hedges,L.V. (1994) *The Handbook of Research Synthesis.* Russell Sage Foundation, New York.

Coppins,B.J. (2002) *Checklist of the lichens of Great Britain and Ireland.* British Lichen Society, London.

Cox,E.S., Marrs,R.H., Pakeman,R.J. & Le Duc,M.G. (2007a) A multi-site assessment of bracken control effectiveness across the UK. *Applied Vegetation Science.* In Press.

Cox,E.S., Marrs,R.H., Pakeman,R.J. & Le Duc,M.G. (2007b) The restoration of heathland and acid grassland on *Pteridium aquilinum* invested land across the UK: a multi site study. *Restoration Ecology.* In Press.

Crawley,M.J. (2005) *Statistics: An introduction to R.* John Wiley & Sons, Chichester, UK.

Daniels,R.E. (1985) Studies in the growth of *Pteridium-aquilinum* (L) Kuhn (Bracken) .1. Regeneration of rhizome segments. *Weed Research,* **25,** 381-388.

Davis,T.J., Klinkenberg,B. & Keller,C.P. (2004) Evaluating Restoration Success on Lyell Island, British Columbia Using Oblique Videogrammetry. *Restoration Ecology,* **12,** 447-455.

De Graaf,M.C.C., Verbeek,P.J.M., Bobbink,R. & Roelofs,J.G.M. (1998) Restoration of species-rich dry heaths: the importance of appropriate soil conditions. *Acta Botanica Neerlandica,* **47,** 89-111.

Deeks,J.J., Altman,D.G., Pakeman,R.J., Oksanen,J. & Marrs,R.H. (2001) Statistical methods for examining heterogeneity and combining results from several studies in meta-analysis. *Systematic Reviews in Health Care: Meta-analysis in Context* (eds M. Egger, G. D. Smith & D. G. Altman), pp. 285-312. British Medical Journal Publishing Group, London.

Dersimonian,R. & Laird,N. (1986) Metaanalysis in Clinical-Trials. *Controlled Clinical Trials,* **7,** 177-188.

DiTomaso,J.M. (2000) Invasive weeds in rangelands: Species, impacts, and management. *Weed Science,* **48,** 255-265.

Duffey,E., Morris,M.G., Sheail,J., Ward,L.K., Wells,D.A. & Wells,T.C.E. (1974) *Grassland Ecology and Wildlife Management.* Chapman and Hall, London.

Dutkowski, G. and Boomsma, D. (1990) Bracken control and tree growth in plantations of radiata pine in the lower south-east of South Australia. *Bracken Biology and Management* (eds J.A. Thompson and R.T. Smith), pp. 277-290.Australian Institute of Agricultural Sciences (NSW) Occasional Publication No. 40.

Dyer,A.F. (1989) Does bracken spread by spores? *Bracken biology and management* (eds J. A. Thomson & R. T. Smith), pp. 35-42. Australian Institute of Agricultural Science, Sydney.

Engelman, H.M. and Nyland, R.D. (2006) Interference to Hardwood Regeneration in Northeastern North America: Assessing and Countering Ferns in Northern Hardwood Forests. *Northern Journal of Applied Forestry*, **23**, 166-175.

Equihua,M. & Usher,M.B. (1993) Impact of carpets of the invasive moss *Campylopus introflexus* on *Calluna vulgaris* regeneration. *Journal of Ecology*, **81**, 359-365.

Evans,I.A. & Galpin,O.P. (1990) Bracken and leukaemia. *The Lancet*, **335**, 231.

Evans,W.C. (1976) Bracken thiaminase-mediated neurotoxic syndromes. *Botanical Journal of the Linnean Society*, **73**, 113-132.

Fenwick,G.R. (1989) Bracken (*Pteridium aquilinum*)- Toxic Effects and Toxic Constituents. *Journal of the Science of Food and Agriculture*, **46**, 147-174.

Frankland,J.C. (1976) Decomposition of bracken litter. *Botanical Journal of the Linnean Society*, **73**, 133-143.

Galpin,O.P., Whitaker,C.J., Whitaker,R. & Kassab,J.Y. (1990) Gastric-cancer in Gwynedd - possible links with bracken. *British Journal of Cancer*, **61**, 737-740.

Ghorbani Pashakolaei,J. (2005) *Restoration of bracken-dominated land: the response of propagule banks*. PhD Thesis, University of Liverpool.

Gimingham,C.H. (1992) *The lowland heathland management handbook*. English Nature, Peterborough.

Gordon,C., Woodin,S.J., Mullins,C.E. & Alexander,I.J. (1999) Effects of environmental change, including drought, on water use by competing Calluna vulgaris (heather) and Pteridium aquilinum (bracken). *Functional Ecology*, **13**, 96-106.

Grime,J.P., Hodgson,J.G. & Hunt,R. (1988) *Comparative plant ecology ; a functional approach to common British species*. Unwin Hyman, London.

Gurevitch,J. & Chester,Jr.S.T. (1986) Analysis of repeated measures experiments. *Ecology*, **67**, 255.

Gurevitch,J. & Hedges,L.V. (1999) Statistical issues in ecological meta-analyses. *Ecology*, **80**, 1142-1149.

Gurevitch,J. & Hedges,L.V. (1999) Combining results of independent experiments. In: *Design and analysis of ecological experiments*. (eds S. M. Scheiner & J. Gurevitch), pp. 347-369. Oxford University Press, Oxford.

Hamilton, L.J., Tolhurst, K.G. & Walker, E. (1990) The distribution, abundance and economic impact of bracken (*Pteridium esculentum*) in Victoria. *Bracken Biology and Management*, (eds J.A. Thompson and R.T. Smith) pp. 115-19. Australian Institute of Agricultural Sciences (NSW) Occasional Publication No. 40.

Harper,J.L. (1977) *Population biology of plants.* Academic Press, London.

Hayes,G.F. & Holl,K.D. (2003) Site-specific responses of native and exotic species to disturbances in a mesic grassland community. *Applied Vegetation Science*, 6, 235-244.

Hedges,L.V. & Olkin,I. (1985) *Statistical methods for meta-analysis.* Academic Press, London.

Hill,M.O., Preston,C.D. & Smith,A.J.E. (1991) *Atlas of the Bryophytes of Britain and Ireland, Volume 1 Liverworts (Hepaticae and Anthocerotae).* Harley Books, Colchester.

Hill,M.O., Preston,C.D. & Smith,A.J.E. (1992) *Atlas of the Bryophytes of Britain and Ireland, Volume 2 Mosses (except Diplolepideae).* Harley Books, Colchester.

Hill,M.O., Preston,C.D. & Smith,A.J.E. (1994) *Atlas of the Bryophytes of Britain and Ireland, Volume 3 Mosses (Diplolepideae).* Harley Books, Colchester.

Hill,M.O. (1996) *TABLEFIT VERSION 1.0, For identification of vegetation types.* ITE Monks Wood, Huntingdon.

Hirono,I., Shibuya,C., Fushimi,K. & Haga,M. (1970) Studies on carcinogenic properties of bracken (*Pteridium aquilinum*). *Journal of the National Cancer Institute*, 45, 179-188.

Hirono,I., Shibuya,C., Shizmu,M. & Fushimi,K. (1972) Carcinogenic activity of processed bracken as human food. *Journal of the National Cancer Institute*, 48, 1245-1250.

Hobbs,R.J. & Norton,D.A. (1996) Towards a Conceptual Framework for Restoration Ecology. *Restoration Ecology*, 4, 93-110.

Hobbs,R.J. & Harris,J.A. (2001) Restoration Ecology: Repairing the Earth's Ecosystems in the New Millennium. *Restoration Ecology*, 9, 239-246.

Hodgson,E.S. (1991) Is Bracken A Health-Hazard. *Lancet*, 337, 493.

Hopkins,A., Wainwright,J., Murray,P.J., Bowling,P.J. & Webb,M. (1988) 1986 survey of upland grassland in England and Wales: changes in age structure and botanical composition since 1970-72 in relation to grassland management and physical features. *Grass and Forage Science*, 43, 185-198.

Hopkins,A. (1990) Bracken (*Pteridium-aquilinum*) - its distribution and animal health implications. *British Veterinary Journal*, 146, 316-326.

Horrill, A. D., Dale, J., and Thomson, A. J. (1978) Asulam - its effects of selected plants, plant communities and animals. *CST Report No. 174.* Nature Conservancy Council.

Hudson,P.J., Norman,R., Laurenson,M.K., Newborn,D., Gaunt,M., Jones,L., Reid,H., Gould,E., Bowers,R. & Dobson,A. (1995) Persistence and transmission of tick-bourne viruses: *Ixodes ricinus* and louping-ill virus in red grouse populations. *Parasitology*, **111**, S49-S58.

Hulme,P.D., Merrell,B.G., Torvell,L., Fisher,J.M., Small,J.L. & Pakeman,R.J. (2002) Rehabilitation of degraded Calluna vulgaris (L.) Hull-dominated wet heath by controlled sheep grazing. *Biological Conservation*, **107**, 351-363.

Humphrey,J.W. & Swaine,M.D. (1997) Factors affecting the natural regeneration of Quercus in Scottish oakwoods .1. Competition from Pteridium aquilinum. *Journal of Applied Ecology*, **34**, 577-584.

Hunter,J.G. (1953) The composition of bracken: some major and trace element constituents. *Journal of Science and Food Agriculture*, **4**, 10-20.

Hytonen,J. & Jylha,P. (2005) Effects of competing vegetation and post-planting weed control on the mortality, growth and vole damages to Betula pendula planted on former agricultural land. *Silva Fennica*, **39**, 365-380.

Jacquemart,A.L., Champluvier,D. & De Sloover,J. (2003) A test of mowing and soil-removal restoration techniques in wet heaths of the High Ardenne, Belgium. *Wetlands*, **23**, 376-385.

Koedam,N., Buscher,P. & Vanspeybroeck,D. (1992) Acidiphily in pteridophytes - assessment of the role of root cation-exchange properties. *Journal of Plant Nutrition*, **15**, 2605-2619.

Lawson,C.S., Ford,M.A., Mitchley,J. & Warren,J.M. (2004) The establishment of heathland vegetation on ex-arable land: the response of *Calluna vulgaris* to soil acidification. *Biological Conservation*, **116**, 409-416.

LCA-4 (1993) *LCA-4 Operating Manual.* Analytical Development Company, UK.

Le Duc,M.G., Pakeman,R.J., Putwain,P.D. & Marrs,R.H. (2000) The variable responses of bracken fronds to control treatments in Great Britain. *Annals of Botany*, **85**, 17-29.

Le Duc,M.G., Pakeman,R.J. & Marrs,R.H. (2003) Changes in the rhizome system of bracken subjected to long-term experimental treatment. *Journal of Applied Ecology*, **40**, 508-522.

Le Duc,M.G., Pakeman,R.J. & Marrs,R.H. (2007a) A restoration experiment on moorland infested by *Pteridium aquilinum*: Plant species responses. *Agriculture, Ecosystems & Environment*, **119**, 53-59.

Le Duc,M.G., Yang,L., Fisher,M.J., Miller,P.G.G., Pakeman,R.J. & Marrs,R.H. (2007b) A database solution for archiving and publishing complex ecological datasets from experiments. *Journal of Vegetation Science*. In Press.

Le Duc,M.G., Tong,C., Grigoriu,A., Cox,E.S., Pakeman,R.J. & Marrs,R.H. (2007c) Can we produce alternative stable states when reversing succession? – a test with a long-term experiment on a bracken-infested Calluna moorland. *Journal of Applied Ecology*. In Press.

Legendre,P. & Legendre,L. (1998) *Numerical Ecology*. Elsevier Science B. V., Amsterdam.

Leimu,R. & Koricheva,J. (2004) Cumulative meta-analysis: a new tool for detection of temporal trends and publication bias in ecology. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 1961-1966.

Leimu,R. & Koricheva,J. (2005) What determines the citation frequency of ecological papers? *Trends in Ecology & Evolution*, **20**, 28-32.

Lowday,J.E. & Marrs,R.H. (1992a) Control of bracken and restoration of heathland: I. Control of bracken. *Journal of Applied Ecology*, **29**, 195-203.

Lowday,J.E. & Marrs,R.H. (1992b) Control of bracken and the restoration of heathland.III. Bracken Litter disturbance and heathland restoration. *Journal of Applied Ecology*, **29**, 212-217.

MAFF. (1993) Environment matters. Environmentally Sensitive Areas. London, Ministry of Agriculture, Fisheries and Food.

MAFF. (1996) Environment matters. The Countryside Stewardship Scheme: Information for farmers and land managers. London, Ministry of Agriculture, Fisheries and Food.

Marrs,R.H. & Hicks,M.J. (1986) Study of vegetation change at Lackenheath Warren: a re-examination of A. S. Watt's theories of bracken dynamics in relation to succession and vegetation management. *Journal of Applied Ecology*, **23**, 1029-1046.

Marrs,R.H. & Lowday,J.E. (1992) Control of bracken and the restoration of heathland .II. Regeneration of the heathland community. *Journal of Applied Ecology*, **29**, 204-211.

Marrs,R.H., Pakeman,R.J. & Lowday,J.E. (1993) Control of bracken and the restoration of heathland .V. Effects of bracken control treatments on the rhizome and Its relationship with frond performance. *Journal of Applied Ecology*, **30**, 107-118.

Marrs,R.H., Johnson,S.W. & Le Duc,M.G. (1998a) Control of bracken and restoration of heathland. VI. The response of bracken fronds to 18 years of continued bracken control or 6 years of control followed by recovery. *Journal of Applied Ecology*, **35**, 479-490.

Marrs,R.H., Johnson,S.W. & Le Duc,M.G. (1998b) Control of bracken and restoration of heathland. VIII. The regeneration of the heathland community after 18 years of continued bracken control or 6 years of control followed by recovery. *Journal of Applied Ecology*, **35**, 857-870.

Marrs,R.H., Johnson,S.W. & Le Duc,M.G. (1998c) Control of bracken and restoration of heathland. VII. The response of bracken rhizomes to 18 years of continued bracken control or 6 years of control followed by recovery. *Journal of Applied Ecology*, **35**, 748-757.

Marrs,R.H., Le Duc,M.G., Mitchell,R.J., Goddard,D., Paterson,S. & Pakeman,R.J. (2000) The ecology of bracken: its role in succession and implications for control. *Annals of Botany*, **85**, 3-15.

Marrs,R.H. & Le Duc,M.G. (2000) Identifying the factors controlling vegetation change in long-term experiments designed to control bracken and restore heathland community in Breckland, UK. *Applied Vegetation Science*, **3**, 135-146.

Marrs,R.H. (2004) Why we should conserve 'limiting factors', at least sometimes! *Journal of Vegetation Science*, **15**, 573-575.

Marrs,R.H., Phillips,J.D.P., Todd,P.A., Ghorbani,J. & Le Duc,M.G. (2004) Control of *Molinia caerulea* on upland moors. *Journal of Applied Ecology*, **41**, 398-411.

Marrs,R.H. & Watt,A.S. (2006) Biological Flora of the British Isles: *Pteridium aquilinum* (L.) Kuhn. *Journal of Ecology*, **94**, 1272-1321.

Marrs,R.H., Galtress,K., Tong,C., Cox,E.S., Blackbird,S.J., Heyes,T.J., Pakeman,R.J. & Le Duc,M.G. (2007) Competing conservation goals, biodiversity or ecosystem services: Element losses and species recruitment in a managed morrland- bracken model system. *Journal of Environmental Management*, **doi;10.1016/j-jenvman.2006.11.011.**

Milligan,A.L., Putwain,P.D. & Marrs,R.H. (2003) A field assessment of the role of selective herbicides in the restoration of British moorland dominated by Molinia. *Biological Conservation*, **109**, 369-379.

Mitchell,R.J., Marrs,R.H., Le Duc,M.G. & Auld,M.H.D. (1997) A study of succession on lowland heaths in Dorset, southern England: Changes in vegetation and soil chemical properties. *Journal of Applied Ecology*, **34**, 1426-1444.

Mitchell,R.J., Marrs,R.H. & Auld,M.H.D. (1998) A comparative study of the seedbanks of heathland and successional habitats in Dorset, Southern England. *Journal of Ecology*, **86**, 588-596.

Mitchell,R.J., Auld,M.H.D., Hughes,J.M. & Marrs,R.H. (2000) Estimates of nutrient removal during heathland restoration on successional sites in Dorset, Southern England. *Biological Conservation*, **95**, 233-246.

Nathwani,D., Hamlet,N. & Walker,E. (1990) Lyme disease: a review. *British Journal of General Practice*, **40**, 72-74.

Ojika,M., Wakamatsu,K., Niwa,H. & Yamada,K. (1987) Ptaquiloside, a potent carcinogen isolated from bracken fern *Pteridium-aquilinum* var *latiusculum* - structure elucidation based on chemical and spectral evidence, and reactions with amino-acids, nucleosides, and nucleotides. *Tetrahedron*, **43**, 5261-5274.

Oksanen,J. (2006) *Multivariate Analysis of Ecological Communities in R: vegan tutorial, version 1.6-10 for windows.*

Osenberg,C.W., Sarnelle,O., Cooper,S.D. & Holt,R.D. (1999) Resolving ecological questions through meta-analysis: Goals, metrics, and models. *Ecology*, **80**, 1105-1117.

Ovenden,G.N., Swash,A.R.H. & Smallshire,D. (1998) Agri-environment schemes and their contribution to the conservation of biodiversity in England. *Journal of Applied Ecology*, **35**, 955-960.

Page,C.N. (1976) The taxonomy and phytogeny of bracken - a review. *Botanical Journal of the Linnean Society*, **73**, 1-34.

Page,C.N. (1995) Structural variation in western European bracken: an updated taxonomic perspective. *Bracken: An Environmental Issue* (eds R. T. Smith & J. A. Taylor), pp. 13-15. International Bracken Group, Aberystwyth.

Pakeman,R.J. & Marrs,R.H. (1992) The conservation value of bracken *Pteridium-aquilinum* (L) Kuhn-dominated communities in the Uk, and an assessment of the ecological impact of bracken expansion or its removal. *Biological Conservation*, **62**, 101-114.

Pakeman,R.J. & Marrs,R.H. (1993) Long-term recovery of bracken (*Pteridium-aquilinum* (L) Kuhn) after Asulam spraying. *Annals of Applied Biology*, **122**, 519-530.

Pakeman,R.J., Marrs,R.H. & Jacob,P.J. (1994) A Model of Bracken (Pteridium-Aquilinum) Growth and the Effects of Control Strategies and Changing Climate. *Journal of Applied Ecology*, **31**, 145-154.

Pakeman,R.J. & Marrs,R.H. (1994) The effects of control on the biomass, carbohydrate content and bud reserves of bracken (*Pteridium-aquilinum* (L.) Kuhn), and an evaluation of a bracken growth-model. *Annals of Applied Biology*, **124**, 479-493.

Pakeman,R.J., Marrs,R.H., Howard,D.C. & Barr,C.J. (1995) Predicting the effects of climate and landuse change on the spread of bracken. *Bracken: An Environmental Issue* (eds R. T. Smith & J. A. Taylor), pp. 69-72. International Bracken Group, Leeds.

Pakeman,R.J. & Marrs,R.H. (1996) Modelling the effects of climate change on the growth of bracken (Pteridium aquilinum) in Britain. *Journal of Applied Ecology*, **33**, 561-575.

Pakeman,R.J. & Hay,E. (1996) Heathland seedbanks under bracken Pteridium aquilinum (L) Kuhn and their importance for re-vegetation after bracken control. *Journal of Environmental Management*, **47**, 329-339.

Pakeman,R.J., LeDuc,M.G. & Marrs,R.H. (1997) Moorland vegetation succession after the control of bracken with asulam. *Agriculture Ecosystems & Environment*, **62**, 41-52.

Pakeman,R.J., Le Duc,M.G. & Marrs,R.H. (1998) An assessment of aerially applied asulam as a method of long- term bracken control. *Journal of Environmental Management*, **53**, 255-262.

Pakeman,R.J., Le Duc,M.G. & Marrs,R.H. (2000) Bracken distribution in Great Britain: strategies for its control and the sustainable management of marginal land. *Annals of Botany*, **85**, 37-46.

Pakeman,R.J., Thwaites,R.H., Le Duc,M.G. & Marrs,R.H. (2002) The effects of cutting and herbicide treatment on Pteridium aquilinum encroachment. *Applied Vegetation Science*, **5**, 203-212.

Pakeman,R.J. (2004) Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. *Journal of Ecology*, **92**, 893-905.

Pakeman,R.J., Small,J.L., Le Duc,M.G. & Marrs,R.H. (2005) Recovery of moorland vegetation after aerial spraying of bracken (Pteridium aquilinum (L.) Kuhn) with asulam. *Restoration Ecology*, **13**, 718-724.

Paterson,S., Marrs,R.H. & Pakeman,R.J. (1997) Efficacy of bracken (Pteridium aquilinum (L) Kuhn) control treatments across a range of climatic zones in Great Britain. A national overview and regional examination of treatment effects. *Annals of Applied Biology*, **130**, 283-303.

Poel,L.W. (1948) Effects of aeration on bracken and heather grown in nutrient solution. *Nature*, **162**, 115.

Poel,L.W. (1951) Soil aeration in relation to *Pteridium aquilinum* (L.) Kuhn. *Journal of Ecology*, **39**, 182-191.

Poel,L.W. (1961) Soil aeration as a limiting factor in the growth of *Pteridium aquilinum* (L.) Kuhn. *Journal of Ecology*, 49, 107-111.

Pottier, J., Pakeman, R. J., Le Duc, M. G., and Marrs, R. H. (2005) Validation of a model for predicting *Pteridium aquilinum* (L.) Kuhn production and control across the UK. BCPC International Congress – Crop Science & Technology 2005. pp. 987-994.

Pullin,A.S. & Knight,T.M. (2001) Effectiveness in conservation practice: Pointers from medicine and public health. *Conservation Biology*, **15**, 50-54.

Pullin,A.S. & Knight,T.M. (2003) Support for decision making in conservation practice: an evidence-based approach. *Journal for Nature Conservation*, **11**, 83-90.

Pullin,A.S. & Stewart,G.B. (2006) Guidelines for systematic review in conservation and environmental management. *Conservation Biology*, **20**, 1647-1656.

Putwain,P.D., Gillham,D.A. & Holliday,R.J. (1982) Restoration of heather moorland and lowland heathland, with special reference to pipelines. *Environmental Conservation*, **9**, 225-235.

Pywell,R.F., Bullock,J.M., Hopkins,A., Walker,K.J., Sparks,T.H., Burke,M.J.W. & Peel,S. (2002) Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology*, **39**, 294-309.

Rasmussen,L.H., Kroghsbo,S., Frisvad,J.C. & Hansen,H.C.B. (2003) Occurrence of the carcinogenic Bracken constituent ptaquiloside in fronds, topsoils and organic soil layers in Denmark. *Chemosphere*, **51**, 117-127.

Rawes,M. (1983) Changes in 2 High-Altitude Blanket Bogs After the Cessation of Sheep Grazing. *Journal of Ecology*, **71**, 219-235.

Roberts,J., Pymar,C.F., Wallace,J.S. & Pitman,R.M. (1980) Seasonal changes in leaf area, stomatal and canopy conductances and transpiration from bracken below a forest canopy. *Journal of Applied Ecology*, **17**, 409-422.

Roberts,J., Wallace,J.S. & Pitman,R.M. (1984) Factors affecting stomatal conductance of bracken below a forest canopy. *Journal of Applied Ecology*, **21**, 643-655.

Robinson,R.C. (1986) Practical herbicide use for bracken control. *Bracken: Ecology, land use and control technology* (eds R. T. Smith & J. A. Taylor), pp. 331-340. Parthenon Publishing Group, Carnforth, Lancs.

Robinson,R.C. (2000) The means to large-scale, effective bracken clearance in the UK. *Bracken fern: toxicity, biology and control* (eds J. A. Taylor & R. T. Smith), pp. 156-162. International Bracken Group, Leeds.

Robinson,R.C. (2007) Steps to more effective bracken management. *Aspects of Applied Biology*, **82**, 143-155.

Rodwell,J.S. (1991a) *British plant communities, Vol. 1: Woodlands and scrub.* Cambridge University Press, Cambridge.

Rodwell,J.S. (1991b) *British plant communities, Vol. 2: Heaths and mires.* Cambridge University Press, Cambridge.

Rodwell,J.S. (1992) *British plant communities, Vol. 3: Grassland and montane communities.* Cambridge University Press, Cambridge.

Rodwell,J.S. (2000) *British Plant Communities: Vol. 5: Maritine communities and vegetation of open habitiats.* Cambridge University Press, Cambridge.

Rowntree,J.K., Lawton,K.F., Rumsey,F.J. & Sheffield,E. (2003) Exposure to Asulox inhibits the growth of mosses. *Annals of botany*, **92**, 547-556.

Rymer,L. (1976) The history and ethnobotany of bracken. *Botanical Journal of the Linnean Society*, **73**, 151-176.

Saito,K., Nagao,T., Matoba,M., Koyama,K., Natori,S., Murakami,T. & Saiki,Y. (1989) Chemical-assay of Ptaquiloside, the carcinogen of *Pteridium- aquilinum*, and the distribution of related-compounds in the pteridaceae. *Phytochemistry*, **28**, 1605-1611.

Sankoh,A.J., Huque,M.F. & Dubey,S.D. (1997) Some comments on frequently used multiple endpoint adjustment methods in clinical trials. *Statistics in Medicine*, **16**, 2529-2542.

SAS (1989) *SAS/STAT User's Guide Version 6.* SAS Institute., Cary, NC.

Scheiner,S.M. & Gurevitch,J. (2001) *Design and Analysis of Ecological Experiments.* Oxford University Press, New York.

Sharp,S. (1998) Meta-analysis regression: statistics, biostatistics, and epidemiology. *Stata Technical Bulletin*, **42**, 16-22.

Sheffield, E., Johns, M., & Rumsey, F. J. (2001) An Investigation of the Effects of Low Doses of Asulox on non-target Species. English Nature Contract EIT20-19-001.

Simmons,M.T. (2005) Bullying the bullies: The selective control of an exotic, invasive annual (Rapistrum rugosum) by oversowing with a competitive native species (Gaillardia pulchella). *Restoration Ecology*, **13**, 609-615.

Smith,R.T. & Lockwood,J.G. (1990) Bracken invasion and bracken replacement: guidelines for the prediction of hydrological changes. *Bracken biology and management* (eds J. A. Thomson & R. T. Smith), pp. 175-185. Australian Institute of Agricultural Science, Sydney.

Smith, R. T. and Taylor, J. (1995) A. Bracken: An environmental issue, Special publication No. 2. Aberystwyth, International Bracken Group.

Sokal,R.R. & Rohlf,F.J. (1995) *Biometry.* W. H. Freeman & Co., New York.

Stace,C. (1997) *New Flora of the British Isles.* CUP, Cambridge.

Stata Corporation (2003) *Stata statistical software: release 8.2.* Stata Corporation, College Station , Texas, USA.

Stewart,G.B., Coles,C.F. & Pullin,A.S. (2005) Applying evidence-based practice in conservation management: Lessons from the first systematic review and dissemination projects. *Biological Conservation,* **126,** 270-278.

Stewart,G.B., Pullin,A.S. & Tyler,C. (2007) The effectiveness of asulam for the control of *P. aquilinum* in Britain: A meta-analysis. *Environmental Management,* In Press.

Stewart, R.E., Cooley, A.W. & Guardigli, A. (1979) Asulam controls western bracken (*Pteridium-aquilinum*) on forest land in Western Oregon. *Weed Science* 27 (6):589-594.

Suding,K.N., Gross,K.L. & Houseman,G.R. (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution,* **19,** 46-53.

Sutherland,W.J., Pullin,A.S., Dolman,P.M. & Knight,T.M. (2004) Response to Griffiths. Mismatches between conservation science and practice. *Trends in Ecology & Evolution,* **19,** 565-566.

Taylor,J.A. (1985) Bracken encroachment rates in Britain. *Journal of Soil Use and Management,* **1,** 53-56.

Taylor, J.A. (1986) The bracken problem: a local hazard and global issue. Bracken Ecology, *Land Use and Control Technology,* (eds R.T. Smith and J.A. Taylor), pp. 21-42. International Bracken Group.

Taylor, J. A. (1999) Perceptions of bracken. *Bracken Perceptions and Bracken Control in the British Uplands International Bracken Group.* Special Publication No.3. pp. 1-7. International Bracken Group.

ter Braak,C.J.K. & Smilauer,P. (1998) *CANOCO 4 Reference manual and user's guide to Canoco for Windows: Software for Canonical Community Ordination.* Microcomputer Power, Ithaca, USA.

The Southern Uplands Partnership. (2001) Bracken Control; A guide to best practise. The Southern Uplands Partnership, Galashields.

Thompson,S.G. & Sharp,S.J. (1999) Explaining heterogeneity in meta-analysis: A comparison of methods. *Statistics in Medicine* , **18,** 2693-2708.

Thompson, J.A., Willoughby, C. and Shearer, C.M. (1986) Factors affecting the distribution, abundance and economic status of bracken (*Pteridium esculentum*) in NSW. *Bracken Ecology, Land Use and Control Technology.* (eds R.T. Smith and J.A. Taylor), pp. 109-119. Internation Bracken Group.

Tong,C., Le Duc,M.G., Ghorbani,J. & Marrs,R.H. (2006) Linking restoration to the wider landscape: A study of a bracken control experiment within a upland moorland landscape mosaic in the Peak District, UK. *Landscape and Urban Planning*, **78**, 115-134.

Tyler,C., Pullin,A.S. & Stewart,G.B. (2006) Effectiveness of management interventions to control invasion by Rhododendron ponticum. *Environmental Management*, **37**, 513-522.

van der Hoeven,J.C.M., Largerweij,W.J., Posthumus,M.A., van Veldhuizen,A., Holterman,H.A. & Aquilide,A. (1983) Aquilide-a, a new mutagenic compound isolated from bracken fern *(Pteridium aquilinum* (L.) Kuhn). *Carcinogenesis*, **4**, 1587-1592.

Varvarigos,P. & Lawton,J.H. (1991) Farmers' perceptions of the scale of the bracken problem on farms in less favoured areas in England and Wales. *Journal of Applied Ecology*, **28**, 988-1003.

Veerasekaran,P., Kirkwood,R.C. & Fletcher,W.W. (1977a) Studies on the mode of action of asulam in bracken (*Pteridium aquilinum* (L.) Kuhn) 2. Biochemical activity in the rhizome buds. *Weed Research*, **17**, 85-92.

Veerasekaran,P., Kirkwood,R.C. & Fletcher,W.W. (1977b) Studies on the mode of action of asulam in bracken (*Pteridium aquilinum* (L.) Kuhn) 1. Absorption and translocation of [^{14}C] asulam. *Weed Research*, **17**, 33-39.

Veerasekaran,P., Kirkwood,R.C. & Fletcher,W.W. (1978) Studies on the mode of action of asulam in bracken (*Pteridium aquilinum* L. Kuhn) 3. Long-term control of field bracken. *Weed Research*, **18**, 315-319.

Veerasekaren,P., Kirkwood,R.C. & Fletcher,W.W. (1976) The mode of action of asulam [methyl (4-aminobenzenesulphonyl) carbamate] in bracken. *Botanical Journal of the Linnean Society*, **73**, 247-268.

Veltkamp,C.J., Chubb,J.C., Birch,S.P. & Eaton,J.W. (1994) A Simple Freeze Dehydration Method for Studying Epiphytic and Epizoic Communities Using the Scanning Electron-Microscope. *Hydrobiologia*, **288**, 33-38.

Venables,W.N., Smith,D.M. & The R Development Core Team (2005) *An Introduction to R. Notes on R: A Programming Environment for Data Analysis and Graphics*. R Foundation for Statistical Computing, Vienna, Austria.

Watrud,L.S., Maggard,S., Shiroyama,T., Coleman,C.G., Johnson,M.G., Donegan,K.K., Di Giovanni,G., Porteous,L.A. & Lee,E.H. (2003) Bracken (Pteridium aquilinum L.) frond biomass and rhizosphere microbial community characteristics are correlated to edaphic factors. *Plant and Soil*, **249**, 359-371.

Watt,A.S. (1940) Contributions to the ecology of bracken (*Pteridium aquilinum*) I. The rhizome. *New Phytologist*, 39, 401-422.

Watt,A.S. (1954) Contributions to the ecology of bracken (*Pteridium aquilinum*) VI. Frost and the advance and retreat of bracken. *New Phytologist*, **53**, 117-130.

Watt,A.S. (1955) Bracken versus heather: a study in plant sociology. *Journal of Ecology*, **43**, 490-506.

Watt,A.S. (1976) The ecological status of bracken. *Botanical Journal of the Linnean Society*, **73**, 217-239.

White,R.A. (1963) Tracheary Elements of the Ferns.II. Morphology of tracheary elements; conclusions. *American Journal of Botany*, **50**, 514-522.

Whitehead,S.J. & Digby,J. (1997a) The morphology of bracken (Pteridium aquilinum (L) Kuhn) in the North York Moors - a comparison of the mature stand and the interface with heather (Calluna vulgaris (L) Hull) .2. The rhizome. *Annals of Applied Biology*, **131**, 117-131.

Whitehead,S.J. & Digby,J. (1997b) The morphology of bracken (Pteridium aquilinum (L) Kuhn) in the North York Moors - a comparison of the mature stand and the interface with heather (Calluna vulgaris (L) Hull) .1. The fronds. *Annals of Applied Biology*, **131**, 103-116.

Wiles,L.J. (2004) Economics of weed management: Principles and practices. *Weed Technology*, **18**, 1403-1407.

Williams,G.H. & Foley,A. (1975) Effect of herbicides on bracken rhizome survival. *Annals of Applied Biology*, **79**, 109-111.

Williams,G.H. & Foley,A. (1976) Seasonal variations in the carbohydrate content of bracken. *Botanical Journal of the Linnean Society*, **73**, 87-94.

Williams,G.H. (1980) Bracken control: a review of progress, 1974 -1979. *Research and development publication No. 12.* The West of Scotland Agricultural College, Auchincruive.

Williams,J.A. & West,C.J. (2000) Environmental weeds in Australia and New Zealand: issues and approaches to management. *Austral Ecology*, **25**, 425-444.

Willis,A.J., Folkes,B.F., Hopesimpson,J.F. & Yemm,E.W. (1959) Braunton Burrows - the Dune System and Its Vegetation .2. *Journal of Ecology*, **47**, 249.

Willis,A.J., Folkes,B.F., Hopesimpson,J.F. & Yemm,E.W. (1959) Braunton Burrows - the Dune System and Its Vegetation .1. *Journal of Ecology*, **47**, 1-24.

Appendix

Published Papers

Either from this thesis or additional work outside the formal scope of the thesis but allied to it.

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Developing an integrated land management strategy for the restoration of moorland vegetation on *Molinia caerulea*-dominated vegetation for conservation purposes in upland Britain

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Abstract

Molinia encroachment is considered a major threat to moorland and heathland conservation in Europe, and there is a need to develop management strategies to control *Molinia* and restore *Calluna* moorland. Here we combined weed control and restoration treatments into an integrated land management strategy (ILMS) to provide a more sympathetic approach than previous prescriptions. We applied the following treatments in factorial combination to a *Molinia*-dominated moorland in the Yorkshire Dales: grazing (ESA prescription level versus no grazing), cutting (0, 1, 2 and 3 cuts), ±application of a graminicide and ±*Calluna* brash addition. The response of the vegetation was assessed for four years. These data were analyzed using a combination of univariate and multivariate analysis of variance based on constrained ordinations but combined with bivariate standard deviational ellipses. This combined approach was extremely useful in identifying trends in this complex dataset.

The only treatment that had consistent effects in the univariate analysis of variance was cutting, where there was increased bare ground, reduced vegetation height, increased species diversity and reduced *Molinia* cover. Cutting three times had the greatest effect, maintaining a reduced *Molinia* cover over four years. The multivariate analysis showed that there were important community level interactions. Grazing generally produced vegetation which had a greater moorland species complement. Where grazing was restricted the vegetation had a greater component of *Molinia* and other acid grassland species. The most effective treatment was the grazed plots, cut thrice, which maintained a low *Molinia* cover for longest and had less variation in moorland species in the fourth year. Graminicide and brash application had marginal effects on species composition, but the best plots were those given herbicide alone, or in combination with brash addition.

These results contrast with other studies, where non-selective herbicide treatment and *Calluna* addition were required to obtain *Molinia* control and *Calluna* regeneration. However, great variation has been found between sites, and managers should be prepared to tailor ILMS for their own site. This is likely to require a knowledge of the initial floristic composition, seed banks and experimentation.

Keywords: *Calluna vulgaris*; Conservation; Cutting; Graminicide; Grazing; Herbicide; Multivariate analysis of variance; Seed addition; Vegetation management

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1. Introduction

British heather moorlands are internationally significant ecosystems, protected under the EC Habitat and Species Directive (92/43/EEC) and the subject of Biodiversity Action Plans (Anon, 1995a,b). Despite this, the quality of remaining moorland is under threat from a

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wide variety of factors, with only 14% of moorland in England assessed as "in favourable condition" (English Nature, 2001). One of the perceived threats to upland moors is the increase in grasses, especially *Molinia caerulea*, at the expense of dwarf shrub heath species like *Calluna vulgaris*, which are important components of these ecosystems from a conservation viewpoint. Here nomenclature follows Stace (1997) for higher plants and Corley and Hill (1981) for bryophytes, but following common practice *Molinia caerulea* and *Calluna vulgaris* are referred to by generic names. Increases in *Molinia* have also been found elsewhere in Europe, for e.g., in Holland large areas of Dutch heathlands have been colonized by *Molinia*, which replaces heath vegetation (Diemont and Heil, 1984; Heil and Diemont, 1983). These observed shifts in vegetation composition from *Calluna* to *Molinia* have been variously attributed to inappropriate burning and/or grazing regimes (Grant et al., 1963; Grant and Maxwell, 1988; Miller et al., 1984) and increased atmospheric nitrogen and sulphur deposition, especially in Holland (Hogg et al., 1995; Lee et al., 1992; Diemont and Heil, 1984; Heil and Diemont, 1983; Roem et al., 2002). Irrespective of the cause of these changes, there is a need to reduce the cover of *Molinia* and restore the characteristic dwarf shrub flora (Marrs et al., in press).

In England and Wales, the funding mechanism for such moorland restoration work is currently being implemented through grant payment under agri-environment schemes, e.g., environmentally sensitive areas (ESA) or countryside stewardship schemes (CSS) (MAFF, 1993, 1996). In such schemes, the policy objectives are to reduce *Molinia* cover and restore the dwarf shrub component of the moorland (Bardgett et al., 1995). However, until recently there has been very limited information available on how to achieve this, and there is still a need to develop cost-effective techniques for achieving these objectives. Recently a multisite study tested factorial combinations of burning, grazing, glyphosate application and seed amendment in both *Molinia*-dominated and mixed *Molinia*/*Calluna* vegetation and showed that it was difficult to derive specific management prescriptions that worked in three regions in England (Todd et al., 2000; Marrs et al., in press). Only one consistent result was found: *Molinia* cover was always reduced by the application of the non-selective herbicide glyphosate. The other treatments either showed site-specific effects, or any impact was found on only one sampling occasion. Moreover, on *Molinia*-dominated sites ('White' moors; Thomas, 1951) litter removal in combination with seed addition was needed to enhance *Calluna* seedling colonization.

The success of glyphosate was important because at present it is the only herbicide approved for grass control on open upland moorland (MAFF No. 06941; PSD/HSE, 1988). However, there are a number of selective herbicides (graminicides), which should only control grasses, that have been identified as being potentially useful for *Molinia* control (Milligan et al., 1999, 2003a,b). Graminicides reduced *Molinia* for at least a period of two years and did not affect *Calluna*. However, extensive, repeated use of selective herbicides on a large scale could be expensive and may lead to the build up of harmful residues (Clay and Stevens, 1991). As most moorland restoration work carried out under agri-environment schemes is done partly for environmental or conservation reasons, the wide-scale use of non-selective herbicides, or even selective ones, may not find favour.

Grazing also plays an important role, and this is bound up with the need to provide grazing livestock with the maximum possible level of nutrition throughout the year (Maxwell et al., 1986). To achieve this there must be an adequate mixture of *Molinia* and *Calluna* (Maxwell et al., 1986). *Molinia* is a highly digestible species but as it has a relatively short growing season (late April–August) it only provides summer feed, and *Calluna*, although having a lower nutritional quality provides winter food (Grant and Maxwell, 1988). *Molinia* is a highly digestible species but as it has a relatively short growing season (late April–August) it only provides summer feed and *Calluna*, although having a lower nutritional quality, provides winter food (Grant and Maxwell, 1988). Summer grazing has been demonstrated to keep *Molinia* in check (Hulme et al., 2002). Thus, any management prescription should not attempt the total eradication of *Molinia*, but achieve a reduction in its dominance and an increase in the dwarf shrub component of the vegetation, especially *Calluna*. Moreover, the final mosaic produced will produce ecosystems with complex interaction between vegetation communities and livestock utilization (Palmer and Hester, 2000).

An alternative would be to include a disturbance treatment such as cutting into the management strategy. Cutting has the advantage of acting as both a control method. Reducing the target *Molinia* and a physical disturbance treatment, which has been shown to enhance dwarf shrub colonisation during *Molinia* control (Todd et al., 2000), presumably through exposure of bare soil and hence creation of regeneration niches (Cloy, 1984; Bakker, 1989). Cutting has long been recognised as an effective method for conservation management of plant communities (Bakker, 1989; Worral and Palmer, 1988; Wells and Cox, 1993) and for controlling invasive perennial species, e.g., *Betula* spp. (Marrs, 1984, 1985, 1987) and *Pteridium aquilinum* (Lowday and Marrs, 1992; Marrs et al., 1998; Le Duc et al., 2003). These species, like *Molinia*, have a considerable potential for rapid recovery after initial good control (Morton, 1977). Cutting *Molinia* in wet grasslands and lowland heathlands can be effective in reducing its abundance, depending on the severity, timing and frequency (Schoppguth et al., 1994; Hogg et al., 1995; Moen, 1995; Grant et al., 1996). Nevertheless the effects of cutting *Molinia* in upland British moorland on a large scale has not been examined experimentally. Moreover no attempt has been made to examine the use of cutting in conjunction with other techniques for reducing *Molinia* and restoring heathland vegetation under experimental conditions.

Here, we tested the effects of: (a) grazing – sheep and rabbit grazing versus no grazing, (b) up to three repeat cuts in the first season, (c) application of selective herbicides, and (d) addition of *Calluna* propagules in the form of brash for the control of *Molinia* and subsequent development of moorland vegetation over a four year period. The aim was to develop an integrated land management strategy (ILMS) combining an integrated weed control (IWC) and a restoration strategy (Mulder and Doll, 1993; Buhler, 2002; Zoschke, 1994). The IWC approach combines more than one weed control technique to control the abundance of a species or species group, and usually this involves both mechanical and herbicide methods (Popay and Field, 1996). However, some of the treatments applied here have a dual function, e.g., cutting and grazing also contribute to restoration.

2. Methods

The experiment was carried out at Ramsgill Bents, North Yorkshire (National grid reference SE41054715; Longitude 1°50′27″ W; Latitude 54°8′27″ N), a *Molinia*-dominated, or 'White' moorland.

2.1. Experimental design

The four factors to be tested (grazing pressure, cutting frequency, herbicide application and *Calluna* propagule addition) were applied in a randomised block ($n = 2$) split–split plot design. Within each block (50×60 m), two grazing treatments were applied as main-plot treatments; the current moorland ESA – prescription sheep grazing pressure (ca. 1.8 ewes ha^{-1} yr^{-1}), which is uncontrolled free-range grazing plus an effect from an unknown rabbit density versus reduced grazing, where sheep and rabbit grazing was prevented by fenced exclosures.

Within each main-plot (48×24 m), four cutting treatments were applied as sub-plot treatments: (a) uncut, (b) cut once (December 1995), (c) cut twice (December 1995 and June 1996) and (d) cut thrice (December 1995, June 1996 and July 1996). Within each sub-plot (24×6 m), further treatment combinations of selective herbicide application (quizalofop-ethyl) and/or *Calluna* brash addition were added in factorial combination at the sub–sub-plot level. Each of the 32 sub–sub-plots in each block measured 5×10 m. All treatment combinations were allocated to plots randomly.

2.2. Field procedures

Cutting was carried out using a tractor-mounted, drum flail-mower. As the intention here was to cut as close to the ground as possible, the height of the cutter was reduced between cuts as vegetation height was progressively reduced. Cutting height was approximately 25 cm from ground surface in cut 1, reducing to 10 cm in cut 2 and 5 cm in cut 3. Because of the undulating ground, stretches of mineral soil were exposed on elevated ground at the third cut. Litter was not removed from the site and did not blow on to uncut plots. The exclosures were erected in July 1996, immediately after the last cut was applied.

The grass-selective herbicide, quizalofop-ethyl (trade name Pilot, AgrEvo Ltd., 0.5 kg ai l^{-1}) was selected for use after preliminary laboratory trials showed it had potential to control *Molinia* whilst leaving *Calluna* relatively unharmed (Milligan et al., 1999, 2003a). It was first applied to the herbicide-treated plots at 0.25 kg ai ha^{-1} (0.5 l ha^{-1}) in July 1996 but after four weeks little effect was noticed. A second dose was, therefore, applied in August 1997 at 0.50 kg ai ha^{-1} (1.0 l ha^{-1}). Both herbicide additions were applied using a knapsack sprayer with an application volume of 170 l ha^{-1} (flat fan nozzle, 2 bar pressure).

Calluna brash, cut and baled at Helmsley, North Yorkshire (National grid reference SE 461583; Longitude 1°3′10″ W; Latitude 54°14′21″ N), during November–December 1996 was spread in the brash addition treatments in January 1997. Two bales were added to each 5×10 m plot. Thirty bales were selected randomly and taken to the laboratory and weighed (mean ± SE; 19.92 ± 0.88 kg). A (ca. 100 g) were taken from each of the thirty bales and the total number of capsules counted (2930 ± 29.7 capsules per sample). Within each subsample 30 capsules were chosen randomly and the number of viable seeds counted (4.36 ± 0.64 seeds per capsule). These data were used to estimate the amount of viable seed applied to each plot (510,000 per plot, 10,200 seeds m^{-2}).

2.3. Assessment procedures

Species cover was assessed visually in three permanent 1 m^2 quadrats within each sub–sub-plot at the following times (a) June 1996 (cut 1 had been applied), (b) July 1996 (cuts 1 and 2 applied), (c) August 1996 (all cuts applied and fence erected) (d) June 1997, (e) August 1997, (f) August 1998 and August 1999. A series of vegetation physiognomic variables were also recorded at each quadrat: cover of bare ground, vegetation height and litter depth. Total species number and the Shannon–Weiner Diversity index were computed (Krebs, 1972). From August 1997, both *Calluna* seedling density and litter depth were recorded. Each 1 m^2 quadrat was sub-divided into 100 sub-sections to allow accurate assessment. The mean values of the three sub-quadrats were computed to provide a sub-sub-plot mean.

2.4. Statistical analysis

Analysis of variance was used to assess treatment effects on the cover of the major species and the physiognomic variables. A randomised block split–split plot model was used with treatments included as they were applied, with repeated measures where appropriate. Data were transformed ($\% = \arcsin(\sqrt{x}/100)$; counts $= \sqrt{x}$) and analyzed using PROC GLM (SAS, 1985) with treatment effects tested using the appropriate error term. Only significant differences ($P < 0.05$) are presented and discussed here; the results presented are of transformed means ± standard errors, but a back-transformation is provided for ease of interpretation.

Multivariate analyses (CANOCO for WINDOWS, Ter Braak and Šmilauer, 1998) were also used to describe changes in the entire community composition using data from the August samples. Initially, a detrended correspondence analysis was used to measure gradient lengths. The gradient lengths were 2.8 and 2.5 without and with the downweighting option for rare species, accordingly linear models redundancy analysis (RDA) were used thereafter (Ter Braak and Šmilauer, 1998). All subsequent analyses used the downweighting option.

Multivariate analysis of variance was then performed using the constrained ordination method, again using CANOCO for Windows (Ter Braak and Šmilauer, 1998). With this approach, the significance of each factor and interaction was determined using separate runs of RDA. In each run the factors and their interactions were included as environmental variables, with experimental blocks included as covariables. Significance was assessed using restricted Monte Carlo permutation tests with 499 permutations. The model used was a split–split–split-split plot design with grazing at the top level, followed by cutting, herbicide and brash addition, and time.

Thereafter, the dispersion of the treatment plots in the species ordination space was examined using bivariate standard-deviational (SD) ellipses for axes 1 and 2. The algorithm used for this purpose was ELLIPSE.SAS, given by Ricklefs and Nealen (1998), implemented in EXCEL (Le Duc et al., in press). The ellipse parameters (size, shape, orientation, Le Duc et al., in press) were inspected but provided little additional information to that provided in the biplots, thus only biplots are presented here.

3. Results

At the start of the experiment, the most common species was *Molinia*, followed by *D. flexuosa*. There were lower amounts (0.5–20%) of *Festuca ovina*, *Anthoxanthum odoratum*, *Galium saxatile*, *Juncus squarrosus*, *Vaccinium. myrtillus*, and very small amounts (0.5%–5%) of *Calluna* and *Erica tetralix*.

3.1. Effects of experimental treatment on individual variables

The significant results from the analysis of variance are summarised (Table 1) but gave limited information partly as a result of the variability in the cover of species at low abundance. The most consistent results were obtained for those variables that were available for measurement in every quadrat (physiognomy and *Molinia* cover). For other variables the results were patchy and significance was most evident when all of the treatments had just been applied, and for the species diversity variables after four years.

3.1.1. Physiognomy

The cover of bare ground was measured only in 1996 when the cutting treatments were applied as there was very little bare ground after 1997 as a result of sward recovery (Table 2(a)). However, during 1996 cutting significantly increased the amount of bare ground. After six months there was no significant effect on bare ground as a result of the first cut applied in winter but after seven months there was a significant increase in bare ground in the plots cut twice and this was maintained until the eight month. However, the main effect was the third cut, which significantly increased the amount of bare ground.

Cutting was also the major treatment to reduce vegetation height, and this was found at each sampling point throughout the period (Table 2(b)); the effect of time was also significant. The effects were more significant early in the study and there was some recovery through time (Table 2(b)). Cutting three times effected the greatest reduction in vegetation height, and a reduction was still found after 44 months, reducing height from 31 to 17 cm; other cutting treatments were similar to untreated values within seven months (cutx1) and 19 months (cut 2).

The only other significant effects on vegetation height were found as a result of herbicide and brash treatments but only at 20 months, although there was also a significant interaction between each of these treatments and time. There were no further significant interactions. Vegetation height was reduced at that time immediately after herbicide spraying (unsprayed mean height = 19 cm (untransformed mean), 4.344 ± 0.197 (transformed mean ± SE); sprayed = 15 cm, 3.880 ± 0.244; $F = 5.30$,

Table 1
Significant responses ($P < 0.05$) detected in univariate analyses of variance of the results of the moorland restoration experiment at Ramsgill Bents between 1996 and 1999

Variable	Sampling date (months from start)						
	June 96 (6)	July 96 (7)	August 96 (19)	July 97 (20)	August 97 (21)	98 (32)	99 (44)
Physiognomy							
Bare ground	ns	C 10.04^{***}	C 14.88^{***}	–	–	–	–
Height	C 10.43^{***}	C 21.93^{***}	C 53.47^{***}	C 10.04^{**}	C 7.91^{*}	C 4.87^{*}	C 15.62^{**}
Litter depth	–	–	–	C 4.83^{*}	ns	ns	ns
Species diversity							
Species number	ns	ns	ns	ns	ns	ns	G 332.0^{*} C 8.49^{*}
Shannon–Weiner	ns	ns	ns	ns	ns	ns	G 235^{*} C 15.33^{*}
Species cover							
M. caerulea	ns	C 20.17^{***}	C 10.59^{**}	ns	C 4.53^{*}	C 11.0^{**}	ns
Seedling density							
C. vulgaris	–	–	–	ns	C 12.95^{**} H 4.68^{*}	C 6.09^{*} G 3238^{*}	C 6.05^{*}

Key to treatments: C – cutting; G – grazing; H – herbicide; B – brash and a dash denoting that no measurement was made at that sampling occasion. *F*-values are presented with an indication of significance as follows: ns – not significant $P > 0.05$.

$^{*}P < 0.05$.

$^{**}P < 0.01$.

$^{***}P < 0.001$.

Table 2
The effects of cutting *Molinia*-dominated moorland on (a) cover of bare ground, (b) vegetation height, and (c) litter depth in a 44 month experiment at Ramsgill Bents. Data are transformed means ±SE, back transformed data are discussed in text; significance levels are presented in Table 1

Month from start	Cutting frequency			
	No cut	Cutx1	Cut2	Cutx3
(a) Bare ground (%, transformation = arcsin)				
7	0.017 ± 0.013	0.010 ± 0.007	0.284 ± 0.059	
8	0.016 ± 0.010	0.032 ± 0.014	0.094 ± 0.042	0.402 ± 0.092
(b) Height (cm, transformation = $\sqrt{x}$)				
6	4.259 ± 0.067	3.905 ± 0.091		
7	5.189 ± 0.127	4.901 ± 0.270	3.892 ± 0.134	
8	5.144 ± 0.127	4.595 ± 0.290	3.793 ± 0.149	2.843 ± 0.136
19	4.239 ± 0.160	4.341 ± 0.281	4.016 ± 0.231	3.112 ± 0.156
20	4.503 ± 0.278	4.476 ± 0.374	4.144 ± 0.278	3.327 ± 0.257
32	5.149 ± 0.155	4.892 ± 0.199	4.565 ± 0.050	3.635 ± 0.257
44	5.597 ± 0.165	5.527 ± 0.236	5.267 ± 0.231	4.092 ± 0.310
(c) Litter depth (cm, transformation = $\sqrt{x}$)				
20	1.865 ± 0.412	1.625 ± 0.387	1.195 ± 0.264	0.452 ± 0.129

$P < 0.01$) and brash application (no brash = 15 cm 3.860 ± 0.2603; +brash = 11 cm, 3.344 ± 0.175; $F = 5.30$, $P < 0.01$).

After 20 months the effects of treatment on both litter cover and depth were assessed. No significant effects were found for litter cover and only one significant treatment effect was found for litter depth. Here cutting three times reduced the litter depth significantly from 3.5 cm to <0.3 cm (Table 2(c)).

3.1.2. *Effects of treatment on species number and diversity*

There were few significant treatment effects on either species number or Shannon–Weiner index. Significant differences were found only in 1999 for both grazing and cutting, no other treatments were significant (species number – grazing $F = 332$, $P < 0.05$, cutting $F = 8.49$, $P < 0.05$; Shannon–Weiner-grazing $F = 235$, $P < 0.05$, cutting $F = 15.33$, $P < 0.01$). Both measures were greater in the ungrazed compared to the grazed plot (species number, ungrazed $= 8.31 \pm 0.43$, grazed $= 6.31 \pm 0.39$; Shannon–Weiner-ungrazed $= 0.42 \pm 0.03$, grazed $= 0.38 \pm 0.03$). In the cut plots both measures increased with increasing intensity of cutting, and in plots cut thrice were markedly greater than the others (species number – uncut $= 6.19 \pm 0.48$, cutx1 $= 6.50 \pm 0.59$, cutx2 $= 6.88 \pm 0.46$, cutx3 $= 9.69 \pm 0.61$; Shannon–Weiner-uncut $= 0.32 \pm 0.03$, cutx1 $= 0.36 \pm 0.03$, cutx2 $= 0.36 \pm 0.03$, cutx3 $= 0.56 \pm 0.02$).

3.1.3. *Effects of treatment on Molinia cover*

Significant effects of cutting were found on *Molinia* cover on four of the seven sampling dates (Table 2) and a significant time × cutting interaction ($F = 54.22$, $P < 0.001$). Cutting once had very little impact compared to the uncut treatment, indeed 6 months after cutting there appeared to be a compensatory increase in *Molinia* cover in the cut once treatment (Fig. 1). Cutting three times gave the greatest reduction in *Molinia* cover with a significant effect found for three years after the cutting was applied. The double cut was intermediate with a reduction compared to the uncut and cut once treatments, but not as effective as the thrice cut. No other treatment either on its own or in interaction had a significant effect on *Molinia* cover.

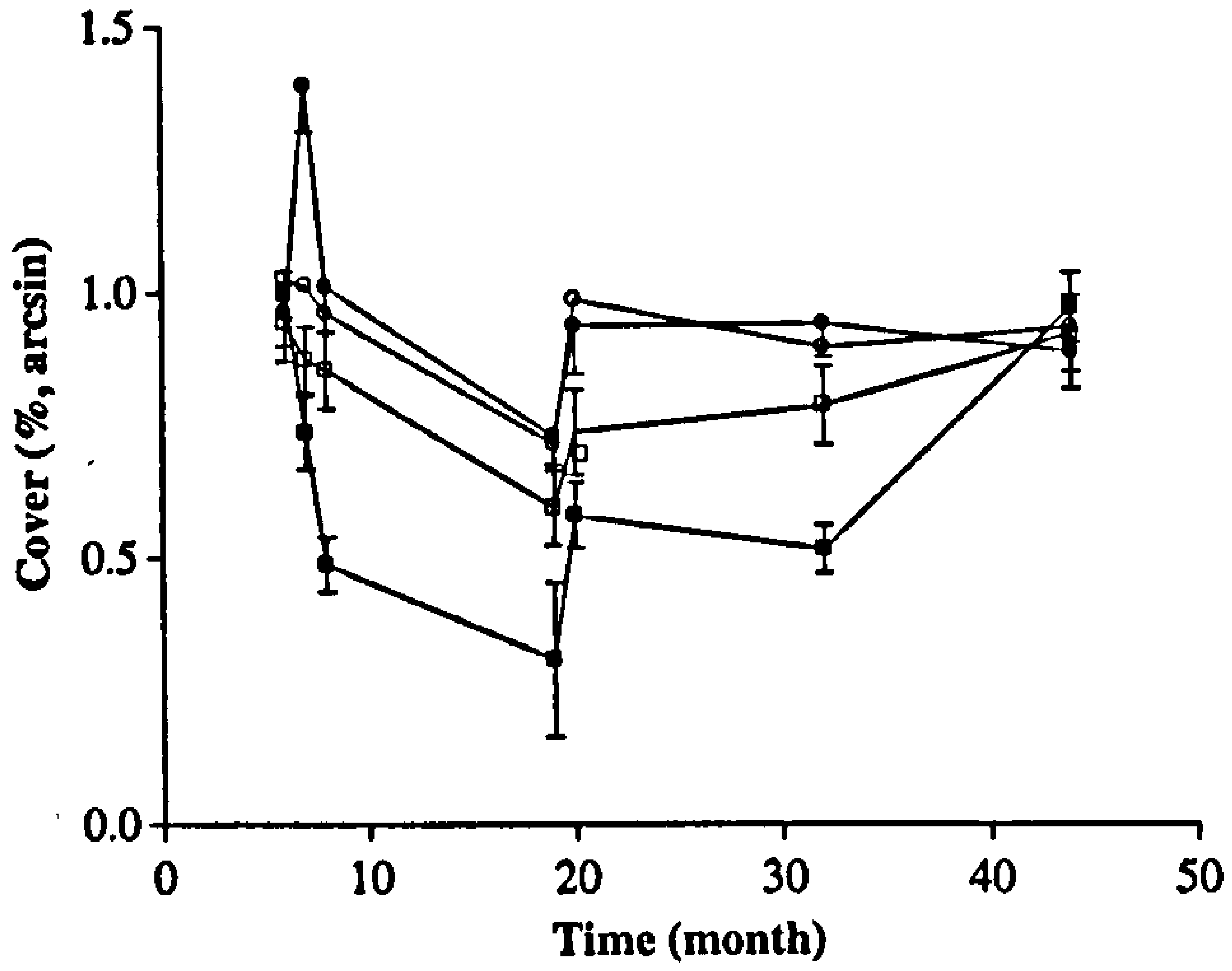

Fig. 1. Effects of cutting once, twice or thrice compared to uncut controls on *Molinia* cover at Ramsgill Bents over a four year period; mean values ±SE are presented of arcsin transformed data. Key: uncut – (○); cutx1 – (●); cutx2 – (□); cutx3 – (■).

3.1.4. *Effects of treatment on Calluna*

There were no significant treatment effects detected on *Calluna* cover but a marked spatial effect between blocks (Fig. 2(a)). Over the experiment as a whole there was a slight increase in *Calluna* cover through time from 0.5% to 2.3%.

Cutting, herbicide and grazing also had an effect on *Calluna* seedling density in at least one of the last three sampling periods (August 1997–1999). In 1997 herbicide application increased *Calluna* seedling density from 0.7

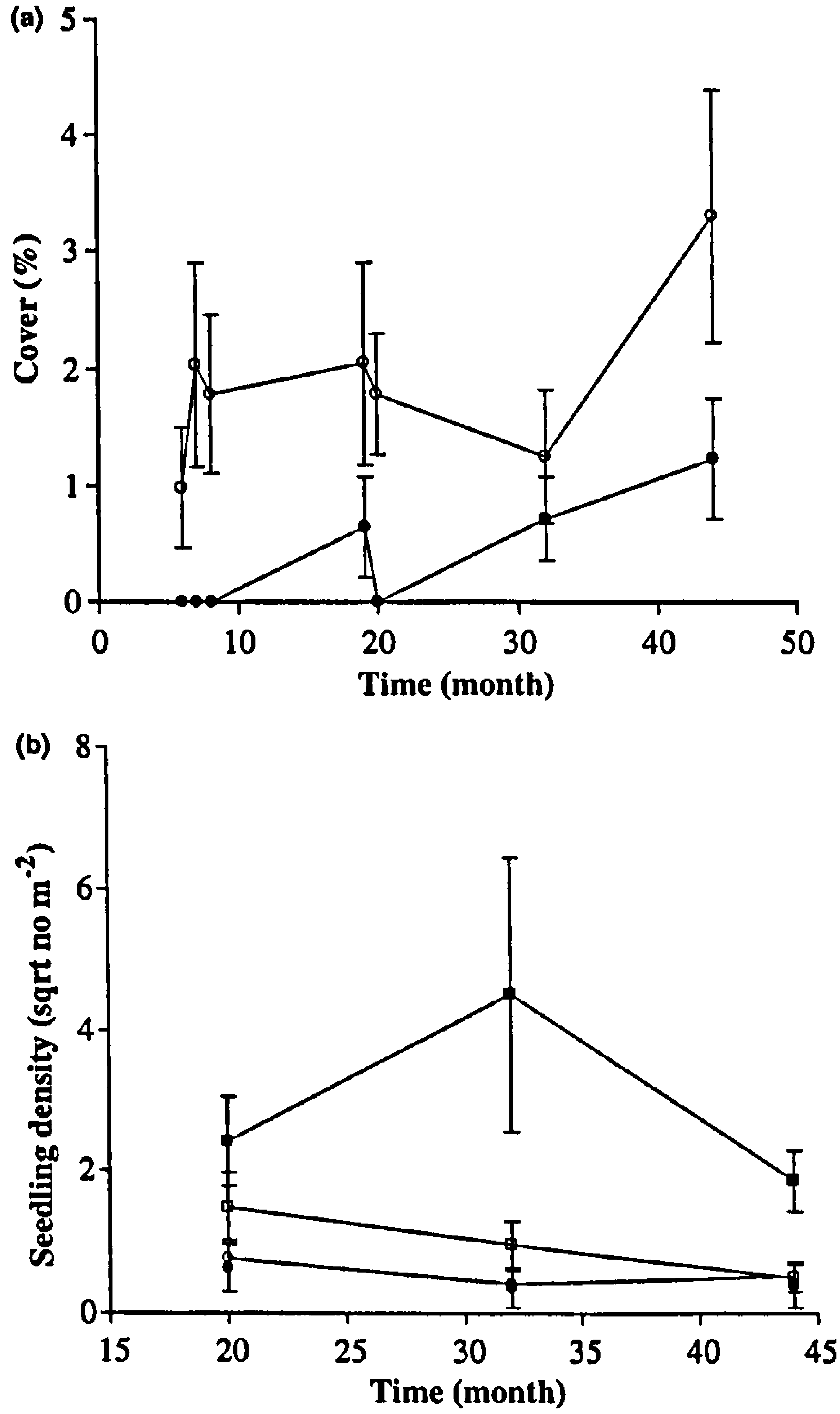

Fig. 2. Effects of (a) spatial position (blocks) on *Calluna* cover (%) and (b) cutting once, twice or thrice compared to uncut controls on *Calluna* seedling densities ($\sqrt{x}$ transformed) at Ramsgill Bents over a four year period; mean values ±SE are presented. Key: (a) block 1 – (○); block 2 – (●); (b) uncut – (○); cutx1 – (●); cutx2 – (□); cutx3 – (■).

(0.832 ± 0.547) to 3.5 (1.826 ± 0.427) seedlings m^{-2} and in 1998 grazing reduced *Calluna* seedling density from 3.7 (1.918 ± 0.339) to 1.1 (1.184 ± 0.415) seedlings m^{-2}. There were significant effects between cutting treatments with cutting twice and thrice having a greater number of seedlings than the uncut and cut once treatments. The cut twice treatment had slightly greater seedling densities at the start and then a slight decline over the three years until they were identical to the uncut and cut once plots. The cut thrice treatment, however, had the greatest density in 1997, and there was a doubling of numbers in 1998 followed by a decline again in 1999 (Fig. 2(b)).

3.2. Community responses to treatment

The multivariate analysis of variance (Table 3) shows that of the main treatment effects only grazing and time were significant, but there were many significant interactions. As the highest order interaction (time × grazing × cutting × herbicide × brash) was significant, the species-plot biplot from this model was used for all subsequent investigations. This significance of this model was re-tested with 9,999 permutations as recommended by Legendre and Legendre (1998); it was highly significant (trace = 0.599, $F = 1.9$. $P < 0.0001$).

The species ordination (Fig. 3) shows a gradient on axis 1 from *Molinia* domination (+ve end) to an acid grassland/moor (−ve end). Axis 2 represents a gradient from wet acid grassland/moorland dominated by *Juncus squarrosus* and *Nardus stricta* (+ve end) to a drier acid grassland dominated by *Festuca ovina* (−ve end). *Calluna vulgaris* and *Deschampsia flexuosa* appear in the upper left quadrant indicating a relatively dry moorland, and *Erica tetralix* and *Vaccinium vitis-idaea* occupy a similar position in the upper right quadrant indicating wetter conditions.

Only a selection of the most interesting treatments and treatment combinations are presented and discussed here. The individual treatments (Fig. 4) show important

Table 3
Results of the multivariate analysis of variance using restricted permutation tests (499 permutations) of an experiment carried out to test the effects of management treatments (grazing versus no grazing, four levels of cutting, herbicide application and *Calluna* brash addition) to control *Molinia* and enhance moorland vegetation over a four year period at Ramsgill Bents

Factor	Phase II				
	Df	N_P	Trace	*F*	*P*
Grazing	1	4	0.063	18.3	0.002
Cutting	3	16	0.026	2.4	0.354
Grazing × cutting	3	16	0.098	4.2	0.002
Herbicide	1	64	0.004	1.1	0.506
Brash	1	64	0.005	1.3	0.416
Herbicide × brash	1	64	0.015	1.4	0.274
Grazing × herbicide	1	64	0.144	14.2	0.002
Grazing × brash	1	64	0.026	1.7	0.002
Grazing × herbicide × brash	1	64	0.021	9.0	0.002
Cutting × herbicide	3	64	0.038	1.5	0.112
Cutting × brash	3	64	0.004	1.6	0.060
Cutting × herbicide × brash	3	64	0.068	1.3	0.102
Grazing × cutting × herbicide × brash	3	64	0.177	1.7	0.002
Time	3	256	0.185	20.7	0.002
Time × grazing	3	256	0.270	14.5	0.002
Time × cutting	9	256	0.227	4.8	0.002
Time × grazing × cutting	9	256	0.654	4.4	0.002
Time × herbicide	3	256	0.198	9.5	0.002
Time × brash	3	256	0.198	9.5	0.002
Time × herbicide × brash	3	256	0.226	5.1	0.002
Time × grazing × herbicide	3	256	0.295	7.4	0.002
Time × grazing × brash	3	256	0.196	4.0	0.002
Time × grazing × herbicide × brash	3	256	0.345	4.2	0.002
Time × cutting × herbicide	9	256	0.279	3.1	0.002
Time × cutting × brash	9	256	0.279	3.1	0.002
Time × cutting × herbicide × brash	9	256	0.364	2.0	0.002
Time × grazing × cutting × herbicide × brash	9	256	0.599	1.8	0.002
Total	255				

Codes are: N_p – number of permutable units; Trace (T_r – total sums of squares); *F*-ratio (*F*) and *P*-value (*P*).

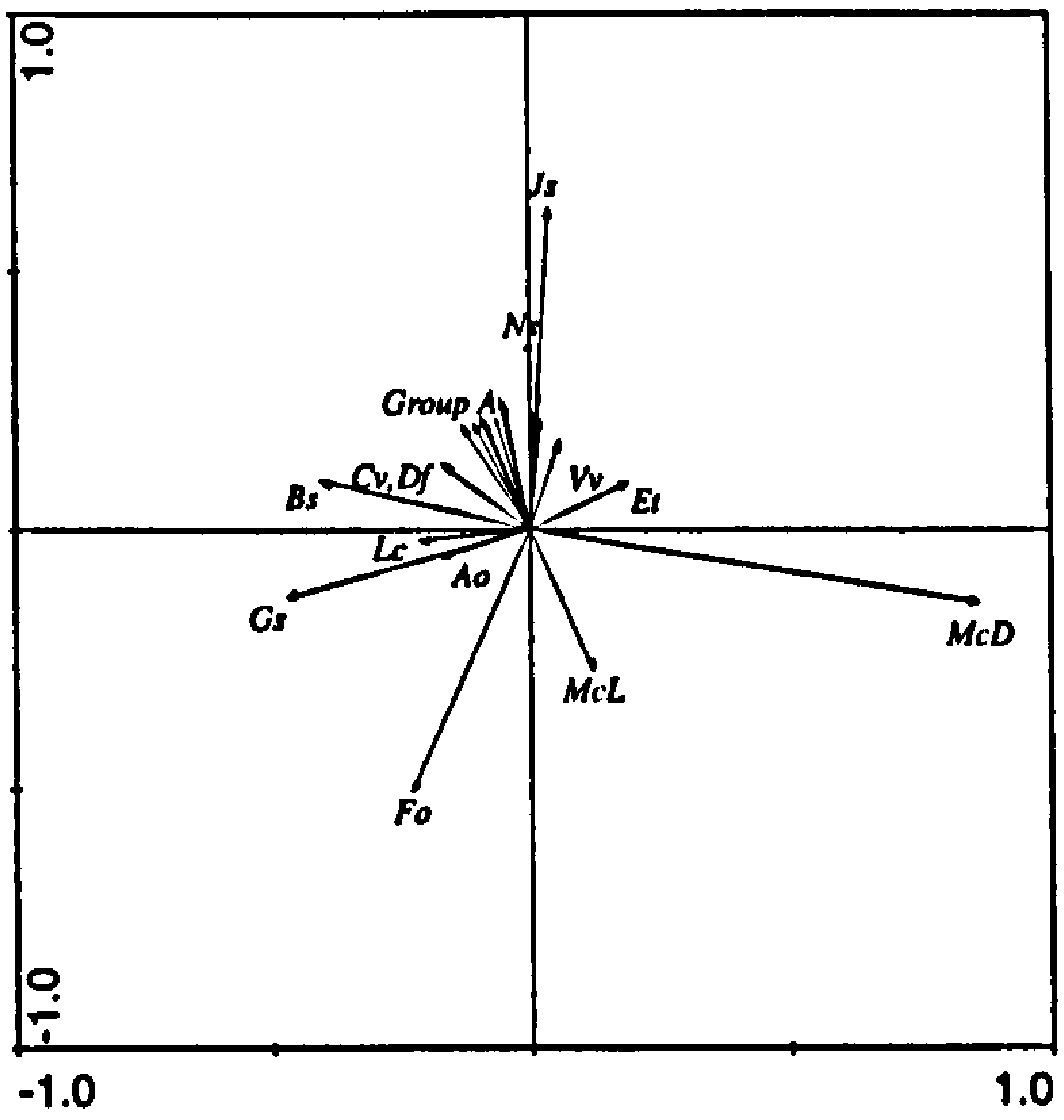

Fig. 3. Species distribution in biplot produced from the RDA ordination testing all experimental treatments in combination (Table 3). Key to species codes: Ao – *Anthoxanthum odoratum*; Bs – *Bryophyte* spp; Cv – *Calluna vulgaris*; Df – *Deschampsia flexuosa*; Et – *Erica tetralix*; Fo – *Festuca ovina*; Gs – *Galium saxatile*; Js – *Juncus squarrosus*; Lc – *Luzula campestris*; Mc – *Molinia caerulea* (L – live; D – dead); Ns – *Nardus stricta*; Vv – *Vaccinium vitis-idaea*. Group A (grouped for clarity) include *Carex* spp, *Eriophorum vaginatum, Polytrichum commune, Racomitrium lanuginosum, Rhytidiadelphus squarrosus, Sphagnum* spp. *Trichophorum cespitosum, Vaccinium myrtillus, Vaccinium oxycoccus.*

differences. The trends through time (Fig. 4(a)) indicate a general change from *Molinia* domination (+ve end axis 1) towards the acid grass/moorland for three years then a slight reversal in the fourth year, perhaps indicating that *Molinia* is recovering. The shape of the ellipses indicate that there was a major increase in the species pool in the second year, followed by a reduction in years three and four, but in these years there was a change towards more moorland species (−ve increase on axis 1 and slight +ve increase axis 2). The effect of grazing (Fig. 4(b)) shows a clear separation with ungrazed plots located more or less below the origin and grazed plots above. This suggests that grazing promoted moorland development, whereas no grazing promoted acid grassland.

The effects of cutting, herbicide application and brash addition, although not significant are presented to illustrate their effect (Fig. 4(c)–(e)). The general trend for cutting is a slight move upwards on the biplot towards moorland, the effect of herbicide application is a slight increase in the species pool with a bias towards moorland species, and the effect of brash addition is barely distinguishable. This latter result is not too surprising given that brash addition is only likely to affect one species (*Calluna vulgaris*), and this species takes many years to establish and contribute to species cover (Gimingham, 1992).

3.2.1. Interaction between grazing and time (Fig. 5)

The ungrazed plots showed ellipses located in the *Molinia* – acid grassland areas. On grazed plots however, there was a difference from the start (one month after the fences were erected) with an increase in cover of acid\grassland\moorland species; this trend increased over the four years with a slow but consistent positive increase on axis 2.

3.2.2. Interaction between cutting and time (Fig. 6)

The three cutting treatments all showed more or less the same pattern of response, although there were subtle differences. All uncut plots moved from *Molinia* domination along axis 1 towards acid grassland in years two and three and then moved back again. The reversal in year four differed between cutting treatments; as the number of cuts increased the area of the ellipse reduced and there was an increasing trend towards moorland. This is illustrated by the year four ellipses, which were centred across axis one in the uncut, cutx1 and cutx2 treatments, but was located in the *Calluna vulgaris* quadrant in the cutx3 treatment.

3.2.3. Interaction between grazing × cutting (Fig. 7)

This analysis produced two distinct types of response, the first where there was a change through time with respect to the treatment combination but a reversal in the direction of the approximate start conditions in year four; this occurred in ungrazed treatments irrespective of cutting treatment, although the cutx3 treatment produced the best effect in year four, with the most of the ellipse clearly over axis 1 in the wet moor quadrant. The grazed cutting treatments show a general trend through time, increasing the size of the species pool in year two, especially in the cutx2 and cutx3 plots. In all grazed plots the ellipse in year four is located within the dry moor quadrant; as number of cuts increased from zero to two there is an increase in ellipse size within the dry moor quadrant. Where three cuts were applied the size of the ellipse is much smaller but it is completely located within the dry moor quadrant.

3.2.4. Interaction between grazing × cutting × herbicide × brash addition

For brevity, only the most successful treatment combination in achieving moorland vegetation (grazing and cut thrice, Fig. 7) is illustrated and discussed here. This treatment combination was examined to assess the effects of herbicide and brash addition alone and in combination (Fig. 8). All of the treatment combinations moved from the *Molinia*-dominated quadrant through to the moorland quadrant, although the trajectories differ. Herbicide application produced a much greater expansion of the species pool in the year after application compared to the unsprayed plots, but this effect declined in years three and four (Fig. 8(a) and (b)).

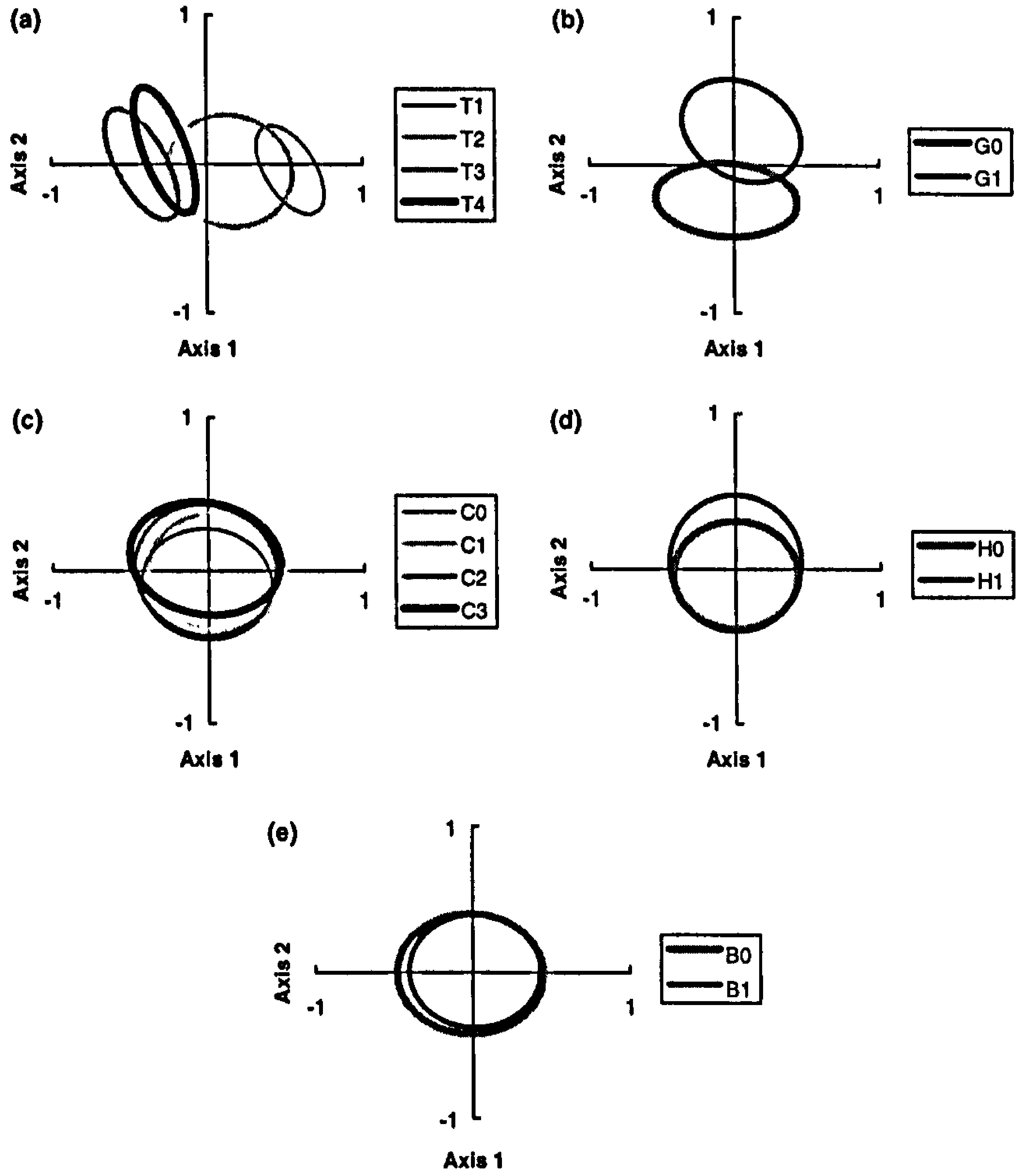

Fig. 4. Distribution of applied treatments in the biplot produced from the RDA testing all treatments in combination (Table 3) – these figures are directly comparable with the species distribution (Fig. 3). The effects of treatments on their own are displayed as bivariate standard-deviational (SD) ellipses for axes 1 and 2: (a) time (T); (b) grazing (G); (c) cutting (C); (d) herbicide application (H); (e) brash addition (B). Codes for G, H and B are 0 – no treatment; 1 – treatment; codes for cutting (C) are 0, 1, 2, 3 for zero, cutx1, cutx2 and cutx3; codes for time (T) are 1, 2, 3, 4 – 1996, 1997, 1998, 1999.

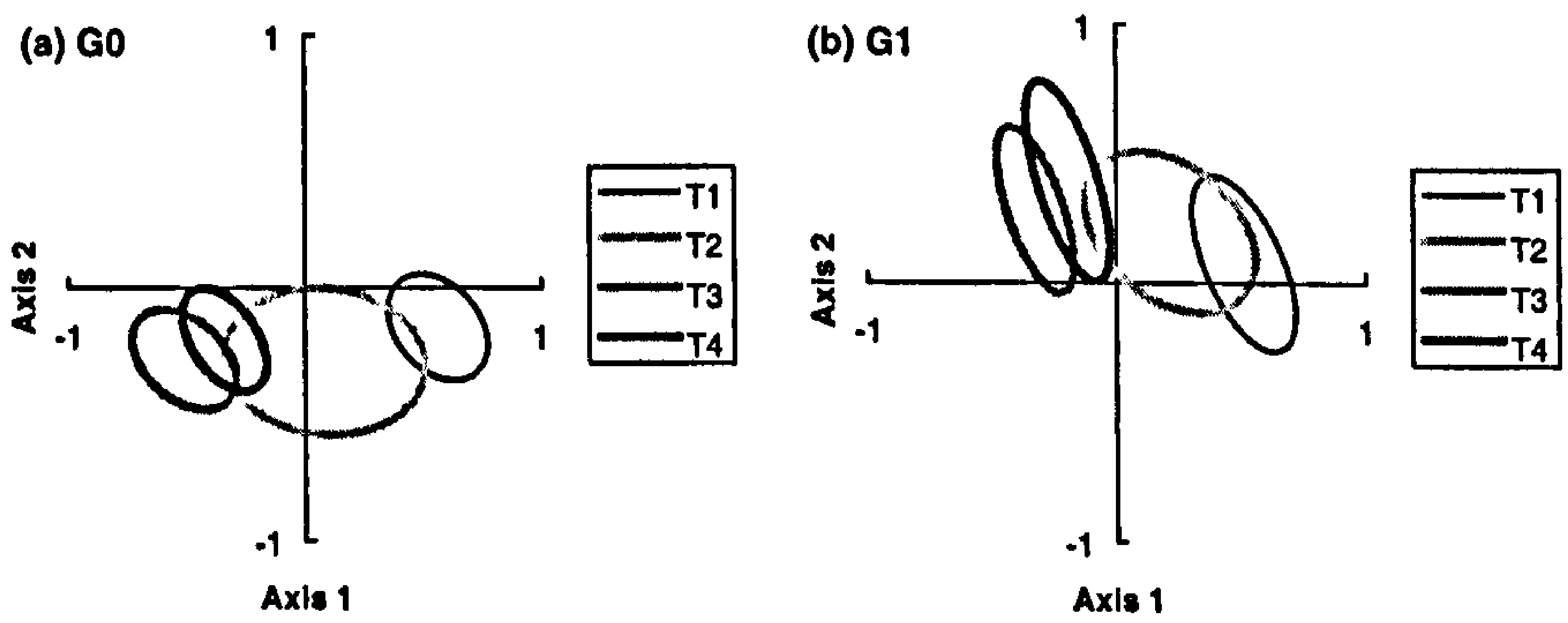

Fig. 5. Distribution of grazing treatments through time in the biplot produced from the RDA testing all treatments in combination (Table 3) – these figures are comparable with the species distribution (Fig. 3). The effects of treatment combinations are displayed as bivariate standard-deviational (SD) ellipses for axes 1 and 2: (a) no grazing (G0), (b) grazing (G1). Codes for time (T) are 1, 2, 3, 4 – 1996, 1997, 1998, 1999.

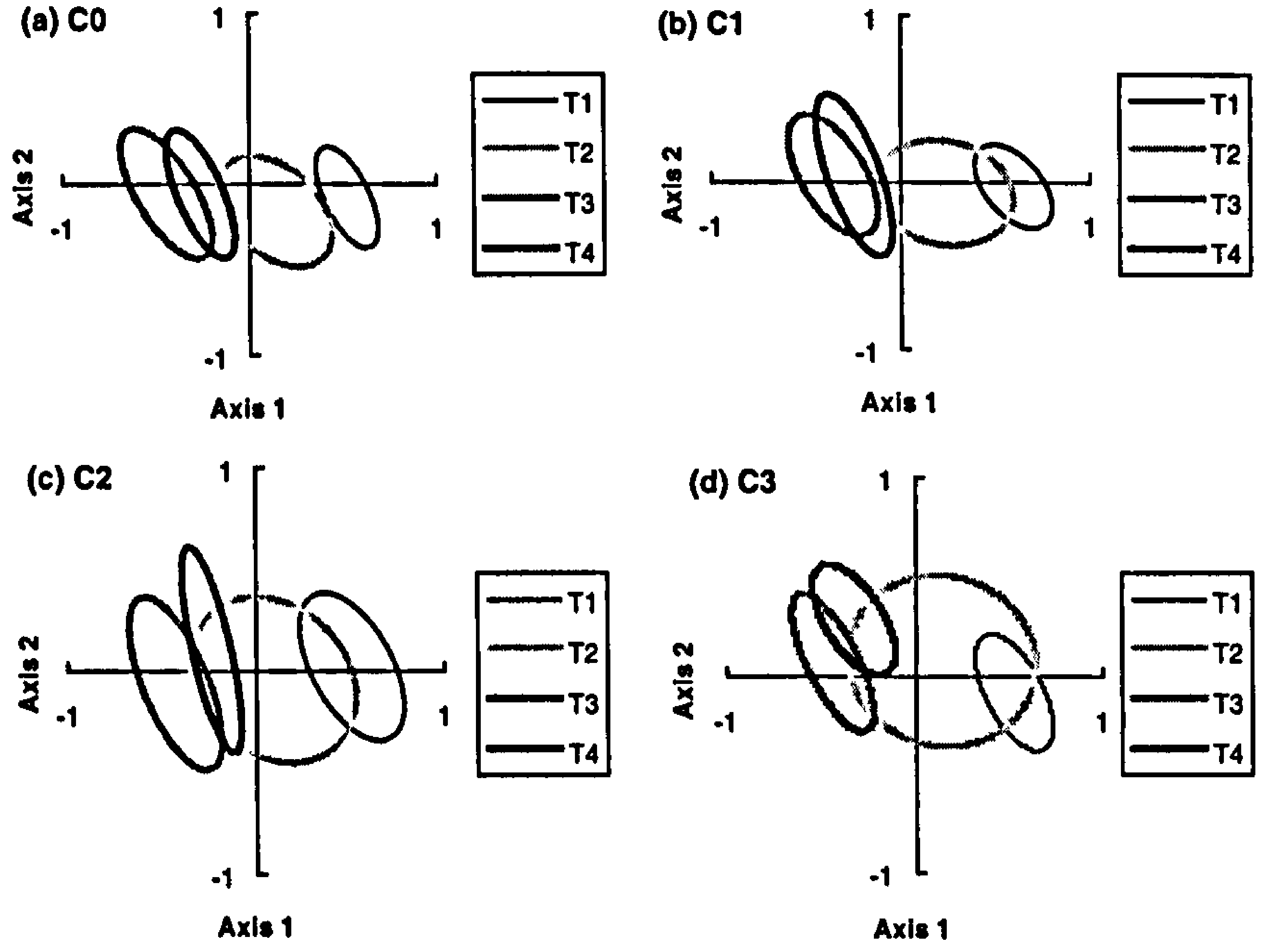

Fig. 6. Distribution of cutting treatments through time in the biplot produced from the RDA testing all treatments in combination (Table 3) – these figures are comparable with the species distribution (Fig. 3). The effects of treatment combinations are displayed as bivariate standard-deviational (SD) ellipses for axes 1 and 2: (a) uncut (C0); (b) cutx1 (C1); (c) cutx2 (C2); (d) cutx3 (C3). Codes for time (T) are 1, 2, 3, 4 – 1996, 1997, 1998, 1999.

Moreover, the increase in species in year two was in the moorland species area. The effect of brash had the opposite effect, here the increase in the species pool occurred where no brash was added, presumably because brash addition prevented species invasion by smothering (Fig. 8(c) and (d)). In the individual treatment combinations, whilst all treatments show a trajectory from *Molinia* to moorland, the size of the ellipses gave different patterns. Where no herbicide or brash was applied the species pools were very small and in year four was edging towards *Nardus stricta*. Where either brash or herbicide alone was applied, there were different trajectories but for each treatment there was an overlap between each year indicating relatively smooth transitions; the brash treatment was also edging towards *Nardus stricta*. However, where both brash and herbicide were applied, the transitions were not as smooth indicating a staccato-type change (Fig. 8(h)), even though the final vegetation was centred on *Calluna*. The treatments that appeared nearest the *Calluna* target were herbicide application alone and combined with brash addition.

4. Discussion

In order to restore *Calluna* and other dwarf shrub heath communities on *Molinia*-dominated moorland for conservation purposes, the *Molinia* abundance must be reduced (Weed Control Phase, Vermeer and Berendse, 1983; Marrs et al., in press), and the heathland species need to be restored (Restoration Phase, Todd et al., 2000; Marrs et al., in press). Effectively, this requires the development of an ILMS. The initial weed control phase should reduce the *Molinia*, if possible create gaps and suitable niches for the establishment of *Calluna* and associated moorland species, before the *Molinia* begins to re-establish from tussock fragments or seed (Sansen and Koedam, 1996). To assure restoration success, a 'window' must be created where the *Molinia* competition is reduced so that *Calluna* can begin to establish before *Molinia* recovers. This 'window' should be at least eighteen months long to ensure *Calluna* becomes established and competes effectively with encroaching or re-establishing *Molinia*. In recent experiments a single application of glyphosate produced a reduction in *Molinia* cover for six years (Marrs et al., in press). We accept that 18 months is only the start of the succession, and further work is needed to judge longer-term success.

During this period, *Molinia* has some short-term advantages. First it sets seed during its first season, whereas *Calluna* takes at least two years from initial seedling establishment to produce seeds in upland Britain (Miles, 1974), and second, *Molinia* can attain its maximum biomass faster than *Calluna*, even though *Calluna* can eventually attain a higher biomass (Aerts and van der Peijl, 1993). Where recruitment is from the seed bank, *Calluna* has an advantage because seed viability is longer (Granström, 1987) than *Molinia* (Miles, 1974).

In order to develop the ILMS, we tested a range of treatments designed to control *Molinia* and enhance

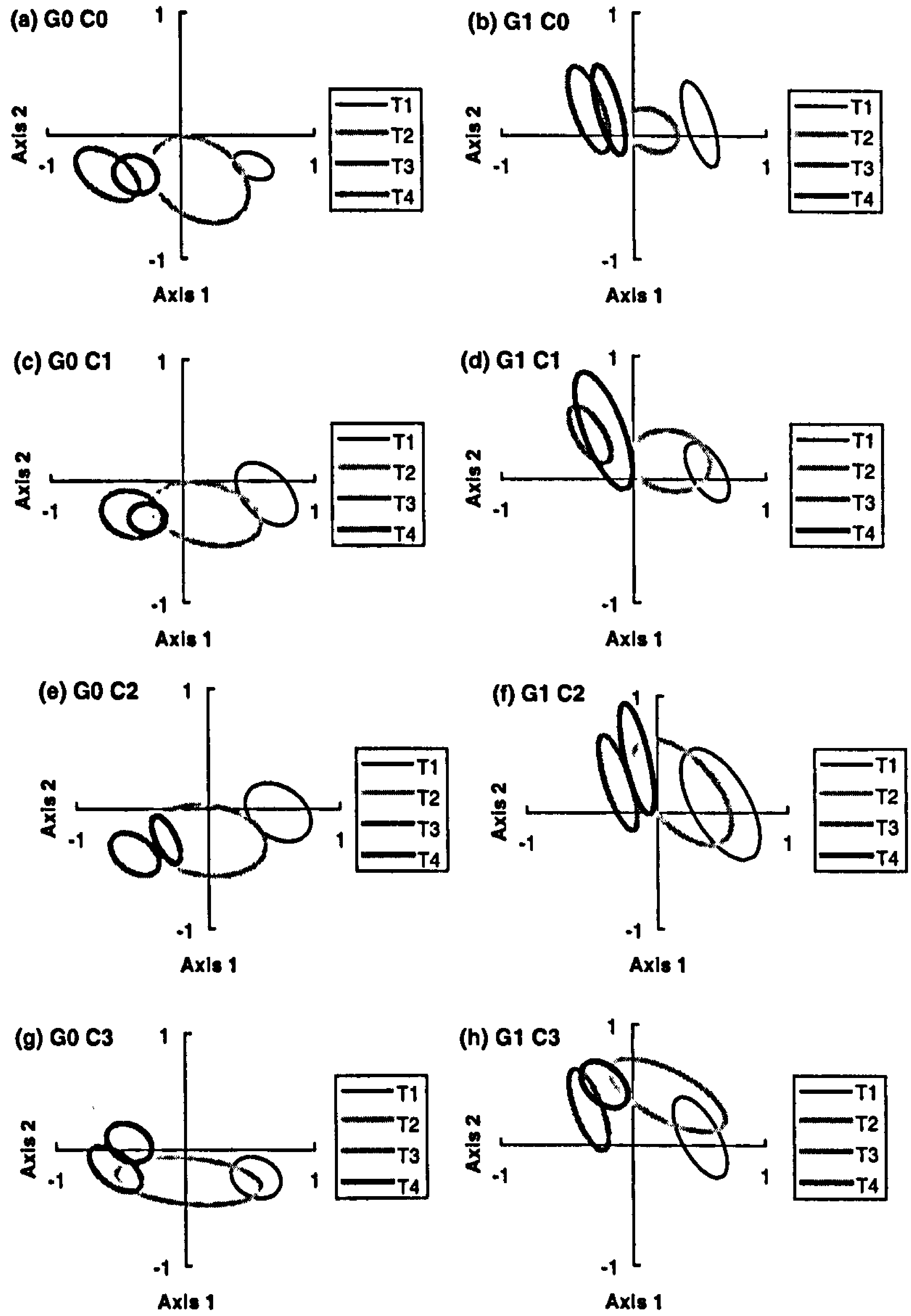

Fig. 7. Distribution of grazing × cutting treatments through time in the biplot produced from the RDA testing all treatments in combination (Table 3) – these figures are directly comparable with the species distribution (Fig. 3). The effects of treatment combinations are displayed as bivariate standard-deviational (SD) ellipses for axes 1 and 2: (a) no grazing + uncut (G0C0); (b) grazing + uncut (G1C0); (c) no grazing + cutx1 (G0C1); (d) grazing + cutx1 (G1C1); (e) no grazing + cutx2 (G0C2); (f) grazing + cutx2, (G1C2); (g) no grazing + cutx3 (G0C3); (h) grazing + cutx3 (G1C3). Codes for time (T) are 1, 2, 3, 4 – 1996, 1997, 1998, 1999.

moorland species without the use of the non-selective glyphosate. The four treatments were: cutting at the start of the experiment at various frequencies; grazing *versus* no grazing, selective herbicide use and brash addition. The first three treatments were aimed mainly at reducing the *Molinia* cover, although cutting and grazing also had disturbance effects, and the last one was intended to increase *Calluna* restoration.

A major feature of this work was the combined use of: (a) univariate and (b) multivariate analysis using constrained ordinations to test for significant differences coupled with the use of bivariate standard deviational ellipses to investigate treatment effects and their interactions. This combination has proved a powerful tool for teasing out important effects and comparing treatment trajectories. It is certainly more informative than methods used hitherto (Milligan et al., 2003a,b; Marrs et al., in press).

4.1. Effects of treatments

Cutting had the greatest effect on *Molinia*, reducing it for up to four years, especially where three cuts were applied. Increasing the number of cuts produced more

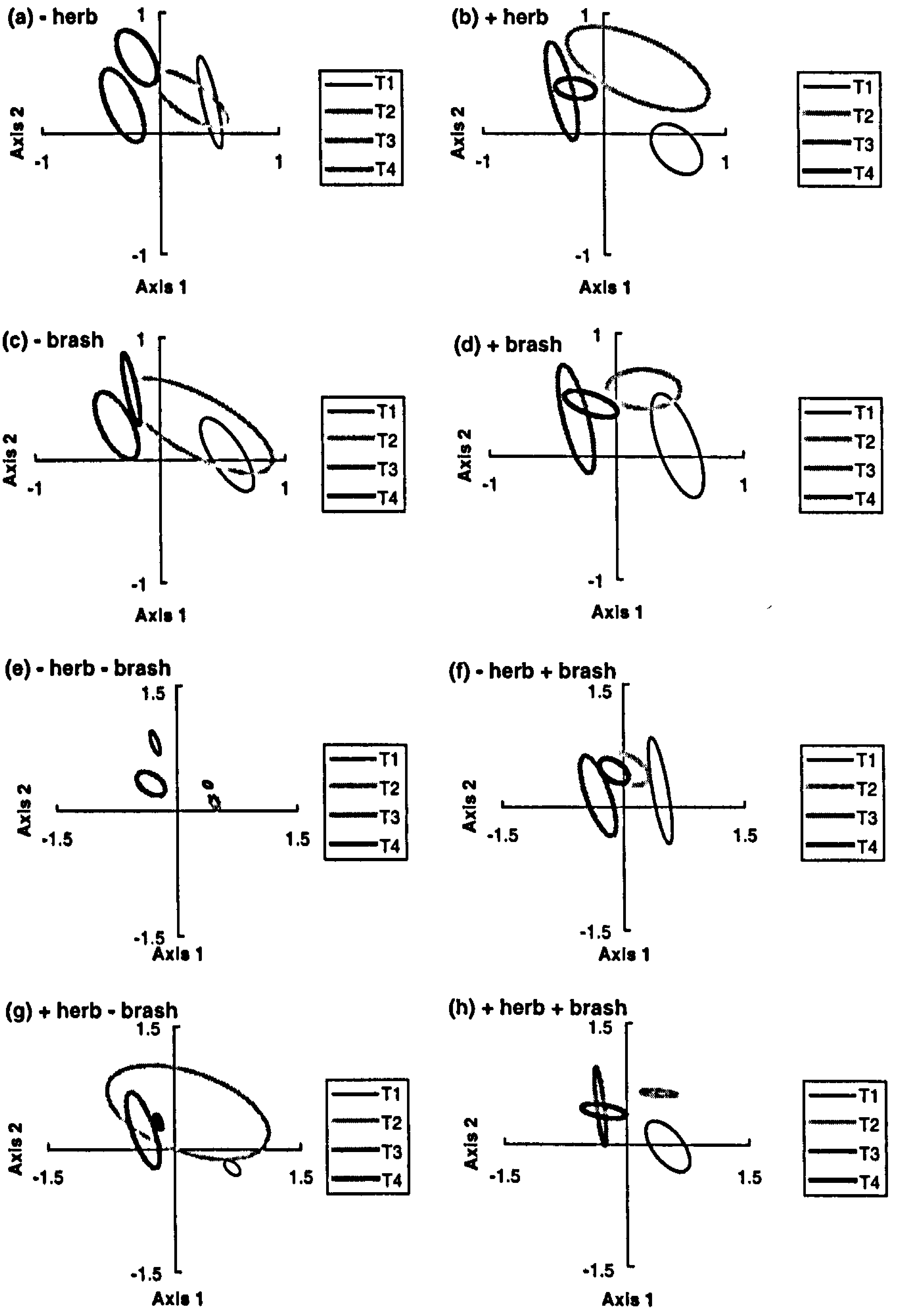

Fig. 8. Distribution of the herbicide and brash addition treatments and their interaction for the most successful grazing and cutting combination (ungrazed + cut three times) through time in the biplot produced from the RDA biplot testing all treatments in combination (Table 3) – these figures are directly comparable with the species distribution (Fig. 3). The treatments are shown as bivariate standard-deviational (SD) ellipses through time on axes 1 and 2: (a and b) herbicide treatments; (b and c) brash treatments, and (e,f,h,i) are the herbicide × brash treatment combinations. Key to time: thick black 1996, Grey 1997, Light grey 1998, Thin black 1999.

bare ground in the first year, which created more regeneration niches (sensu Grubb, 1977). Grazing had a lesser effect on *Molinia*, but the community analysis showed that it had a major effect on the development of moorland communities with a much more diverse vegetation developing on the plots grazed at the ESA prescription level than those ungrazed. The reduced sheep grazing and natural rabbit grazing pressure combined to produce plant communities that contained more moorland species; whereas where this grazing pressure prevented *Molinia* and other grasses such as *Festuca ovina* dominate. The grazed, cut treatments were the most effective in developing a moorland species composition and given the effect of the cut thrice treatment on

Calluna seedlings this is the recommended treatment Where grazing was applied there was an increasing trend towards moorland species, and where there was no grazing the trend was to a species-poor grassland.

The sheep grazing pressure at Ramsgill was calculated at 1.8 ewes ha^{-1}, an intermediate pressure in upland areas (ranges: 0.01 sheep ha^{-1} for *Pteridium aquilinum*-dominated areas to 3.01 sheep ha^{-1} on *Nardus stricta Vaccinium myrtillus*-dominated areas; ADAS, 1997), but perhaps a little high with respect to sub-dominant heather moorland sites (0.57–1.18; ADAS, 1997). It is slightly greater than that suggested as possibly suitable for holding *Molinia* in check (0.6–1.4 sheep ha^{-1}, Hulme et al., 2002). The size of the rabbit population at Ramsgill is unknown but was substantially reduced in spring/summer 1996 (A. Swainston, pers. commun.). This reduction may have helped to establish and maintain *Calluna* and other moorland species. However, the interactions are potentially complex. For example, field observations suggested that cutting prolonged the sheep-grazing season, with *Molinia* in plots cut twice and three times being preferentially grazed. Cutting may, therefore, have increased the attractiveness of *Molinia* and lengthened the grazing period; this may be important as sheep and other grazers are known not to graze *Molinia* toward the end of summer, preferring more palatable grasses and ericaceous species (Welch, 1984, 1986; Grant et al., 1985). The reasons are unclear but may result from more palatable regrowth or greater accessibility. However, it is possible that too high sheep pressures may damage *Calluna* growth and we suggest that in such circumstances it may be wise to graze the remaining *Molinia* hard in spring and early summer to ensure continued reductions (Hulme et al., 2002). Left ungrazed, *Molinia* will increase in vigour and begin to encroach again (McAdam, 1992; Marrs et al., in press).

Application of selective herbicides was less effective; they reduced vegetation height on some sampling occasions but had no significant effect on *Molinia* cover. However, selective herbicides have been shown to be effective for *Molinia* under some circumstances (Milligan et al., 2003a). As there is some discrepancy in the value of using selective herbicides more wide scale studies are needed to assess their effects under a range of different application conditions.

The addition of brash reduced vegetation height in the year after application but there was no discernable effect on recruitment of *Calluna* seedlings. This implies that natural regeneration from the soil seed bank was adequate at this site, especially in the most disturbed plots, where the greatest densities were found. Here disturbance gave better results than brash addition. The *Calluna* seed bank at Ramsgill Bents was estimated to be 5000 seeds m^{-2}, although the variability was high (SE = 3870, $n = 10$, Milligan, 1998). We added a further 10,000 in the brash, but even this rate was much lower than the 40000 seeds m^{-2} recommended for good *Calluna* establishment (Putwain and Rae, 1988). Here *Calluna* seed was added in brash and there is a physical limit to the amount that can be added, because even with this amount there was some evidence of a smothering effect. Its is possible that better quality brash could be obtained with a greater number of viable seeds, or alternatively seed can be extracted from the brash and given smoke treatment to increase its viability. Smoke-treated seeds can be applied to moorland using hydraulic sprayers (GC Eyre, personnel communication).

4.2. *Potential of integrated land management schemes*

The combined application of techniques used in this study provided evidence of important interactions with respect to restoration for conservation purposes. Cutting (especially thrice) in combination with light grazing produced a vegetation trajectory towards a moorland species complement and cutting-thrice increased *Calluna* seedling densities. The most successful treatment combination thus provided a 'window' of *Molinia* reduction with associated increased bare ground and decreased litter depths and provided opportunities for developing a moorland vegetation with a mixed species complement. At this site the background natural *Calluna* regeneration was sufficient to allow *Calluna* to regenerate, especially in plots cut thrice, but on sites with a poorer *Calluna* seed bank, addition of seeds via brash or other techniques would be essential (Todd et al., 2000; Marrs et al., in press). However, whilst natural regeneration provided successful results, the community analysis indicated that herbicide addition alone or in combination with brash addition was closer to the *Calluna* position in the biplot and had a larger pool of moorland species.

One drawback to this study has been the short length of time needed for moorland development and clearly longer-term research is needed to assess the most appropriate and economic treatment in the longer-term. It may also be worthwhile considering the use of selective herbicides to reduce *Molinia* recovery during the moorland re-establishment phase (Milligan et al., 2003a,b; GC Eyre, pers. comm.). *Molinia* has been shown to re-establish and become dominant even after sustained disturbance (Sansen and Koedam, 1996). Therefore the continued management of established *Calluna* plants within the *Molinia* mosaic is extremely important to ensure success. Sensitive grazing regimes, which reduce *Molinia* during the summer, yet protect *Calluna* plants from overgrazing in winter is strongly recommended.

A further drawback is that little is known of the effects of cutting on the fauna of these habitats. Cutting was timed to occur after the main breeding season for grouse (*Lagopus lagopus*) and curlew (*Numenius arquata*), which are common visitors to the study site. However the use of the cut sites by these species remains unknown. Further work is also necessary to clarify the effects of cutting on moorland invertebrates although increases and decreases will depend on the species present (Morris, 1981).

This study has shown that an ILMS using a combination of grazing and cutting here would be beneficial. Although costly initially, it would provide considerable conservation gains as the *Calluna* seedlings develop within a mosaic of other moorland species. Moreover, Marrs et al. (in press) have shown that there is a large variability in response of *Molinia* communities across the UK, and any attempt to develop site-specific ILMS may require further modifications, which will require additional experimentation.

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References

ADAS, 1997. Biological monitoring of moorland in the north Peak ESA 1988–1998. Report to Ministry of Agriculture, Fisheries and Food, London.

Aerts, R., van der Peijl, M.J., 1993. A simple model to explain the dominance of low productive perennials in nutrient – poor habitats. Oikos 66, 144–147.

Anon, 1995a. Biodiversity UK Steering Group Report, vol 1. Action Plans. HMSO, London.

Anon, 1995b. Biodiversity UK Steering Group Report, vol 1. Meeting the Rio Challenge. HMSO, London.

Bakker, J.P, 1989. Nature Management by Grazing and Cutting. Kluwer, Dordecht.

Bardgett, R.D., Marsden, J.H., Howard, D.C., 1995. The extent and condition of heather moorland in the uplands of England and Wales. Biological Conservation 71, 155–161.

Buhler, D.D., 2002. Challenges and opportunities for integrated weed management. Weed Science 50, 273–280.

Clay, D.V., Stevens, R.J., 1991. Herbicide use in industrial and amenity areas: current practice and future prospects. In: Brighton Crop Protection Conference Proceedings, pp. 1141–1146.

Cloy, C.J., 1984. Mechanical weed control. Aspects of Applied Biology 5, 355–360.

Corley, M.F.V., Hill, M.O, 1981. Distribution of Bryophytes in the British Isles. Bryological Society of the British Isle, Cardiff.

Diemont, W.H., Heil, G., 1984. Some long-term observations on cyclical and seral processes in Dutch heathlands. Biological Conservation 30, 283–290.

English Nature, 2001. State of nature: the upland challenge. English Nature, Peterborough.

Gimingham, C.H., 1992. The Lowland Heathland Management Handbook. English Nature, Peterborough.

Granström, A., 1987. Seed viability of fourteen species during five years of storage in forest soil. Journal of Ecology 75, 321–331.

Grant, S.A., Maxwell, T.J., 1988. Hill vegetation and grazing by domesticated herbivores: the biology and definition of management options. In: Usher, M.B., Thompson, D.B.A. (Eds.), Ecological Change in the Uplands. Blackwell Scientific Publications, Oxford, pp. 201–211.

Grant, S.A., Bolton, G.R., Torvell, L., 1985. The responses of blanket bog vegetation to controlled grazing by hill sheep. Journal of Applied Ecology 22, 739–751.

Grant, S.A., Hunter, R.F., Cross, C., 1963. The effect of muirburning *Molinia*-dominated communities. Journal Of The British Grassland Society 18, 249–257.

Grant, S.A., Torvell, L., Common, T.G., Sim, E.M., Small, J.L., 1996. Controlled grazing studies on *Molinia* grassland: effects of different seasonal patterns and levels of defoliation *Molinia* growth and responses of swards to controlled grazing by cattle. Journal of Applied Ecology 33, 1267–1280.

Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Review 52, 107–145.

Heil, G., Diemont, W.H., 1983. Raised nutrient levels change heathland into grassland. Vegetatio 53, 113–120.

Hogg, P., Squires, P., Fitter, A.H., 1995. Acidification, nitrogen deposition and rapid vegetation change in a small valley mire in Yorkshire. Biological Conservation 71, 143–153.

Hulme, P.D., Merrell, B.G., Torvell, L., Fisher, J.M., Small, J.L., Pakeman, R.J., 2002. Rehabilitation of degraded *Calluna vulgaris* (L.) Hull-dominated wet heath by controlled sheep grazing. Biological Conservation 107, 351–363.

Krebs, C.J., 1972. Ecology. Harper and Row, New York.

Le Duc, M.G., Pakeman, R.J., Marrs, R.H., 2003. Changes in the rhizome system of bracken when subjected to long-term experimental treatment. Journal of Applied Ecology 40, 508–522.

Le Duc, M.G., Pakeman, R.J., Marrs, R.H., in press. Extracting information from noisy survey data on temporal change in vegetation following disturbance. Ecological Modelling.

Lee, J.A., Caporn, S.J.M., Read, D.J., 1992. Effects of increasing nitrogen deposition and acidification on heathlands. In: Schneider, T. (Ed.), Acidification Research. Evaluation and Policy Applications. Elsevier, Amsterdam, pp. 97–106.

Legendre, P., Legendre, N., 1998. Numerical Ecology, second edn. Elsevier, Amsterdam.

Lowday, J.E., Marrs, R.H., 1992. Control of bracken and the restoration of heathland. I. Control of bracken. Journal of Applied Ecology 29, 195–203.

McAdam, J.H, 1992. The effect of sheep grazing density on heathland vegetation. Aspects of Applied Biology 29, 371–376.

MAFF, 1993. Environment matters. Environmentally Sensitive Areas. MAFF, London.

MAFF, 1996. Environment matters. The Countryside Stewardship Scheme: Information for Farmers and Land Managers. MAFF, London.

Maxwell, T.J., Grant, S.A., Milne, J.A., Sibbald, A.R., 1986. Systems of sheep production on heather moorland. In: O'Toole M. (edn.), Hill Land Symposium, Galway, 1984, An Foras Taluntais, Dublin, pp. 188–211.

Marrs, R.H., 1984. Birch control on lowland heaths: mechanical control and the application of selective herbicides by foliar spray. Journal of Applied Ecology 21, 703–716.

Marrs, R.H., 1985. Birch control by the treatment of cut stumps with herbicides. Arboriculture Journal 9, 173–182.

Marrs, R.H., 1987. Studies on the conservation of lowland *Calluna* heaths. I. Control of birch and bracken and its effect on heath vegetation. Journal of Applied Ecology 24, 163–175.

Marrs, R.H., Johnson, S.W, Le Duc, M.G., 1998. Control of bracken and restoration of heathland. VI. The response of bracken fronds to 18 years of continued bracken control or six years of control followed by recovery. Journal of Applied Ecology 35, 479–490.

Marrs, R.H., Phillips, J.D.P, Todd, P.A., Ghorbani, J., Le Duc, M.G., in press. Control of *Molinia caerulea* on upland moors. Journal of Applied Ecology.

Miles, J., 1974. Experimental establishment of new species from seed in *Callunetum* in North-east Scotland. Journal of Ecology 62, 527–551.

Miller, G.R., Miles, J., Heal, O.W., 1984. Moorland Management: A Study of Exmoor. Institute of Terrestrial Ecology, Cambridge.

Milligan, A.L., Putwain, P.D., Marrs, R.H., 1999. A laboratory assessment of the relative sensitivity of *Molinia caerulea* (L.) Moench and *Calluna vulgaris* (L.) Hull to a range of herbicides. Annals of Applied Biology 135, 503–508.

Milligan, A.L., Putwain, P.D., Marrs, R.H., 2003a. A field assessment of the role of selective herbicides in the restoration of British moorland dominated by *Molinia*. Biological Conservation 109, 369–379.

Milligan, A.L., Putwain, P.D., Marrs, R.H., 2003b. Testing selective herbicides for *Molinia caerulea* (L.) Moench control in British upland moorland. British Crop Prot Conference.

Moen, A., 1995. Vegetational changes in boreal rich fens induced by Haymaking; management plan for the Sølendet nature reserve. In: Wheeler, B.D., Shaw, S.C., Fojt, W.J., Robertson, R.A. (Eds.), Restoration of Temperate Wetlands. Wiley, Chichester, pp. 167–181.

Morris, M.G., 1981. Responses of grassland invertebrates to management by cutting. III. Adverse effects on Auchenorhyncha. Journal of Applied Ecology 18, 107–123.

Morton, A.J., 1977. Mineral nutrient pathways in *Molinietum* in autumn and winter. Journal of Ecology 65, 993–999.

Mulder, T.A., Doll, J.D., 1993. Integrating reduced herbicide use with mechanical weeding in Corn (*Zea mays*). Weed Technology 7, 382–389.

Palmer, S.C.F., Hester, A.J., 2000. Predicting spatial variation in heather utilization by sheep and red deer within heather/grass mosaics. Journal of Applied Ecology 37, 616–631.

Popay, I., Field, R., 1996. Grazing animals as weed control agents. Weed Technology 10, 217–231.

PSD/HSE, 1988. The Pesticides Register. PSD/HSE, London.

Putwain, P.D., Rae, P.A.S., 1988. Heathland Restoration: A Handbook of Techniques. British Gas, Southampton.

Ricklefs, R.E., Nealen, P., 1998. Lineage-dependent rates of evolutionary diversification: analysis of bivariate ellipses. Functional Ecology 12, 871–888.

Roem, W.J., Klees, H., Berendse, F., 2002. Effects of nutrient addition and acidification on plant species diversity and seed germination in heathland. Journal of Applied Ecology 39 (5), 937–948.

SAS, 1985. SAS/STAT User's Guide. Release 6.03 Edition. SAS Institute Inc., Cary, NC.

Sansen, U., Koedam, N., 1996. Use of sod cutting for restoration of wet heathlands; revegetation and establishment of typical species in relation to soil conditions. Journal of Vegetation Science 7, 483–486.

Schoppguth, A., Maas, D., Pfadenhauer, J., 1994. Influence of amanagement of the seed production and seed bank of calcareous fen species. Journal of Vegetation Science 5, 569–578.

Stace, C.A., 1997. New Flora of the British Isles, second edn. Cambridge University Press, Cambridge.

Ter Braak, C.J.F., Šmilauer, P., 1998. CANOCO 4 Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca.

Thomas, B., 1951. The moorland grazings. British Agricultural Bulletin 15, 126–132.

Todd, P.A., Phillips, J.D.P., Putwain, P.D., Marrs, R.H., 2000. Control of *Molinia caerulea* on moorland. Grass and Forage Science 55, 181–191.

Vermeer, J.G., Berendse, F., 1983. The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. Vegetatio 53, 121–126.

Welch, D., 1984. Studies in the grazing of heather moorland in north-east Scotland. I. Site descriptions and patterns of utilisation. Journal of Applied Ecology 21, 179–195.

Welch, D., 1986. Studies in the grazing of heather moorland in north-east Scotland. V. Trends in *Nardus stricta* and other unpalatable graminoids. Journal of Applied Ecology 23, 1047–1058.

Wells, T.C.E., Cox, R., 1993. The long term effects of cutting on the yield, floristic composition and soil nutrient status of chalk grassland. English Nature Research Report no. 71. English Nature, Peterborough.

Worral, D., Palmer, C., 1988. The use of mowing and herbicides for vegetation management on the Island of Flat Holm. Aspects of Applied Biology 16, 393–401.

Zoschke, A., 1994. Towards reduced herbicide rates and adapted weed management. Weed Technology 8, 376–386.

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Competing conservation goals, biodiversity or ecosystem services: Element losses and species recruitment in a managed moorland–bracken model system

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Abstract

Conservation management in Europe is often geared towards restoring semi-natural ecosystems, where the objective is to reverse succession and re-establish early-successional communities, to comply with national and international conservation targets. At the same time, it is increasingly recognised that ecosystems provide services that contribute to other, possibly conflicting policy requirements. Few attempts have been made to define these conflicts. Here, we assess some potential conflicts using a *Calluna vulgaris*-dominated moorland invaded by bracken (*Pteridium aquilinum*) as a model system, where the current policy is to reverse this process and restore moorland. We examined impacts of bracken control treatments on services (stocks and losses of C and mineral nutrients), litter turnover and biodiversity within a designed experiment over 7 years. Bracken litter was $>2000\,\mathrm{g\,m^{-2}}$ in untreated plots, and treatments reduced this quantity, and its element content, to varying degrees. Cutting twice per year was the most successful treatment in reducing bracken litter and its element content, increasing litter turnover, and increasing both mass and diversity of non-bracken vegetation. Diversity was greatest where bracken litter had been reduced, but species composition was also influenced by light sheep grazing. There was a significant loss of some chemical elements from bracken that could not be accounted for in other pools, and hence potentially lost from the system. In absolute terms large amounts of C and N were lost, but when expressed as a percentage of the total amount in the system, Mg was potentially more important with losses of almost a third of the Mg in the surface soil-vegetation system.

There is, therefore, a potential dilemma between controlling a mid-successional invasive species for conservation policy objectives, especially when that species has evolved to sequester nutrients, and the negative effect of increasing environmental costs in terms of carbon accounting required, the potential input of nutrients to aquatic systems, and long-term nutrient loss. There is, therefore, a need to balance conservation goals against potential damage to biogeochemical structure and function.

Keywords: Moorland; Model systems; Litter turnover; Nutrient compartmentation; Decomposition; Restoration; Land management; Carbon stocks; Kyoto; Water Framework Directive

1. Introduction

The value of both ecosystem services and natural capital is increasingly being recognised and incorporated into international legislation and protocols (Constanza et al., 1997; Moss et al., 2003). On the one hand, there are policies designed to control biogeochemical processes, for example, the Kyoto Protocol (KP), and the European Union (EU) Water Framework Directive (WFD); the KP aims to limit C emissions and increase C storage (Watson, 2001; Grace, 2004), and the WFD aims to improve water quality, by minimising inputs of N and P to aquatic systems (Moss et al., 2003). On the other hand, there are policies designed

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to conserve biodiversity; at the international level, the Convention on Biological Diversity (CBD), and a range of EU Directives (Habitats Directive-92/43/EEC; Birds Directive-79/409/EEC), and at the national scale, the UK has developed Biodiversity Action Plans (Anon, 1995). In addition, the UK has designated areas under Agri-Environment Schemes to reduce agricultural damage and produce environmental benefits (MAFF, 1993).

There can be potential conflict between some of these policies. For example, most research to support biogeochemical policy implementation has been carried out, either on relatively pristine systems such as forests, peatlands and tundra (Olsen et al., 1985; Cannell et al., 1999 Worrall et al., 2003), or on agro-ecosystems (Grace, 2004). Where pristine systems are to be conserved, or where succession is occurring towards late-successional communities, we might expect organic matter accumulation (Odum, 1969). Thus, conservation action under these circumstances would support policies affecting biogeochemistry processes.

However, a great deal of conservation management in northern Europe is focused on conserving early- or mid-successional, semi-natural communities. These ecosystems were created by human activities, and they must be managed actively to prevent succession and maintain the target communities (Gimingham, 1992). Most semi-natural communities occur on infertile soils, and one of the objectives of conservation management is to deliberately reduce and/or maintain a low nutrient status (Marrs, 1993). Where such conservation management is applied, biotic control (*sensu* Bormann and Likens, 1979) is likely to be reduced, and nutrients will be released where they either prevent the restoration of the target biotope (Dorland et al., 2003), or they are lost through increased outflows. Here, there is a potential conflict between policies designed to enhance conservation, and those designed to conserve biogeochemical processes.

Unfortunately, very little information is available on the effect of conservation management in semi-natural systems on C and nutrient stocks. Accordingly, here we attempt to assess the impact of various management treatments on both element stocks and biodiversity concurrently, using a *Calluna vulgaris*-moorland invaded by dense bracken, where the conservation objective is to reverse invasion and restore moorland. We refer to *Pteridium aquilinum* and *C. vulgaris* as bracken and *Calluna* throughout; otherwise nomenclature follows Stace (1997) and Corley and Hill (1981).

This is an ideal model system for testing management processes and conservation hypotheses. Heathlands/moorlands have been used as model systems previously for describing regeneration and succession (Watt, 1947, 1955; Marrs, 1988), partly because they are species-poor systems (Rodwell, 1991), making it easier to derive underlying mechanisms that can be extrapolated to more complex ones (Vitousek, 2004). The extension of this model to include a successional component with bracken can be justified on the basis that bracken often invades alone, and can substantially reduce the complement of heath species (Pakeman and Marrs, 1992). There are also good practical reasons for studying this system as bracken-dominated land currently occupies large areas of the UK. Bracken is present on approximately 17,100 km^2 of land (7.3% of the total land area), with 4800 km^2 directly referable to the model system referred to here (Pakeman et al., 1995). However, this situation could change markedly, in different directions, as a result of changing management policies. The area of dense bracken could either reduce if control/restoration policies are implemented to increase biodiversity, or it could increase through a combination of reduced stocking policies implemented under Agri-Environment schemes, coupled with global warming (Pakeman et al., 2000a).

There are four main mechanisms through which bracken can maintain dominance (Marrs, 1988; Marrs et al., 1998a): (1) Competition through the production of a dense frond canopy; (2) Persistence, the clonal habit allows bracken to persist on sites for a very long time (>1500 years; Oinonen, 1967); (3) Resilience, through the large perennial rhizome network, containing a large store of carbohydrates, nutrients, and perenniating buds; and (4) Inhibition, through the production of deep litter, which prevents species invasion (Lowday and Marrs, 1992). Bracken control treatments impinge on fronds, rhizomes and litter in different ways and to different degrees, depending on control methods used (Marrs et al., 1998a). There are two major control options; mechanical and herbicidal.

Mechanical control has a direct effect, shredding and compacting fronds and litter, but the aim is to continuously deplete the rhizome stores. As cutting proceeds there are also indirect effects as frond production declines over time, and hence litter inputs are also reduced (Marrs et al., 1998a). In contrast, herbicide (usually asulam in the UK) is usually applied once in late summer, when it is translocated to rhizome buds. Most frond-producing buds on the rhizome (95–99%) are killed resulting in a large reduction in fronds in the year after spraying; however, there is usually rapid recovery if follow-up treatments are not applied (Marrs et al., 1998a).

In the year after spraying litter inputs should reduce to almost zero, followed by an increase paralleling frond recovery. No information is available on whether litter turnover changes after bracken control treatment.

The effectiveness of control treatments on bracken performance and restoration treatments on vegetation development have been reported elsewhere (Marrs et al., 1998a, b; Le Duc et al., 2000, 2003, 2007). Here, we report the results of an experiment in a dense bracken stand where experimental bracken control has been combined with heathland restoration treatments at a site in the Peak District of the UK. After 7 years we measured: (1) C and mineral elements in various ecosystem pools; (2) selected fluxes including litter turnover; and (3) changing

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biodiversity. The bracken control treatments were designed to (a) variably interfere with the mass of vegetation and litter, and by inference element stocks, and (b) produce a heath-grass target biotope with increased plant diversity. We tested four hypotheses: (1) Successful bracken control treatments changes the distribution of elements between bracken, litter and soil pools; (2) Bracken control influences element losses; (3) Bracken control treatment accelerates litter turnover; and (4) Bracken control, as a result of reduced bracken (fronds and litter), accelerates the invasion of species of grass/moor communities.

2. Methods

2.1. The study site

The experiment was set up at Hordron Edge in Derbyshire, UK (Latitude, Longitude; 53°23′N, 1°41′W), the site is within the Peak District National Park and the North Peak Environmentally Sensitive Area ESA. At the start of the experiment the entire site was covered in dense bracken fronds (10 fronds m^{-2} in untreated control plots in 1994) and a deep litter layer (>80% cover and 18 cm deep, Ghorbani et al., 2006). The underlying vegetation was extremely species-poor, consisting of a few scattered *Calluna* bushes and very little else (Le Duc et al., 2007). The soil is a podzol with a pronounced organic layer and the site is grazed by sheep at a low stocking density, which is a condition of the ESA prescription (ca. 0.5 ha^{-1}; Pakeman et al., 2000b).

2.2. The experimental design

The experiment was set up in 1993 to test a range of bracken control/vegetation restoration treatments. The full experimental protocol is detailed in Le Duc et al. (2000, 2003), so only a resumé is given here. The experiment used a split–split plot design with three replicate blocks (each 70 × 60 m). Six bracken control treatments were applied within the main-plots (each 60 × 10 m), these were: (1) experimental control; (2) cutting once per year (early July); (3) cutting twice per year (early July and mid-August); (4) asulam application in first year only; (5) asulam application in first year followed by single cut in second; and (6) cutting in first year followed by asulam in second. Here these treatments are coded: untreated, cut once per year, cut twice per year, asulam, asulam + cut, cut + asulam, respectively. All asulam applications were applied using a knapsack sprayer at 4.4 kg a.i. ha^{-1} in late summer. Each main-plot was split into two sub-plots (each 30 × 10 m), one was enclosed to prevent grazing, and the other remained open to light sheep grazing. Within each of these sub-plots three seeding treatments were imposed to assist with *Calluna* regeneration; these were not considered here so sampling was confined to the unseeded sub-sub-plots. Treatments were allocated randomly at all levels.

Each year between 1994 and 2003 we measured: (1) summer bracken frond biomass (June and August); (2) bracken litter cover and depth (June) and (3) cover (%) of all species in the understorey vegetation (June). In 2000, bracken rhizomes were sampled and separated in long- and short-shoots (Marrs and Watt, 2006), oven-dried, weighed and archived (Le Duc et al., 2003). These archived samples were analysed as described below. The data on rhizome biomass from Le Duc et al. (2003) were used to compute element mass ($g\,m^{-2}$) for the rhizome system.

2.3. Litter, vegetation and soil sampling

In October 2000, 7 years after the experiment started, litter, vegetation and soils were sampled after the fronds had died back. A 0.25 m^2 quadrat was located at pre-selected random co-ordinates in each unseeded split–split plot ($n = 36$) and the following samples taken in order: (1) the standing, senescent fronds were cut at ground level (uncompacted bracken litter); (2) the remaining vegetation (biomass + necromass including compacted bracken litter) was cut at ground level; (3) two 15-cm deep soil cores were taken using an auger (5.08 cm diameter), which were then divided into three fractions: fibrous organic material (A_{00} horizon), dark, amorphous organic material (A_0 horizon) and mineral material (A_1 horizon). Vegetation samples were sub-sampled randomly and sorted into bracken litter (compacted bracken litter) and non-bracken plant vegetation/litter. The latter fraction included all non-bracken material, both living and dead. All fractions were oven-dried (85 °C, 48 h) and data converted to $g\,m^{-2}$.

2.4. Estimation of nutrient concentrations

All samples were ground to a fine powder with a Kika-Labortechnik A10 mill. C and N concentrations were measured using a Carlo Erba Instruments NC2500 elemental analyser. Sub-samples were digested in acid and P, K, Ca, and Mg concentrations then estimated using standard methods (Allen, 1989). For each fraction, data were calculated on an area basis ($g\,m^{-2}$). Statistical analysis was performed on transformed data ($g\,m^{-2}$), but arithmetic means are also presented for ease of interpretation and comparison (converted to $Mg\,ha^{-1}$ for C; $kg\,ha^{-1}$ for all other elements). Standard errors were calculated for composite variables by adding the variances for each variable and then correcting with the covariance using the method described in Beaumont (1986). C:N and C:P ratios were calculated. Two derived variables were computed, these were the total mount of elements in the litter/plant component (all litter fractions + rhizomes) and the entire litter/plant/soil system (all litter fractions + rhizomes + soil).

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2.5. Calculation of bracken litter turnover

A litter turnover index (*K*) was calculated as the current year's litter input (L, g m^{-2}) divided by the total above-ground (i.e. standing+compacted) crop of litter (X_L, g m^{-2}) (Swift et al., 1979). L was computed for bracken treatments as follows: (1) for control and non-cut treatments using the uncompacted litter mass (one input of fronds at the end of season); (2) for the cut once per year treatment as the sum of the uncompacted litter mass and the June frond biomass (two inputs, cut+end of season), and (3) for the cut twice per year treatment as the sum of the uncompacted litter mass and both the June and August frond biomass (three inputs, two cuts plus end of season).

2.6. Estimating effects on diversity

Floristic data was collected in the summer of 2000, 3 months before the litter sampling. Both floristic and litter data were collected from identical locations. The effects of bracken control treatment on species richness and diversity (using the Shannon–Weiner index) was assessed and correlation and the relationships between species composition and litter components were explored.

2.7. Data analysis

Hypothesis 1:. "Successful bracken control changes the distribution of elements between bracken, litter and soil pools" was tested by assessing the effects of treatment on the measured mass and nutrient contents of all bracken, litter and soil pools using univariate ANOVA.

Hypothesis 2:. "Bracken control influences element losses" was tested using univariate ANOVA. Here, we might expect two possibilities, either (a) element losses from the changing bracken pools would be counteracted by uptake from the developing grass/moor vegetation, viz. no net loss, or (b) if element losses from bracken pools could not be accounted for by developing vegetation, there would be a potential loss from the system. These hypotheses were tested by comparing the difference between treatments where bracken control was applied and the untreated state.

Hypothesis 3:. "Bracken control accelerates litter turnover and the invasion of species of grass/moor communities" was tested by assessing the effects of treatment on litter turnover index univariate ANOVA.

Hypothesis 4:. "Bracken control accelerates the invasion of species of grass/moor communities" was tested by assessing the effects of treatment on diversity measures (species richness, Shannon–Wiener index) and species cover using a combination of univariate ANOVA, correlation analysis and multivariate analysis.

Univariate analysis of variance was performed using PROC ANOVA (SAS, 1989) using a randomised block split-plot design. All variables apart from the Shannon–Wiener diversity index were transformed using $\log_e(y+1)$ (Sokal and Rohlf, 1995). These analyses produced significant effects only for the bracken control treatments. Therefore, only the means for the main-plot bracken control treatments, i.e. the pooled mean of the two grazing treatments, are discussed here.

Kendal rank correlation coefficients were calculated between litter turnover rates, measures of biodiversity and soil-litter chemical variables (PROC CORR; SAS, 1989). Bonferroni correction was used to adjust for the Type I error rate (Cabin and Mitchell, 2000; Sokal and Rohlf, 1995).

Multivariate analysis using CANOCO for WINDOWS v4.5 (ter Braak and Šmilauer, 1998) was also employed to determine which factors were influencing species community composition. Gradient lengths of the first axis, measured using Detrended Correspondence Analysis, were always <2.5 so linear redundancy analysis (RDA) was used thereafter (ter Braak and Šmilauer, 1998). Species data were $\ln(y+1)$ transformed, the downweighting option for rare species was not used; and significance was tested using a Monte Carlo test with 999 permutations. Forward Selection was used to select those environmental variables (e.g. bracken litter depth, grazing, etc.), that accounted for a significant proportion of the explained variation ($P<0.05$). A final RDA was then done using just those selected environmental variables.

3. Results

3.1. General description of changes during the experiment

The untreated plots had the greatest bracken cover in June, with all bracken control treatments reducing its cover (Table 1). Cutting twice per year resulted in the greatest reduction of bracken cover (<1% cover) compared to the untreated control (8%). These apparently low bracken cover values reflect the slow emergence in the spring of 2000; the sampling time in June is designed to measure species diversity rather than bracken. In August, however, the two cutting treatments were more effective than asulam alone, or in combination, with cutting treatments. Species richness and the cover of all of the common species were lowest in the untreated plot and greater where bracken control had been applied. The most common species was the grass *Deschampsia flexuosa*, and there was a much greater bryophyte cover in the plots where cutting was applied. The temporal development of the vegetation in this experiment is detailed in Le Duc et al. (2007).

3.2. Hypothesis 1: Successful bracken control changes the distribution of elements between bracken, litter and soil pools

3.2.1. Element distribution in untreated stands

The element distribution in the untreated bracken-dominated communities (Table 2) showed that there

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Table 1
Mean species richness (number m^{-2}) and cover (%) of the 10 most abundant species plus total bryophytes in each bracken control treatment at Hordron Edge, Derbyshire in June 2000, after 7 years of treatment *Pteridium aquilinum* cover in August is also presented

Species richness & cover (%)	Bracken control treatment					
	Untreated control	Cut 1 pa	Cut 2 pa	CutSpray	SprayCut	Spray
Species richness	**3.19** (1.79±0.71)	**7.29** (2.70±0.73)	**7.68** (2.77±0.71)	**6.65** (2.58±0.70)	**4.48** (2.12±0.76)	**6.67** (2.59±0.65)
Deschampsia flexuosa	**3.44** (1.49±1.06)	**16.53** (2.86±1.00)	**16.75** (2.88±1.04)	**12.15** (2.58±1.08)	**17.81** (2.93±1.09)	**15.06** (2.78±0.92)
Pteridium aquilinum	**8.39** (2.24±0.73)	**2.63** (1.29±0.68)	**0.84** (0.61±0.74)	**2.59** (1.28±0.78)	**5.87** (1.93±0.67)	**2.40** (1.22±0.90)
Pteridium aquilinum August	**48.37** (3.90±1.01)	**31.55** (3.48±1.16)	**36.84** (3.63±0.98)	**62.04** (4.14±0.57)	**62.74** (4.15±0.70)	**49.24** (3.92±0.69)
Galium saxatile	**0.24** (0.21±0.67)	**6.29** (1.99±1.05)	**14.09** (2.71±0.84)	**2.71** (1.31±0.92)	**1.35** (0.86±0.98)	**1.56** (0.94±1.01)
Festuca ovina	**0.06** (0.06±0.42)	**1.72** (1.00±1.14)	**6.68** (2.04±1.22)	**3.33** (1.47±1.21)	**1.14** (0.76±1.12)	**1.55** (0.94±0.99)
Hypnum jutlandicum	**0.81** (0.59±0.86)	**2.43** (1.23±0.90)	**1.21** (0.79±0.78)	**1.65** (0.97±1.06)	**0.63** (0.49±0.86)	**0.88** (0.62±0.79)
Agrostis castenella	**0.03** (0.03±0.36)	**0.63** (0.49±0.92)	**2.35** (1.21±1.13)	**0.33** (0.29±0.81)	**0.44** (0.37±0.88)	**0.92** (0.65±1.12)
Campylopus introflexus	**0.05** (0.05±0.40)	**1.12** (0.75±0.85)	**0.70** (0.53±0.91)	**0.88** (0.63±1.00)	**0.50** (0.41±0.90)	**0.27** (0.24±0.88)
Potentilla erecta	**0.01** (0.01±0.12)	**0.38** (0.32±0.83)	**0.50** (0.41±0.79)	**0.80** (0.59±0.87)	**0.12** (0.11±0.47)	**0.98** (0.69±0.93)
Vaccinium myrtyllus	**0.09** (0.09±0.44)	**0.40** (0.34±0.74)	**0.25** (0.22±0.70)	**0.55** (0.44±0.92)	**0.40** (0.33±0.80)	**0.37** (0.31±0.77)
Nardus stricta	**0.04** (0.04 ±0.33)	**0.20** (0.18±0.76)	**0.00** (0.00 ±0.00)	**0.83** (0.60±1.07)	**0.09** (0.09±0.54)	**1.26** (0.82±1.26)
Total Bryophytes	**1.00** (0.69±0.96)	**12.39** (2.59±1.37)	**6.11** (1.96±1.23)	**6.85** (2.06±1.38)	**2.29** (1.19±1.28)	**2.41** (1.23±1.27)

Data are presented as back-transformed means ($n = 18$) in bold with transformed means±SE in parentheses.
Data transformed ($Y' = \log_e(Y+1)$, except species richness ($Y' = (Y)^{0.5}$) and litter depth ($Y' = (Y+0.5)^{0.5}$).

Table 2
Element distribution in a dense unmanaged bracken stand at Hordron Edge, Derbyshire in 2000; (a) mean values±SE ($n = 6$) of untransformed data are presented

	C	N	P	K	Ca	Mg
(*a*) *Element mass*						
Bracken litter (compacted + uncompacted)	9.4±2.8	439±148	21.0±10.0	67±23	22±4	11±3
Other vegetation/litter	0.6±0.4	35±24	2±1	7.5±5.0	0.3±0.2	0.1±0.04
Soil (0–15 cm depth)	84.6±10.9	3766±410	606±69	6240±680	326±64	401±70
Total (surface litter—15 cm depth) = (x)	94.7±12.1	4240±432	629±70	6315±673	348±65	413±71
Bracken rhizomes = (y)	8.1±0.3	306±21	129±21	925±160	249±27	276±39
Total measured ($z = x+y$)	102.8±12.3	4546±447	758±73	7240±686	597±70	689±91
(*b*) *% of total measured* (z)						
Bracken litter (compacted + uncompacted)	9.2	9.7	2.8	1.0	3.7	1.6
Other vegetation/litter	0.6	0.8	0.3	0.1	0.1	0.01
Soil (0–15 cm depth)	82.3	82.8	79.9	86.2	54.6	58.2
Bracken rhizomes	7.9	6.7	17.0	12.8	41.7	40.1

Units: C = Mg ha^{-1}, others = kg ha^{-1}, and (b) % calculated on the total measured.

is a considerable proportion of C and N (almost 10%) within the bracken litter fraction, almost nothing in the non-bracken vegetation/litter but a substantial amount of C, N, P and K (7–17%), and especially Ca and Mg (40%) within the bracken rhizomes. The total amounts measured are in accord with published values (Perkins, 1978; Wilson and Puri, 2001; Prentice, 2001).

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Table 3
Effects of bracken control treatments on the elements in the three litter components in the bracken control/moorland restoration experiment at Hordron Edge, Derbyshire after 7 years treatment

Measure		Untreated	Asulam + cut	Cut + asulam	Asulam	Cut 1/yr	Cut 2/yr	$F_{5,10}$	Significance
Uncompacted bracken litter	Mass	**3.8**	**3.7**	**3.2**	**0.6**	**0.9**	**0.1**		
		5.841a	5.850a	5.568a	4.058b	4.245b	1.805c	8.94	*
	C	**1.8**	**1.8**	**1.5**	**0.7**	**0.5**	**0.05**		
		5.103a	5.109a	4.830ab	3.444bc	3.523bc	1.354	9.62	*
	N	**85**	**49**	**46**	**26**	**13**	**2**		
		2.065a	1.725ab	1.601b	1.003bc	0.782cd	0.137d	8.14	*
	Ca	**19**	**13**	**13**	**4**	**2**	**0.4**		
		1.020a	0.827a	0.758a	0.308b	0.219b	0.035b	18.51	**
	Mg	**3.9**	**3.7**	**4.5**	**2.2**	**0.9**	**0.2**		
		0.322a	0.312a	0.348a	0.187ab	0.081b	0.016b	6.47	**
Compacted bracken litter	Mass	**16.4**	**14.4**	**2.2**	**0.9**	**0.6**	**0.1**		
		7.004a	6.807ab	5.018abc	4.614bcd	3.828cd	2.401d	6.11	*
	C	**7.6**	**6.7**	**1.1**	**2.9**	**0.3**	**0.1**		
		6.268a	6.073a	4.295ab	3.971b	3.121bc	1.746c	6.78	*
	N	**354**	**251**	**47**	**91**	**11**	**3**		
		3.200a	2.860a	1.465b	1.380b	0.667b	0.232b	7.87	*
	Ca	**3**	**4**	**0.7**	**0.7**	**0.2**	**0.1**		
		0.258a	0.346a	0.068b	0.068b	0.020b	0.006b	7.34	**
Non-bracken vegetation/litter	Mass	**1.4**	**1.9**	**7.5**	**7.5**	**7.8**	**10.1**		
		3.328a	2.688a	6.462b	5.619b	6.538b	6.880b	3.93	*
	N	**35**	**43**	**169**	**137**	**170**	**199**		
		1.009a	0.861a	2.682b	2.318b	2.794b	3.012b	6.42	*
	Ca	**0.3**	**0.1**	**2.2**	**1.2**	**1.8**	**2.2**		
		0.030a	0.012a	0.190b	0.119b	0.154b	0.202b	11.61	*
*K*1 (max. possible litter input)		**0.31**	**0.53**	**0.54**	**0.43**	**1.66**	**5.40**		
		0.329a	0.408ab	0.405ab	0.251a	0.872b	1.725c	12.18	**
*K*2 (min. possible litter input)		**0.26**	**0.62**	**0.31**	**0.31**	**0.69**	**5.40**		
		0.227a	0.477a	0.261a	0.256a	0.503a	1.725b	14.27	**

Analysis was performed on transformed data ($\log_e + 1$, $n = 6$; $g\,m^{-2}$) and means significantly different from each other are denoted by different letters. Significance coded as: *$P<0.05$; **$P<0.01$. Arithmetic means are also presented in bold for interpretation and have been expressed as $Mg\,ha^{-1}$ for mass and C and $kg\,ha^{-1}$ for all other elements.

3.2.2. Effects of treatment on element compartmentation

There were no significant effects of applied treatment ($P<0.05$) on nutrient concentration in any soil variable, but significant effects of bracken control treatment were detected in the three litter pools (Table 3).

Bracken control treatment had a significant effect on the mass of uncompacted, compacted and total bracken litter. Cutting and asulam-treatment plots had significantly less bracken litter than untreated plots; plots with the combination treatments (asulam + cut; cut + asulam) were not significantly different from untreated plots (Table 3). Cutting twice per year reduced uncompacted and total bracken litter mass significantly compared to all other treatments, and cutting twice per year also produced the greatest reductions in compacted bracken litter, and these were significantly lower than for all other treatments except cutting once per year (Table 3). Treatment in most cases increased the mass of non-bracken vegetation relative to untreated plots but asulam + cut was an exception. Cutting twice per year resulted in the greatest increase (Table 3).

For chemical elements the effects of the bracken treatments varied for each element pool in terms of significance; C, N and Ca were significantly reduced by the cutting and asulam treatments in both bracken litter fractions, with Mg also significantly reduced in the uncompacted fraction (Table 3). Both N and Ca were significantly increased in the no-bracken litter. For the two bracken litter components the greatest amount of all elements was usually in the untreated plots or the plots with combined cutting/asulam treatment with the order: untreated > asulam + cut > cut + asulam, asulam, cut once per year > cut twice per year. In all cases the cut twice per year treatment was the lowest. The opposite results were found for the non-bracken vegetation, where the untreated vegetation had the lowest amounts of all nutrients, and there were greater amounts in the treated plots, increasing through to the cut 2 per year treatment (Table 3).

Bracken control treatments had a significant effect on the N, C, Mg, Ca and K stocks in the rhizome long-shoots, but not P (Table 4). The general treatment responses were in order untreated > combination treatments > asulam > cut once per year > cut twice per year. No significant reduction was found in the short-shoots or total rhizome biomass.

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Table 4
Effects of bracken control treatment on rhizome mass and element content in the long-shoots (all $g m^{-2}$) in the bracken control/moorland restoration experiment at Hordron Edge, Derbyshire after 7 years treatment

Compartment	Untreated	Asulam + cut	Cut + asulam	Asulam	Cut 1/yr	Cut 2/yr	LSD ($P<0.05$)	$F_{5,10}$	P
Long shoot biomass	**12.8**	**11.7**	**11.7**	**10.5**	**9.6**	**5.0**			
	7.151	6.999	6.994	6.823	6.854	6.100	0646	6.56	*
	a	a	a	a	a	b			
Short shoot biomass	**5.7**	**4.0**	**1.7**	**3.0**	**3.5**	**3.0**			
	6.297	4.855	4.515	4.841	5.729	5.196	2.199	1.80	—
Total biomass	**18.5**	**15.7**	**13.4**	**13.6**	**13.0**	**8.0**			
	7.521	7.266	7.136	7.047	7.162	6.570	0.914	2.33	—
Long shoots element content									
C	**5.6**	**5.0**	**5.0**	**4.4**	**4.0**	**2.1**			
	6.318a	6.157a	6.157a	5.973a	5.952a	5.259b	0.640	6.74	*
N	**214**	**171**	**110**	**138**	**96**	**60**			
	3.073a	2.801ab	2.423bc	2.568bc	2.249cd	1.795d	0.593	11.14	*
Mg	**244**	**176**	**220**	**137**	**215**	**7.8**			
	3.168a	2.884a	3.001a	2.575ab	2.964a	1.866b	0.654	10.34	*

Analysis was performed on transformed data ($\log_e + 1$, $n = 6$; $g m^{-2}$), and means significantly different from each other are denoted by different letters. Significance coded as: *$P<0.05$; **$P<0.01$. Arithmetic means are also presented in bold for interpretation and have been expressed as $Mg ha^{-1}$ for mass and C and $kg ha^{-1}$ for all other elements.

Table 5
Effects of bracken control treatment in the nutrient content (C = $Mg ha^{-1}$; rest = $kg ha^{-1}$) of two ecosystem pools at Hordron Edge, Derbyshire over 7 years

Variable	Element	Untreated	Asulam + cut	Cut + asulam	Asulam	Cut 1/yr	Cut 2/yr	$F_{1,10}$	Significance
(a) Total litter/vegetation	C	**17.4**	**14.9**	**11.4**	**11.5**	**9.5**	**7.9**		
		7.461	7.304	7.040	7.045	6.857	6.679	3.70	*
		a	a	abc	abc	bc	c		
	N	**713.0**	**533.0**	**374.1**	**382.3**	**306.8**	**282.8**		
		4.281	3.994	3.648	3.670	3.456	3.377	8.36	**
		a	ab	bc	bc	c	c		
	P	**138.8**	**140.1**	**125.4**	**124.6**	**100.7**	**62.2**		
		2.707	2.709	2.529	2.600	2.320	1.978	2.02	ns
	K	**892.8**	**849.7**	**661.9**	**806.8**	**849.6**	**339.2**		
		4.503	4.454	4.208	4.403	4.454	3.553	3.06	+
		a	a	ab	a	a	b		
	Ca	**263.5**	**144.3**	**119.4**	**119.3**	**192.7**	**89.5**		
		3.309	2.736	2.561	2.560	3.009	2.297	1.55	ns
	Mg	**272.4**	**206.2**	**219.1**	**151.3**	**211.3**	**74.6**		
		3.341	3.073	3.132	2.781	3.097	2.135	8.16	**
		a	ab	ab	b	ab	c		
(b) Soil	C	**81.8**	**86.5**	**77.7**	**82.1**	**80.3**	**74.4**		
		9.010	9.065	8.958	9.012	8.991	8.914	0.32	ns
	N	**3687.7**	**3577.7**	**3489.2**	**3793.5**	**3305.4**	**3247.4**		
		5.907	5.877	5.852	5.936	5.798	5.780	0.72	ns
	P	**582.6**	**433.4**	**476.7**	**524.6**	**592.8**	**652.0**		
		4.082	3.792	3.885	3.979	4.099	4.179	1.14	ns
	K	**603.1**	**5659.4**	**5452.3**	**5549.0**	**8103.6**	**5150.2**		
		6.401	6.337	6.299	6.317	6.696	6.242	1.37	ns
	Ca	**320.9**	**373.7**	**434.1**	**296.1**	**422.9**	**374.9**		
		3.437	3.594	3.748	3.354	3.721	3.597	1.22	ns
	Mg	**391.9**	**330.0**	**307.6**	**281.4**	**326.2**	**342.6**		
		3.642	3.466	3.393	3.301	3.454	3.504	0.81	ns

The pools were: (a) the total vegetation and litter which was directly targeted by treatment, and (b) the soil pool which would have been indirectly affected by treatment. Analysis was performed on transformed data ($\log_e + 1$, $n = 6$; $g m^{-2}$) and means significantly different from each other are denoted by different letters. Arithmetic means are also presented in bold for interpretation. Significance coded as: ns = $P>0.10$, + = $P<0.10$, * = $P<0.05$; ** = $P<0.01$.

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Table 6
Effects of bracken control treatments on litter turnover index (*K*) in the bracken control/moorland restoration experiment at Hordron Edge, Derbyshire after seven years treatment

Measure	Untreated	Asulam + cut	Cut + asulam	Asulam	Cut 1/yr	Cut 2/yr	$F_{5,10}$	Significance
K	**0.26**	**0.62**	**0.31**	**0.31**	**0.69**	**5.40**		$P<0.01$
	0.227a	0.477a	0.261a	0.256a	0.503a	1.725b	14.27	

Analysis was performed on transformed data ($\log_e + 1$, $n = 6$; $g\,m^{-2}$) and means significantly different from each other are denoted by different letters. Arithmetic means are also presented in bold for interpretation.

3.3. *Hypothesis 2: Bracken control influences element losses*

Bracken control reduced the element stocks in both (a) the litter/vegetation/rhizomes and (b) the soil pools relative to the untreated plots (Table 5), but variability was high. In the bracken litter/vegetation/rhizome pool, the fraction directly affected by treatment application a general trend was found for all elements in that they all were less than the untreated plots and the greatest reduction was found where cutting (especially twice per year) was applied. Significant effects were found for C, N, Mg and K, albeit only weakly significant for K; the effects for P and Ca were not significant, although they followed the general trend of the other elements (Table 5a). The data for elements in soil fraction also for the most part followed this general trend, although the effects were not significant ($P>0.10$, Table 5b). The soil in the treated plots and especially the cut plots had the lowest element content compared to untreated plots, P was an exception.

These results taken together, suggest that after 7 years, bracken treatment has reduced the stock of at least four elements in the vegetation, litter and rhizome pools. In addition, there is no evidence to support the hypotheses that for (a) uptake by developing vegetation counterbalances the amounts lost from the bracken rhizomes and litter, and (b) any overall loss from the litter-vegetation is not taken up by the soil; the results here suggest that the soil is also being affected by treatment but a longer time period will be needed for this to be measurable.

Assuming that at the start of the study that the treated plots were similar to the untreated controls the amount of nutrients lost from the litter/vegetation in the cut twice per year treatment would be $9.5\,Mg\,C\,ha^{-1}\,yr^{-1}$, $430\,kg\,N\,ha^{-1}\,yr^{-1}$, $554\,kg\,K\,ha^{-1}yr^{-1}$, $198\,kg\,Mg\,ha^{-1}\,yr^{-1}$, which is equivalent to 9.2%, 9.4%, 7.6% and 29% of the total pools for each element, respectively, in the untreated plots (Table 3). Calculating similar losses for the most commonly-used bracken control treatment in the UK ,asulam application on its own, gives values of $5.9\,Mg\,C\,ha^{-1}\,yr^{-1}$, $331\,kg\,N$
$ha^{-1}\,yr^{-1}$, $86\,kg\,K\,ha^{-1}\,yr^{-1}$, $121\,kg\,Mg\,ha^{-1}\,yr^{-1}$, equivalent to 5.7%, 7.3%, 1.1% and 18% on a percentage basis; but here a significant reduction was only found for N and Mg.

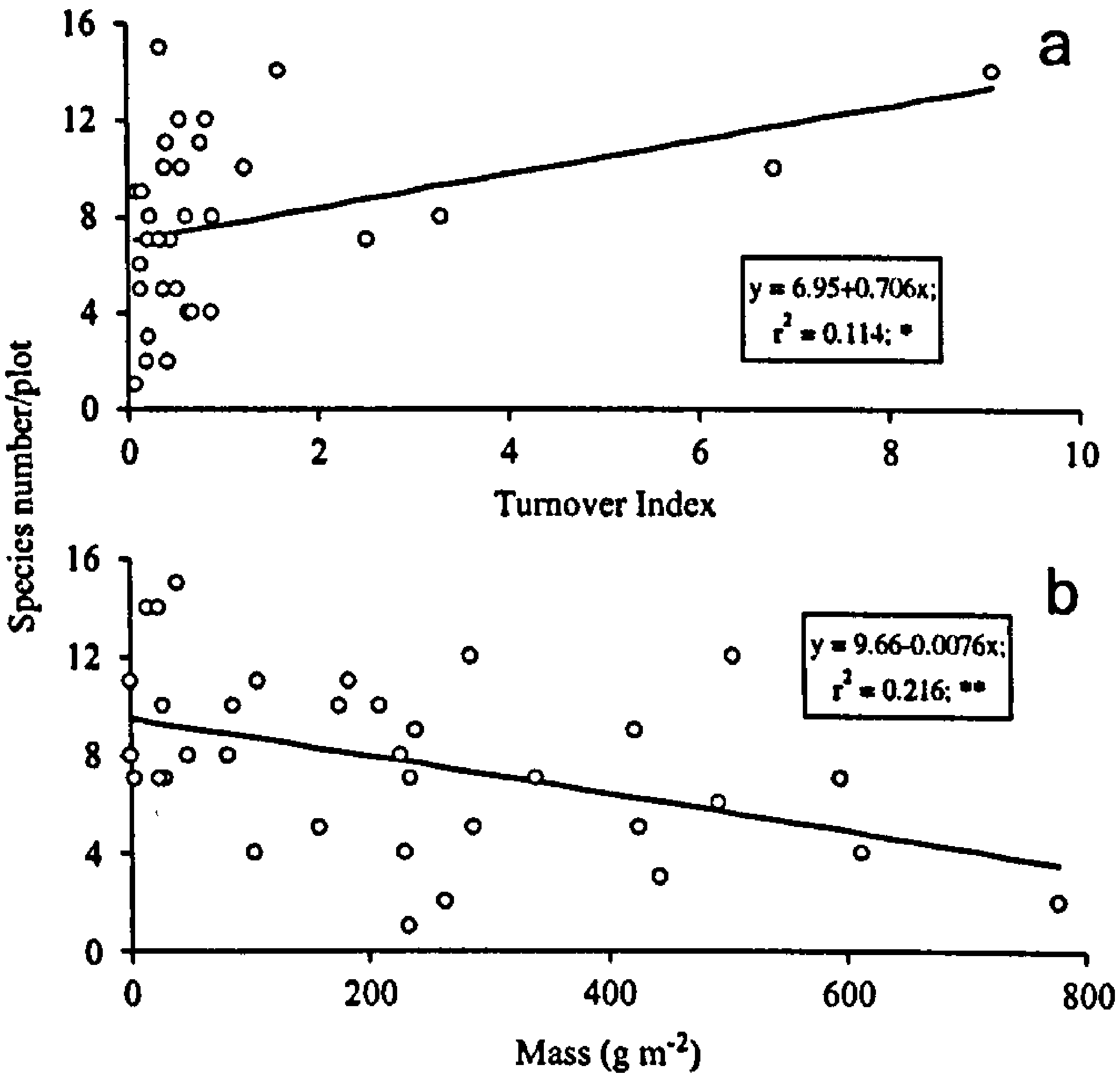

Fig. 1. Relationship between species number and (a) bracken litter turnover, and (b) uncompacted bracken litter mass,; the linear regression and variation accounted for by the regression (r^2) and significance are shown: $^*P<0.05$ and $^{**}P<0.01$.

3.4. *Hypothesis 3: Bracken control accelerates litter turnover*

Cutting, especially twice/yr was the only treatment to significantly increase bracken litter turnover ($P<0.001$) being between three to twenty times faster than all other treatments (Table 6). Litter turnover also showed a significant positive relationship ($P<0.05$) with species richness (Fig. 1a).

3.5. *Hypothesis 4: Bracken control accelerates the invasion of species of grass/moor communities*

No significant differences were found between bracken control main-plot treatments and their interaction with the grazing sub-treatments on total species number/plot or Shannon–Weiner index. However, grazing significantly increased species richness compared to the ungrazed treatment: 9.3 versus 6.3 species/plot, respectively (LSD

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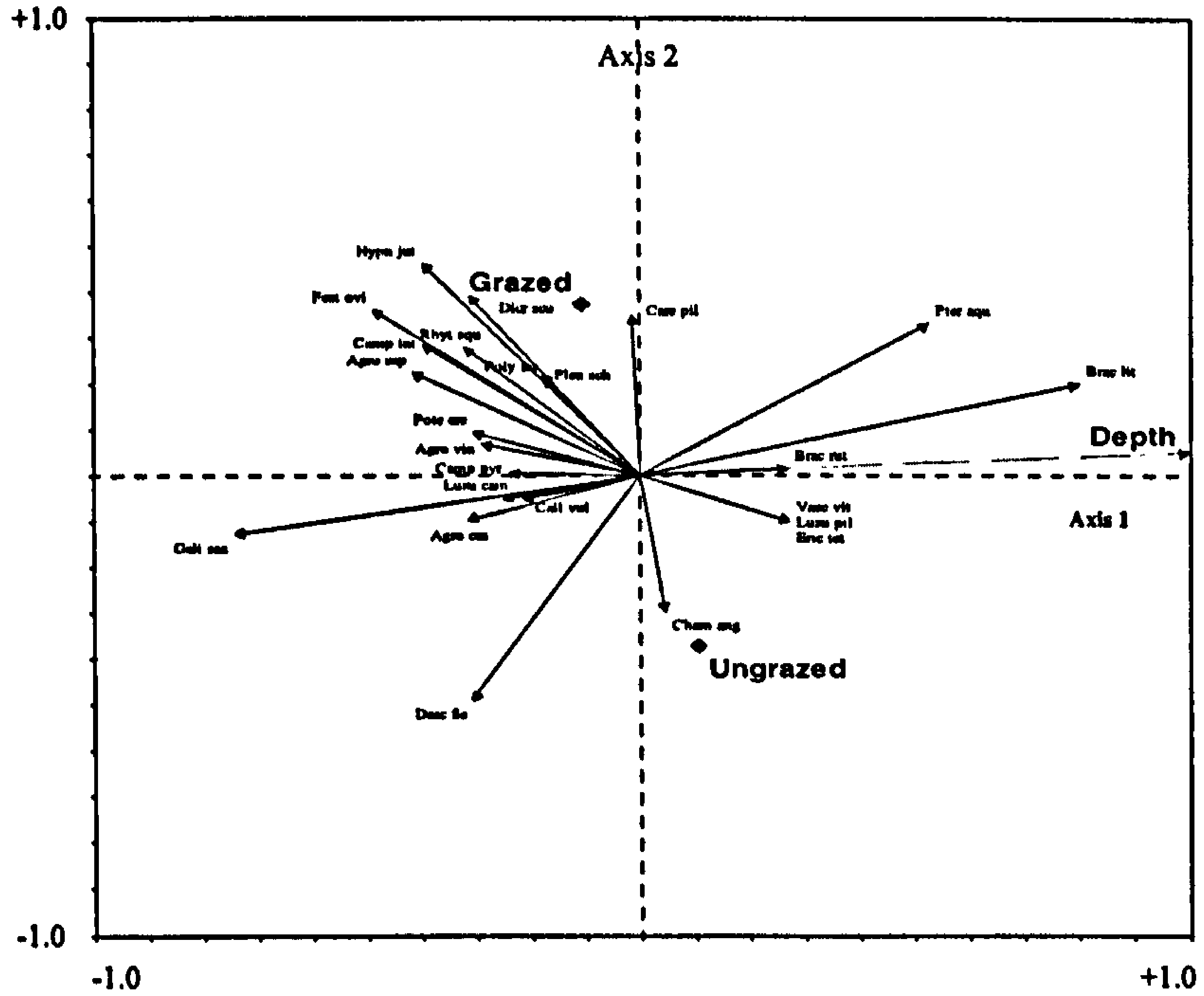

Fig. 2. RDA biplot of the most abundant species and explanatory variables from: (a) Analysis 1, using the 2000 floristic data with the environmental variables found significant after the Forward Selection procedure. Codes for species: Agro cap = *Agrostis capillaris*; Agro cas = *Agrostis castellana*; Agro vin = *Agrostis vinealis*; Brac lit = bracken litter; Brac rut = *Brachythecium rutabulum*; Call vul = *Calluna vulgaris*; Camp int = *Campylopus introflexus*; Camp pyr = *Campylopus pyriformis*; Care pil = *Carex pilulifera*; Cham ang = *Chamerion angustifolium*; Desc fle = *Deschampsia flexuosa*; Dicr sco = *Dicranum scoparium*; Eric tet = *Erica tetralix*; Fest ovi = *Festuca ovina* agg; Gali sax = *Galium saxatile*; Holc mol = *Holcus mollis*; Hypn jut = *Hypnum jutlandicum*; Loph bid = *Lophocolea bidentata*; Luzu cam = *Luzula campestris*; Luzu pil = *Luzula pilosa*; Nard str = *Nardus stricta*; Pleu sch = *Pleurozium schreberi*; Poly for = *Polytrichum formosum*; Pote ere = *Potentilla erecta*; Pter aqu = *Pteridium aquilinum*; Rhyt squ = *Rhytidiadelphus squarrosus*; Vacc myr = *Vaccinium myrtillus*; Vacc vit = *Vaccinium vitis-idaea*. Grazing treatments (nominal variables) are shown as centroids and bracken litter depth as a vector.

($P<0.05$) = 2.38, $F_{1,12} = 7.22$; $P<0.05$) and Shannon–Weiner index 2.05 versus 1.37, respectively (LSD ($P<0.05$) = 0.459, $F_{1,12} = 10.36$, $P<0.01$). Both species number (Fig. 1b) and Shannon–Weiner index showed a significant negative relationship with all bracken litter biomass variables ($P<0.01$). Non-bracken biomass showed no significant relationship with any diversity measure.

The multivariate analysis produced a significant final model (first axis, $F = 9.031$; model, $F = 6.731$, both $P<0.001$) and the eigenvalues (λ) for the first four axes were $\lambda_1 = 0.215$, $\lambda_2 = 0.075$, $\lambda_3 = 0.194$ and $\lambda_4 = 0.097$. Both litter depth and the grazing treatment were selected by Forward Selection as environmental variables in this model. The biplot (Fig. 2), revealed a diversity gradient along axis 1, corresponding positively with increasing bracken litter depth. As litter depth decreased, there was a transition from a bracken-dominated community at the positive end of axis 1 to an acid heath/grassland at the negative end. Grazing was extremely influential on axis 2, with grazed plots having a greater positive score and ungrazed ones having a negative one. Where bracken litter mass was low and sheep grazing occurred, there was a relatively diverse mixture of grasses, dicotyledons and bryophytes typical of an acid heath/grassland community, whereas ungrazed plots were dominated by *D. flexuosa*. Where bracken litter mass was high, grazing had a lesser impact, but on ungrazed plots typical heath species (*Erica tetralix* and *Vaccinium vitis-idaea*) were found, possibly because these species were grazed in preference to the less palatable bracken where sheep were present.

4. Discussion

Bracken is an important mid-successional invasive species that causes problems for conservation managers (Pakeman and Marrs, 1992). Accordingly bracken control and the subsequent restoration of early-successional communities is a high priority, especially where the restored communities feature within UK Biodiversity Action Plans or Agri-environment schemes (Anon, 1995). Whilst it has been appreciated for some time that the deep litter layer produced by bracken impedes re-establishment of many species (Lowday and Marrs, 1992), there have been no studies of the impact of bracken control strategies on litter dynamics and element pools. This is the first study to quantify element stocks within a bracken-dominated stand in combination with bracken control, and to test the

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relationship between management treatments, litter turnover and plant biodiversity.

4.1. *Quantification of the nutrient stock in dense bracken stands*

The stock of C and mineral elements in the dense bracken was considerable, and of the same order of magnitude as other upland ecosystems in the UK (Perkins, 1978; Wilson and Puri, 2001; Prentice, 2001). Interestingly, bracken appears to be able to sequester certain elements (P, Ca, Mg) in relatively large amounts in its rhizomes, and this may be an important element conservation mechanism in these nutrient-poor systems (Gimingham, 1992).

If data for total element stocks for dense bracken in Table 2 were extrapolated to the countrywide scale using the estimate of 4800 km^2 of dense bracken in the open within the UK (Pakeman et al., 1995), this biotope could contribute 0.5 Gt C to the UK Kyoto account in either the "agricultural" or "open" category (http://unfccc.int/resource/docs/convkp/kpeng.pdf). This value assumes that the data presented here were typical, or at least close to, the value of the countrywide mean; this remains to be tested. A similar calculation for the UK for mineral elements indicates stocks of $N = 21.8$, $P = 3.6$, $K = 34.7$, $Ca = 2.9$, $Mg = 3.3$ (all Mt).

These predicted values are subject to considerable uncertainty, first the estimates for element stock have been derived from just the one site sampled here, and the UK estimates for dense bracken cover have very large standard errors (Pakeman et al., 1995). Moreover, the amount of dense bracken in subject to considerable flux over quite short time intervals (Pakeman et al., 1995), positively as a result of encroachment from linear features, change from sparse stands to dense bracken and deforestation, and negatively through bracken control measure and afforestation (Marrs and Watt, 2006). Thus, at the countrywide-scale the element stocks in this biotope are potentially large, are important for nutrient conservation in these upland, nutrient-poor areas, and as through management changes could be a potential source of element inputs to air and water. The data presented here and the inferences to the countrywide scale can, of course, only be considered as preliminary estimates, but they do point out the potential importance of this biotope and management.

4.2. *Effects of bracken control treatments on ecosystem pools and fluxes, litter turnover and plant species biodiversity*

The bracken control treatments influenced the size and element content of litter pools, litter turnover and diversity measures. The most successful treatment overall was the cut twice per year treatment, and this result was unsurprising as it has emerged the most successful treatment in a range of single- and multi-site studies (Lowday and Marrs, 1992; Marrs and Lowday, 1992; Marrs et al., 1998a–c; Le Duc et al., 2000, 2003, 2007). This technique was, however, the most intensive treatment applied, and is successful because it causes a greater depletion of the rhizome carbohydrate reserves compared to cutting once per year. Asulam application attacks the developing frond buds on the rhizome and a single application never achieves a 100% kill do there is continued recovery. Cutting is preferable to asulam spraying on their own because it also breaks up the litter layer and assists in species colonisation (Lowday and Marrs, 1992).

Here, we tested four hypotheses relating bracken treatment to nutrient pools, fluxes and plant species diversity.

4.2.1. *Hypothesis 1: Successful bracken control changes the distribution of elements between bracken, litter and soil pools*

There was clear evidence to support the hypothesis that bracken control treatment reduced the size and element content of bracken pools (litter, rhizomes) and increased the nutrient content in the developing vegetation pool, but there was no effect on any soil parameter measured. This implies that there is at least some transfer of nutrients from

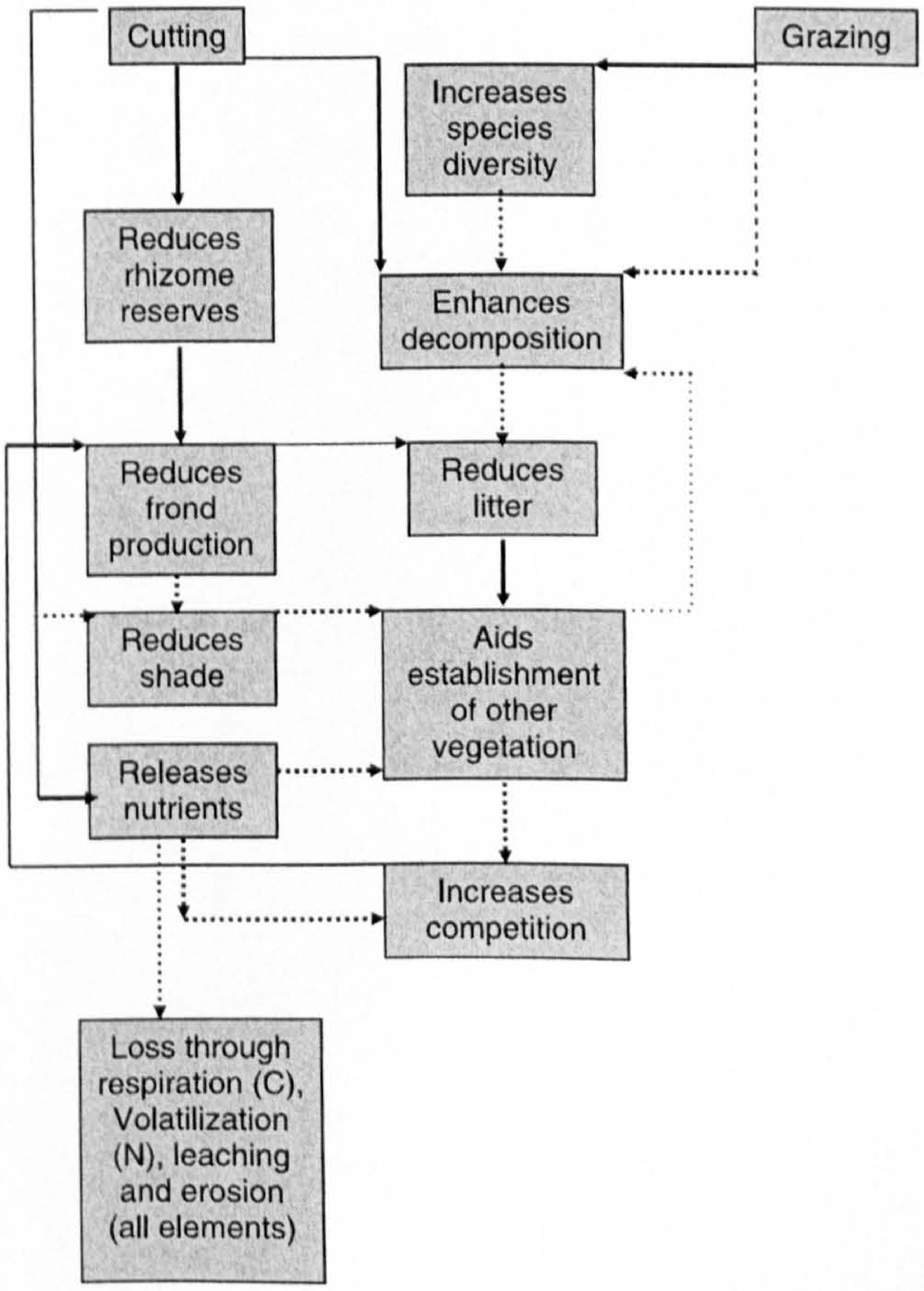

Fig. 3. Potential mechanisms through which cutting and grazing can influence bracken litter abundance: mechanisms for which there is evidence in the results of this study are represented by solid lines; potential relationships are noted with a dotted line.

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bracken to developing vegetation during the control process. The complexity of the potential mechanisms whereby cutting and grazing can affect bracken litter abundance and the establishment of other species is summarised in Fig. 3. Cutting *Pteridium*, for example, reduces rhizome reserves and frond production over several seasons and this reduces shade from fronds and releases nutrients, especially from the declining rhizome reserves. Galtress (2001) has also demonstrated a reduction in cation concentrations as the new uncompacted litter moves into the older compacted form, which suggest there is some leaching losses during senescence. These leachates will be less likely to be taken up by the rhizomes, as they too have been reduced, so these leachates must either be captured by another pool (developing vegetation, mineral matrix) or they too will be lost to the system.

4.2.2. Hypothesis 2: Bracken treatment influences element fluxes

For the most successful treatment (cutting twice per year), relatively large amounts of mineral elements were released from bracken litter. The data were highly variable and there were significant results for three of the six elements studied (C, N and Mg), with a weak significance for K. In absolute terms, bracken management released more C and N but in proportionate terms a very large amount of Mg was released, presumably through losses from the rhizomes. Whilst we have no knowledge of where these elements go, they are no longer present in the surface soil or vegetation, indeed our estimates of losses based solely on the plant-litter fraction are probably underestimates as the soil fraction show similar, albeit non-significant trends. The evidence presented here, however, supports the hypothesis that bracken control can lead to reductions in elements in the surface litter-plant layer, and there is no evidence to support the hypothesis that these losses are captured in the soil.

For C, losses are presumably to the atmosphere, although losses might also have occurred as Dissolved Organic C, which is predicted to rise under global warming (Freeman et al., 2004), and for other elements the pathways would included leaching, erosion loss of particulates, and for N, volatilisation (Fig. 3). It is also possible that some of the elements may not have been totally lost from the system, being re-sequestered further down the soil profile. However, these elements are no longer in the surface rooting zone and hence are unavailable in the short-term within this ecosystem where most plants are shallow-rooted (Grime et al., 1988).

If these elements are lost through leaching or particulate erosion, then they may have impacts elsewhere within the catchment, and potentially impact on water quality, which is subject to legislation under the WFD. Rainfall in the area around the study site is relatively high (1998–2003 mean = 1400 mm (annual range 1120–1850 mm; from nearest weather station; Sheffield, Latitude, Longitude; 3°15.5′N, 1°54.2′W), and such losses would be expected to be high. However further quantification is needed at the catchment scale to quantify this. Impacts will differ between elements; N addition to waterways would be viewed as negative (Moss, 1998), but Mg addition might be viewed as positive as they might help reduce the effects of acidification.

It is not possible to extrapolate the results for cutting to provide national statistics because cutting is not commonly quantified. However, a rough estimate can be made for asulam spraying as detailed records are kept of aerially applied herbicides in the UK (e.g. Wardman and Thomas, 2003). Between 1980 and 2002, asulam was applied to bracken over a total area of 1057 km^2 (0.45%) of the land area (Pakeman et al., 2005). This value is a crude estimate of land sprayed, as it does not include land sprayed using ground-based sprayers, and some applications may be repeat sprayings. However, if this figure is accepted as a notional estimate of treated land then the potential loss of mineral elements from the surface plant-soil layer of these systems over a 7-year period after spraying would be (using the data in Section 3.3); $C = 6236$, $N = 350$, $K = 91$, and $Mg = 128\,\text{t ha}^{-1}$.

The relative importance of these losses needs to be evaluated, but could lead to soil degradation and impacts elsewhere. There are clearly many assumptions made in these calculations and further work is needed to validate this extrapolation, quantify the pools and fluxes in other sites and reduce the variability of estimates detected in this present study. Here the sample size and within plot replication was at a statistically valid level, but would have benefited from greater numbers of sub-sampling to improve precision. This was not possible here because it was not possible to sacrifice larger areas for destructive sampling through the need to maintain experimental integrity for sampling vegetation, the raison d'être of this study.

It would also be useful to have comparative data on nutrient contents of a range of ecosystems in order to assess the relative contribution that fluxes from managed bracken-invaded stands make to the national C and nutrient accounts. Such information is lacking at present.

4.2.3. Hypothesis 3: Bracken control accelerates litter turnover

There was partial support for the hypothesis that bracken control accelerates litter turnover, in that one treatment (cutting twice per year) accelerated litter turnover. However, the litter turnover index used here is a very crude measure (Swift et al., 1979) as it does not consider all aspects of litter transfers. One obvious input which has been ignored is the litter derived from fronds during the growing season. This was ignored for two reasons, first these inputs are likely to be small in relation to end-of-year inputs, and intensive within-season sampling was not possible within the confines of this experiment. It is also interesting that Galtress (2001) found no evidence of resource change in the bracken litter pools as a result of the

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control treatments suggesting that litter comminution (Swift et al., 1979) through the passage and operation of machinery (Pakeman et al., 2000b) is the over-riding factor controlling bracken litter decomposition at this site rather than resource quality, which has been shown as an important controlling variable elsewhere (Anderson and Hetherington, 1999; Hector et al., 2000). This conclusion needs to be tested further experimentally.

4.2.4. Hypothesis 4: Bracken control accelerates the invasion of species of grass/moor communities

There is clear evidence that bracken control treatment increased plant species diversity, and this was correlation significantly with litter turnover index. The multivariate analysis also indicated a significant relationship with both litter depth and the grazing treatments. These results indicate that species diversity is increased at low litter depth, but the composition is influenced by grazing. A mixed grass–heath community with *C. vulgaris* is found where light grazing was present but a *D. flexuosa*-dominated grassland where grazing was prevented. This response to grazing is consistent with Rawes (1981).

We hypothesise that as the grass-moorland communities develop, increased competition will have a negative feedback on frond productivity (Marrs et al., 1998a) Grazing interacts with this process, through, for example differential species selection, increased nutrient cycling (Marrs et al., 1980), and increased gap creation for colonisation (Wardle et al., 2002). This hypothesis remains to be tested in the ongoing, longer-term studies of the vegetation being carried out on this experiment.

4.3. Policy contexts and conflicts

Our results show that land managers and their advisors face a dilemma as they attempt to develop policies of sustainability. Removal of bracken to conserve biodiversity, for amenity and other purposes, will lead to the loss of both C and mineral elements as an unintended consequence. On the one hand conservation management is delivering appropriate outputs with respect to conservation of important national biotopes. On moorland this action will help conserve species which may either have economic (e.g. Red grouse, *Lagopus lagopus*) or have conservation value (e.g. Hen Harrier, *Circus cyaneus*; Golden Plover, *Pluvialis apricaria*). Indeed, as the moorland target is a biotope of infertile soils (Gimingham, 1992) any reduction in nutrient status would be viewed as positive. However, care must be taken in data interpretation, as there is the potential paradox; viz. an overall reduction in total nutrient content but an increase in available nutrient supply as has been shown in Dutch heathlands where topsoil has been stripped (Dorland et al., 2003). We did not measure available nutrients in our study and it is quite possible that at least for part of the period, there was an increased nutrient supply even though the overall total was reducing.

On the other hand, successful conservation action could produce a net release of elements; in the most successful treatment in this study we detected a potential release of $950\,\mathrm{g\,C\,m^{-2}}$ over 7 years or $1.4\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$. This must be viewed in context of the C sink in a north Pennine catchment estimated to be $15.4\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Worrall et al., 2003), and the predicted reduction from 170 predicted to reduce to $70\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ within 50 years in German forests as a result of ageing (Karjalainen et al., 2002). Moreover, other elements were available for leaching and could infringe requirements under the WFD. Policy makers, therefore, face a dilemma in the case bracken management, and possibly in the management of other mid-successional biotopes. The action required to meet biodiversity conservation targets can conflict with the objectives of the Kyoto Protocol, and possibly also the WFD.

This dilemma has not yet been widely recognised or addressed. We do not know what all of the issues are yet, but in order to resolve the conflicting environmental goals of conservation management the first step must be to identify possible issues, quantify the rates of change, and develop models to help resolve conflicts. The work reported here is a first step in this process, and we suggest that the bracken–*Calluna* system is a useful model system (Vitousek, 2004) to tackle these issues.

4.4. Conclusions

We have shown here a potential dilemma between controlling a mid-successional invasive species for conservation policy objectives to increase biodiversity, and the potentially negative effects of increasing environmental costs in terms of carbon accounting, polluting aquatic systems, and long-term site degradation through nutrient loss. We accept that this work requires verification in other situations but suggest that the need to balance competing conservation goals will be a major issue in the future.

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References

Allen, S.E. (Ed.), 1989. Chemical Analysis of Ecological Materials. Blackwells, Oxford.

Anon, 1995. Biodiversity UK Steering Group Report, vol. I. Action Plans. HMSO, London.

Anderson, J.M., Hetherington, S.L., 1999. Temperature, nitrogen availability and mixture effects on the decomposition of heather (*Calluna vulgaris* (L.) Hull) and bracken (*Pteridium aquilinum* (L.) Kuhn) litters. Functional Ecology 13 (Suppl. 1), 116–124.

Beaumont, G.P., 1986. Probability and Random Variables. Ellis Horwood Ltd, Chichester.

Bormann, F.H., Likens, G.E., 1979. Pattern and Processes in a Forested Ecosystem. Springer, New York.

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Cabin, R.J., Mitchell, R.J., 2000. To Bonferroni or not to Bonferroni: when and how are the questions. Bulletin of the Ecological Society of America 81, 246–248.

Cannell, M.G.R., Milne, R., Hargreaves, K.J., Brown, T.A.W., Cruickshank, M.M., Bradely, R.I., Spencer, T., Hope, D., Billiett, M.F., Adger, W.N., Subak, S., 1999. National inventories of terrestrial carbon sources and sinks: the UK experience. Climate Change 42, 505–530.

Constanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskins, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and capital. Nature 387, 255–260.

Corley, M.F.V., Hill, M.O., 1981. Distribution of Bryophytes in the British Isles. Bryological Society of the British Isles, Cardiff.

Dorland, E., Bobbink, R., Messelink, J.H., Verhoeven, J.T.A., 2003. Soil ammonium accumulation after sod cutting hampers the restoration of degraded wet heathlands. Journal of Applied Ecology 40, 804–814.

Freeman, C., Fenner, N., Ostle, N.J., Kang, H., Dowrick, D.J., Reynolds, B., Lock, M.A., Sleep, D., Hughes, S., Hudson, J., 2004. Export of dissolved organic carbon from peatlands under elevated carbon dioxide levels. Nature 430, 195–198.

Galtress, K., 2001. The effects of bracken [*Pteridium aquilinum* (L.) Kuhn] control treatments on bracken litter dynamics and the potential consequences for species diversity and composition. BSc (Hons) Thesis, University of Liverpool, Liverpool.

Ghorbani, J., McAllister, H.A., Pakeman, R.J., Marrs, R.H., Le Duc, M.G., 2006. Effects of the litter layer of Pteridium aquilinum on seed dynamics under experimental restoration. Applied Vegetation Science 9, 127–136.

Gimingham, C.H., 1992. The Lowland Heathland Management Handbook. English Nature, Peterborough.

Grace, J., 2004. Understanding and managing the global carbon cycle. Journal of Applied Ecology 92, 189–202.

Grime, J.P., Hodgson, J.G., Hunt, R., 1988. Comparative Plant Ecology: a Functional Approach to Common British Species. Unwin Hyman, London, UK.

Hector, A., Beale, A.J., Minns, A., Otway, S.J., Lawton, J.H., 2000. Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. Oikos 90, 357–371.

Karjalainen, T., Pussinen, A.S., Liski, J., Nabuurs, G.J., Erhard, M., Eggers, T., Sonntag, M., Mohren, G.M.J., 2002. An approach towards an estimate of the impact of forest management and climate change on the European forest sector carbon budget: Germany as a case study. Forest Ecology and Management 162, 97–103.

Le Duc, M.G., Pakeman, R.J., Putwain, P.D., Marrs, R.H., 2000. The variable responses of bracken fronds to control treatments in Great Britain. Annals of Botany 85B, 17–29.

Le Duc, M.G., Pakeman, R.J., Marrs, R.H., 2003. Changes in the bracken rhizome system subjected to long-term experimental treatment. Journal of Applied Ecology 40, 508–522.

Le Duc, M.G., Pakeman, R., Marrs, R., 2007. A restoration experiment on moorland infested by *Pteridium aquilinum*: plant species responses. Agro-Ecosystems & Environment 119, 53–59.

Lowday, J.E., Marrs, R.H., 1992. Control of bracken and the restoration of heathland. III. Bracken litter disturbance and heathland restoration. Journal of Applied Ecology 29, 212–217.

MAFF, 1993. Environment matters. Environmentally Sensitive Areas. MAFF, London.

Marrs, R.H., 1988. Vegetation change on lowland heaths and its relevance for conservation management. Journal of Environmental Management 27, 127–149.

Marrs, R.H., 1993. Soil fertility and nature conservation in Europe: theoretical considerations and practical management solutions. Advances in Ecological Research 24, 241–300.

Marrs, R.H., Lowday, J.E., 1992. Control of bracken and the restoration of heathland. II. Regeneration of the heathland community. Journal of Applied Ecology 29, 204–211.

Marrs, R.H., the late Watt, A.S., 2006. Biological flora of *Pteridium aquilinum*. Journal of Ecology 94, 1272–1321.

Marrs, R.H., Granlund, I.H., Bradshaw, A.D., 1980. Ecosystem development on reclaimed china clay wastes. IV. Recycling of above-ground plant nutrients. Journal of Applied Ecology 17, 803–813.

Marrs, R.H., Johnson, S.W., Le Duc, M.G., 1998a. Control of bracken and restoration of heathland. VI. The response of bracken fronds to 18 years of continued bracken control or 6 years of control followed by recovery. Journal of Applied Ecology 35, 479–490.

Marrs, R.H., Johnson, S.W., Le Duc, M.G., 1998b. Control of bracken and restoration of heathland. VII. Effects of bracken control treatments on the rhizome and its relationship with frond performance. Journal of Applied Ecology 35, 748–757.

Marrs, R.H., Johnson, S.W., Le Duc, M.G., 1998c. Control of bracken and restoration of heathland. VIII. The regeneration of the heathland community after 18 years of continued bracken control or six years of control followed by recovery. Journal of Applied Ecology 35, 857–870.

Moss, B., 1998. Ecology of Fresh Waters: Man and Medium, Past to Future, third ed. Blackwells, Oxford.

Moss, B., Stephen, D., Alvarez, C., Becares, E., Van de Bund, W., Collings, S.E., Van Don, E., De Eyto, E., Feldmann, T., Fernandez-Alaez, C., Fernandez-Alaez, M., Franken, R.J.M., Garcia-Criado, F., Gross, E.M., Gyllstrom, M., Hansson, L.A., Irvine, K., Jarvalt, A., Jensen, J.P., Jeppesen, E., Kairesalo, T., Kornijow, R., Krause, T., Kunnap, H., Laas, A., Lille, E., Lorens, B., Luup, H., Miracle, M.R., Noges, P., Noges, T., Nykanen, M., Ott, I., Peczula, W., Peeters, E.T.H.M., Phillips, G., Romo, S., Russell, V., Salujoe, J., Scheffer, M., Siewertsen, K., Smal, H., Tesch, C., Timm, H., Tuvikene, L., Tonno, I., Virro, T., Vicente, E., Wilson, D., 2003. The determination of ecological status in shallow lakes—a tested system (ECOFRAME) for implementation of the European Water Framework Directive. Aquatic Conservation-Marine and Freshwater Ecosystems 13, 507–549.

Odum, E.P., 1969. Strategy of ecosystem development. Science 164, 262–270.

Oinonen, E., 1967. The correlation between the size of Finnish bracken (*Pteridium aquilinum* (L.) Kuhn) clones and certain periods of site history. Acta Forestalia Fennica 83, 1–51.

Olsen, J.S., Watts, J.A., Allison, L.J., 1985. Carbon in live vegetation of major world ecosystems. Report to the US Department of Energy, Contract No. W-7405-eng-26. Oak Ridge National Laboratory Publication ORNL-5862, Oak Ridge, Tennessee.

Pakeman, R.J., Marrs, R.H., 1992. The conservation value of bracken (*Pteridium aquilinum* (L.) Kuhn) dominated communities in the UK, and an assessment of the ecological impact of bracken expansion or its removal. Biological Conservation 62, 101–114.

Pakeman, R.J., Marrs, R.H., Howard, D.C., Barr, C.J., Fuller, R.M., 1995. The bracken problem in Great Britain; its present extent and future changes. Applied Geography 16, 65–86.

Pakeman, R.J., Le Duc, M.G., Marrs, R.H., 2000a. Bracken distribution in Great Britain: strategies for its control and the sustainable management of marginal land. Annals of Botany 85B, 37–46.

Pakeman, R.J., Thwaites, R.H., Le Duc, M.G., Marrs, R.H., 2000b. Vegetation re-establishment on land previously subject to control of *Pteridium aquilinum* by herbicide. Applied Vegetation Science 3, 95–104.

Pakeman, R.J., Small, J.L., Le Duc, M.G., Marrs, R.H., 2005. Recovery of moorland vegetation after aerial spraying of bracken (*Pteridium aquilinum* (L.) Kuhn) with asulam. Restoration Ecology 13, 718–724.

Perkins, D.F., 1978. The distribution and transfer of energy and nutrients in the *Agrosto-Festuca* grassland ecosystem. In: Heal, O.W., Perkins, D.F. (Eds.), Production Ecology of British Moors and Montane Grasslands. Springer, Berlin, pp. 375–395.

Prentice, I.C. (Ed.), 2001. The carbon cycle and atmospheric carbon dioxide. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P. J., Xiaosu, D. (Eds.), Climate Change 2001: The

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Scientific Basis, Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, pp. 183–237.

Rodwell, J.S., 1991. British Plant Communities: Mires and heaths. Cambridge University Press, Cambridge.

SAS, 1989. SAS/STAT User's Guide Version 6, fourth ed., vols. 1 and 2. SAS Institute, Cary, NC.

Sokal, R.R., Rohlf, F.J., 1995. Biometry, third ed. Freemans, New York.

Stace, C.A., 1997. New Flora of the British Isles, second ed. Cambridge University Press, Cambridge.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. Blackwells, Oxford.

ter Braak, C.J.F., Šmilauer, P., 1998. CANOCO 4 Reference Manual and User's Guide to Canoco for Windows. Micro-computer Power, New York.

Vitousek, P., 2004. Nutrient Cycling and Limitation: Hawai'i as a Model System. Princeton University Press, Princeton.

Wardle, D.A., Bonner, K.I., Barker, G.M., 2002. Linkages between plant litter decomposition, litter quality and vegetation responses to herbivores. Functional Ecology 16, 585–595.

Wardman, O.L., Thomas, M.R., 2003. Aerial applications, Great Britain 2002. Pesticide Usage Survey Report 186, Central Science Laboratory, York.

Watson, R. (Ed.), 2001. Climate Change 2001: Synthesis Report. Cambridge University Press, Cambridge.

Watt, A.S., 1947. Pattern and process in the plant community. Journal of Ecology 35, 1–22.

Watt, A.S., 1955. Bracken versus heather: a study in plant sociology. Journal of Ecology 43, 490–506.

Wilson, B., Puri, G., 2001. A comparison of pinewood and moorland soils in the Abernethy Forest Reserve, Scotland. Global Ecology and Biogeography 10, 291–303.

Worrall, F., Reed, M., Warburton, J., Burt, T., 2003. Carbon budgets for a British upland peat catchment. Science of the Total Environment 312, 133–146.

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Vegetation management

Bracken control: a multi-site assessment of effectiveness

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Summary

Six experiments were set up at four different regional locations in the UK on acid grassland and heathland sites infested with *Pteridium aquilinum.* Six bracken control treatments were applied to all sites in combination with site-specific vegetation restoration treatments. Bracken response variables (*P. aquilinum* cover, frond length, frond density) were monitored in August between 1993 and 2003. Repeated-measures ANOVAs with polynomial contrasts found significant between- and within-site spatial variation. Treatment with the selective herbicide Asulam resulted in a rapid reduction in frond performance followed by a continued recovery taking approximately 10 years to return to untreated values. Cutting treatments had a slower impact at the start but an increasing one over time, especially cutting twice per year. Restoration treatments had a limited impact; the only significant effect was grass seeding on frond length at Sourhope.

Keywords: *Pteridium aquilinum,* heathland, acid grassland, herbicide, asulam, cutting

Introduction

There is an increasing need for applied ecologists to be able to assist in the development of national weed control strategies to help implement agri-environments schemes (MAFF, 1993: 1996) or deliver Biodiversity Action Plans (Anon., 1995). Advice to policy-makers needs to be cost-effective and must be deliverable in a wide range of situations which provides a broad coverage of the likely scenarios where weeds need to be controlled.

Restoration management often involves a combination of weed control treatments coupled with specific treatments to restore vegetation, and in many situations the weed control phase produces mixed results (Le Duc *et al.*, 2000). A good example of such a problem is *Pteridium aquilinum* (nomenclature follows Stace, 1997) control in the UK, where the policy objective is to reduce the *P. aquilinum* infestation and restore a vegetation type with a greater conservation value (Pakeman & Marrs, 1992). *P. aquilinum* is a serious invasive weed of upland and marginal land (Pakeman & Marrs, 1992). *P. aquilinum* is a long-lived robust clonal species (Le Duc *et al.*, 2003) that produces a dense litter layer (Frankland, 1976), which competes effectively with heathland and grassland species, at best reducing their cover but in some cases eliminating them leaving a very depauperate flora with depleted seed banks (Pakeman & Marrs, 1992; Pakeman & Hay, 1996).

The multi-site study

One of the major issues highlighted in *P. aquilinum* control is the high variability in success rates (Le Duc *et al.*, 2000, 2003). In order to investigate this problem and develop a national policy a multi-site experimental study was set up to ensure that results apply to: (a) a broad geographical coverage, and (b) a reasonable coverage of the types of restoration problem likely to be encountered.

Here we summarize the results of this multi-site study. Six experiments were set up at four regional locations, and within each experiment the efficacy of six *P. aquilinum* control treatments was tested in a range of contrasting ecological situations. These six *P. aquilinum* control treatments were combined with site-specific treatments designed to restore appropriate heathland or grassland vegetation at the local scale.

Our study started in 1993 or 1994 and has been monitored twice per year for 9 or 10 years. The study has produced a voluminous dataset (Le Duc *et al.*, in press) and here we present a small subset of the results on *P. aquilinum* performance along with an overall summary. We tested 3 main hypotheses:

(1) Does geographical location (between- and within-sites) affect the response of *P. aquilinum* to control treatments through time?
(2) Are the *P. aquilinum* control treatments successful at all sites, and if so which ones?
(3) Do the treatments applied at the individual site level to restore vegetation influence the performance of *P. aquilinum* through time?

Methods

Experimental sites

Six experiments were set up at four different regional locations in the UK; Cannock Chase (2°2'W, 52°46'N) in the English midlands; Hordron Edge (1°41'W, 53°23'N), North Peak Environmentally Sensitive Area in the Peak District National Park, northern England; the Carneddau Estate (3°58'W, 53°13'N) in Snowdonia National Park, North Wales; and Sourhope (2°14'W, 55°28'N) in the Cheviot Hills, on the England/Scotland border. Sites are referred to hereafter as Cannock, Carneddau, Peak and Sourhope. The methods have been published elsewhere (Le Duc *et al.*, 2000) so only a brief summary is given here.

The six sites cover a range of different physical and vegetation characteristics leading to differing amounts of litter abundance, rhizome mass and above ground *P. aquilinum* cover. The untreated control plots give an estimate for initial conditions at the six sites. The acid grassland sites, Sourhope 2 and Carneddau, were most species-rich sites with the Cannock sites having the lowest number of species. In August the lowest *P. aquilinum* cover was recorded at Sourhope 2 (41 %) and Carneddau (48%) the most species-rich sites, the species-poor Cannock sites had the highest *P. aquilinum* cover. Despite having the highest bracken litter cover (84%) and the deepest litter (18 cm) Peak had the smallest rhizome mass (Le Duc *et al.*, 2003).

Experimental design

A split-split-plot design was used throughout. Within each experiment each block (70 × 40 m) was divided into six main plots (10 × 40 m) which received one of six bracken control treatments. These were separated by 2 m untreated buffers. Each main plot was further divided into two (10 × 18 m) or three sub-plots (10 × 12 m) according to the experiment which received vegetation restoration treatments. These were separated by 4 m or 2 m buffer zones. Further splitting was carried out in a similar fashion, dividing sub-plots into two or three sub-sub-plots (10 × 5 m).

Treatments

Six main-plot, bracken control treatments were applied to all experiments: (1) untreated (experimental control); (2) cut once per year in June (Cut1pa); (3) cut twice per year in both June and August (Cut2pa); (4) a single June cut in year one followed by asulam spraying in year two (CutSpray); (5) asulam in year one only (Spray); (6) asulam in year one followed by a single June cut in year two (SprayCut). Cutting was applied using a petrol-driven flail mower (Logic MFG series 300), trailed by a quad four-wheel-drive ATV (Kawasaki KLF 300) up to and including 1999, and subsequently using a hand operated AEBI model HC55 flail mower. Asulam (Asulox, Bayer CropScience), was sprayed in late August or early September at 4.4 kg active ingredient ha^{-1} (11 litres Asulox ha^{-1}) in 400 litres water ha^{-1} using a standard knapsack sprayer. In two experiments (Sourhope 1 and Cannock 2) plots treated to a single application of herbicide were re-treated with asulam in 1996, three years after first treatment. On that occasion the herbicide was applied using a weed wiper (Rotowiper, Bisset Engineering International Ltd., New Zealand) trailed by the ATV.

The site-specific sub- and sub-sub-treatments were designed to match the restoration requirements of each individual site. They included: grass seeding with the mix *Festuca ovina*:*Agrostis capillaris*:*Poa pratensis* at a ratio of 5:4:3, with an application rate of 60 kg ha^{-1}; *Calluna vulgaris* seeding with brash comprising 20 cm stems at 13 t ha^{-1} and nurse crop, *Agrostis castellana*, at 12 kg ha^{-1}; *C. vulgaris* seeding with *Calluna* litter at 1.2 t ha^{-1}, vacuum collected from under mature heather, together with the same nurse crop; stock-proof fencing; fertilizer (ENMAG, Zeneca) application at 150 kg ha^{-1}; harrowing (ATV small chain harrow, Logic). In addition, spot-spraying with asulam was applied, as a sub-sub-treatment, at Carneddaau in late summer 1997. The application was from a knapsack using the same strength mixture as above.

Monitoring

All experiments were monitored twice per year in June and August. Here, we concentrate on results from the late-summer, August sampling, when frond expansion is at a maximum. The early-summer June samples should have provided better comparison between-treatments, but this early sampling proved problematic for two reasons. First, *P. aquilinum* performance was affected by late frosts in some years, and second the staggered sampling times between-experiments introduced a considerable bias as sampling is occurring in the most active part of the frond expansion phase (Marrs & Watt, 2006). However, the June results more or less supported those from August.

In each case these were carried out before application of bracken control treatments. Quadrats were placed at pre-selected random co-ordinates on 1 m grids within each sub- (sub-) plot. Two sets of measurements were made: (1) 1 × 1-m quadrat to estimate *P. aquilinum* cover, and (2) 0.5 × 0.5 m quadrat positioned concentrically with the first were bracken performance was measured; all fronds were cut at ground level, counted and length measured.

A full description of the data collection methods is presented along with all raw data in a bespoke database available at www.appliedvegetationdynamics.co.uk (Le Duc *et al.*, in press).

Data analysis and presentation

Data were transformed using standard procedures (Sokal & Rohlf, 1995), number of fronds per quadrat using $(Y + 0.5)^{0.5}$, and individual frond length, and cover estimates using $\ln(Y + 1)$. Estimates of values per treatment combination per block were obtained by combining data per quadrat after transformation by sub- (sub-) plot.

Individual variables were analyzed for change through time for each site individually. As our objective was to measure the shape of response curves through time, we used repeated-measures

ANOVAs with polynomial contrasts (Gurevitch & Chester, 1986). Time was denoted as elapsed time (ET), with the start year designated ET=0. This was carried out by means of PROC GLM in SAS version 8.02 (SAS, 1989). For each site we used the appropriate analysis of variance model; however for Cannock and Sourhope we initially analyzed both experiments together, with experiment included as the first level in a split-split-split plot design.

Bonferroni correction was used to adjust for the Type I error rate (Cabin & Mitchell, 2000). The number of comparisons at all sites was 3 for the August sampling, with $\alpha = 0.05$ the critical probability level of 0.0167 was used to assess significance.

The analyses allowed the three hypotheses to be tested on data, as follows: (1) was assessed by the significance between (a) the different experiments (Cannock and Sourhope) and the interactions between these experiments and applied treatment, and (b) significant block effects at Carneddau and Peak. (2) Was assessed by the significance of bracken control treatment effects and interactions through time. (3) Was assessed by significance of restoration treatments through time.

Results

Spatial effects and interactions

At Sourhope, only frond density showed significant spatial variation between experiments, with Sourhope 1 having the greater frond density at the start of the study, although the difference reduced through time.

At Cannock there was a significant experiment × bracken control interaction for all bracken response variables. The cutting treatments at both experiments tended to have a greater frond density than the untreated control with the Cut2pa being greater for most of the period at Cannock 1 and Cut1pa at Cannock 2. At both experiments Spray and SprayCut both showed an immediate reduction in length and density, followed by a slow recovery over the 10 years. For frond length the cutting treatments reduced length, until years 5 or 6; thereafter Cut1pa recovered to near untreated values but Cut2pa continued to decline. The *P. aquilinum* cover results were similar to the frond length.

Spatial variation was also detected at block level for frond density at Peak and Carneddau and *P. aquilinum* cover at Peak. At both these sites the significant effects reflected different *P. aquilinum* performance across the site.

Effects of treatments applied to control P. aquilinum

Significant bracken control treatment effects were found for all three *P. aquilinum* response variables at all sites, but only one example (*P. aquilinum* cover at Peak) is discussed here (Fig 1). Initially, at Peak the spray treatments with asulam were superior to cutting-only treatments. However the impact of the spray treatments consistently reduced as bracken cover increased over the 10 years, until they were not significantly different from the untreated controls. The Cut2pa treatment showed an increasing impact through time. At this site (Peak) there were significant fluctuations, especially in the cutting treatments. Similar responses were found with two other measures of frond performance (data available from senior author). By the final year of monitoring the cutting treatments where the most effective method of control for all bracken response variables at Carneddau and Sourhope.

At Carneddau spot spraying significantly reduced frond density immediately after application, followed by a steady recovery. There were also two significant interactions: (a) seeding × spot spray on frond length, and (b) bracken control × spot spray on cover (Fig. 2). Frond length remained approximately constant in the unsprayed spot treatment, but was consistently lower immediately after spot spraying. In the spot sprayed treatment where no seeding was applied the frond length remained approximately constant, but where seeding and seeding+fertilizer was applied frond length partly recovered but remained lower than non spot sprayed treatments until year 8, when they started to recover. The bracken control x spot spray interaction showed that spot spraying reduced bracken cover significantly in all treatments, with the exception of Cut2pa where the reduction was minimal (Fig. 2).

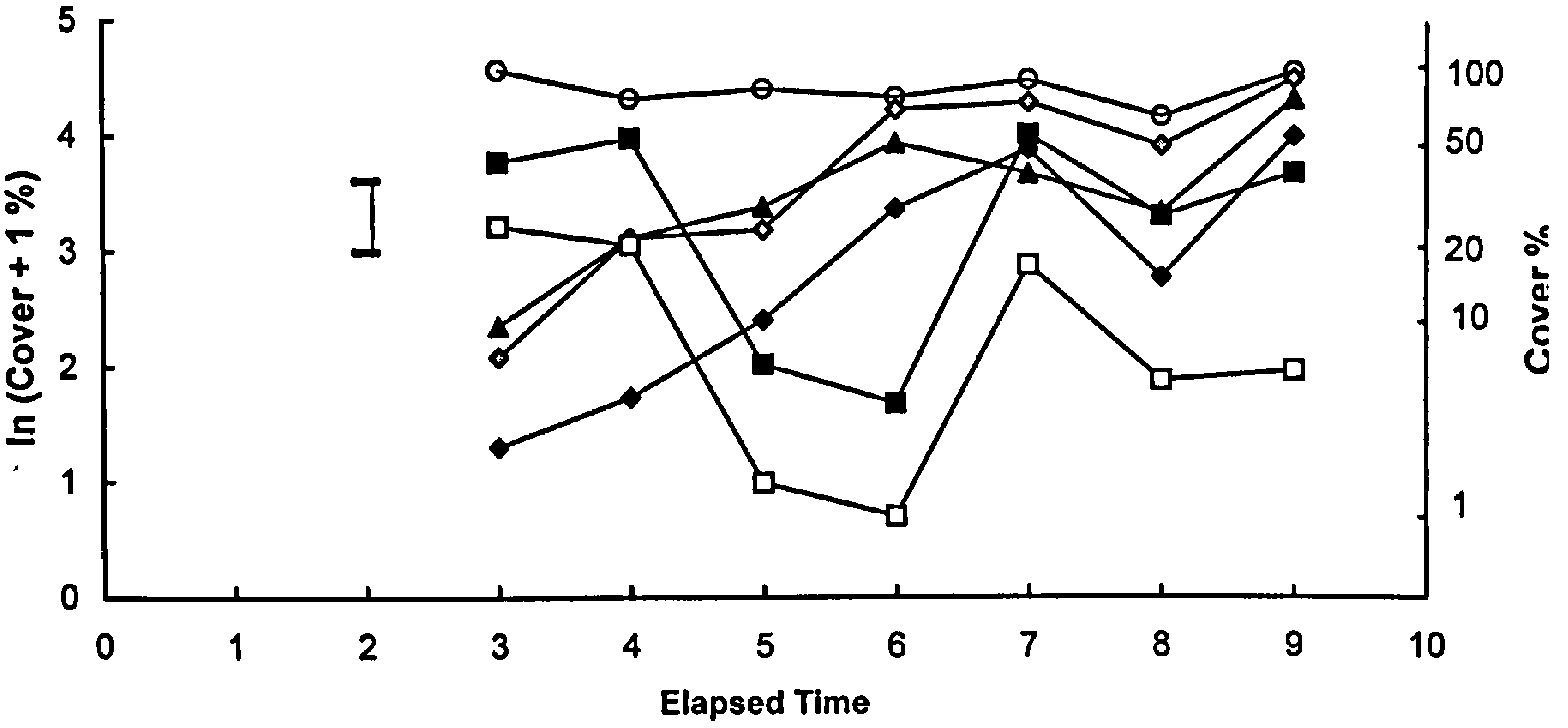

Fig. 1. Bracken control treatment effect on *P. aquilinum* cover at Peak in August (no treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond); 1st order, $F_{(5,10)}$=38.74 n=18. Elapsed Time = 0 is 1993.

Effects of treatments applied to restore vegetation

Generally restoration treatments had no effect on *P. aquilinum* performance with only one significant effect detected. At Sourhope grass seeding reduced frond length between years 2 and 4, after year 4 there was no difference from the untreated plots in year 6.

Discussion

Does geographical location (between- and within-sites) affect the response of P. aquilinum *to control treatment through time?*

One of the obvious problems, is that whilst all measures of bracken performance give more or less similar results in that usually bracken control treatments usually reduce bracken performance (except cutting on frond density, and this is well known, Lowday & Marrs, 1992), there were often subtle differences in rank order of best to worst treatment at the different sites. This might reflect site-specific differences in climatic conditions, starting rhizome biomass, litter depth and amount and composition of understorey vegetation.

An interesting result was the different responses that were found between experiments set up on the same site within relatively short distances of each other (< 2.5 km). At Sourhope there was no difference between the two experiments for bracken density in June, but by August the two experiments were markedly different at the start. The Sourhope result for the June sampling was particularly surprising given that the Sourhope sites show marked differences in modeled rhizome equilibrium biomass (Pottier *et al.*, 2005), these authors hypothesized that Sourhope 1 was particularly sensitive to microclimatic effects, especially the period of frost-free growth, which delimits the growing season.

These overall results are not surprising, but this longer term analysis suggests that within-site variability is perhaps less than suggested from analysis of shorter-term data (Le Duc *et al.*, 2000).

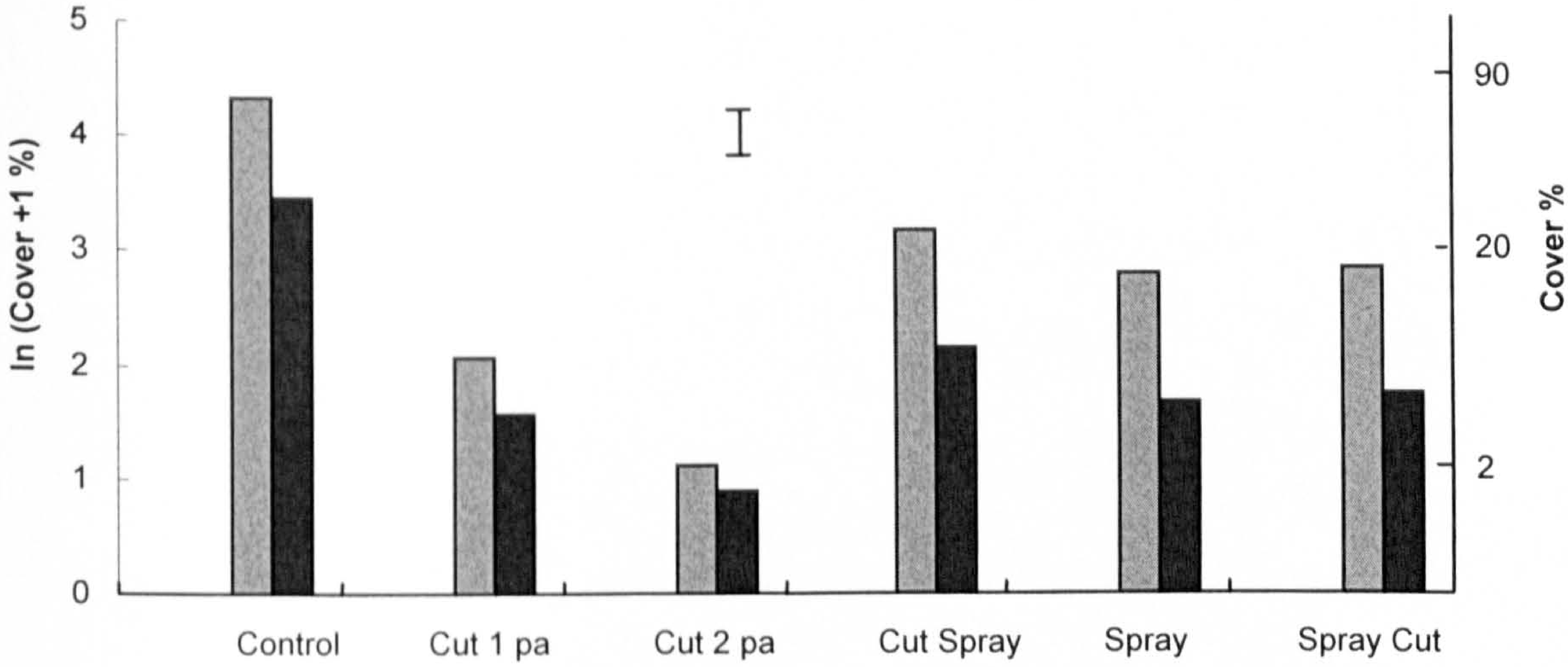

Fig. 2. Effect of bracken control x spot spray interaction on *P. aquilinum* cover at Carneddau in August (no treatment= grey; spot spray= black); Cover (overall effect, $F_{(5,36)}=3.47$ n=54).

Are the P. aquilinum *control treatments successful at all sites, and if so which ones?*

The effects of bracken control treatments showed a pattern similar to that described elsewhere (Lowday & Marrs, 1992; Marrs *et al.*, 1998). After asulam treatment, there was a rapid reduction in frond performance, usually followed by a continued recovery to, or near to, untreated values in approximately 10 years. This result for the UK uplands contrasts with a much shorter recovery rate of approximately 6 years found in lowland Britain where the climate is more equitable (Marrs *et al.*, 1998). Frond density showed a typical response to cutting, were densities are increased but the frond length is much reduced (Lowday & Marrs, 1992). However, cutting treatments tended to have an initially slow impact but increasing with time.

The most effective significant treatment for all sites and all measures in the final year of sampling is summarized in Table 1. Overall, 15 significant bracken control treatment effects were found, of these 13 involved a continuous cutting treatment. However, where spraying is most effective even when combined with a cut this will be a more cost-effective option as only one or two operations will be required, compared to the 20 cuts applied in the cutting twice per year treatment.

The effects of spot spraying with asulam was generally effective in reducing bracken performance, this is in line with manufacturer's recommendations (Robinson, 2000). A full test of the recently introduced manufacturer's recommended good practice i.e. continued spot spraying without respite (Robinson, 2000) has not been tested here. This practice will be included in revised experimental protocols on two of these experiments from 2004.

Table 1. *The most effective treatment for reducing bracken in final year of monitoring*

Treatment	Bracken Measure			Site		
		Cannock 1	Cannock 2	Carneddau	Peak	Sourhope 1 & 2
Experiment × Bracken Control	*P. aquilinum* Cover	Cut2pa	Cut2pa			
	Frond Length	Cut2pa	Cut2pa			
	Frond Density	CutSpray	CutSpray			
Bracken Control	*P. aquilinum* Cover	Cut2pa	Cut2pa	Cut2pa	Cut2pa	Cut1pa/ Cut2pa
	Frond Length	Cut2pa	Cut2pa	Cut2pa	Cut2pa	Cut1pa
	Frond Density	CutSpray	CutSpray	Cut2pa	Cut2pa	Cut2pa
Seeding	Frond Length					Seeding
Spot Spraying	Frond Density			Spot Spray		
Seed × Spot Spray	Frond Length			No treatment, Spot Spray		
Bracken Control × Spot Spray	*P. aquilinum* Cover			Cut2pa, Spot Spray		

Do the treatments applied at the individual site level to restore vegetation influence the performance of P. aquilinum *through time?*

There is some evidence to suggest that vegetation can inhibit bracken recovery, with frond length initially being reduced in seeded plots at Sourhope. However, the evidence is limited as the treatments merge after 3 years and none of the seeded grasses increase significantly over time (Cox *et al.*, pers. comm.). This was the only restoration treatment to have a significant effect on any of the *P. aquilinum* response variables in August. Two other significant restoration treatment interactions; bracken control treatments × fertilizer × time at Cannock and grass seeding × spot spray × time at Carneddau (Table 1) show mixed results with the treatments designed to control *P. aquilinum* having the clearest impact on reducing frond length.

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References

Anon. 1995. *Biodiversity: UK steering group report. Vol. 1: Meeting the Rio challenge.* London: HMSO.

Cabin R J, Mitchell R J. 2000. To Bonferroni or not to Bonferroni: when and how are the questions. *Bulletin of the Ecological Society of America* 81:246-248.

Frankland J C. 1976. Decomposition of bracken litter. *Botanical Journal of the Linnean Society* 73:133-143.

Gurevitch J, Chester Jr S T. 1986. Analysis of repeated measures experiments. *Ecology* 67:255.

Le Duc M G, Pakeman R J, Marrs R H. 2003. Changes in the bracken rhizome system subjected to long-term experimental treatment. *Journal of Applied Ecology* 40:508-522.

Le Duc M G, Pakeman R J, Putwain P D, Marrs R H. 2000. The variable responses of *Pteridium aquilinum* fronds to control treatments in Great Britain. *Annals of Botany* 85B:17-29.

Le Duc M G, Yang L, Fisher M J, Miller P G G, Pakeman R J, Marrs R H. In press. A database solution for archiving and publishing complex ecological datasets from experiments. *Journal of Vegetation Science.*

Lowday J E, Marrs R H. 1992. Control of bracken and the restoration of heathland.III. Bracken litter disturbance and heathland restoration. *Journal of Applied Ecology* 29:212-217.

MAFF. 1993. *Environment matters. Evironmentally Sensitive Areas.* London: MAFF.

MAFF. 1996. *Environment matters. The Countryside Stewardship Scheme: Information for farmers and land managers.* London: MAFF.

Marrs R H, Johnson S W, Le Duc M G. 1998. Control of bracken and restoration of heathland. VI. The response of bracken fronds to 18 years of continued bracken control or 6 years of control followed by recovery. *Journal of Applied Ecology* 35:479-490.

Marrs R H, Watt A S. 2006. Biological flora of *Pteridium aquilinum. Journal of Ecology* 94: 1272-1321.

Pakeman R J, Hay E. 1996. Heathland seedbanks under bracken *Pteridium aquilinum* (L) Kuhn and their importance for re-vegetation after bracken control. *Journal of Environmental Management* 47:329-339.

Pakeman R J, Marrs R H. 1992. The conservation value of bracken *Pteridium-aquilinum* (L) Kuhn- dominated communities in the UK, and an assessment of the ecological impact of bracken expansion or its removal. *Biological Conservation* 62:101-114.

Pottier J, Pakeman R J, Le Duc M G, Marrs R H. 2005. Validation of a model for predicting *Pteridium aquilinum* (L.) Kuhn production and control across the UK *BCPC International Congress – Crop Science & Technology* 2005:987-994.

Robinson R A. 2000. The means of large-scale, effective bracken clearance in the UK. In *Proceeding of the International Bracken Group Conferrence Manchester 1999*, pp 156-162.(Eds JA Taylor, RT Smith). Aberystwyth: International Bracken Group.

SAS. 1989. *SAS/STAT User's Guide Version 6* (4th Edn). SAS Institute.

Sokal R R, Rohlf F J. 1995. *Biometry* (3rd Edn). New York: W. H. Freeman & Co..

Stace C. 1997. *New Flora of the British Isles* (2nd Edn). Cambridge: Cambridge University Press.

A multi-site assessment of bracken control effectiveness across the UK

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Abstract

Questions: The objectives of this study were to assess the effect of bracken control treatments, at the national scale, and the impact of restoration practices, at the local scale, on *Pteridium aquilinum* performance.

Hypotheses: 1. Geographical location (locally between and within sites) affects the control of *Pteridium aquilinum* through time. 2. Are the *P. aquilinum* control treatments successful at all sites, and if so which ones? 3. The treatments applied at the individual site level to restore vegetation influences the performance of *P. aquilinum* through time.

Location: Four geographically distinct acid grassland and heathland sites invested with *Pteridium aquilinum* across the UK.

Methods: Six main-plot, bracken control treatments were applied to all sites with site-specific vegetation restoration treatments. Bracken response variables (*P.aquilinum* cover, frond length and density) were monitored twice yearly, in June and August between 1993 and 2003.

Results: Between- and within-site spatial variation was found, although impact is perhaps less than suggested from shorter-term data. Despite local variation all sites responded similarly to bracken control treatments; asulam treatment resulted in a rapid reduction in frond performance followed by a continued recovery taking approximately ten years to return to untreated values. Cutting treatments tended to have a slower impact at the start but an increasing one over time, especially cutting twice per year. Restoration treatments had a limited impact; the only significant effect in August was grass seeding on frond length at Sourhope. In June only, the plots were sheep were fenced out showed a significant reduction in *P .aquilinum* cover at Peak.

Conclusions: Long-term control of bracken at all sites and on all measures was best achieved using a continuous cutting treatment, preferably twice per year.

Keywords: *Pteridium aquilinum,* heathland, acid grassland, herbicide, asulam, cutting.

Abbreviations: ET = Elapsed Time.

Nomenculture: Stace (1997) for higher plants; Hill, et al. (1991, 1992, 1994) for bryophytes; Coppins (2002) for lichens.

Introduction

There is an increasing need for applied ecologists to be able to assist in the development of national weed control strategies, for example in the implementation of agri-environments schemes developed by the European Union (MAFF 1993, 1996) or the delivery of Biodiversity Action Plans to meet conservation objectives (Anon 1995 a, b). Advice to policy-makers needs to be cost-effective and must be deliverable in a wide range of situations which provides a broad coverage of the likely scenarios where weeds need to be controlled.

Restoration management which involves a weed control phase often produces mixed results (Le Duc et al. 2000, 2003; Hytonen & Jylha, 2005). Such management usually involves a combination of control treatments and specific treatments designed to restore vegetation. Together they can control the problematic weed and create more desirable target vegetation (DiTomaso 2000). This is particularly important when weed infestation is high (Simmons 2005), and the aim is to establish vegetation which increases resistance to invasion and prevents the weed infestation from recurring (Blumenthal et al. 2003).

A good example of such a problem is *Pteridium aquilinum* control in the United Kingdom, where the policy objective is to reduce the *P. aquilinum* infestation and restore a vegetation type with a greater conservation value (Pakeman & Marrs 1992). *P. aquilinum* is a serious invasive weed of upland and marginal land in many parts of the world (Page 1995; Pakeman & Marrs 1992). In the UK dense *P. aquilinum* is a problem species for agriculture and conservation in most situations, as it is a long-lived robust clonal species (Le Duc et al. 2003) that produces a dense litter layer (Frankland 1976), which competes effectively with heathland and grassland species, at best reducing their cover but in some cases eliminating them leaving a very depauperate flora (Pakeman & Marrs 1992). This eventually leads to impacts on seed banks which are also depauperate under bracken (Pakeman & Hay 1996).

One of the major issues highlighted in *P. aquilinum* control is the high variability in success rates (Le Duc et al. 2000, 2003), and a cost-effective control strategy has proved elusive. In order to investigate this problem and develop a national policy a multi-site experiment is needed to ensure that results apply to: (a) a broad geographical coverage of situations, and (b) a reasonable coverage of the types of restoration problem likely to be encountered. Surprisingly there have been relatively few attempts to carry out such large-scale, multi-site experiments in ecological restoration especially over the longer-term, and none on *P. aquilinum* control. Most multi-site studies have been either single site or of short duration (< 8 years) (Pywell et al. 2002; Pakeman 2004; Marrs et al. 2004).

Techniques for bracken control

There are three strategies that are generally used to control *P. aquilinum*, these are:

1. *Mechanical control.* Fronds are cut or bruised during early summer, before and up to the point of maximum frond expansion, with the aim of withdrawing the maximum amount of carbohydrates and nutrients from the rhizome reserves (Hunter 1953; Williams & Foley 1976). When this strategy is used it is advisable to cut the fronds before the new assimilates start being translocated from the fronds to the rhizomes in large amounts (late July/early August in Britain) (Williams & Foley 1976). Cutting can be carried out one, two or three times annually (Braid 1959; Williams 1980). This strategy also has important benefits in that it breaks up and fragments the litter layer, hence assisting other species to colonize (Lowday & Marrs 1992a).
2. *Herbicidal control.* Herbicide action is unlikely to have a direct effect on the amount of rhizome carbohydrate reserves in the short term, and herbicides which attack frond buds on the rhizome are most successful. Asulam [methyl (4-aminobenzenesulphonyl) carbamate] is the most widely used herbicide; it is translocated into the rhizome and accumulates in both active and dormant buds, where it effects a lethal action (Veerasekaran, Kirkwood & Fletcher 1976, 1977a,b, 1978). Asulam frequently produces a very good reduction in fronds in the year after spraying, but there is often rapid frond recovery unless other treatments are applied in subsequent years (Robinson 1986; Lowday & Marrs 1992b). Herbicide action has a limited impact of bracken litter (Marrs et al. 2007).
3. *Inhibition by other vegetation.* Usually where dense bracken is to be controlled, managers want to remove the bracken and replace it with some other vegetation. There is some evidence that when competitive vegetation develops during a *P. aquilinum* control program, there is a reduction in frond performance (Watt 1955; Lowday & Marrs 1992b; Le Duc et al. 2000, 2007a).

The multi-site study

Here we report the results of a multi-site study carried out with the objective of testing these techniques to help develop a national policy for bracken control in the UK. A series of experiments have been set up at four regional locations throughout the UK; at two of these locations replicated experiments were set up to assess local spatial effects. The experiments assessed the efficacy of five treatments designed to control *P. aquilinum* relative to an untreated comparison in a range of contrasting ecological situations. Moreover, these *P. aquilinum* control treatments were combined with site-specific treatments designed to restore appropriate heathland or grassland vegetation. Thus, the experiments were a compromise to assess bracken control at the national scale and the impact of potential control/restoration practices at the local scale. In this paper we only consider the effects on *P. aquilinum* performance.

We tested the following hypotheses: (1) Geographical location (locally between and within sites) affects the control of *Pteridium aquilinum* through time.

(2) Are the *P. aquilinum* control treatments successful at all sites, and if so which ones?

(3) The treatments applied at the individual site level to restore vegetation influences the performance of *P. aquilinum* through time.

Our study started in 1993 or 1994 and has been monitored twice per year for 9 or 10 years. With six experiments and multiple, replicated treatments a voluminous dataset has been produced. The analysis is, therefore, large and complex and presentation of such data in published form is difficult. To accommodate this we have developed a stepwise series of electronic outputs to minimize presentation problems and to make these data and results available for inspection to ensure quality assurance and quality control as well as an audit trail through the analyses (Le Duc et al. 2007b).

Methods

Experimental sites

Six experiments were set up at four different regional locations in the UK (Fig. 1); Cannock Chase in the English midlands; Hordron Edge, North Peak Environmentally Sensitive Area in the Peak District National Park, northern England; the Carneddau Estate in Snowdonia National Park, North Wales; and Sourhope in the Cheviot Hills, on the England/Scotland border. Sites are referred to hereafter as Cannock, Carneddau, Peak and Sourhope. If the bracken patch was large enough three blocks were used, otherwise two blocks were used and the entire experiment was replicated nearby (< 2.5 km distant). Site details are provided in Table 1.

Fig. 1. Map of UK showing the location of the sites.

The sites cover two main types of target vegetation; acid grassland and *Calluna* heath. The untreated control plots give an estimate for initial conditions at the six sites (Table 2). The acid grassland sites, Sourhope 1 & 2 and Carneddau, were most species-rich sites with the *Calluna* heath sites, Cannock 1 & 2 and Peak, having the lowest number of species. The lowest *P. aquilinum* cover was recorded at Sourhope 2 (41 %) and Carneddau (48%) the most species-rich sites, the species-poor Cannock sites had the highest *P. aquilinum* cover. Despite having the highest bracken litter cover (84%) and the deepest litter (18 cm) Peak had the smallest rhizome mass.

Table 1. Description of the experiments. Entries for experimental designs represent: number of blocks/number of plots per block/number of sub-plots per plot/number of sub-sub-plots per sub-plot. These codes are truncated from the right when lower experimental levels do not exist. More than one design for a single experiment indicates successive splitting in time. The National Vegetation Classification (NVC, Rodwell 1991a, b, 1992) descriptions (the codes are explained in the footnote) represent the pre-treated condition, the data in brackets being the results obtained when bracken was left out of the calculations. The measured fit was obtained using the computer program TABLEFIT version 1.0 (Hill 1996), and are rated: > 80 very good, > 70 good, > 60 fair, < 60 poor. † - additional fertilizer was added at Cannock 1 in 1996.

Table 2. Species richness (number of species m^{-2}) in standing vegetation, *P. aquilinum* cover and litter abundance and the total rhizome mass in untreated control plots at each of the experiments. Back-transformed means are in bold and transformed means ⬅ SE in parentheses ($Y' = (Y+0.5)^{0.5}$ for species richness and litter depth; $Y' = \ln(Y+1)$ for *P. aquilinum* cover and litter cover). Mean total dry mass of rhizomes are presented in bold, SE in parentheses (Le Duc et al. 2003).

Experimental design

Use of all-terrain vehicle (ATV) equipment to apply the treatments constrained the layout of the experiments. A basic split-plot design was used throughout, with the main plots receiving one of six bracken control treatments, and the sub-plots receiving vegetation restoration treatments in addition.(Table 1).

Within each experiment each block (70 x 40-m) was divided into six plots (10 x 40-m) separated by 2-m untreated buffers. Each plot was divided into two (10 x 18-m) or three sub-plots (10 x 12-m) according to the experiment, with 4-m or 2-m buffer zones. Further splitting was carried out in a similar fashion, dividing sub-plots into two or three sub-sub-plots (10 x 5-m).

Treatments

Six main-plot, bracken control treatments were applied to all experiments: (1) untreated (experimental control); (2) cut once per year in June (Cut1pa); (3) cut twice per year in both June and August (Cut2pa); (4) a single June cut in year one followed by asulam spraying in year two (CutSpray); (5) asulam in year one only (Spray); (6) asulam in year one followed by a single June cut in year two (SprayCut). In two experiments (Sourhope 1, Cannock 2, Table 1) plots treated to a single application of herbicide were re-treated with asulam in 1996, three years after first treatment. On that occasion the herbicide was applied using a weed wiper. Details and a full description of methods have been published in Le Duc et al. 2000.

Unlike the main treatments, the sub- and sub-sub-treatments were site-specific; vegetation restoration treatments (with the exception of spot-spraying, see below) were designed to match individual site characteristics (Table 1). At the acid grassland sites a grass seed mix *Festuca ovina:Agrostis capillaris:Poa pratensis*, plus a small quantity of *Rumex acetosa* was applied. Two different approaches were taken at the *Calluna* heath sites; at Peak, *Calluna vulgaris* seeding with brash and nurse crop, *Agrostis castellana, C. vulgaris* seeding with *Calluna* litter and stock-proof fencing were tested at Cannock the addition of fertilizer and harrowing were tested.

In addition, spot-spraying with asulam was applied, as a sub-sub-treatment, at Carneddaau in late summer 1997. The spot-spraying was applied strictly within the experimental design with each sub-plot being split into two sub-sub-plots whether it had been sprayed with asulam earlier or not. In June 1997 flash flooding prevented access to Sourhope 2. Consequently, that year the cutting treatments were both replaced by a single cut in August.

Monitoring

All experiments were monitored twice per year in June and August. In each case these were carried out before application of bracken control treatments. Quadrats were placed at pre-selected random co-ordinates on 1-m grids within each sub- (sub-) plot. Using a 0.5 x 0.5-m bracken performance was measured; all fronds were cut at ground level, counted and length measured. Generally experiments split to the sub-plot level were monitored using three quadrats per sub-plot in June and two in August. When further split, experiments had two quadrats per sub-sub-plot in June and one in August.

A full description of the data collection methods is presented along with all raw data in a bespoke database available at www.appliedvegetationdynamics.co.uk (Le Duc et al. 2007b).

Data analysis and presentation

Data were transformed using standard procedures (Sokal & Rohlf 1995), number of fronds per quadrat using $(Y + 0.5)^{0.5}$, and individual frond length, and cover estimates using $\ln(Y + 1)$. After transformation the mean frond length per quadrat was calculated. Estimates of values per treatment combination per block were obtained by combining data per quadrat after transformation by sub- (sub-) plot.

Individual variables were analyzed for change through time for each site individually. As our objective was to measure the shape of response curves through time, we used repeated-measures ANOVAs with the method of polynomial contrasts (Gurevitch & Chester 1986). Time was denoted as elapsed time (ET), with the start year designated year=0. This was carried out by means of PROC GLM in SAS version 8.02 (SAS 1989). The value of this approach is that it is possible to test for treatment effects as in ANOVA, but the shape of the temporal trends of these treatment effects can also be identified. This approach becomes more useful with longer-term datasets (Le Duc et al. 2007a). For each site we used the appropriate analysis of variance model; however for Cannock and Sourhope we initially analyzed both experiments together, with experiment included as the first level in a split-split-split plot design.

The analysis of variance model changed when new treatment combinations were added into an experiment, usually changing the design from a split-plot to a split-split-plot one; thus different segments of the time series were analyzed using different models. A Sourhope there was an additional problem in 2001 because data could not be collected because of the Foot and Mouth epidemic in Britain. At this site the experiments were also started in different years, and accordingly the loss of the 2001 data resulted in the loss of two years information from the repeated measures analysis. Where a gap in temporal data was present this is indicated graphically as a dashed line.

Bonferroni correction was used to adjust for the Type I error rate (Cabin & Mitchell 2000; Sokal & Rohlf 1995). For the June sampling there were a large number of comparisons done as all species identified were analyzed, i.e. 144, 85, 44 and 131 analyses at Cannock, Carneddau, Peak and Sourhope respectively. With $\alpha = 0.05$ the critical probability levels of 0.0006, 0.0004, 0.0005 and 0.0004 were used to assess significance. For August the number of comparisons at all sites was 3, with $\alpha = 0.05$ the critical probability level of 0.0167 was used to assess significance.

Both the June and August data was analyzed separately. Here, we concentrate on results from the late-summer, August sampling, the point when *P.aquilinum* reaches maximum frond expansion with all significant results being described. The early-summer June samples should have provided better comparison between-treatments, but this early sampling proved problematic for two reasons. First, *P. aquilinum* performance was affected by late frosts in some years, and second the staggered sampling times between-experiments would have introduced a considerable bias as sampling is occurring in the most active part of the frond expansion phase (Marrs & Watt 2006). The June results more or less supported those from August, and where they diverged the differences are discussed in the text.

The analyses allowed the three hypotheses to be tested on data collected in early- and late-summer, as follows:

(1) Geographical location (locally between and within sites) affects the control of *Pteridium aquilinum* through time. This was assessed by the significance between (a) the different experiments (Cannock and Sourhope) and the interactions between these experiments and applied treatment, and (b) significant block effects at Carneddau and Peak.

(2) Are the bracken control treatments successful at all sites, and if so which ones? This was assessed by the significance of bracken control treatment effects and interactions through time.

(3) The treatments applied at the individual site level to restore vegetation influences the performance of *P. aquilinum* through time. This was assessed by significance of restoration treatments through time.

Results

Effects through time

Significant mean variations over time were found for *P .aquilinum* cover at all sites; for frond density at all sites except Cannock; and frond length at all sites except Sourhope (Table 3). However where these overall significant mean effects were found there were also significant bracken control treatment effects, suggesting that the mean variation is not independent of treatment effects.

Table 3. Bracken response variables which showed significant variation through time (mean effects).

Geographical location (locally between and within sites) affects the control of Pteridium aquilinum *through time.*

There were spatial variations between experiments at both Sourhope and Cannock. At Sourhope, only frond density was significant at this level, with Sourhope 1 having a much greater frond density than Sourhope 2 at the start of the study, although the differences between the experiments reduced through time (Fig. 2).

At Cannock there was a significant experiment x bracken control interaction for all bracken response variables (Fig. 3). *P. aquilinum* cover, frond density and length were more or less constant for the untreated controls; the cutting treatments at both experiments had a greater density than the untreated control with the Cut2pa being greater for most of the period at Cannock 1 and Cut1pa at Cannock 2. For frond length Cut1pa reduced length, until years 5 or 6, after which there was recovery to near untreated values whereas there was a continued decline with the Cut2pa treatment. At both experiments the sprayed treatments showed an immediate reduction in cover, length and density, followed by a slow recovery over the 10 years. The CutSpray treatment was initially the most effective at both sites; but at Cannock 1 there were large fluctuations with lows in years 6 and 8.

Significant spatial variations were found between blocks at Carneddau (frond density, $F_{(2,36)}$=6.53) and Peak (frond density, $F_{(2,48)}$=9.19; *P. aquilinum* cover, $F_{(2,48)}$=9.87 at Peak). The blocks are random effects and are reported as indicative, nevertheless if suggests differential *P.aquilinum* responses across the site.

Fig. 2. Experiment effect through time on frond density at Sourhope in August (Sourhope 1= square, Sourhope 2= triangle); 5th order, $F_{(1,2)}=103.33$ n=24, overall effect $F_{(1,2)}=69.47$ n=216. Elapsed Time=0 is 1993 for Sourhope 1, 1994 for Sourhope 2.

Fig. 3. Experiment x bracken control interactions in August sampling at Cannock (no treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond); (a) frond density (9th order, $F_{(5,10)}=11.37$ n=6) (b) frond length (3rd order effect, $F_{(5,10)}=5.47$ n=6) (c) *Pteridium aquilinum* cover (2nd order, $F_{(5,10)}=5.74$ n=6). Elapsed Time= 0 is 1993.

Table 4. Bracken response variables and non-living cover which showed spatial effects (Block) at the Carneddau and Peak sites; significant effects of temporal change have been identified using repeated measures analysis of variance using polynomial contrasts, the largest F-value is presented. Carneddau was analysed in two phases to accommodate the addition of sub-sub-treatments in 1998. The presence of species in blocks is also presented (n=3, A, B, C).

Are the bracken control treatments successful at all sites?

Significant bracken control treatment effects were found for all three *P. aquilinum* response variables at all sites (Fig 4). At the acid grassland sites (Carneddau, Sourhope) and the *Calluna* heath sites (Peak, Canncok) the treatments including asulam were initially superior to cutting-only treatments (Fig. 4) The bracken cover of these spray treatments consistently increased over the 10 years, until they were either converging (Sourhope), or were not significantly different from the untreated controls (Peak and Cannock). At Carneddau there was no significant difference through time, just an overall significant difference between the treatments (Fig. 4 a) with Cut2pa being the most effective. The cut treatments showed an increasing impact at Sourhope through time as they maintained a low bracken cover, whereas at Peak an increasing impact was only found in the Cut2pa treatment. At Peak there was clear evidence of significant fluctuations, especially in the cutting treatments. A similar picture was found with two other measures of frond performance at Carneddau, Cannock and Sourhope, with minor differences in the overall rankings of the treatments (Data in Electronic Appendix).

Fig. 4. Bracken control treatment effect on *Pteridium aquilinum* cover in August (no treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in

the second= black diamond; sprayed in the first year cut in the second= grey diamond); (a) Carneddau (98-03) (overall effect, $F_{(5,10)}$=50.69 n=18 (Cut2pa n=17)) (b) Sourhope (1st order, $F_{(5,10)}$=8.9 n=8; overall effect, $F_{(5,10)}$=13.24 n=56) (c) Peak (1st order, $F_{(5,10)}$=38.74 n=18). Data for Cannock can be found in Fig.2. Elapsed Time = 0 is 1993 for Carneddau, Peak and Sourhope 1, 1994 for Sourhope 2.

At Carneddau spot spraying significantly reduced frond density immediately after application, followed by a steady recovery (Fig. 5a). There were also two significant interactions at this site: (a) seeding x spot spray on frond length, and (b) bracken control x spot spray on cover. Frond length remained approximately constant in the unsprayed spot treatment, but was consistently lower immediately after spot spraying (Fig. 5b). In the spot sprayed treatment where no seeding was applied the frond length remained approximately constant, but where seeding and seeding+fertilizer was applied frond length partly recovered but remained lower than non spot sprayed treatments until year 8, when they started to recover (Fig. 5b). The bracken control x spot spray interaction showed that spot spraying reduced bracken cover significantly in all treatments (Fig. 5c), with the exception of Cut2pa where the reduction was minimal.

Fig. 5. Effect of spot spraying, restoration and bracken control treatments at Carneddau in August ((a and b) no treatment= square; spot spray= triangle; no restoration treatment= white; fertilizer= black; fertilizer and grass seed= grey; (c) no treatment= grey; spot spray= black) (a) spot spray on frond density (1st order, $F_{(1,36)}$=20.27 n=54) (b) restoration treatment x spot spray interaction on frond length (1st order , $F_{(2,36)}$=6.84 n=18 (Frt_GrS & No SbSbTr n=17) (c) bracken control x spot spray interaction on *Pteridium aquilinum* cover (overall effect, $F_{(5,36)}$=3.47 n=54). Elapsed Time = 0 is 1993.

The treatments applied at the individual site level to restore vegetation influences the performance of P. aquilinum *through time.*

Grass seeding had a significant effect at Sourhope, with frond length declining between years 2 and 4. After year 4 frond length increases, converging with the control in year 6 (Fig. 6). Otherwise there were no other significant effects of the restoration treatments.

Fig. 6. The effect of grass seeding on frond length at Sourhope in August (No seeding treatment= square; grass seeding= triangle) (6th order, $F_{(1,12)}$=8.95 n=24). Elapsed Time = 0 is 1993 for Sourhope 1 & 1994 for Sourhope 2. Seed treatment applied ET=1.

Significant differences between June and August

There were only five additional single-treatment effects found in the June data that were not significant in the August data. Four of the five these single-treatment effects were, however, significant in higher order interaction in the August analyses so they are not discussed further here. The exception was a significant effect of fencing at Peak on *P. aquilinum* cover (2nd order effect, $F_{(1,12)}=24.24$, n=54; mean fenced cover is 9.2% compared to a mean unfenced cover of 10.6%, transformed means are 2.32 and 2.45 respectively, 2xSED=0.17).

Discussion

Geographical location (locally between and within sites) affects the control of Pteridium aquilinum *through time.*

An interesting result was that different responses were found between experiments set up on the same site within relatively short distances of each other (< 2.5 km) and on the same vegetation type. At Cannock the bracken treatments produced the same responses at the two sites in both samplings; however at Sourhope the two experiments were markedly different at the start, with frond density being significantly different at the two sites. The Sourhope sites show marked differences in modeled rhizome equilibrium biomass (Pottier et al. 2005), these authors hypothesized that Sourhope 1 was particularly sensitive to microclimatic effects, especially the period of frost-free growth as a result of exposure and shelter, which delimits the growing season.

The inter-annual fluctuations noted at Cannock, are almost solely observed in Cannock 1 for the CutSpray treatment. This variation may be due to the patchiness of recovery (Pakeman et al. 2005), in the years with low cover, length and density there was a high percentage quadrats containing 5% or less *P. aquilinum* cover (67, 58 and 42% for ET3, 6 and 8 respectively) compared to other years (25, 0, 0 and 8% for ET4, 5, 7 and 9 respectively). This effect may have been highlighted due to the random nature of the sampling and did not occur in other sprayed treatments as recovery was much more uniform.

These overall results are not too surprising, but this longer term analysis suggests that within-site variability is perhaps less than suggested from analysis of shorter-term data (Le Duc et al. 2000).

Are the P. aquilinum *control treatments successful at all sites, and if so which ones?*

Despite local variation, at all sites the continuous cutting treatments, normally Cut2pa, were the most effective at reducing bracken performance in the final year of monitoring (Table 4), with the exception of frond density at the Cannock sites. The cutting treatments generally became most successful at reducing *P. aquilinum* in ET5 or 6 (1998 or 1999) with an increasing impact over time, showing a pattern similar to that described elsewhere (Lowday & Marrs 1992b; Marrs et al. 1998, Pakeman et al. 2002). Recovery from the initially successful spray treatments to untreated levels occurred approximately 10 years, contrasting with a much shorter recovery rate of approximately 6 years found in lowland Britain where the climate is more equitable (Lowday & Marrs 1992b; Marrs et al. 1998). It is clear that a single application of asulam to control bracken is not enough and findings here support current good practice guidelines (Anon 2005). For the heath sites Cut2pa has still not yet reduced frond cover to the same level as the initial CutSpray reduction, at the acid grassland sites the cutting treatments have significantly reduced frond cover below that of the spray treatments in the initial years of the experiment. This might reflect the greater *P._aquilinum* cover, litter cover, litter depth or being initially species poor at the start. It may also reflect other site-specific differences in climatic conditions and other abiotic factors that have not been tested here (see Table 2 for a summary of estimated initial covers).

Table 4. The most effective treatment for reducing bracken in final year of monitoring for all data presented.

However, at the Cannock sites the cutting treatments were not the most effective at reducing frond density, the effect of cutting on frond density (i.e. the production of smaller but more numerous fronds) is well known (Lowday & Marrs 1992a). Possibly due to the high rhizome biomass at this site (Le Duc et al. 2003) and the greatest initial frond cover, if the cutting treatment were to continue the frond density will no doubt decease over time. It was not until the penultimate year of monitoring, ET9, that cutting had the greatest impact on frond density at the Sourhope sites.

The effects of spot spraying with asulam was generally effective in reducing bracken performance, this is in line with manufacturer's recommendations (Anon 2005; Robinson 2000). However, a full test of the recently introduced manufacturer's recommended good practice i.e. continued spot spraying without respite (Anon 2005; Robinson 2000; The Southern Upland Partnership 2001) has not been tested here. This practice will be included in revised experimental protocols on two of these experiments from 2004.

The treatments applied at the individual site level to restore vegetation influences the performance of P. aquilinum *through time.*

In August only one restoration treatment had a significant effect on any of the *P. aquilinum* response variables. There is some evidence to suggest that vegetation can inhibit bracken recovery with frond length initially being reduced in seeded plots at Sourhope, however the evidence is limited as the treatments merge after 3 years and this result is only significant in August monitoring with none of the seeded grasses having a significant increase over time (Cox et al. submitted). In June only, the exclusion of sheep grazing at Peak had a significant effect on *P. aquilinum* cover. Plots were sheep were fenced out showed a reduction in *P .aquilinum* cover, in August this effect was no longer significant. This contradicts other results which report reduced *P. aquilinum* cover (Pakeman et al. 1997; Williams 1980) or *P. aquilinum* litter cover (Le Duc et al. 2007a) with moderate grazing

Issues in the analysis of multi-site data

In spite of the need for good experimentally-derived information to guide restoration policies there have been surprisingly relatively few attempts to carry out large-scale, long-term, multi-site experiments for the control of pernicious weeds. Most studies either being single-site or short-term. Where multi-site studies have been reported in restoration ecology a mixture of analytical techniques has been used. Pywell et al. (2002) used standard ANOVA with repeated measures to assess the factors limiting success when attempting to restore species-rich grassland on arable land in a four-year experiment. Pakeman (2004) preferred a combination of Residual Maximum Likelihood (REML) analysis to test for complex relationships between species response and measured covariables in a 7-year study. In contrast, Marrs et al. (2004) used a combination of univariate and multivariate analyses of variance to describe a multi-site experiment on *Molinia caerulea* control. Here, as we used properly-designed classical experiments, we used a variant of the former approach, using standard ANOVA with repeated measures, but extending its usefulness using polynomial contrasts (Gurevitch & Chester 1986; Le Duc et al. 2007a). The value of this approach is that it is possible to test for treatment effects as in ANOVA, but the temporal trends of these treatment effects can also be identified. This approach becomes more useful with longer datasets. This approach enabled both recovery trajectories to be identified and the detection of peaks and troughs which are almost certainly linked to annual difference in weather factors (Lowday & Marrs 1992a; Le

Duc et al. 2003). This approach has been used successfully to detect change in single sites (Le Duc et al. 2007a).

General conclusions

Despite local variation, all sites reacted in a similar manner to the bracken control treatments. From these data it is clear that long-term control of bracken at all sites and on all measures was best achieved using a continuous cutting treatment, preferably twice per year. Although, this may not be the most cost-effective method as treatment will need to be applied twice a year essentially indefinitely. It is clear that a single application of herbicide is not an effective treatment for long term control, current advice recommends following up with spot spray, yearly, until no new fronds appear (Anon 2005), but this has not been tested experimentally yet.

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References

Anon. 1995a. *Biodiversity UK Steering Group Report, Vol II. Action Plans.* London, HMSO.

Anon. 1995b. *Biodiversity: UK steering group report. Volume 1: Meeting the Rio challenge.* HMSO, London.

Anon. 2005. *Bracken control, vegetation restoration and land management.* Rural Development Service Technical Advice Note 23. RDS, Defra, London.

Blumenthal, D.M., Jordan, N.R. & Svenson, E.L. 2003. Weed control as a rationale for restoration: The example of tallgrass prairie. *Conserv. Ecol.* 7(1): 6

Braid, K.W. 1959. *Bracken: a review of the literature.* Commonwealth Agricultural Bureaux, Hurley, Berkshire.

Cabin, R.J. & Mitchell, R.J. 2000. To Bonferroni or not to Bonferroni: when and how are the questions. *Bull. Ecol. Soc. Am.* 81: 246-248.

Coppins, B.A. 2002. *Checklist of the lichens of Great Britain and Ireland.* British Lichen Society, London.

Cox, E.S., Marrs, R.H., Pakeman, R.J. & Le Duc, M.G. In press. The restoration of heathland and acid grassland on *Pteridium aquilinum* invested land across the UK: a multi site study. *Restor. Ecol.* Submitted.

DiTomaso, J.M. 2000. Invasive weeds in rangelands: Species, impacts, and management. *Weed Sci.* 48: 255-265.

Frankland, J.C. 1976. Decomposition of bracken litter. *Bot. J. Linn. Soc.* 73: 133-143.

Gurevitch, J. & Chester, Jr. S.T. 1986. Analysis of repeated measures experiments. *Ecology*. 67: 255.

Hill, M.O., Preston, C.D. & Smith, A.J.E. (eds.) 1991. *Atlas of the Bryophytes of Britain and Ireland; Volume 1 Liverworts (*Hepaticae *and* Anthocerotae*).* Harley Books, Colchester.

Hill, M.O., Preston, C.D. & Smith, A.J.E. (eds.) 1992. *Atlas of the Bryophytes of Britain and Ireland; Volume 2 Mosses (except* Diplolepideae*).* Harley Books, Colchester.

Hill, M.O., Preston, C.D. & Smith, A.J.E. (eds.) 1994. *Atlas of the Bryophytes of Britain and Ireland; Volume 3 Mosses* (Diplolepideae). Harley Books, Colchester.

Hill, M.O. 1996. *Tablefit Version 1.0 For identification of vegetation types.* ITE Monks wood, Huntingdon.

Hunter,J.G. 1953. The composition of bracken: some major and trace element constituents. *Journal of Science and Food Agriculture* 4: 10-20.

Hytonen, J. & Jylha, P. 2005. Effects of competing vegetation and post-planting weed control on the mortality, growth and vole damages to Betula pendula planted on former agricultural land. *Silva Fennica* 39: 365-380.

Le Duc, M.G., Pakeman, R.J. & Marrs. R.H. 2003. Changes in the bracken rhizome system subjected to long-term experimental treatment. *J.Appl. Ecol.*40: 508-522.

Le Duc, M.G., Pakeman, R.J. & Marrs, R.H. 2007a. A restoration experiment on moorland infested by *Pteridium aquilinum*: Plant species responses. *Agriculture, Ecosystems & Environment.* 119: 53-59.

Le Duc, M.G., Pakeman, R.J., Putwain, P.D. & Marrs. R.H. 2000. The variable responses of *Pteridium aquilinum* fronds to control treatments in Great Britain. *Ann. Bot.* 85: (Supplement B) 17-29.

Le Duc, M.G., Yang, L., Fisher, M.J., Miller, P.G.G., Pakeman, R.J. & Marrs, R.H. 2007b. A database solution for archiving and publishing complex ecological datasets from experiments. *J. Veg. Sci.* Accepted.

Lowday,J.E. & Marrs,R.H. 1992a. Control of bracken and restoration of heathland: I. Control of bracken. *J. Appl. Ecol.* 29: 195-203.

Lowday,J.E. & Marrs,R.H. 1992b. Control of bracken and the restoration of heathland.III. Bracken Litter disturbance and heathland restoration. *J. Appl. Ecol.* 29: 212-217.

MAFF. 1993. *Environment matters. Evironmentally Sensitive Areas.* London, Ministry of Agriculture, Fisheries and Food.

MAFF. 1996. *Envirnoment matters. The Countryside Stewardship Scheme: Information for farmers and land managers.* London, Ministry of Agriculture, Fisheries and Food.

Marrs, R. H., Galtress, K., Tong, C., Cox, E.S., Blackbird, S.J., Heyes, T.J., Pakeman, R.J. & Le Duc, M.G. 2007. Competing conservation goals, biodiversity or ecosystem services: element losses and species recruitment in a managed moorland-bracken model system. *J. Environ. Manage.* Accepted.

Marrs, R.H., Johnson, S.W. & Le Duc, M.G. 1998. Control of bracken and restoration of heathland. VI. The response of bracken fronds to 18 years of continued bracken control or 6 years of control followed by recovery. *J. Appl. Ecol.* 35: 479-490.

Marrs, R.H., Phillips, J.D.P., Todd, P.A., Ghorbani, J. & Le Duc, M.G. 2004. Control of Molinia caerulea on upland moors. *J. Appl. Ecol.* 41: 398-411.

Marrs, R. H. & Watt, A. S. 2006. Biological flora of *Pteridium aquilinum. J. Ecol.* Accepted.

Page,C.N. 1995. Structural variation in western European bracken: an updated taxonomic perspective. In: Smith,R.T. & Taylor,J.A. (eds.), Bracken: An Environmental Issue, pp. 13-15. International Bracken Group, Aberystwyth.

Pakeman, R.J. 2004. Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. *J. Ecol.* 92: 893-905.

Pakeman, R.J. & Hay, E. 1996. Heathland seedbanks under bracken Pteridium aquilinum (L) Kuhn and their importance for re-vegetation after bracken control. *J. Environ. Manage.* 47: 329-339.

Pakeman, R.J., Le Duc, M.G. & Marrs, R.H. 2000. Bracken distribution in Great Britain: strategies for its control and the sustainable management of marginal land. *Ann. Bot. (Lond.)* 85: 37-46.

Pakeman, R.J., LeDuc, M.G. & Marrs, R.H. 1997. Moorland vegetation succession after the control of bracken with asulam. *Agriculture Ecosystems & Environment* 62: 41-52.

Pakeman, R.J. & Marrs, R.H. 1992. The conservation value of bracken *Pteridium-aquilinum* (L) Kuhn-dominated communities in the UK, and an assessment of the ecological impact of bracken expansion or its removal. *Biol. Conserv.* 62: 101-114.

Pakeman, R.J., Small, J.L., Le Duc, M.G. & Marrs, R.H. 2005. Recovery of moorland vegetation after aerial spraying of bracken (*Pteridium aquilinum*) with Asulam. *Restor. Ecol.* 13:718-724.

Pottier, J., Pakeman R.J., Le Duc, M.G. & Marrs, R.H. 2005. Validation of a model for predicting *Pteridium aquilinum* (L.) Kuhn production and control across the UK *BCPC International Congress – Crop Science & Technology 2005*. pp. 987-994.

Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W. & Peel, S. 2002. Restoration of species rich grassland: assessing the limiting processes using a multi-site experiment. *J. Appl. Ecol.* 39: 294-309.

Robinson,R.C. 1986. Practical herbicide use for bracken control. In: Smith,R.T. & Taylor,J.A. (eds.), *Bracken: Ecology, land use and control technology*, Parthenon Publishing Group, *Carnforth, Lancs.* pp. 331-340.

Robinson, R.A. 2000. The means of large-scale, effective bracken clearance in the UK. *Proceedings of the International Bracken Group Conferrence, Manchester 1999.* International Bracken Group, Aberystwyth. pp 156-162.

Rodwell, J.S. 1992. *British plant communities, Vol. 3: Grassland and montane communities.* Cambridge University Press, Cambridge.

Rodwell, J.S. 1991a. *British plant communities, Vol. 1: Woodlands and scrub.* Cambridge University Press, Cambridge.

Rodwell, J.S. 1991b. *British plant communities, Vol. 2: Heaths and mires*. Cambridge University Press, Cambridge.

SAS. 1989. SAS/STAT User's Guide Version 6. 4th Edition. SAS Institute, Cary, NC.

Simmons, M.T. 2005. Bullying the bullies: The selective control of an exotic, invasive annual (Rapistrum rugosum) by oversowing with a competitive native species (Gaillardia pulchella). *Restor. Ecol.* 13: 609-615.

Sokal, R.R. & Rohlf, F.J. 1995. *Biometry, 3rd Edition.* 3rd ed. W. H. Freeman & Co., New York.

Stace, C. 1997. *New Flora of the British Isles.* 2nd ed. CUP, Cambridge.

Veerasekaren,P., Kirkwood,R.C. & Fletcher,W.W. 1976. The mode of action of asulam [methyl (4-aminobenzenesulphonyl) carbamate] in bracken. Bot. J. Linn. Soc. 73: 247-268.

Veerasekaran,P., Kirkwood,R.C. & Fletcher,W.W. 1977a. Studies on the mode of action of asulam in bracken (*Pteridium aquilinum* (L.) Kuhn) 1. Absorption and translocation of $[^{14}\text{C}]$ asulam. *Weed Res.* 17: 33-39.

Veerasekaran,P., Kirkwood,R.C. & Fletcher,W.W. 1977b. Studies on the mode of action of asulam in bracken (*Pteridium aquilinum* (L.) Kuhn) 2. Biochemical activity in the rhizome buds. *Weed Res.* 17: 85-92.

Veerasekaran,P., Kirkwood,R.C. & Fletcher,W.W. 1978. Studies on the mode of action of asulam in bracken (*Pteridium aquilinum* L. Kuhn) 3. Long-term control of field bracken. *Weed Res.* 18: 315-319.

Watt, A.S. 1955. Bracken versus heather: a study in plant sociology. *J. Ecol.* 43: 490-506.

Williams, G.H. & Foley,A. 1976. Seasonal variations in the carbohydrate content of bracken. Botanical *J. Linn. Soc.* 73: 87-94.

Williams, G. H. 1980. *Bracken control: a review of progress, 1974 -1979.* Research and Development Publication No. 12. The West of Scotland Agricultural College, Auchincruive.

Table 1. Description of the experiments. Entries for experimental designs represent: number of blocks/number of plots per block/number of sub-plots per plot/number of sub-sub-plots per sub-plot. These codes are truncated from the right when lower experimental levels do not exist. More than one design for a single experiment indicates successive splitting in time. The National Vegetation Classification (NVC, Rodwell 1991a, b, 1992) descriptions (the codes are explained in the footnote) represent the pre-treated condition, the data in brackets being the results obtained when bracken was left out of the calculations. The measured fit was obtained using the computer program TABLEFIT version 1.0 (Hill 1996), and are rated: > 80 very good, > 70 good, > 60 fair, < 60 poor. † - additional fertilizer was added at Cannock 1 in 1996.

Location	Sourhope Estate		Hordron Edge	Carneddau Estate	Cannock Chase	
Latitude: Longitude:	2° 14' W 55° 28' N		1° 41' W 53° 23' N;	3° 58' W 53° 13' N	2° 2' W 52° 46' N	
Experiment:						
- Name	Sourhope 1	Sourhope 2	Peak	Carneddau	Cannock 1	Cannock 2
- Started	1993	1994	1993	1993	1993	1993
- Design	1994-03 = 2/6/2	1995-03 = 2/6/2	1994-03= 3/6/2/3	1993=3/6 1994-97 =3/6/3 1998-03 =3/6/3/2	1994-03= 2/6/3	1994-03= 2/6/3
National grid reference	NT 861 202	NT 846 210	SK2187	SH6871	SJ 976 200	SJ 987 181
- Main treatments (bracken control)*	All + weed-wiping	All	All	All	All	All + weed-wiping
- Sub-treatments	Grass seeding		Stock fencing	Grass seeding & fertilizer	Harrowing & fertilizer†	
- Sub-sub-treatments	-	-	*Calluna* seeding (brash & litter)	Spot-spray	-	-
Physical:						
- altitude (m)	325	285	290	350	145	165
- aspect (°)	280	130	275	190	140	125
- slope (°)	16	22	9	20	20	18
Vegetation:						
- NVC class	U4e (U4e)	U4a (U4a)	U20 (H18)	U4a (U4a)	W16 (U2b)	W16 (U2b)
- fit	75 (77)	61 (64)	77 (83)	74 (79)	78 (67)	61 (55)

NVC classes represented are:

U2b	*Vaccinium myrtillus* sub-community of *Deschampsia flexuosa* grassland
U4a	Typical sub-community of *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland
U4e	Vaccinium myrtillus-Deschampsia flexuosa sub-community of *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland
U20	*Pteridium aquilinum-Galium saxatile* community
H18	*Vaccinium myrtillus-Deschampsia flexuosa* heath
W16	*Quercus* spp.-*Betula* spp.-*Deschampsia flexuosa* woodland

Main treatments: (1) Untreated control; (2) Cut once per year; (3) Cut twice per year; (4) Cut in year 1 and sprayed with herbicide in year 2; (5) Sprayed only; (6) Sprayed in year 1 and cut in year 2.

Table 2. Species richness (number of species m^{-2}) in standing vegetation, *P. aquilinum* cover and litter abundance and the total rhizome mass in untreated control plots at each of the experiments. Back-transformed means are in bold and transformed means – SE in parentheses (Y' = (Y+0.5)$^{0.5}$ for species richness and litter depth; Y' – Ln (Y+1) for *P. aquilinum* cover and litter cover). Mean total dry mass of rhizomes are presented in bold, SE in parentheses (Le Duc et al. 2003).

Site	**Species richness**	***P.aquilinum* Cover (%) August**	**Litter cover (%)**	**Litter depth (cm)**	**Rhizome Mass (kg m^{-2})**
***Calluna* Heath Sites**					
Cannock 1	**2.88** (1.84–0.01)	**96.23** (4.58–0.02)	**69.13** (3.97–0.96)	**11.74** (3.28–1.24)	**5.14** (–0.16)
Cannock 2	**3.43** (1.98–0.01)	**83.65** (4.44–0.03)	**61.46** (3.86–0.92)	**15.82** (3.81–1.35)	**2.67** (–0.08)
Peak	**5.19** (2.39–0.01)	**80.60** (4.67–0.05)	**84.02** (4.41–0.28)	**17.56** (4.2–0.64)	**1.85** (–0.04)
Acid Grassland Sites					
Carneddau	**9.59** (3.18–0. 01)	**47.75** (3.89–0.20)	**33.59** (3.54–0.13)	**7.63** (2.79–0.05)	**4.58** (–0.08)
Sourhope 1	**10.76** (3.35–0.02)	**59.99** (4.11–0.08)	**6.48** (1.21–1.18)	**2.54** (1.64–0.6)	**2.89** (–0.09)
Sourhope 2	**12.14** (3.56–0.02)	**41.48** (3.75–0.16)	**3.77** (1.15–0.94)	**1.96** (*1.96–0.88*)	**3.00** (–0.11)

Table 3. Bracken response variables which showed significant variation through time (mean effects).

	Site	Other significant treatments	df	Effect	n	F Value
Pteridium aquilinum Cover	Cannock	Experiment x Bracken Control	1,24	3rd	72	117.77
Pteridium aquilinum Cover	Carneddau 98-03	Bracken Control x Spot Spray	*1,36*	*1st*	*108*	*41.98*
Pteridium aquilinum Cover	Peak	Block & Bracken Control	1,48	1st	108	1859.93
Pteridium aquilinum Cover	Sourhope	Bracken Control	1,12	3rd	48	15.82
Frond Length	Cannock	Experiment x Bracken Control & Bracken Control x Fertilizer	1,24	1st	72	97.29
Frond Length	Carneddau 93-94	-	1,4	1st	9	72.79
Frond Length	Carneddau 95-97	-	1,24	1st	54	22.71
Frond Length	Peak	Bracken Control	1,48	1st	108	139.03
Frond Density	Carneddau 98-03	Block & Bracken Control x Spot Spray	1,36	1st	108	12.00
Frond Density	Peak	Block & Bracken Control	1,48	8th	108	62.60
Frond Density	Sourhope	Experiment & Bracken Control	1,12	1st	48	11.42

Table 4. The most effective treatment for reducing bracken in final year of monitoring for all data presented.

		Site			
Treatment	**Bracken Measure**	**Cannock 1 & 2**	**Carneddau**	**Peak**	**Sourhope 1 & 2**
Experiment x Bracken Control	*P. aquilinum* Cover	Cut2pa			
	Frond Length	Cut2pa			
	Frond Density	CutSpray			
Bracken Control	*P. aquilinum* Cover	Cut2pa	*Cut2pa*	Cut2pa	Cut1pa/ Cut2pa
	Frond Length	Cut2pa	Cut2pa	*Cut2pa*	*Cut1pa*
	Frond Density	CutSpray	Cut2pa	Cut2pa	Cut2pa
Seeding	Frond Length				Seeding
Spot Spraying	Frond Density		Spot Spray		
Seed x Spot Spray	Frond Length		No treatment, Spot Spray		
Bracken Control x Spot Spray	*P. aquilinum* Cover		Cut2pa, Spot Spray		

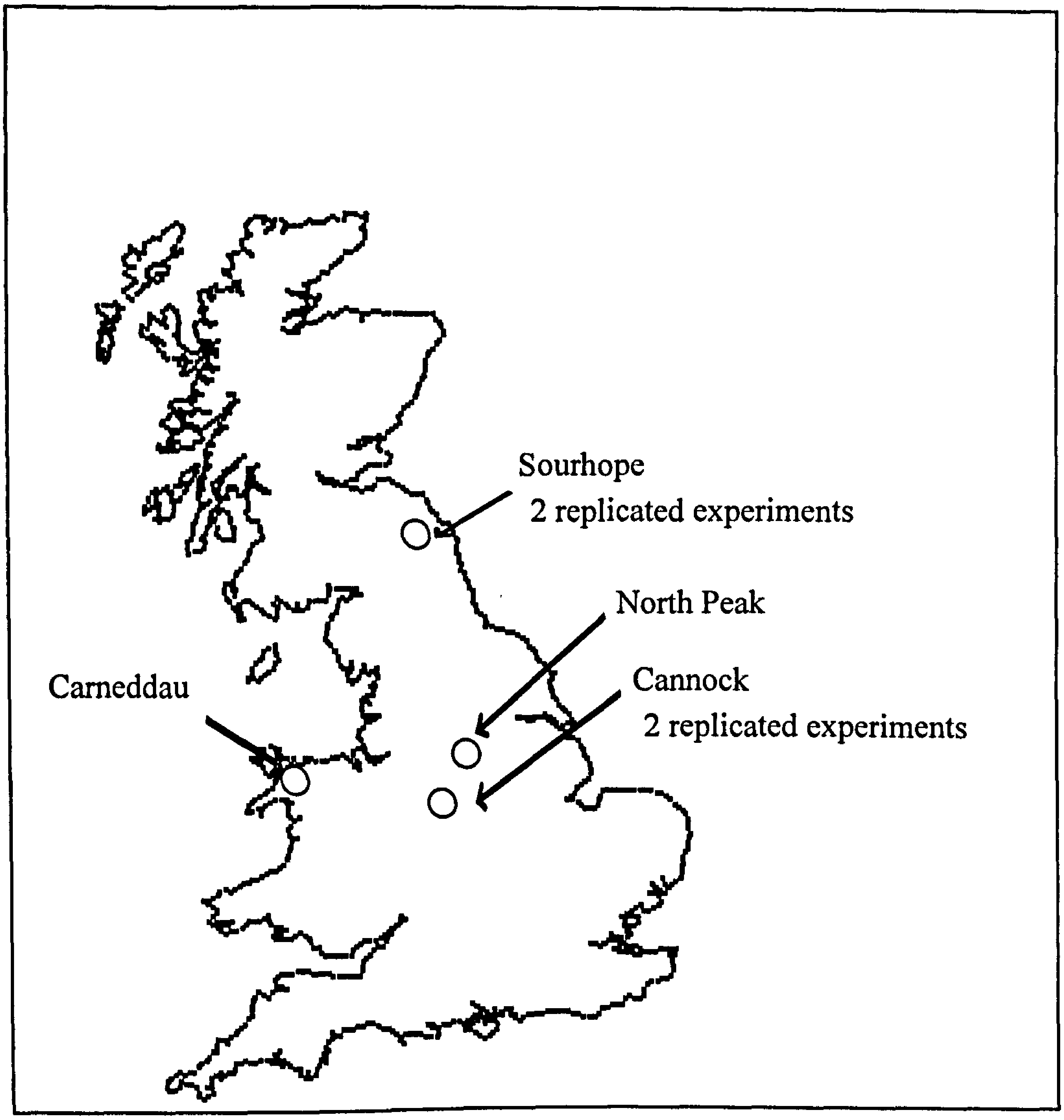


Fig. 1. Map of UK showing the location of the sites.

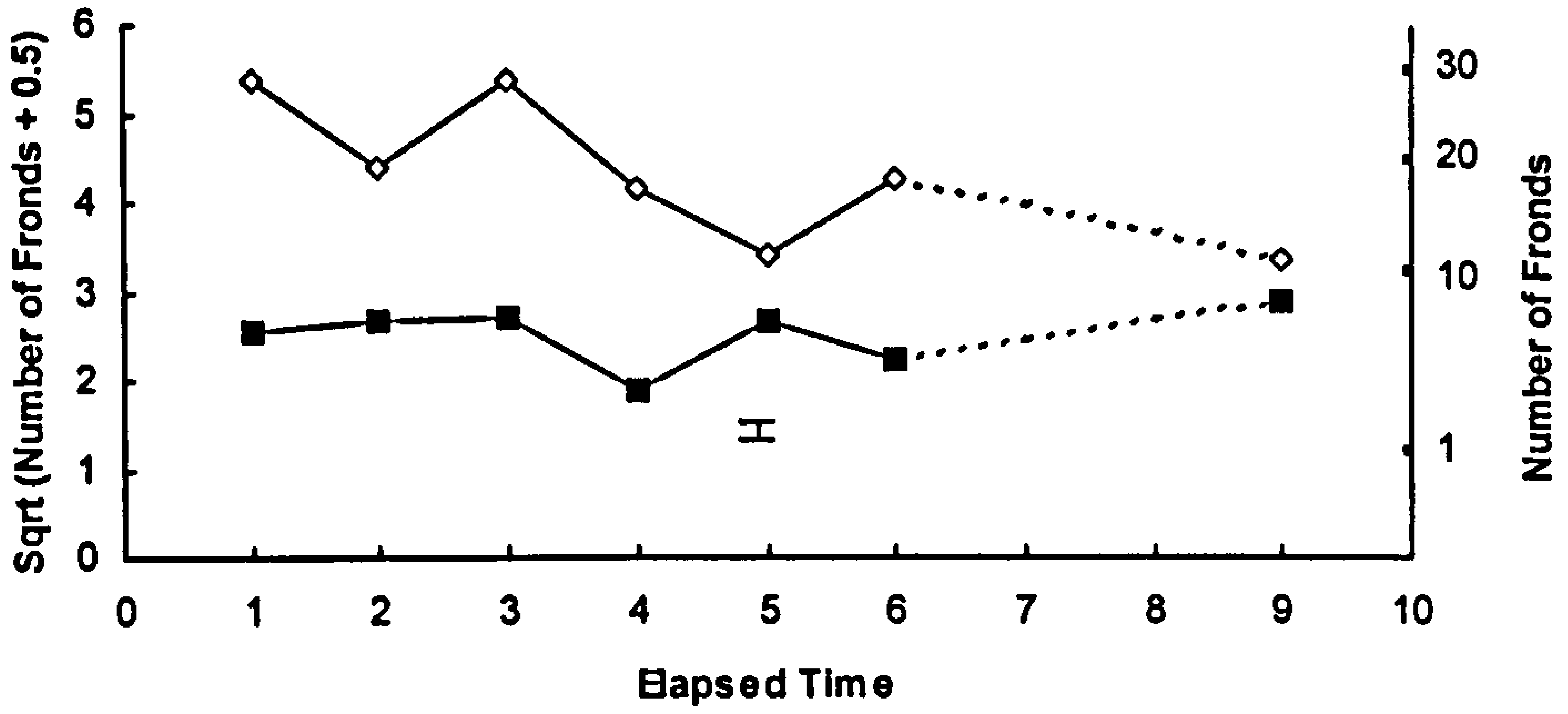
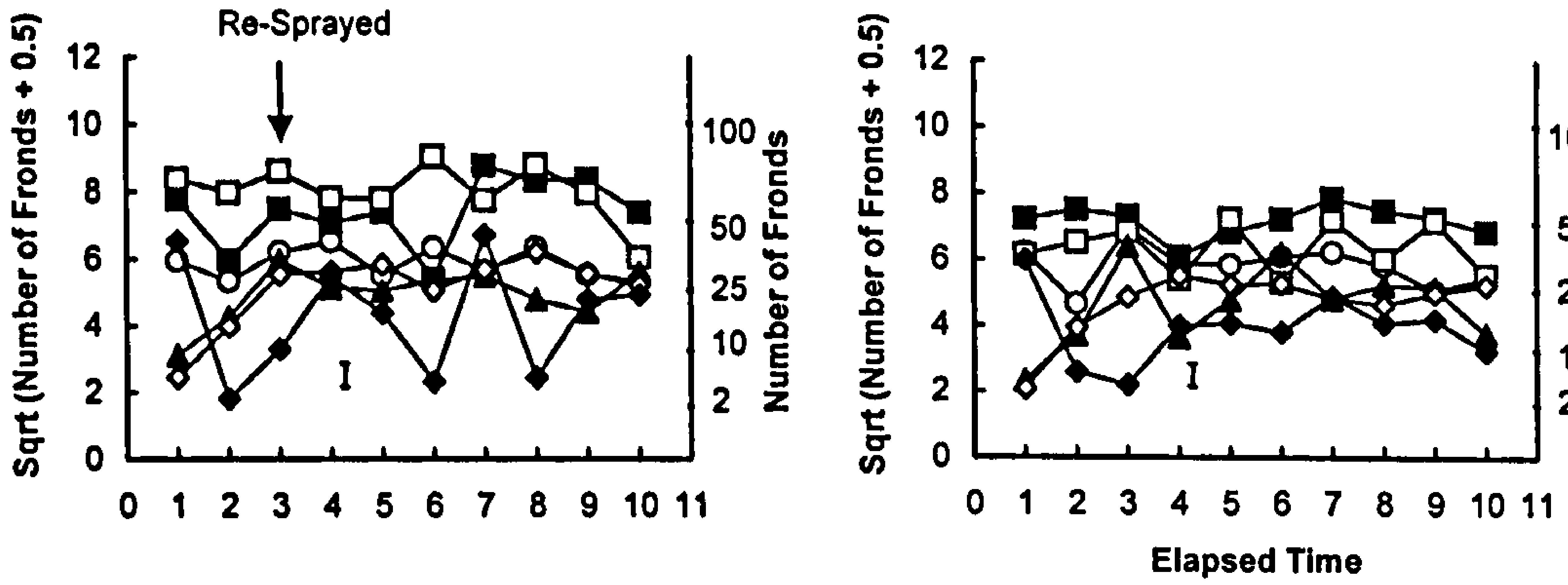
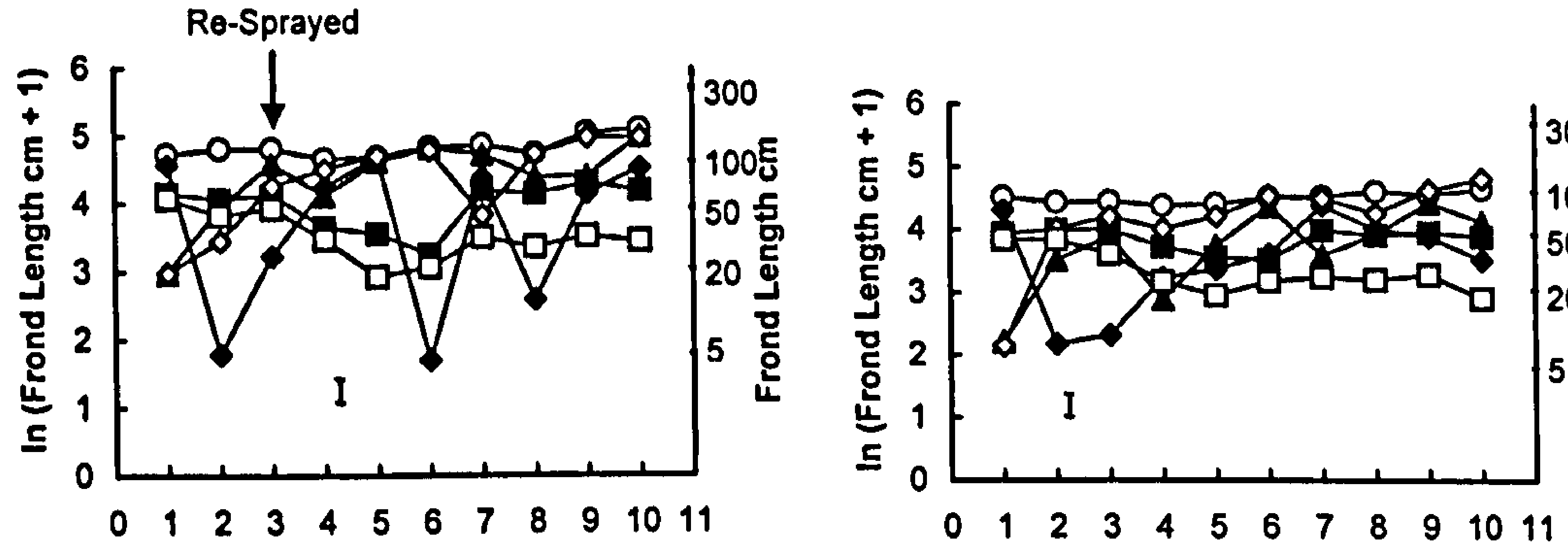


Fig. 2. Experiment effect through time on frond density at Sourhope in August (Sourhope 1= square, Sourhope 2= diampnd); 5th order, $F_{(1,2)}$=103.33 n=24, overall effect $F_{(1,2)}$=69.47 n=216. Elapsed Time=0 is 1993 for Sourhope 1, 1994 for Sourhope 2.

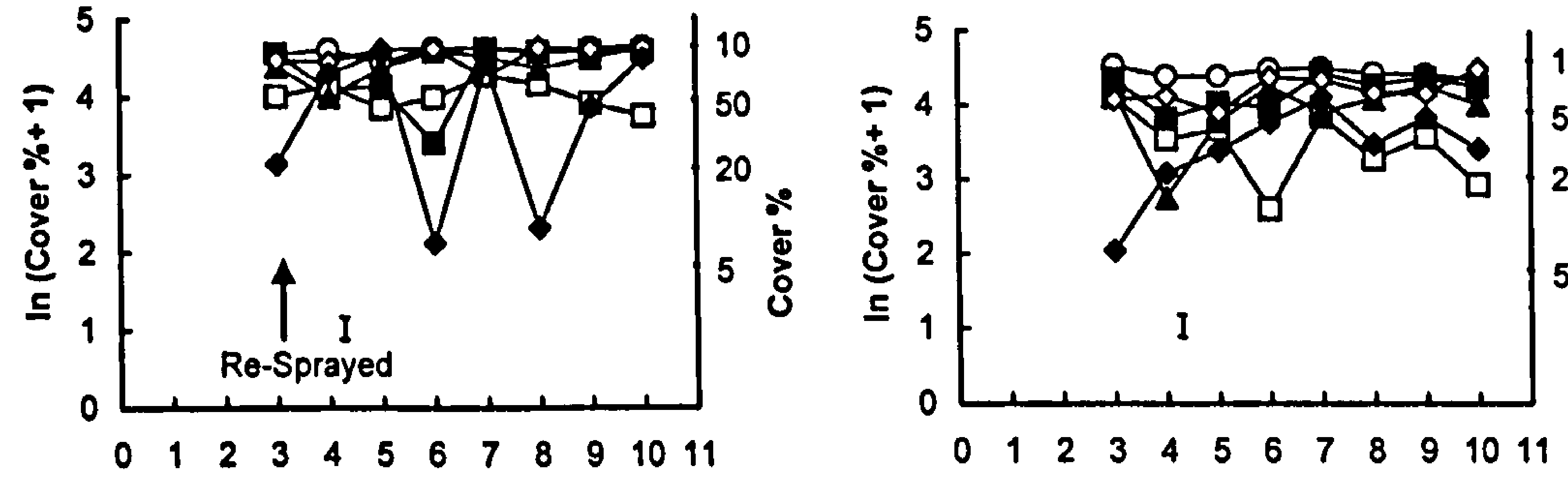
(a) Frond Density; (i) Cannock 1 (ii) Cannock 2



(b) Frond Length; (i) Cannock 1 (ii) Cannock 2



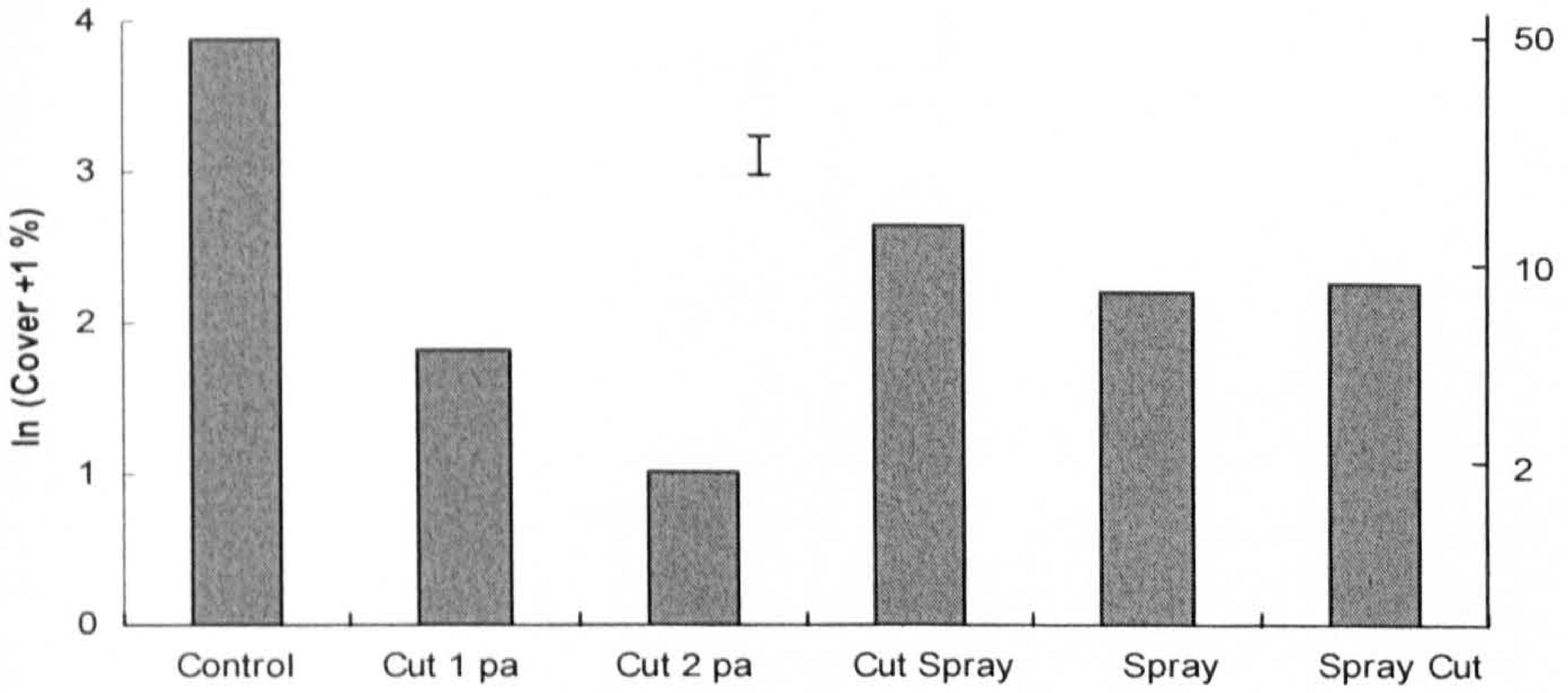
(c) *Pteridium aquilinum* Cover; (i) Cannock 1 (ii) Cannock 2



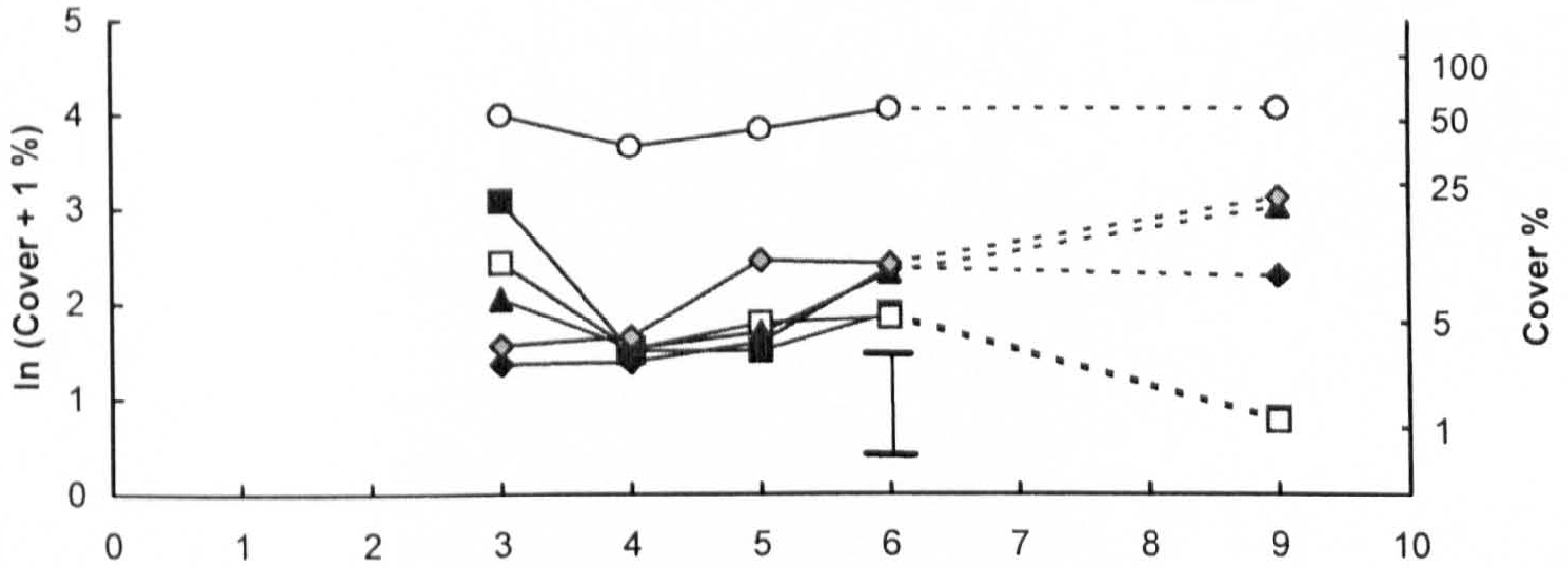
Elapsed Time

Fig. 3. Experiment x bracken control interactions in August sampling at Cannock (no treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond); (a) frond density (9^{th} order, $F_{(5,10)}$ =11.37 n=6) (b) frond length (3^{rd} order effect, $F_{(5,10)}$=5.47 n=6) (c) *Pteridium aquilinum* cover (2^{nd} order, $F_{(5,10)}$=5.74 n=6). Elapsed Time= 0 is 1993.

(a) Carneddau (1998-2003)



(b) Sourhope



(c) Peak

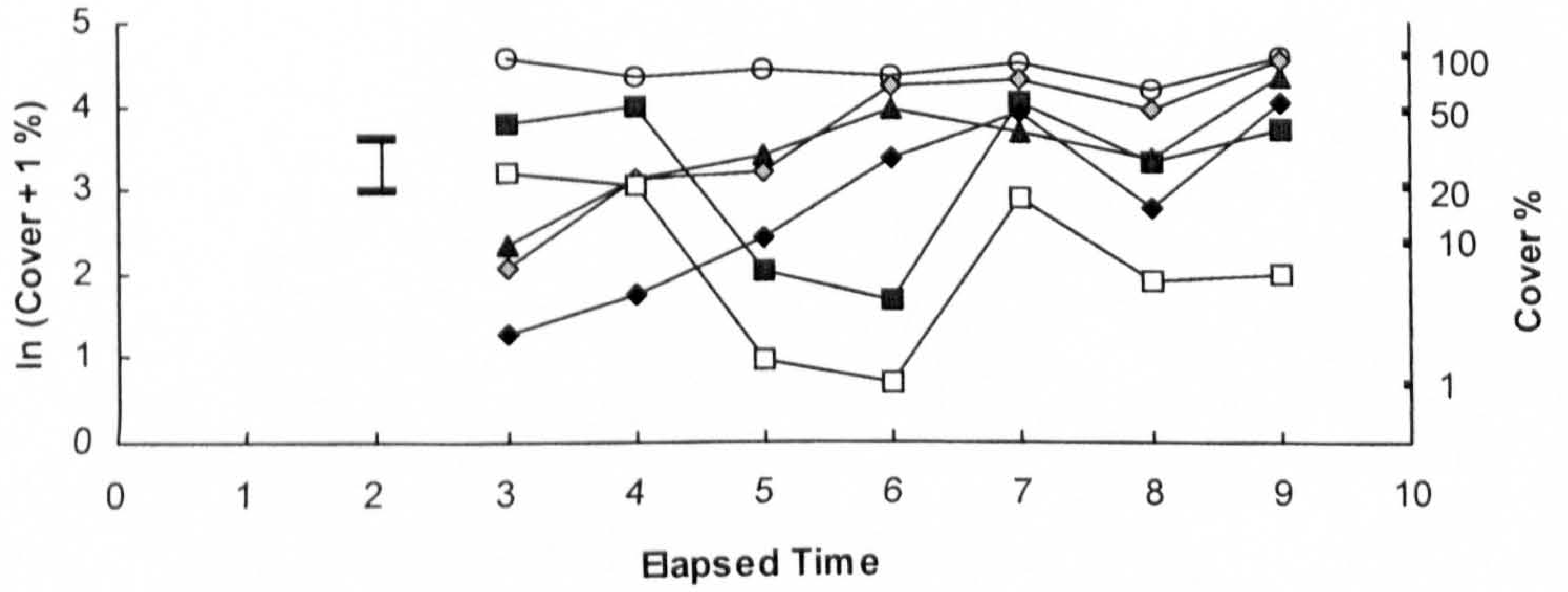
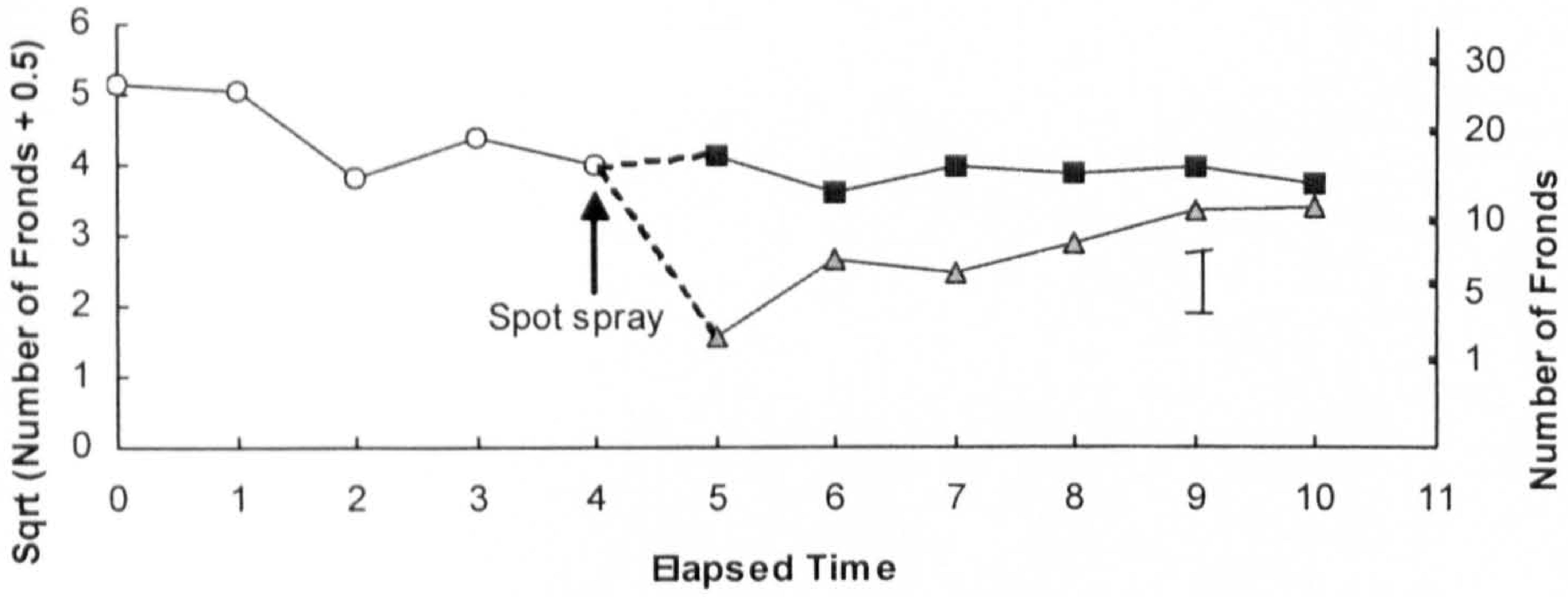
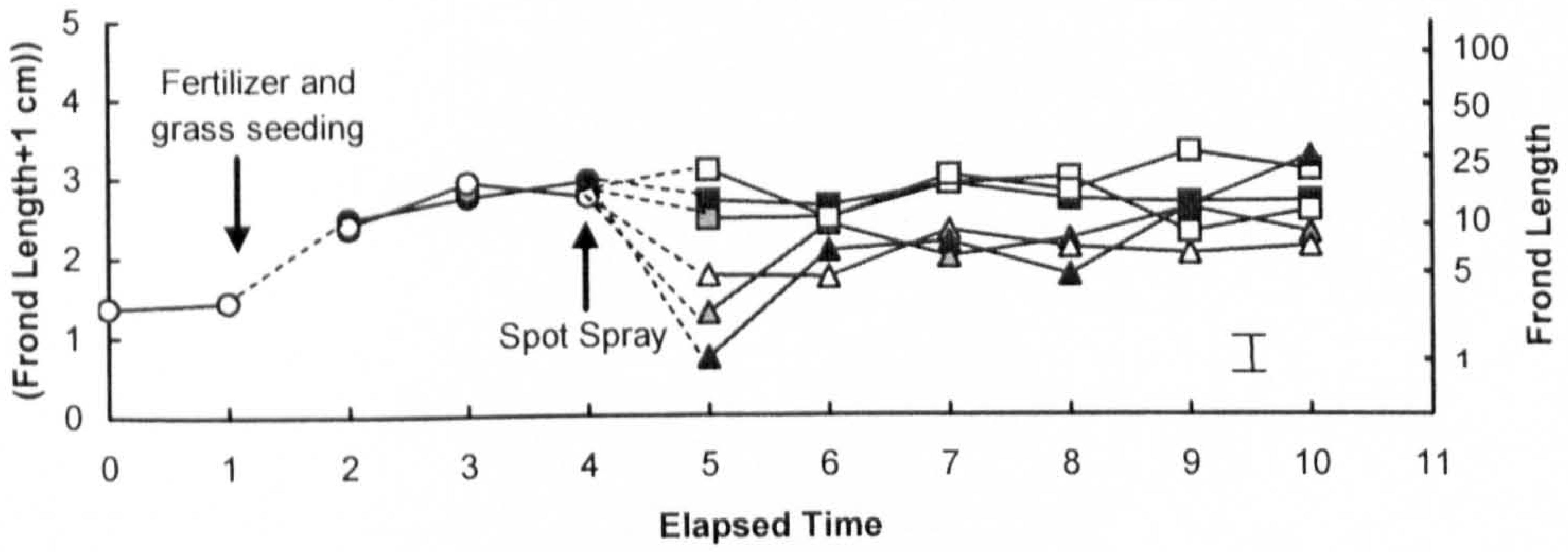


Fig. 4. Bracken control treatment effect on *Pteridium aquilinum* cover in August (no treatment= white circle; cut1pa= black square; cut2pa= white square; spray= black triangle; cut in the first year spray in the second= black diamond; sprayed in the first year cut in the second= grey diamond); (a) Carneddau (98-03) (overall effect, $F_{(5,10)}$=50.69 n=18 (Cut2pa n=17)) (b) Sourhope (1st order, $F_{(5,10)}$=8.9 n=8; overall effect, $F_{(5,10)}$=13.24 n=56) (c) Peak (1st order, $F_{(5,10)}$=38.74 n=18). Data for Cannock can be found in Fig.2. Elapsed Time = 0 is 1993 for Carneddau, Peak and Sourhope 1, 1994 for Sourhope 2.

(a) Spot Spray on Frond Density



(b) Restoration Treatment x Spot Spray Interaction on Frond Length



(c) Bracken Control x Spot Spray Interaction on *Pteridium aquilinum* Cover

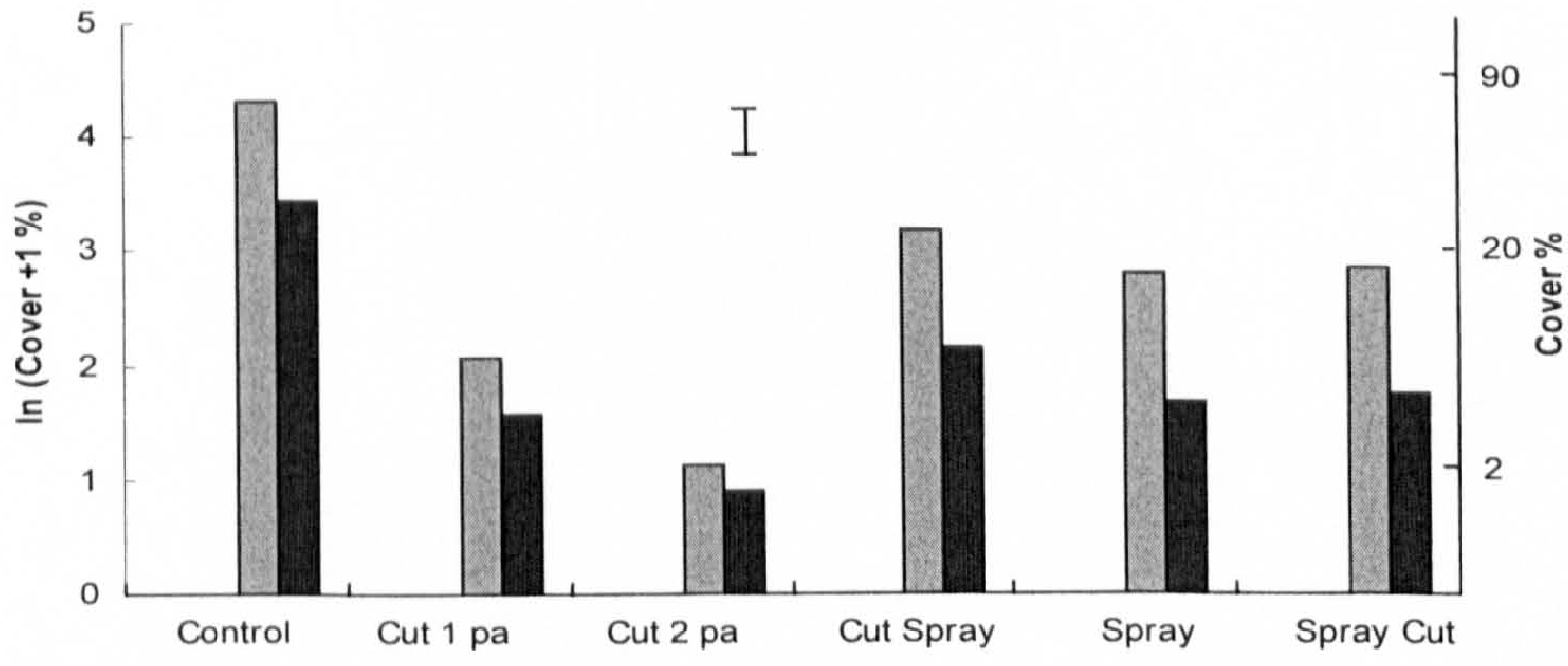


Fig. 5. Effect of spot spraying, restoration and bracken control treatments at Carneddau in August ((a and b) no treatment= square; spot spray= triangle; no restoration treatment= white; fertilizer= black; fertilizer and grass seed= grey; (c) no treatment= grey; spot spray= black) (a) spot spray on frond density (1st order, $F_{(1,36)}$=20.27 n=54) (b) restoration treatment x spot spray interaction on frond length (1st order , $F_{(2,36)}$=6.84 n=18 (Frt_GrS & No SbSbTr n=17) (c) bracken control x spot spray interaction on *Pteridium aquilinum* cover (overall effect, $F_{(5,36)}$=3.47 n=54). Elapsed Time = 0 is 1993.

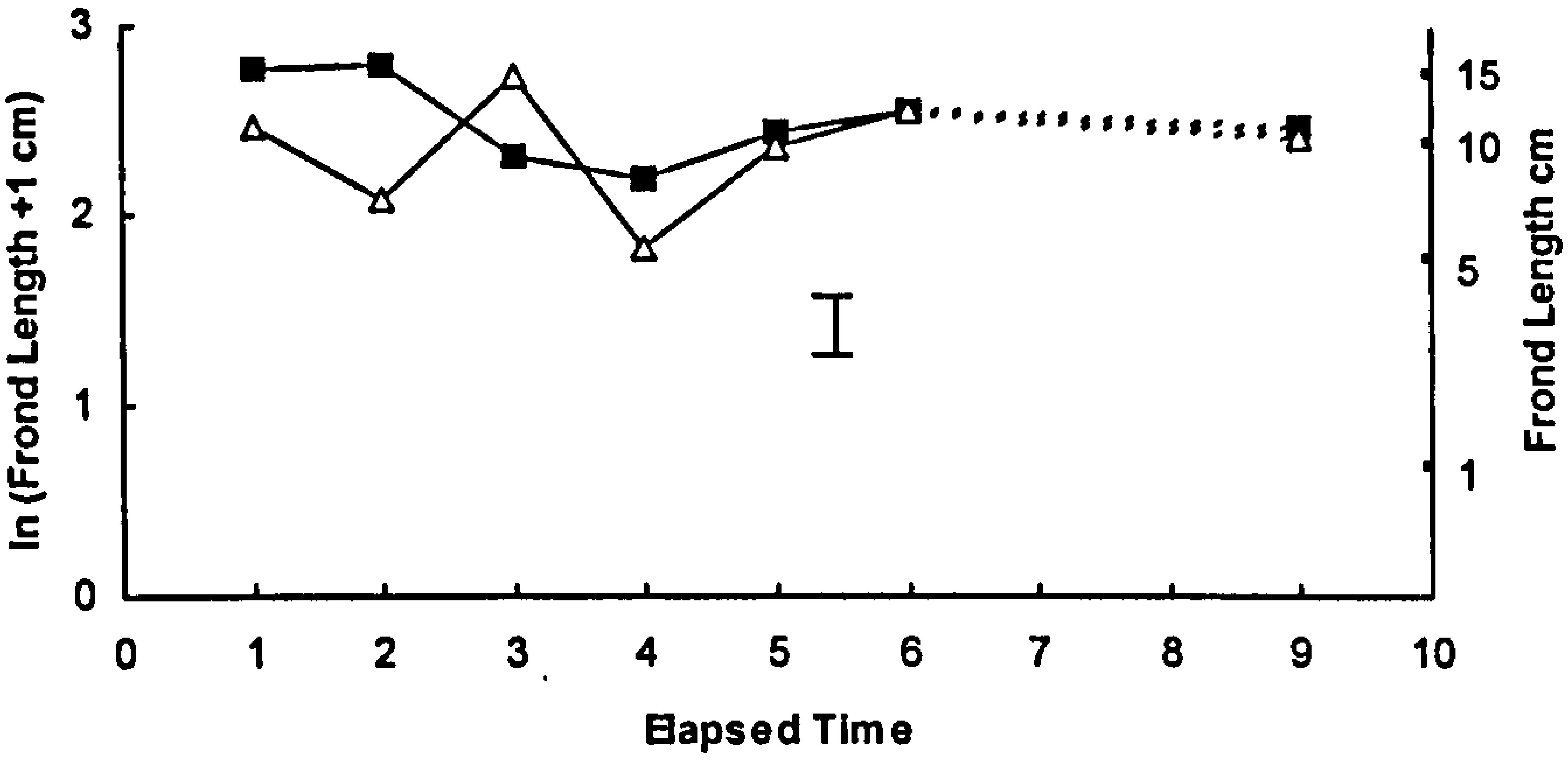


Fig.6. The effect of grass seeding on frond length at Sourhope in August (No seeding treatment= square; grass seeding= triangle) (6th order, $F_{(1,12)}$=8.95 n=24). Elapsed Time = 0 is 1993 for Sourhope 1 & 1994 for Sourhope 2. Seed treatment applied ET=1.

Factors affecting the restoration of heathland and acid grassland on *Pteridium aquilinum*-infested land across the UK: a multi site study

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Restoration Ecology
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Implications for practice

- It will be difficult to develop a one-size-fits-all policy for vegetation restoration after *P.aquilinum* control at the UK scale, because of the spatial effects found between- and within-sites.
- The isolated use of bracken control treatments has relatively little influence on the subsequent long-term vegetation development.
- Seeding with desired species produced varied results and is probably unnecessary for the restoration of acid grassland where there is some extant vegetation under the *P.aquilinum*.
- Seeding is needed where *Calluna vulgaris* heathland is the target and the *P.aquilinum* cover is dense.

Abstract

The variability in the success of *Pteridium aquilinum* (bracken) control and vegetation restoration has been highlighted as a major issue in the UK. Experiments were set up at *four different regional locations to assess* bracken control at the national scale and the impact of restoration practices at the local scale. Bracken control treatments (cutting once or twice per year, a combination of cutting and asulam spraying and asulam in year one), were combined with site-specific treatments designed to restore appropriate heathland or acid grassland vegetation. This paper considers the effects on the developing understorey vegetation, testing the hypotheses: (1) Local differences between sites would affect community change; (2) Treatments applied to control *P.aquilinum* (same at all sites) influences community change; and, (3) Treatments applied at the individual site level to restore vegetation influences community change towards the target vegetation.

There were a considerable number of spatial effects. It is, therefore, difficult to develop a one-size-fits-all policy for vegetation restoration within a national *P.aquilinum* control strategy. Few bracken control treatment effects were found and, where they were detected, it was only at single sites Thus, the development of target vegetation requires a combination of control and restoration treatments that take into consideration the aspects of that site. Only three species; *Deschampsia flexuosa*, *Galium saxatile* and *Campylopus introflexus* increased as a direct effect of the control treatments. Vegetation restoration was most successful in the cutting twice per year plots, the treatment with the greatest reduction in *P.aquilinum* cover.

Keywords: Bracken, Control, Vegetation recovery, *Calluna vulgaris*, Community change, Heath

Introduction

There is an increasing need for restoration ecology to assist in the development of national strategies, for example in the implementation of agri-environments schemes developed by the European Union (MAFF 1993, 1996) and Biodiversity Action Plans set to meet conservation objectives (Anon 1995a b). Policy-makers require practical management strategies that are cost-effective and deliverable in a wide range of situations. Inevitably, this will require some form of multi-site experiment to ensure that there is: (a) a broad geographical coverage, and (b) a reasonable coverage of the types of restoration problem likely to be encountered. Surprisingly, there have been relatively few attempts to carry out such large-scale, multi-site experiments in ecological restoration especially over the longer-term; most studies have been either single-site or of short duration (< 8 years) (e.g. Pywell et al. 2002; Pakeman 2004; Marrs et al. 2004).

The difficulty in providing general advice to policy makers becomes more complex when the restoration aims are to control a single invasive weed which invades a range of community types and establish new understorey vegetation as the required target vegetation will vary in different situations. One example of this problem is *Pteridium aquilinum* (L.) Kuhn (bracken) (nomenclature; Stace (1997), for higher plants; Hill et al. (1991, 1992, 1994) for bryophytes; Coppins (2002) for lichens) control in the United Kingdom, were the policy aim is to reduce *P.aquilinum* infestations and restore either heathland or grassland vegetation. Dense *P.aquilinum* is a problem species for conservation in most situations, as it is a long-lived robust clonal species (Le Duc et al. 2003) producing a dense litter layer that prevents the establishment of other species (Frankland 1976) and competes effectively with heathland and grassland species, resulting in a reduction in diversity of plant species (Pakeman & Marrs 1992).

Thus, ecological restoration of dense *P.aquilinum* patches requires at least two treatment strategies: control of the *P.aquilinum*, and restoration of suitable target vegetation. Under experimental conditions, and in practice, *P.aquilinum* control is often highly variable and gives conflicting results (Le Duc et al. 2000) and vegetation development during bracken control is often slow and unpredictable, especially in upland areas of the UK (Marrs et al. 1998a). This variability in the success may be due either to regional effects (climate, geology), or to localized effects interacting with the management applied. Localized effects might be ascribed to (1) local microclimate or soil conditions,

(2) local standing vegetation, (2) its derived seed rain, (4) recruitment from the soil propagule bank, and (5) potential seed rain derived from the surrounding landscape.

In order to develop a national policy for bracken control and restoration, a series of experiments were set up at four regional locations throughout the UK; at two of these locations replicated experiments were set up to assess local scale effects. The experiments assessed the efficacy of five treatments (cutting once or twice per year, a combination of cutting or asulam spraying in year one followed by asulam spraying or cutting in year two and asulam in year one only) designed to control *P.aquilinum* relative to an untreated comparison in a range of contrasting ecological situations (Le Duc et al. 2007; Cox et al. 2007). Accordingly, these control treatments were combined with site-specific treatments designed to restore appropriate heathland or grassland vegetation, as thought appropriate to the site. Thus, the experiments were a compromise to assessing the success bracken control at the national scale and local scale control/restoration practices.

We hypothesized that: (1) Local differences between sites would affect community change; (2) Treatments applied to control *P.aquilinum* (same at all sites) influences community change; and, (3) Treatments applied at the individual site level to restore vegetation influences community change towards the target vegetation. The experiments started in 1993 or 1994 and were monitored for 9 or 10 years.

Methods

Experimental sites

Six experiments were set up at four different regional locations in the UK (Fig. 1, Table 1).; Cannock Chase; Hordron Edge, North Peak Environmentally Sensitive Area,; Carneddau; and SourhopeSites are referred to hereafter as Cannock, Carneddau, Peak and Sourhope.

Target vegetation for Cannock and Peak is *Calluna* heath and acid grassland for Carneddau and Sourhope. The four sites cover a range of different physical and vegetation characteristics leading to differences in litter abundance, rhizome mass and above ground cover of *P.aquilinum* (Table 1). The untreated plots give an estimate of initial conditions at each site. After *P.aquilinum,* bracken litter has the greatest percentage cover. The acid grassland sites, Sourhope and Carneddau, were most species-rich sites with the heath Cannock sites having the lowest number of species. In August the lowest *P.aquilinum* cover was recorded at the acid grassland sites Sourhope (41 %) and Carneddau (48%) the most species-rich sites, the species-poor Cannock sites had the greater *P.aquilinum* cover.

Experimental design

A split-plot design was used throughout, with the main plots receiving one of five bracken control treatments or left untreated as a control, and the sub-plots receiving vegetation restoration treatments. The experiment at Peak had a split-split-plot design from the start, and the one at Carneddau was changed to a split-split-plot design during its course to accommodate additional spot-spraying treatment (Table 1). At Carneddau and Peak the bracken patch was large enough to accommodate three blocks, but at Cannock and Sourhope only two blocks were possible so the entire experiment was replicated nearby (< 2.5 km distant) (Le Duc et al. 2000). Each block was divided into six plots (10 × 40 m) separated by 2 m buffers. Plots were split into two (10 × 18 m) or three sub-plots (10 × 12 m) according to the experiment, with 4 m or 2 m buffer zones. Further splitting was carried out in a similar fashion, dividing sub-plots into two or three sub-sub-plots (10 × 5 m).

Treatments

Six main-plot, bracken control treatments were applied to all experiments: (1), untreated (experimental control); (2) cut once per year in June (Cut1pa); (3) cut twice per year in both June and August (Cut2pa); (4) a single June cut in year one followed by asulam spraying in year two (CutSpray); (5)

asulam in year one only (Spray); (6) asulam in year one followed by a single June cut in year two (SprayCut). Asulam (Asulox, Bayer CropScience PLC) was sprayed in late August or early September at 4.4 kg active ingredient ha^{-1} (11 litres Asulox ha^{-1}) in 400 litres water ha^{-1} using a standard knapsack sprayer. In two experiments (Sourhope 1, Cannock 2, Table 1) plots treated to a single application of herbicide were re-treated with asulam in 1996, three years after first treatment (Le Duc et al. 2000).

Unlike the main treatments, the sub- and sub-sub-treatments were site-specific vegetation restoration treatments designed to match individual site characteristics (Table 1). The sub-treatments and sub-sub-treatments were all associated with vegetation restoration. They included: grass seeding with *Festuca ovina*:*Agrostis capillaris*:*Poa pratensis* at 5:4:3, plus a small quantity of *Rumex acetosa*, at an application rate of 60 kg ha^{-1}; *Calluna vulgaris* seeding with brash comprising 20 cm stems at 13 t ha^{-1} and nurse crop, *Agrostis castellana*, at 12 kg ha^{-1}; *Calluna vulgaris* seeding with *Calluna* litter at 1.2 t ha^{-1}, sucked from under mature heather, together with the same nurse crop; stock-proof fencing; fertilizer (ENMAG, Zeneca) application at 150 kg ha^{-1}; harrowing using a chain harrow. In addition, spot-spraying with asulam (same strength mixture as above) was applied at Carneddaau in late summer 1997.

Monitoring

Vegetation was monitored in June each year before application of bracken control treatments. Quadrats (1 m × 1 m) were placed at pre-selected random co-ordinates on 1 m grids within each sub- (sub-) plot and cover of all plant species present was estimated visually. Two quadrats were examined each year in the smaller plots at Careneddau and Peak and three in the larger plots at Cannock and Sourhope.

Data analysis and presentation

Data were transformed using standard procedures (Sokal & Rohlf 1995), species richness using $(Y + 0.5)^{0.5}$, and species cover using $\ln(Y + 1)$. Estimates of values per treatment combination per block were obtained by combining data per quadrat, after transformation, by sub- (sub-) plot.

Individual response variables (species cover, species richness and measured abiotic factors) were analyzed for change through time for each site separately. Some taxa (eg *Cladonia* spp. *Betula* spp., *Carex* spp. and *Festuca* spp.) were grouped into aggregate taxa, denoted spp. As our objective was to measure the response of species through time, repeated-measures ANOVAs with the method of polynomial contrasts were used (Gurevitch & Chester 1986). The value of this approach is that it is possible to test for treatment effects as in ANOVA, but the shape of the temporal trends of these treatment effects can also be identified. This approach becomes more useful with longer-term datasets. Results are presented in the text as; the order number (referring to the shape of the polynomial curve, 1st order being linear, and subsequent orders being the equivalent polynomial (i.e. 2nd order = quadratic), the *F*-test statistic and n. As only significant results after Bonferroni correction are discussed here, they are conservative.

Time was denoted as elapsed time, with the start year designated year=0. Analysis was carried out using PROC GLM (SAS 1989). For each site we used the appropriate analysis of variance model; however for Cannock and Sourhope we initially analyzed both experiments together, with experiment included as the first level in a split-split-split plot design. Where a significant difference was indicated but that species was absent from one experiment, the analysis was repeated for the single experiment where the species was present.

The analysis of variance model changed when new treatment combinations were added into an experiment, changing the design from a split-plot to a split-split-plot one; thus different segments of the time series were analyzed using different models. At Sourhope there was an additional problem in 2001, data could not be collected because of the Foot and Mouth epidemic in Britain. At this site the experiments were also started in different years, and accordingly the loss of the 2001 data resulted in the absence of two years information.

Bonferroni correction was used to adjust for the Type I error rate (Sokal & Rohlf 1995; Cabin & Mitchell 2000). For the June sampling there were 85, 131, 110 and 144 analyses at Cannock, Carneddau, Peak and Sourhope respectively. With $\alpha = 0.05$ the critical probability levels of 0.0006, 0.0004, 0.0005 and 0.0004 were used to assess significance. A common problem with this type of data is that many species datasets contain a large number of zero entries. Here, only species which were present in at least 20% of all recorded quadrats are presented. Data for other species where a significant response was found are available from the corresponding author.

A very large number of significant results were derived, even after Bonferroni correction. In order to simplify the presentation and interpretation of the results a three level approach to data presentation and analysis audit has been used. Level 1 is the raw data held in the web database; www.appliedvegetationdynamics.co.uk, Level 2 includes all the significant results in graphical form along with tables of all significant results from the repeated measures ANOVA using polynomial contrasts, held in an electronic Appendix as an Excel worksheets, and Level 3 are the data presented here, which includes just the lowest significant order found in the polynomial contrast analysis.

Results

Hypothesis 1: Local differences between sites would affect community change

Effects through time

Significant variation in time was found for 10 species across all four sites (Table 2). Three main response patterns for time effects were detected (Table 2); Type 1, are species starting from zero or a very low level, increasing to reach a peak before falling again; Type 2, are species increasing steadily over time and Type 3 are species declining over time.

Species richness showed a Type 1 response at the acid grassland site Carneddau with a significant decline starting in 1998 (ET=5) after an initial increase. Declining from 10.5 species m^{-2} in 1998 to 9 species m^{-2} in 2003 (1st order, $F_{(1,10)}=29.85$ n=216). For individual species different responses were detected at different sites and in different time periods on the same sites e.g. *Galium saxatile* at the Carneddau acid grassland site (1st order, $F_{(1,10)}=136$ n= 162) and the Peak heath site (3rd order, $F_{(1,10)}=239$ n= 216). Although *G.saxatile* had similar % cover at both sites (ranging from 0.7 to 10.0 %) and a dip in year 7 (2000) the two sites showed different response patterns. At Peak an overall increase through time was observed, perhaps influenced by this species' significant response to bracken control treatments. At Carneddau, *G.saxatile* cover increased to reach a peak in year 4 (1997) before declining; no other significant effects were observed.

Spatial effects and interactions

Between-experiment spatial effects

Two types of responses were detected. The first included species that were present at one experiment but not the other, these species normally appeared in small quantities in a limited number of years. At Cannock these were: *F.ovina, Dicranum bonjeanii* and *Quercus* spp. present only at Cannock 1; *Pinus sylvestris* and *Vaccinium vitis-idaea* present only at Cannock 2, and at Sourhope: *Dactylis glomerata* and *Helictotrichon pratense* were found only at Sourhope 2. Only *V.vitis-idaea* appears in more than 20% of quadrats. The second were species that were present on both experiments but there was a significant difference in cover between experiments. *R. acetosella* (6th order, $F_{1,2}=3207$ n=36) with greater cover at Cannock 1 compared to Cannock 2 and *Agrostis vinealis* with a greater cover at Sourhope 1 (1st order, $F_{1,2}=13741$ n=24). Superimposed on the site responses for *A. vinealis* at

Sourhope was an obvious cyclic effect for at least 6 years, as there was no data between years 7-9 so no inference can be drawn for this period.

Significant experiment × bracken control × restoration treatment interactions

D.flexuosa (2nd order, $F_{(5,12)}$ =12 n=2) at Sourhope displayed a complex series of responses (Fig. 2), with a differential cover between the experiments, being greater at Sourhope 1 (1-25%) compared to Sourhope 2 (0.5-5%). At Sourhope 1 (Fig. 2i & ii), where no seeding was applied *D. flexuosa* cover was lowest in the Spray plots. This was followed by a recovery period until declining again after year 6. In the seeded treatment SprayCut follows a similar pattern with the increase in *D. flexuosa* cover being greater but again declining after year 6. At Sourhope 2 (Fig. 2iii & iv), *D. flexuosa* was greater in the CutSpray treatment regardless of whether or not seed was applied.

Hypothesis 2: Treatments applied to control *P.aquilinum* (same at all sites) influences community change

Of the 470 species tested across the four sites, bracken control treatments on their own increased only three species; two higher plants and one bryophyte, at the heath sites. No positive effects were found at the acid grassland sites (summarized, Table 3). All bracken control treatments increased *D. flexusoa* cover (1st order, $F_{(5,10)}$= 17.31 n=12, Fig.3a), *Campylopus introflexus* (1st order, $F_{(5,10)}$= 12.1 n=12, Fig. 3b) at Cannock and *G.saxatile* (5th order, $F_{(1,12)}$=13.6 n=18, Fig. 3c) at Peak in comparison to the untreated plots. A steady increase in cover over time resulted in the Cut2pa plots having the greatest cover for all three species by the final year of sampling. Maximums of 20% (*D.flexuosa*) and 24% (*G.saxatile*) were reached in the final year, with *C.introflexus* reaching 4.5% in the penultimate year. The increase in *D.flexuosa* occurred from an initially small cover (1.25%) despite having the greatest cover of any species, after *P.aquilinum* and litter, in the untreated plots at Cannock 1. A similar pattern was seen for *G.saxatile* at Peak with a 0.5% cover in untreated plots. The increase in already common species could be replacing the previously dominant bracken litter which fell from 65 and 85% in untreated plots to 19 and 1% in cut twice per year plots at Cannock and Peak, respectively.

Pseudoscleropodium purum (overall effect, $F_{(5,10)}$=14.09 n=108,) at Carneddau was most abundant in the untreated plots. This species had comparatively low cover, reaching a maximum of 0.4%.

All bracken control treatments at Peak increased species richness in a linear model (1st order, $F_{(5,10)}=27.01$ n=18) compared to the untreated plots, and by 2003 the cutting treatments were the most successful.

Hypothesis 3: Treatments applied at the individual site level to restore vegetation influences community change towards the target vegetation

Grazing at the Peak Calluna *heath*

Two species showed an overall effect of grazing (Table 4). *D.flexuosa* (overall effect, $F_{(1,12)}=32.5$ n=540) had a greater cover in the fenced treatment. In contrast, *F.ovina* (overall effect, $F_{(1,12)}=33.2$ n=540) and species richness (overall effect, $F_{(1,12)}=40.8$ n=540) were greater in the unfenced treatment. Three species (*F.ovina* (3rd order effect, $F_{(1,12)}=26.5$ n=54), *F.rubra* (1st order effect, $F_{(1,12)}=23.2$ n=54), *Hypnum jutlandicum* (1st order effect, $F_{(1,12)}=25.1$ n=54) showed a significant time × fencing interaction, increasing in the unfenced treatment.

Fertilizer/disturbance at the Cannock Calluna *heath*

Fertilizer addition produced a lower *Calluna vulgaris* cover at Cannock 2 (4th order, $F_{2,24}=10.5$ n=12) either no treatment or surface disturbance + fertilizer until year 9 when it increased inline with the other two treatments (Fig. 4). Although found at both sites *C.vulgaris* was consistently greater at Cannock 2 (Fig. 4), restoration treatments were significant only at this site.

Seeding at the Peak Calluna *heath site*

At Peak *Calluna* brash addition increased *C.vulgaris* cover to 0.19% (overall effect, $F_{(2,48)}=9.63$ n=360), whereas *Calluna* seeding had very little impact when compared to untreated plots, both with a cover of 0.07%.

Grass seeding at the acid grassland sites

There were no significant effects of seeding or any of its interactions on any species at Carneddau or Sourhope, this included the sown species.

Effects of spot spraying at the Carneddau acid grassland

F.ovina showed an increase in cover in sprayed plots, (overall effect; 12% compared to 8%; $F_{1,36}=29.24$ n=54).

Discussion

This series of long-term experiments allowed us to test a series of treatments deigned to control an invasive species (*P.aquilinum*) and restore different target communities. The results assist in developing national implementation policies.

Hypothesis 1: Local differences between sites would affect community change

There were a considerable number of spatial effects detected, between experiments on the same site and as a result of spatial effects in interaction with applied treatments. This result might appear an obvious one, in that it confirms that local spatial effects control restoration processes. Results were, however, complex and contradictory. For example, at Sourhope two experiments located < 2.5 km from each other showed; (1) Complex significant results, including synchronous peaks of *A.vinealis* in the different experiments, which were started in different years, suggesting that weather was the main driver for this species, although this remains to be confirmed experimentally. (2) *D.flexuosa* responds differently to the same treatments at the two Sourhope sites. Observations at the Peak heathland in March 2005 illustrate the importance of local spatial effects. All of the mature tree specimens (*Betula pubescens, Sorbus acuparia* and *Quercus petraea*) in the experimental area were in the un-grazed plots of Block A, and all were approximately 10 years old (M.G. Le Duc & H.A. McAllister, personal communication). This suggests that recruitment occurred as the *P.aquilinum* vegetation was initially controlled and this particular block was nearest to the seed sources (Tong et al. 2006) or had better access to dispersal vectors. There is also potential for similar colonization at other sites with *Betula* stands common in the vicinity of Cannock, Sourhope (Ghorbani 2005). However, natural colonization can take many years where bracken had been controlled (Marrs & Lowday 1992). With bracken litter acting as a potential trap for *C.vulgaris* (Ghorbani 2005) and, potentially, other seeds.

Taken collectively, these spatial effects suggest that it is almost impossible to develop a "one-size-fits-all" national policy that will guarantee the development of a predicted target vegetation community, because community development involves so many uncontrollable factors, for example, the regional and local seed pool, dispersal of seed on to a given site, which will depend on micro-climatic factors, the site propagule bank and the site conditions when the seeds arrive or begin to germinate (Harper 1977). *C.vulgaris* was found to be common in the seed bank at both Cannock sites (Ghorbani 2005). Although less potential is seen for development of target species from existent seed banks at Sourhope and Carneddau in addition the heavily grazed dense sward at Carneddau limiting colonization (Ghorbani 2005).

Hypothesis 2: Treatments applied to control *P.aquilinum* (same at all sites) influences community change

Relatively few effects of the bracken control treatments were found on the cover of other plant species, and where they were detected, it was only at single sites. At the acid grassland sites (Carneddau and Sourhope) no species where found to increase significantly. At the *Calluna* heath sites (Cannock and Peak) no target species were significantly increased although two common higher plants and one bryophyte did increase their cover. Experiments aimed at restoring oligotrophic heathland in the Netherlands found mixed results, after 25 years of cutting there had been an increase in target species but the community still resembled the original one, typical of eutrophic conditions (Bakker et al. 2002). Jacquemart et al. (2003) also cutting as a control treatment reduced the problem species (*Molinia*) it had little impact on vegetation composition. With added problems when trying to regenerate *Calluna* heath including; evidence that *Calluna* establishment from seed can be hindered by competition (Allison & Ausden, 2004), as it is able to establish and grow well on arable soil in the absence of other species (Lawson et al., 2004); and the establishment of *Calluna* from seed may also be hindered by the presence of bracken litter. Experiments conducted on old *Pinus* plantation land found the removal of the litter and humus layers increased *Calluna* establishment (Allison & Ausden, 2006).

The increase of *D.flexuosa*, *G.saxatile* and *C.introflexus* by treatment particularly in cutting twice per year compares to the greatest reduction in *P.aquilinum* cover by the later years of sampling. The increase of *C.introflexus* at Cannock where the desired habitat is *Calluna* heath could have mixed effects. Carpets of *C.introflexus* were shown to have a negative effect on seed germination but a positive effect on seedling performance once germination had occurred (Equihua & Usher 1993).

Whilst it is accepted that it is unreasonable to expect different species to respond to the same main treatments at every site, it is important to remember that the sites were replicated on relatively similar vegetation (heathland and acid grassland). It must be concluded that bracken control treatments, on their own, have relatively little influence on the subsequent long-term development of vegetation

Hypothesis 3: Treatments applied at the individual site level to restore vegetation influences community change towards the target vegetation

At Peak, the response of *D.flexuosa* to grazing was predictable. The reduction of *D.flexuosa* with sheep grazing is well known (Rawes 1983; Anderson & Radford 1994; Pakeman 2004) and it is noted that the species is often preferentially grazed (Duffey et al. 1974).

It is clear that seeding worked best at Peak (with *C.vulgaris* when applied as brash and seeded *A.castellana* increasing) and produced less satisfactory results elsewhere, even though the treatment combinations were designed to produce site-specific targets. The selection of sites was designed to provide a range of bracken control scenarios across the UK, and they can broadly represent high bracken infestation on acid grassland sites and heathland sites. At the grassland sites, there was a depauperate understory flora, rather than no existing flora, at the start of the experiment and the results suggest that in such situations it is unnecessary to add additional species or spend a great deal of effort in vegetation restoration; natural colonization processes will be sufficient to establish acid grassland. For sites like Peak and Cannock where the original target vegetation was *Calluna* heath and restoration treatments were designed to target this, both Marrs et al. (1998b) and Le Duc et al. (2007) conclude that grass heath vegetation is the most likely outcome on sites. Increased soil nutrients may be a factor here as *C. vulgaris* tends to be found on infertile soils (Gimingham 1992), although fertilizer addition has been prescribed for heathland restoration elsewhere in the uplands (Anon 1988). High frond biomass is also associated with increased levels of nitrogen (Watrud et al. 2003)

Conclusions

The isolated use of bracken control treatments has relatively little influence on the subsequent long-term development of target vegetation, with a few already abundant species increasing their cover. Thus the development of target vegetation requires a combination of control and restoration treatments that take into consideration the aspects of that site. This may include management for more than one factor, for example, soil condition and the present seed bank (De Graaf et al. 1998).

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References

Allison,M. & Ausden,M. 2004. Successful use of topsoil removal and soil amelioration to create heathland vegetation. Biological Conservation **120:** 221-228.

Allison,M. & Ausden,M. 2006. Effects of removing the litter and humic layers on heathland establishment following plantation removal. Biological Conservation **127:** 177-182.

Anderson, P. & E. Radford. 1994. Changes in vegetation following reduction in grazing pressure on The National-Trust Kinder Estate, Peak District, Dersbyshire, England. Biological Conservation 69: (1) 55-63.

Anon. 1995a. Biodiversity UK Steering Group Report, Vol I. Action Plans. HMSO, London.

Anon. 1995b. Biodiversity UK Steering Group Report, Vol I. Meeting the Rio Challenge. HMSO, London.

Anon. 1988. Heathland restoration: A handbook of techniques. British Gas plc, Southampton.

Bakker, J.P. & Berendse, F. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology and Evolution **14:** (2) 63-68.

Cabin, R.J. & R.J. Mitchell. 2000. To Bonferroni or not to Bonferroni: when and how are the questions. Bulletin of the Ecological Society of America **81:** 246-248.

Coppins, B.J. 2002. Checklist of the lichens of Great Britain and Ireland. British Lichen Society, London.

Cox, E.S., R. H. Marrs, R.J. Pakeman, and M.G. Le Duc. 2007. A multi-site assessment of bracken control effectiveness across the UK. Applied Vegetation Science (Accepted).

De Graaf, M.C.C., Verbeek, P.J.M., Bobbink,R., Roelofs,J.G.M. 1998. Restoration of species-rich dry heaths: the importance of appropriate soil conditions. Acta Botanica Neerlandica **7:** (1) 89-111.

Duffey, E., M.G. Morris, J. Sheail, L.K. Ward, D.A. Wells, and T.C.E. Wells. 1974. Grassland Ecology and Wildlife management. Chapman and Hall, London, 281pp.

Equihua,M. & Usher,M.B. 1993. Impact of carpets of the invasive moss *Campylopus introflexus* on *Calluna vulgaris* regeneration. Journal of Ecology **81:** 359-365.

Frankland, J.C. 1976. Decomposition of bracken litter. Botanical Journal of the Linnean Society **73:** 133-143.

Ghorbani, J. 2005. Restoration of bracken-dominated land: the response of propagule banks. PhD thesis. University of Liverpool.

Gimingham, C.H. 1992. The lowland heathland management handbook. English Nature, Peterborough.

Gurevitch, J., and S.T. Chester, Jr. 1986. Analysis of repeated measures experiments. Ecology **67:** 251-255.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, London.

Hill, M.O. 1996. TABLEFIT VERSION 1.0, For Identification of Vegetation Types. ITE, Huntingdon.

Hill, M.O., C.D. Preston, and A.J.E. Smith. (eds). 1991. Atlas of the Bryophytes of Britain and Ireland, Volume 1 Liverworts (Hepaticae and Anthocerotae). Harley Books, Colchester.

Hill, M.O., C.D. Preston, and A.J.E. Smith. (eds). 1992. Atlas of the Bryophytes of Britain and Ireland, Volume 2 Mosses (except Diplolepideae). Harley Books, Colchester.

Hill, M.O., C.D. Preston, and A.J.E. Smith. (eds). 1994. Atlas of the Bryophytes of Britain and Ireland, Volume 3 Mosses (Diplolepideae). Harley Books, Colchester.

Jacquemart,A.L., Champluvier,D. & De Sloover,J. 2003. A test of mowing and soil-removal restoration techniques in wet heaths of the High Ardenne, Belgium. Wetlands **23:** 376-385.

Lawson,C.S., Ford,M.A., Mitchley,J. & Warren,J.M. 2004. The establishment of heathland vegetation on ex-arable land: the response of *Calluna vulgaris* to soil acidification. Biological Conservation **116:** 409-416.

Le Duc, M.G., R.J. Pakeman, P.D. Putwain, and R.H. Marrs. 2000. The variable responses of *Pteridium aquilinum* fronds to control treatments in Great Britain. Annals of Botany **85:** (Supplement B) 17-29.

Le Duc, M.G., R.J. Pakeman, and R.H. Marrs. 2003. Changes in the bracken rhizome system subjected to long-term experimental treatment. Journal of Applied Ecology **40:** 508-522.

Le Duc, M.G., R.J. Pakeman, and R.H. Marrs. 2007. A restoration experiment on moorland infested by *Pteridium aquilinum*: Plant species responses. Agro-Ecosystems & Environment **119:** 53-59.

MAFF. 1993. Environment matters. Environmentally Sensitive Areas. Ministry of Agriculture, Fisheries and Food, London.

MAFF. 1996. Environment matters. The Countryside Stewardship Scheme: Information for farmers and land managers. Ministry of Agriculture, Fisheries and Food, London.

Marrs, R.H., and J.E. Lowday. 1992. Control of bracken and the restoration of heathland. II. Regeneration of the heathland community. Journal of Applied Ecology 29: 204-211.

Marrs, R.H., S.W. Johnson, and M.G. Le Duc. 1998a. Control of bracken and the restoration of heathland. VI. The response of fronds to 18 years of continued bracken control or 6 years of control followed by recovery. Journal of Applied Ecology 35: 479-490.

Marrs, R.H., S.W. Johnson, and M.G. Le Duc. 1998b. Control of bracken and the restoration of heathland. VIII. The regeneration of the heathland community after 18 years of continued bracken control or 6 years of control followed by recovery. Journal of Applied Ecology 35: 857-870.

Marrs, R.H., J.D.P. Phillips, P.A. Todd, J. Ghorabani, and M.G. Le Duc. 2004. Control of Molinia caerulea on upland moors. Journal of Applied Ecology 41: 398-411.

Pakeman, R.J. 2004. Consistency of plant species and trait responses along a productivity gradient: a multi-site analysis. Journal of Ecology 92: 893-905.

Pakeman, R.J., and R.H. Marrs. 1992. The conservation value of bracken *Pteridium aquilinum* (L.) Kuhn - dominated communities in the UK, and an assessment of the ecological impact of bracken expansion and removal. Biological Conservation 62: 101-114.

Pywell, R.F., J.M. Bullock, A. Hopkins, K.J. Walker, T.H. Sparks, M.J.W. Burke, and S. Peel. 2002. Restoration of species-rich grassland: assessing the limiting processes using a multi-site experiment. Journal of Applied Ecology 39: 294-309.

Rawes, M. 1983. Changes in two high altitude blanket bogs after the cessation of sheep grazing. Journal of Ecology 71: 219-235.

Rodwell, J.S. 1991a. British Plant Communities: Vol. 1. Woodlands and scrub. Cambridge University Cambridge.

Rodwell, J.S. 1991b. British Plant Communities: Vol. 11. Mires and heaths. Cambridge University Cambridge.

Rodwell, J.S. 1992. British Plant Communities: Vol. 111. Grasslands and montane communities. Cambridge University Cambridge.

SAS. 1989. SAS/STAT User's Guide Version 6. 4th edn. SAS Institute, Cary, NC.

Sokal, R.R., and F.J. Rohlf. 1995. Biometry. 3rd ed. W.H. Freeman & Co., New York.

Stace, C. 1997. New Flora of the British Isles, 2nd edn. CUP, Cambridge.

Tong, C., M.G. Le Duc, J. Ghorbani, and R.H. Marrs. 2006. Linking restoration to the wider landscape: A study of a bracken control experiement within a upland moorland landscape mosaic in the Peak District, UK, Landscape and Urban Planning 78 (1-2): 115-134.

Watrud,L.S., Maggard,S., Shiroyama,T., Coleman,C.G., Johnson,M.G., Donegan,K.K., Di Giovanni,G., Porteous,L.A. & Lee,E.H. 2003. Bracken (Pteridium aquilinum L.) frond biomass and rhizosphere microbial community characteristics are correlated to edaphic factors. Plant and Soil 249: 359-371.

TABLE 1. Description of the experiments. Entries for experimental designs represent: number of blocks/number of plots per block/number of sub-plots per plot/number of sub-sub-plots per sub-plot. These codes are truncated from the right when lower experimental levels do not exist. More than one design for a single experiment indicates successive splitting in time. Species richness (number of species m^{-2}) in standing vegetation, *P.aquilinum* cover and litter abundance and the total rhizome mass in untreated control plots are presented; back-transformed means with transformed means ± SE in parentheses ($Y' = (Y+0.5)^{0.5}$ for species richness; $Y' = \text{Ln}(Y+1)$ for *P.aquilinum* cover and litter cover). Mean total dry mass of rhizomes are presented, SE in parentheses (Le Duc et al. 2003).The National Vegetation Classification (NVC, Rodwell 1991a,b & 1992) descriptions (the codes are explained in the footnote) represent the pre-treated condition, the data in brackets being the results obtained when bracken was left out of the calculations. The measured fit was obtained using the computer program TABLEFIT version 1.0 (Hill 1996), and are rated: > 80 very good, > 70 good, > 60 fair, < 60 poor. † - additional fertilizer was added at Cannock 1 in 1996.

Location	Sourhope Estate		Hordron Edge	Carneddau Estate	Cannock Chase	
Latitude:	2° 14' W		1° 41' W	3° 58' W	2° 2' W	
Longitude;	55° 28' N		53° 23' N;	53° 13' N	52° 46' N	
Experiment:						
- Name	Sourhope 1	Sourhope 2	Peak	Carneddau	Cannock 1	Cannock 2
- Started	1993	1994	1993	1993	1993	1993
- Design	1994-03 = 2/6/2	1995-03 = 2/6/22/6/2	1994-02= 2/6/23/6/2/3	1993=3/6 1994-97 =3/6/3 1998-03 =3/6/3/2	1994-03= 2/6/3	1994-03= 2/6/3
National grid reference	NT 861 202	NT 846 210	SK2187	SH6871	SJ 976 200	SJ 987 181
- Main treatments (bracken control)*	All + weed-wiping	All	All	All	All	All + weed-wiping
- Sub-treatments	Grass seeding		Stock fencing	Grass seeding & fertilizer	Harrowing & fertilizer†	
- Sub-sub-treatments	-	-	*Calluna* seeding (brash & litter)	Spot-spray	-	-
Physical:						
- altitude (m)	325	285	290	350	145	165
- aspect (°)	280	130	275	190	140	125
- slope (°)	16	22	9	20	20	18
Vegetation:						
P.aquilinum Cover (%) August	59.99 (4.1±0.1)	41.48 (3.6±0.2)	80.60 (4.7±0.1)	47.75 (3.9±0.2)	96.23 (4.6±0.0)	83.65 (4.4±0.0)
Litter cover (%)	6.48 (1.2±1.2)	3.77 (1.2±0.9)	84.02 (4.4±0.3)	33.59 (3.5±0.1)	69.13 (4.0±1.0)	61.46 (3.9±0.9)
Dominant Species	Holcus mollis	Agrostis capillaris	Deschampsia flexuosa	Agrostis capillaris	Deschampsia flexuosa	Vaccinium myrtillus
Species Richness	10.76 (3.35±0.02)	12.14 (3.56±0.02)	5.19 (2.39±0.01)	9.59 (3.18±0. 01)	2.88 (1.84±0.01)	3.43 (1.98±0.01)
- NVC class	U4e (U4e)	U4a (U4a)	U20 (H18)	U4a (U4a)	W16 (U2b)	W16 (U2b)
- fit	75 (77)	61 (64)	77 (83)	74 (79)	78 (67)	61 (55)

NVC classes represented are:

U2b	*Vaccinium myrtillus* sub-community of *Deschampsia flexuosa* grassland
U4a	Typical sub-community of *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland
U4e	Vaccinium myrtillus-Deschampsia flexuosa sub-community of *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland
U20	*Pteridium aquilinum-Galium saxatile* community
H18	*Vaccinium myrtillus-Deschampsia flexuosa* heath
W16	*Quercus* spp.-*Betula* spp.-*Deschampsia flexuosa* woodland

**Main treatments: (1) Untreated control; (2) Cut once per year; (3) Cut twice per year; (4) Cut in year 1 and sprayed with herbicide in year 2; (5) Sprayed only; (6) Sprayed in year 1 and cut in year 2.

TABLE 2. Species with significant variation through time not associated with any treatment. Type 1, are species starting from zero or a very low level, increasing to reach a peak before falling again; Type 2, are species increasing steadily over time, and Type 3 are species declining over time. After Bonferroni correction P= 0.0006, 0.0004, 0.0005 and 0.0004 for Cannock, Carneddau, Peak and Sourhope respectively.

Species	**Site**	**Pattern Type**	**Order of Effect**	**Df**	**F Value**
Deschampsia flexuosa	Peak	3	2nd	1,10	106
Festuca ovina	Carneddau 98-03	3	4th	1,10	615
Festuca rubra	Carneddau 98-03	2	2nd	1,10	242
Galium saxatile	Carneddau 94-97	1	1st	1,10	136
Galium saxatile	Peak	2	3rd	1,10	249
Pleurozium schreberi	Carneddau 98-03	2	3rd	1,10	57.9
Rhydtidiadelphus squarrosus	Carneddau 94-97	1	1st	1,10	31.8
Rhydtidiadelphus squarrosus	Carneddau 98-03	1	4th	1,10	123
Rumex acetosella	Cannock	2	6th	1,10	3077
Species Richness	Carneddau 98-03	2	1st	1,10	29.85

TABLE 3. A summary of the significant species responses to the multi-site bracken control treatments. Experiment in the Significant Effect column refers to a significant difference between Sourhope 1 and Sourhope 2.

Site	Species	Species Response	Treatments which increased species cover	Significant Effect
Cannock	*Deschampsia flexuosa*	Increased	Cutting twice per year	Bracken Control
Cannock	*Campylopus introflexus*	Increased	Cutting twice per year	Bracken Control
Peak	*Galium saxatile*	Increased	Cutting twice per year	Bracken Control
Sourhope	*Deschampsia flexuosa*	Complex	-	Experiment × Bracken Control × Grass Seeding
Carneddau	*Pseudoscleropodium purum*	Decreased	-	Bracken Control

TABLE 4. Fencing at the Peak heath site; back-transformed mean percent cover values, df= 1,12

Species	Unfenced	Fenced	Order of Effect	F Value
Deschampsia flexuosa	7.17%	17.21%	Overall	32.5
Festuca ovina	1.23%	0.29%	Overall	33.2
			3rd	26.5
Festuca rubra	1.38%	0.58%	1st	23.2
Hypnum jutlandicum	1.28%	0.47%	1st	25.1

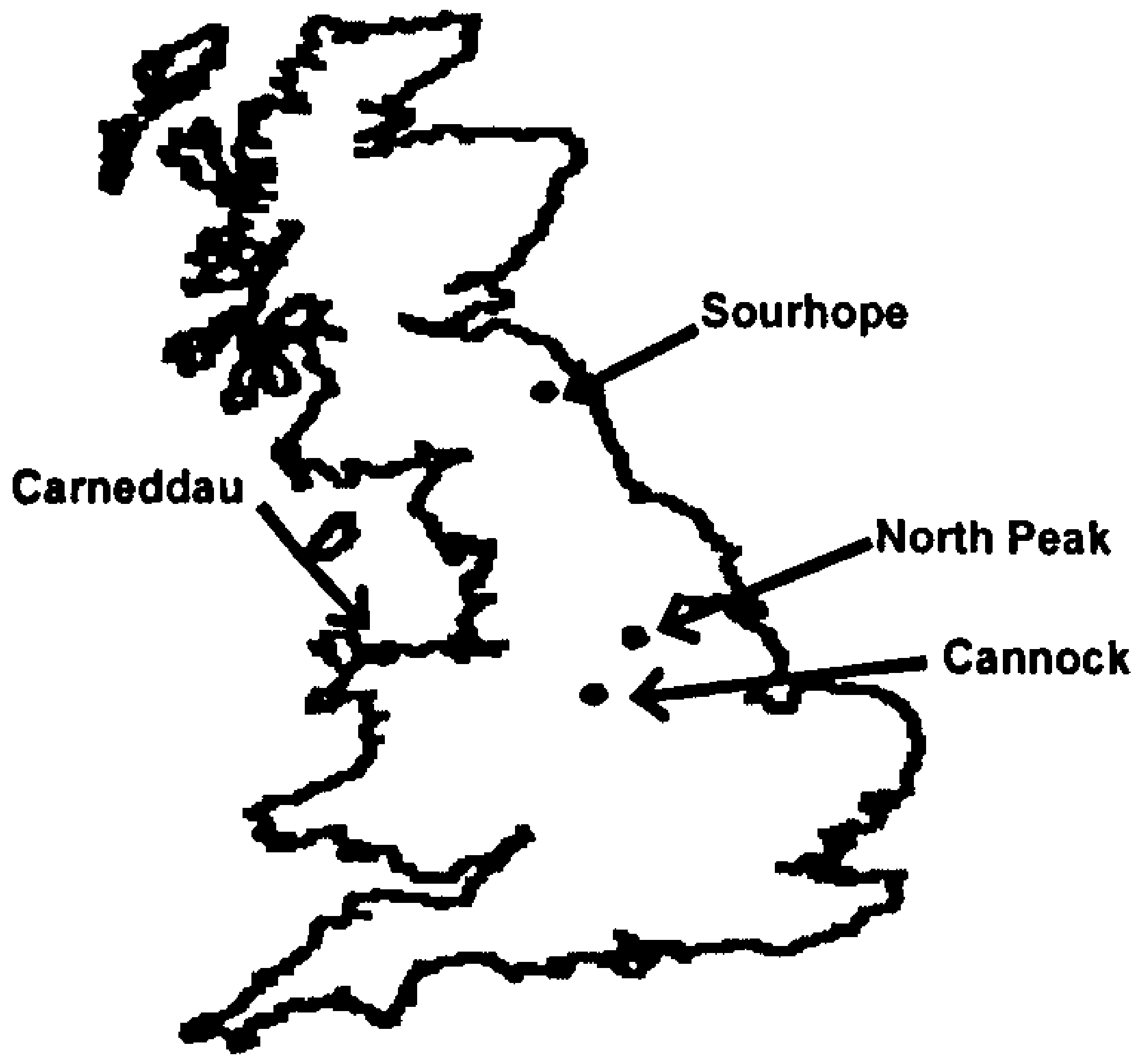
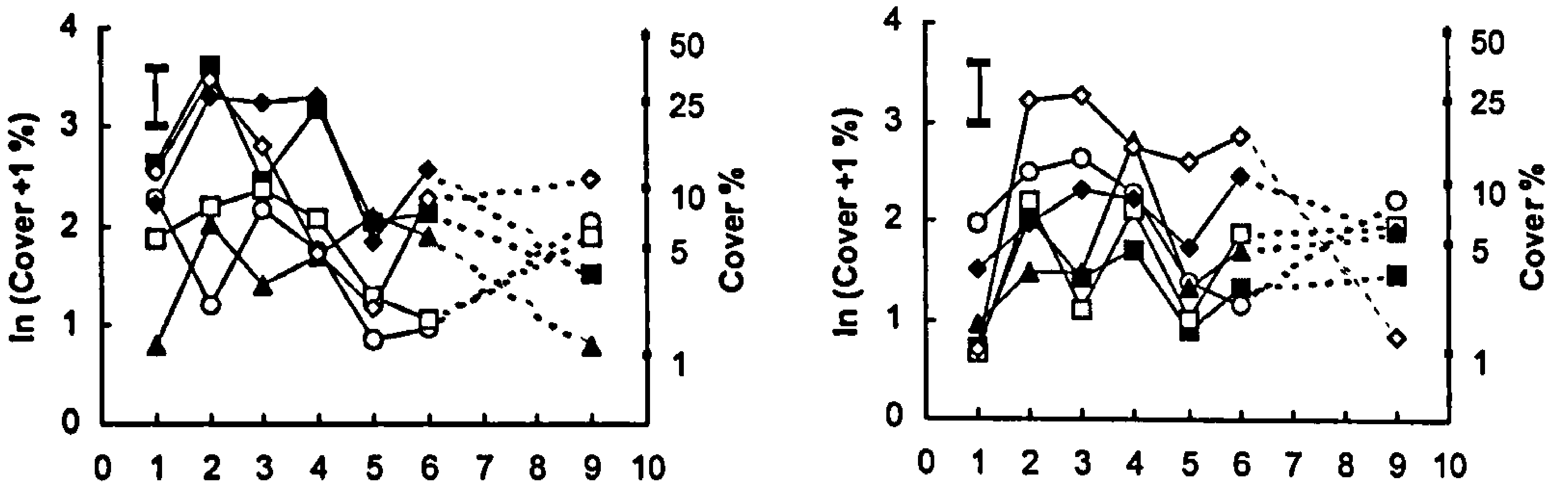


Fig. 1. Map of the UK displaying site locations.

(i) Sourhope 1, no treatment (ii) Sourhope 1, grass seeding



(iii) Sourhope 2, no treatment (iv) Sourhope 2, grass seeding

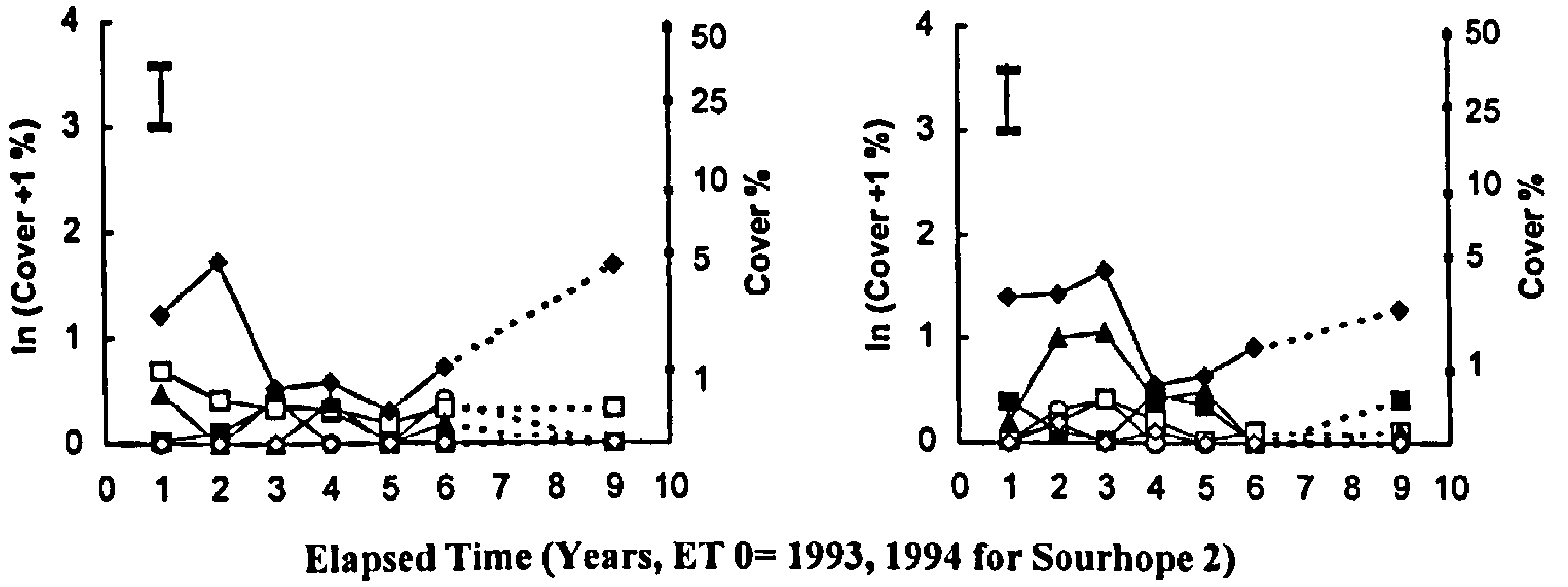
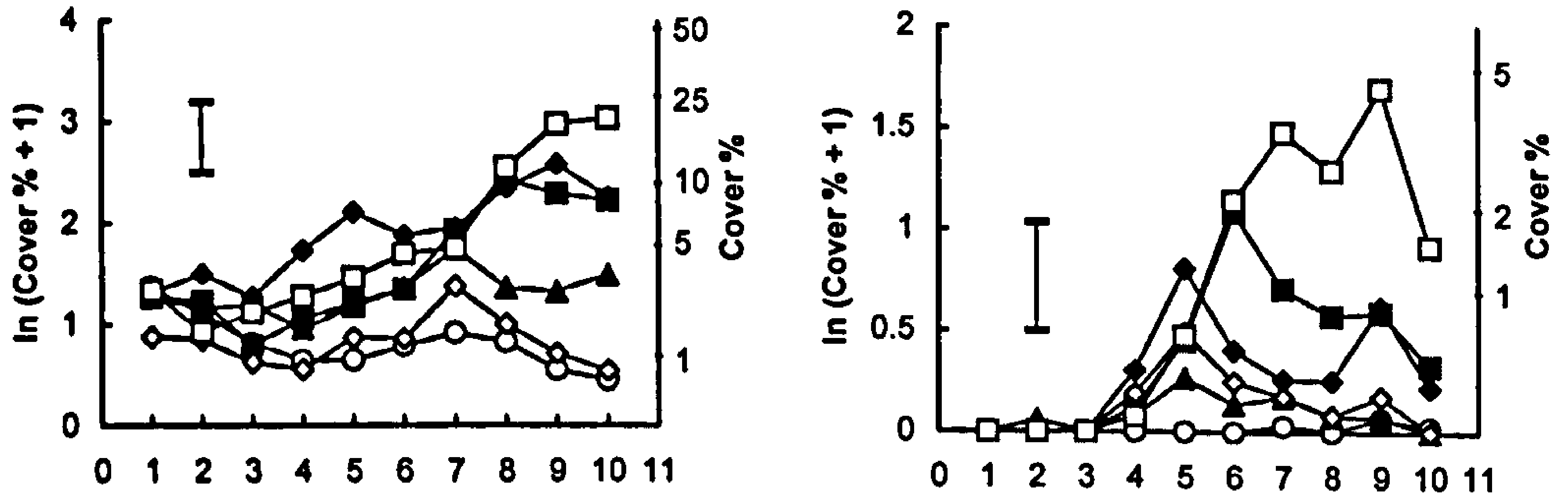


Fig. 2. Effects of space (experiment), bracken control and restoration treatments on species *Deschampsia flexuosa* at Sourhope (2nd order, $F_{(5,12)}$ =12 n=2) (i) Sourhope 1, no restoration treatment (ii) Sourhope 1, grass seeding (iii) Sourhope 2, no restoration treatment (iv) Sourhope 2, grass seeding. No treatment= white circle; Cut1pa= black square; Cut2pa= white square; Spray= black triangle; CutSpray= black diamond; SprayCut= grey diamond. Error bars are ± 2S.E.D (standard error of the difference between two means (Sokal & Rohlf 1995)).. Gaps in the temporal data are presented as a dashed line.



(a) *Deschampsia flexuosa* at Cannock

(b) *Campylopus introflexus* at Cannock

(c) *Galium saxatile* at Peak

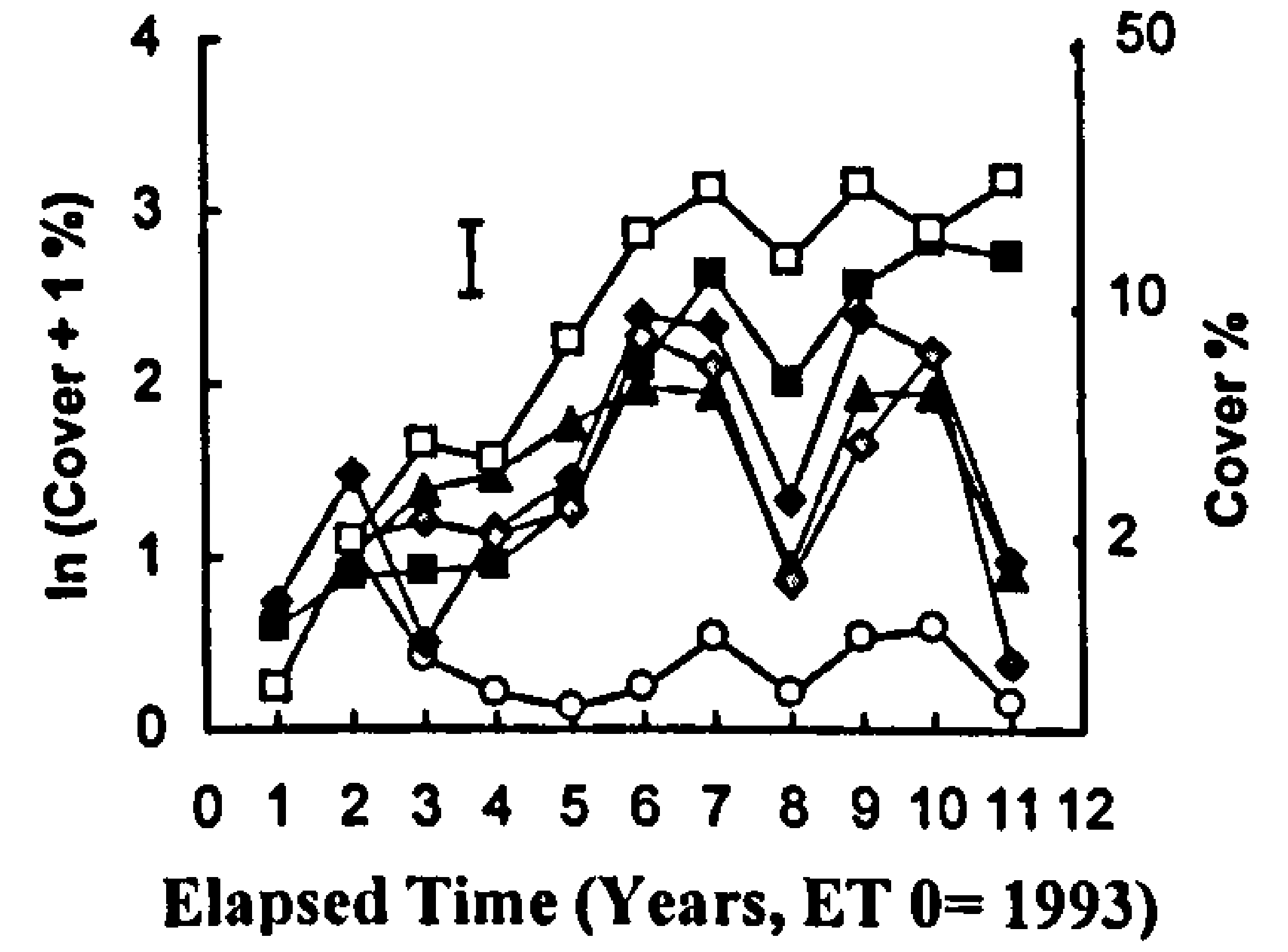


Fig. 3. Effect of bracken control treatments on (a) *Deschampsia flexuosa* at Cannock (1st order, $F_{(5,10)}$= 17.31 n=12), (b) *Campylopus introflexus* at Cannock (1st order, $F_{(5,10)}$= 12.1 n=12), (c) *Galium saxatile* at Peak (5th order, $F_{(1,12)}$=13.6 n=18). No treatment= white circle; Cut1pa= black square; Cut2pa= white square; Spray= black triangle; CutSpray= black diamond; SprayCut= grey diamond. Error bars are ± 2S.E.D (standard error of the difference between two means (Sokal & Rohlf 1995))..

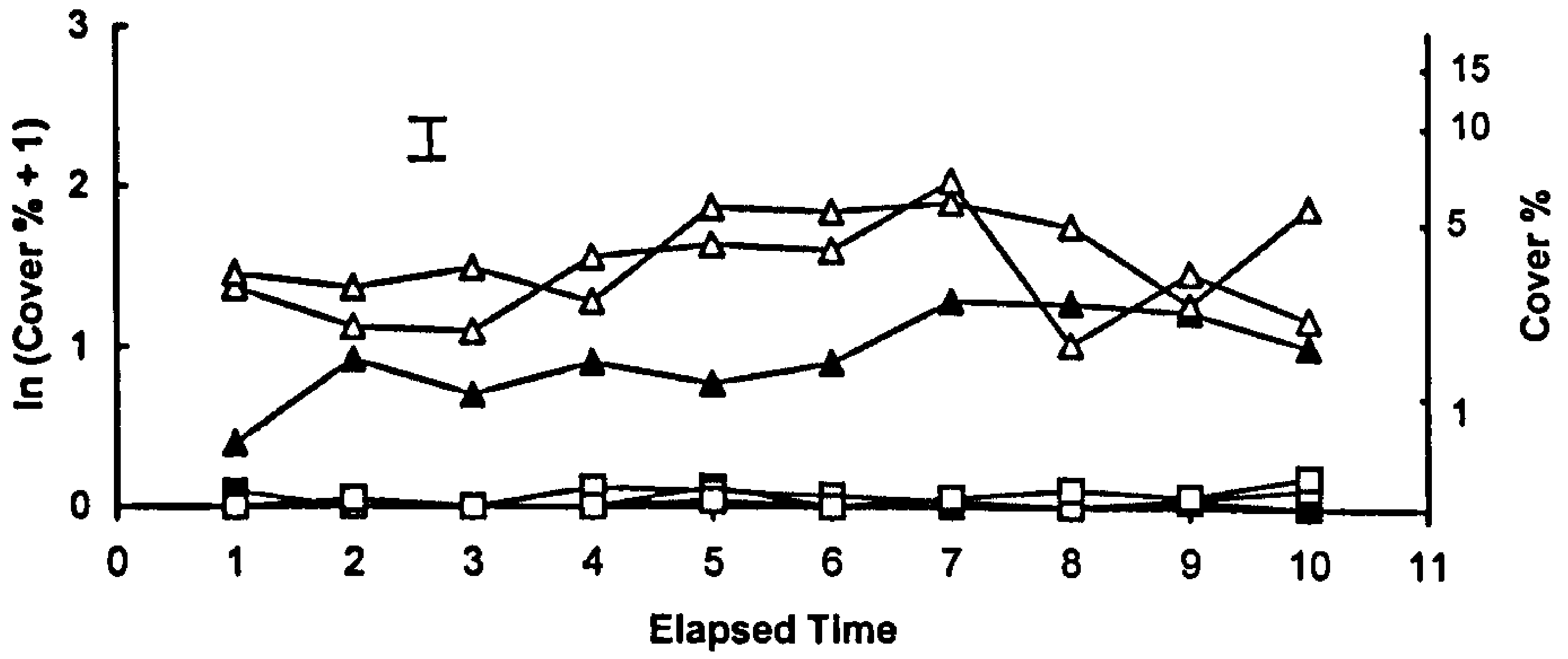


Fig. 4. Significant effect of space (experiment) × restoration treatment through time on *Calluna vulgaris* cover at Cannock (Cannock 1= square; Cannock 2 = triangle; no treatment= white; fertilizer= black; fertilizer and surface disturbance= grey); 4th order, $F_{(2,24)} = 10.5$ n=12. Elapsed Time=0 is 1993. Error bars are ± 2S.E.D (standard error of the difference between two means (Sokal & Rohlf 1995)).