Aspects of the ecology of the Lepidoptera associated with Calluna vulgaris on managed northern heath

Haysom, Karen A.

Aspects of the Ecology of the Lepidoptera Associated with *Calluna vulgaris* on Managed Northern Heath

by

Karen Haysom B.Sc. (Dunelm)

A thesis presented in candidature for the degree of Doctor of Philosophy

Department of Biological Sciences

University of Durham

1994

I certify that all material in this thesis which is not my own has been identified and that no material is included for which a degree has previously been conferred on me.

Abstract

Aspects of the ecology of the Lepidoptera associated with *Calluna vulgaris* on managed northern heaths were studied between 1991-1993 at five study areas in Durham, Northumberland and southern Scotland. The study areas were northern heaths that were managed by rotational burning and each comprised a mosaic of even-aged *Calluna* stands. Lepidoptera were studied in the larval stage of development. A range of even-aged *Calluna* stands, with different ages and vegetation structures were selected as sample sites and the larval assemblages in the different stands were monitored by sweepnet sampling. A total of 29 species of macrolepidoptera and 3 species of microlepidoptera larvae were recorded. Species lists were similar at the five study areas, but the relative abundance of individual species varied between sites. The degree of similarity between communities was not related to the distance between study areas. The densities of many macrolepidoptera species were closely correlated with *Calluna* height. Intercorrelation between vegetation architecture variables meant that other factors *e.g.* green shoot density or flower density could also have been responsible. Lepidoptera diversity varied with *Calluna* height, due to changes in the dominance of common species and the presence of additional rare species at certain heights. However patterns in diversity were not consistent between study areas. The concentrations of total leaf nitrogen, total phenolics and water were significantly higher in current year's *Calluna* leaves than in the shoots formed in previous years. In same-aged leaves, there was no relationship between plant age and the concentrations of leaf nitrogen or phenolics. The water content of same-aged leaves was negatively correlated with stand age at some sites and at certain sampling times. Larvae offered different choices of ericaceous plants exhibited significant preferences for different plant species and also for the current year's *Calluna* leaves rather than previous years' growth. Mechanisms that could be responsible for the observed distribution patterns of larvae in different heights of *Calluna* are discussed. The maintenance of a mosaic of different-aged *Calluna* stands on northern heath represents the best conservation strategy for Lepidoptera by maintaining species diversity at a site.

Acknowledgements

I would like to thank Dr John Coulson and Dr Val Standen of Durham University and Mr Angus MacDonald of Scottish Natural Heritage for providing help and encouragement while supervising this study.

N.E.R.C. and Scottish Natural Heritage financed the work through a Case Research Studentship and Professor P.R. Evans provided facilities in the Department of Biological Sciences.

Access to study areas was provided by Lambton Estates, Langholm Estates, Lord Crewe Estates, Mr D. Knowles, Miss Little, Mr Elliot and Mr S. Scott. I would like to thank the gamekeepers and farmers on these areas for their support, especially Andy Walker, Dennis Dodds, Mr and Mrs Colclough and Brian Mitchell.

Chris Baddenoch, Robin, Reuben and the rest of the Scottish Natural Heritage office at Galashiels gave invaluable assistance in Scotland by finding suitable study areas, arranging contact and access with landowners, giving information on S.S.S.I.'s and providing accommodation and hospitality on my visits to the borders. Steve Redpath's research team provided hospitality and a bed at Langholm-Newcastleton Hills S.S.S.I.

Gerry Haggett identified various macrolepidoptera larvae, Mr T.C. Dunn the microlepidoptera adults and Andy Buckham some macrolepidoptera adults. All three were very generous with their time and shared their enthusiasm for Lepidoptera with me.

Dr Susan Hartley of I.T.E., Banchory taught me the chemical analysis techniques used in Chapter Seven, and with Jim Kerslake, showed me their winter moth study areas. I am grateful to both Sue and Jim for advice and correspondence. Dr Alan Pearson provided laboratory facilities, equipment and advice for chemical analysis work in Durham.

The comparison of the extraction efficiencies of the Blow-Vac and D-Vac suction techniques (section 4.4.4) was in collaboration with Iain Downie.

I would like to thank Susan Haysom, David Wood, Iain Downie, Mathew Parsons, Jane Borthwick, Andy Hoodless, Rob Evans, Chris Tapp and Eric Henderson, for

lending a hand with fieldwork and enduring rain, snow and point quadrats. Eric Henderson gave much help with technical problems.

Cathy Thompson, Gilbert Roberts, Iain Downie and Chris Tapp gave advice on computing. For advice on other aspects of the study and general discussions I am grateful to Brian Eversham, Lewis Davies, Phil Hulme, Ann Smithson and Carol Fielding.

I thank Susan Raven, David Wood and Ken Durose for their help during the final days of this thesis and Monica Calado, Rachel Koktava, Gary Wheelhouse, Susan Haysom, Ann Smithson, Steve Palmer, Penny Andrews, Mathew Parsons, Simon Lawrence, Tom Hibbert, Jon Booker and Rebecca Godsell for general encouragement.

Table of Contents

Chapter One

Introduction

Calluna vulgaris (L.) Hull, commonly known as heather or ling, is an evergreen dwarf shrub species with a distribution through temperate oceanic and sub-oceanic climatic regions in western Europe (Gimingham 1960; Gimingham *et al.* 1979). It is native in Britain, where it is in its optimum ecological range (Beijerinck 1940), occurring in all the British vice-counties (Gimingham 1960). *Calluna* is tolerant of a wide range of environmental conditions. The plant is found between latitudes 36-71°N and in Britain, between sea-level and 1036m a.s.l. (Gimingham 1960). It is usually associated with freely-drained acidic soils, mor humus and peat (Gimingham 1960) and is recorded in 25 vegetation types in the National Vegetation Classification (Rodwell 1991 in Armstrong 1991).

Calluna is an important food-plant for several mammals and birds including sheep *Ovis aries*, mountain hares *Lepus timidus*, red deer *Cervus elaphus* and red grouse *Lagopus lagopus scoticus* (Hewson 1962; Moss *et al.* 1972; Moss & Miller 1976; Gimingham 1972; Gimingham *et al.* 1979; Heal 1980; Moss 1989). A variety of invertebrates feed on *Calluna* or utilise other features of the habitats in which it occurs *e.g.* Lepidoptera, Hemiptera, Coleoptera, Diplopoda, Acarina, Opiliones, Araneae, Collembola and Thysanoptera (Barclay-Estrup 1974; Gimingham *et al.* 1979; Heal 1980; Gimingham 1985; Webb 1986, 1989; Coulson 1988 and others). Much has been published concerning the life history, growth characteristics and productivity of *Calluna* in different habitats under different management practices (*e.g.* Barclay-Estrup 1969, 1970; Forrest 1971; Grant 1971; Gimingham 1972; Chapman *et al.* 1975; Miller 1979) and the wide-variety of *Calluna* growth forms, leaf and flower characteristics displayed across its range (Gimingham 1960; Grant & Hunter 1962). In fact, *Calluna vulgaris* is one of the most extensively studied of native British plant species (Gimingham 1989). Given this, and the fact that the Order Lepidoptera often forms the largest proportion of the total insect fauna on woody shrubs (Southwood 1961; Lawton & Schröder 1978) it is surprising that until recently (Fielding unpublished Ph.D. thesis 1992), the Lepidoptera species associated with *Calluna* have received little attention except for certain pests *e.g.* winter moth *Operophtera brumata.*

This study concerns the Lepidoptera associated with the plant community described by Gimingham (1972) as northern heath. Northern heath occurs in the uplands of

eastern Scotland and northern England at altitudes below 500m above sea-level (Gimingham 1972). In this habitat, *Calluna vulgaris* is the dominant plant species and may be associated with several other ericoids including *Vaccinium myrtillus*, *V. vitis-idaea*, *V. uliginosum* and *Empetrum nigrum* and several mosses (Gimingham 1972; Gimingham *et al.* 1979). The northern heaths are less floristically diverse, with fewer lichen species, but a richer bryophyte flora than the dry lowland heaths in the south (Gimingham *et al.* 1979), and two ericaceous plants also found on southern heaths, *Erica tetralix* and *E. cinerea*, may be present. The soils of northern heaths are acidic such as peaty podsols or shallow peats, have high carbon/nitrogen ratios and are usually moist because of a medium to high rainfall (Gimingham 1972; Coulson 1988). The underlying rocks are usually base-poor (Gimingham 1972; Coulson 1988). This habitat differs from the blanket bog that occurs at high altitudes where the average daily temperature is cooler, the rainfall is much higher and soils may be saturated with water for most of the year (Pearsall 1950; Coulson 1988). On blanket bog *Calluna* is co-dominant with *Eriophorum* and *Sphagnum* spp. and peat layers may be as deep as 2m (Pearsall 1950; Coulson 1988).

This study was restricted to northern heaths because the effects of management practices on the Lepidoptera associated with *Calluna* were of particular interest. The *Calluna* that grows in blanket bogs is usually less productive than at lower altitude sites (Gimingham *et al.* 1979) and exists in a steady state in which increase in plant height is restricted because of strong winds and snow and the bog surface grows upwards (Forrest 1971). For these reasons management practices applied on northern heaths *e.g.* burning are less appropriate and should be less frequently used (Hobbs & Gimingham 1980; Hobbs 1984; Usher & Thompson 1993). Present day management techniques on upland estates aim to maintain high stocks of sheep and red grouse, and in some areas red deer. Commonly, strips of *Calluna* on northern heath are burned or cut on a regular rotation to ensure regeneration of the most nutritive young plant growth, and to create a diverse range of plant ages for territorial red grouse. Where burning or cutting is practised intensively, a "mosaic" of different aged patches results. In northern England and Scotland the burning of *Calluna* for the management of red grouse dates to approximately 1840 and peaked at the turn of the century (Ratcliffe & Thompson 1988). The influence of man however, extends back over a much longer period so that below the tree-line, *Calluna* heath is a semi-natural habitat (Ratcliffe & Thompson 1988). Heathland in its present form originated when man began to deforest the uplands as early as 5000BP (Turner 1965). The process of deforestation became extensive between 3900-3000BP (Birks 1988). In the northern Pennines, the earliest period of extensive forest clearance occurred at 2500BP (Turner *et al.* 1973). Dwarf shrub heaths comprising species such as *Calluna*, *Erica tetralix*, *E. cinerea*, *V. myrtillus* and

Empetrum nigrum replaced the trees and clearance of the remaining forest, and subsequent expansion of heather moor has continued into historical times (Conway 1954). *Calluna* heathland is a plagio-climax community. In the south, fire and tree clearance check its succession to woodland, while in the north grazing by vertebrates is the main-factor limiting change of vegetation type (Miller *et al.* 1982). Only above the natural tree-line is heathland a climax vegetation and here the habitat is usually blanket bog.

Guidelines for the length of the burning rotation on managed northern heath are based on the natural life cycle of the dominant plant species *Calluna vulgaris*. The natural lifespan of a plant is approximately 25-40 years (Gimingham 1960, 1972, 1985) and as the plant ages it undergoes several structural changes. Watt (1947, 1955) identified four phases of development within the life-cycle, the pioneer, building, mature and degenerate phases. These were further characterised by Barclay-Estrup and Gimingham (1969), Barclay-Estrup (1970, 1971) and Gimingham (1960, 1972). The rates at which plants pass through the different phases are partly controlled by environmental factors so they vary at different locations. The details in the following summary of the *Calluna* lifecycle follow Gimingham (1972).

The cycle begins with the pioneer phase which usually lasts 3-6 years. In this phase plants establish from seed, contribute approximately 10% of ground cover and have little woody tissue. Other plants *e.g. V. myrtillus* and *E. tetralix* may coexist with or be dominant to the *Calluna*. In the building and mature phases (plant ages 7-13 years and 12-28 years respectively), plants gain height, extra foliage and woody growth. Ground cover becomes virtually complete and other plant species are outcompeted. By the end of the mature phase, the larger heavier plant stems start to bow and some plants begin to die off. The effect may be accelerated by external factors such as heavy snow lying on the branches and a less dense canopy results. By the degenerate stage (plant ages 16-40 years) there is widescale death of plants and gaps open within the canopy, allowing lichens and higher plants to recolonise. By this stage, *Calluna* contributes approximately 40% to ground cover and wood, rather than foliage, constitutes the bulk of the *Calluna* biomass.

These changes in the structure and floral composition of the community occur repetitively over a period of time and Gimingham *et al.* (1979) state that it may sometimes take 50 years for one pioneer phase to be replaced by a subsequent pioneer. Changes within the habitat are mediated endogenously because of the characteristics of different ages of *Calluna*, the dominant plant (Gimingham 1972) and are accompanied by variations in microclimate (Barclay-Estrup 1971; Gimingham 1972; Mallick 1986). In an unmanaged heathland, neighbouring plants may be in different phases and the

moorland is uneven-aged. Recent studies have suggested that in unmanaged heathlands patterns of vegetation change are not always cyclical (Diemont & Heil 1984; Marrs 1986; Gimingham 1988). External factors *e.g.* herbivore attack, climatic extremes or changes in nutrient status may instigate a change in the pattern of vegetation development and differences in environmental variables at a site may determine whether vegetation change is cyclical or seral (Diemont & Heil 1984; Marrs 1986, 1993).

Burning imposes a common date of regeneration, so plants in stands that have been burned have similar chronological and physiological ages. It is recommended that *Calluna* be burned when it reaches the late building or early mature phase (Gimingham 1972; Mowforth & Sydes 1989), but it should not be more than 30cm tall (Gimingham 1972). The corresponding time period for such a rotation on northern heath should be approximately 10-15 years (Gimingham 1972, 1981; Gill & Groves 1981; Muirburn Working Party 1977 in Hester & Sydes 1992). *Calluna* burned at these intervals regenerate most quickly, since vigorous vegetative growth arises from the buds of burned stems. Such a burning regime maintains *Calluna* in the most productive younger stages, when there is a high ratio of foliage: wood on the plants for grazing animals. Lack of management, fertilisation, over-grazing and fires that are too hot or too frequent can convert *Calluna* heathland to grassland (Gimingham 1981).

Although Coulson (1988) calculated that the Lepidoptera represented 33% of the invertebrate standing crop on northern heath, the number of Lepidoptera species feeding on *Calluna* heath has been severely underestimated in the past. Webb (1989) considered that approximately 40 invertebrate species were dependent on heather for food, but in a comprehensive literature review Fielding (unpublished Ph.D. thesis 1992) found that the number of species of Lepidoptera larvae reported to feed on *Calluna vulgaris*, *Vaccinium myrtillus* and *Erica* spp. was 86, 76 and 47 respectively. Fielding suggested that the actual number of Lepidoptera species utilising *Calluna* as a food resource could be nearer 100, because authors do not list all the food-plants of widely polyphagous species, so these are probably under-recorded. These figures represent the total number of species that feed on the plants in all their British habitats, so include records for both northern and southern heaths, the high altitude blanket bogs and rarer habitats. However, even in a more limited field study of several northern heaths and blanket bogs in County Durham, Fielding found 26 species of Lepidoptera larvae utilising *Calluna*. A total of 19 species were found as larvae and these represented 45% of the species with known associations with the plant that have been recorded in the county (Fielding unpublished Ph.D. thesis 1992). Altitude affected the number of species found at any location and on a gradient from 290-650m a.s.l. there was a loss of

approximately three macrolepidoptera species for every 100m rise in altitude. This agreed with some work on other invertebrate groups (Greenslade 1968; Coulson 1988 both in Fielding unpublished Ph.D. thesis 1992) but not with the work of Lawton *et al.* (1987) quoted in Fielding (unpublished Ph.D. thesis 1992). This was probably because Lawton *et al.* (1987) considered results based on single altitude transects to be misleading and that a large number of sites in different geographical locations should be examined (Fielding unpublished Ph.D. thesis 1992). Coulson maintained that the temperature effects associated with change in altitude could be the most important factor limiting the distribution of invertebrates in the uplands. Pearsall (1950) stated that almost all of the Lepidoptera found in the uplands were moths rather than butterflies and Ratcliffe (1977) listed only five upland butterflies. These were the small heath *Coenonymphas pamphilus*, large heath *C. tullia*, Scotch argus *Erebia aethiops*, mountain ringlet *Erebia epiphron* and the dark green fritillary *Argynnis aglaja*. Fielding's work confirmed the dominance of moths in the upland Lepidoptera community, but other literature accounts were queried. For example, 61% of the larvae Fielding found occurred outside the periods listed in literature sources. This suggests that, even for such a generally well-studied group as the Lepidoptera, there is still much to learn regarding their basic ecology on upland *Calluna* heaths.

Perhaps one of the reasons why research on upland Lepidoptera has been largely neglected is that they are a surprisingly difficult group to sample quantitatively. With a few exceptions (*e.g.* fox moth *Macrothylacia rubi*, northern eggar *Lasiocampa quercus callunae*, emperor moth *Pavonia pavonia*) the moths of *Calluna* heathland are small, inconspicuous and difficult to identify in flight. These characteristics make them unsuitable candidates for transect surveys which are often used to assess the densities of butterfly imagoes (*e.g.* Pollard *et al.* 1975; Pollard 1977). Similarly light traps, although designed for moths, have limited value because they discriminate against certain species and catch from a wide area that may include the area outside the immediate habitat. Catch size may be affected by variations in external factors such as moonlight and air temperature and trap efficiency also varies in different habitats (Southwood 1978). Quantitative data from light traps should be interpreted cautiously (Southwood 1978). Depending on the habitat, eggs, larvae and pupae may also be difficult to locate. In this study only one stage of the lifecycle, the larva is examined. Although this stage may also be difficult to locate, when found information about an animal's utilisation of the habitat can be determined very precisely. An investigation of larvae restricts study to species which have established a breeding population on heathlands and excludes most transient migrants from other habitats. Chapter Four assesses the efficiency of several methods of sampling Lepidoptera larvae and describes the techniques that were used in this study.

On heathlands that are managed for grouse or sheep it is possible to study the Lepidoptera community at each stage of the *Calluna* "succession" or cycle, because there are a range of *Calluna* stands with different average plant ages and various plant structures. Lawton (1978, 1983) identified a number of relationships between the characteristics of a host-plant species and its invertebrate community. For example, within Britain widely distributed plant species host more species of phytophagous insects than plants with narrower distributions. Insect species richness is also related to host-plant growth-form, decreasing in the order woody shrubs, perennial herbs, weeds and annuals, monocots (Lawton 1983). Lawton (1978) suggested that some of these effects were due to variation in the exposure of a plant in space and time to insect herbivores. Seasonal variation in insect diversity could also be related to differences in structural complexity that change the number of niches available for exploitation *e.g.* the development of flowers and seeds, or seasonal changes in plant chemistry (Lawton 1978). There is overlap between Lawton's hypotheses and the theories of plant "apparentness" or "predictability" and their influence on the type of structural or chemical anti-herbivore defences possessed by different plant species (Feeny 1970; Rhoades & Cates 1976). Lawton (1983) identified a need for studies of the insect community on single plant species to determine whether the patterns of insect utilisation found on the wider growth-form scale, continued within the more limited range of ages, sizes and structures exhibited by single species.

This study monitors the Lepidoptera larvae found on *Calluna* stands with different average plant ages and different architectures at several sites in Durham, Northumberland and southern Scotland. Chapter Two describes these study areas and Chapter Five compares the Lepidoptera larvae communities that were found at each site. Chapter Six examines the density of different species of larvae and Lepidoptera heterogeneity and considers whether there are patterns related to the architectural characteristics of different *Calluna* stands. Characteristics of the vegetation are described in Chapter Three. Chapter Seven investigates whether the chemical composition of *Calluna* foliage changes with plant and leaf age and considers the implications for Lepidoptera larvae.

This is not the first study to examine the populations of invertebrates associated with *Calluna* stands at different stages after burning. Work on both northern and southern heaths has examined communities on all stages after fire, from bare ground through to mature and degenerate heather. Groups studied include ants (Brian *et al.* 1976), spiders (Merrett 1976; Usher & Smart 1988), carabids (Gardner & Usher 1989) and cryptostigmatid mites (Webb 1972). As recently as 1992, Fielding (unpublished Ph.D. thesis) reported that a geometrid lepidopteran, the July highflyer *Hydriomena furcata*

was recorded most frequently in the tallest mature stands of *Calluna*. Such studies are valuable not only for their intrinsic academic interest, but also because there is now much concern regarding recent losses of all types of *Calluna* heathland (Moore 1962; Gimingham *et al.* 1979; Sheail 1979; Webb & Haskins 1980; Anderson & Yalden 1981; Gimingham 1981; Mowforth & Sydes 1989; Armstrong 1991). For example, it is reported that 16% of English upland heathlands were lost to unimproved grassland between 1947 and 1980 (Armstrong 1991). Major losses of heathland have also occurred through conversion of *Calluna* to forestry, agriculture and buildings. In the south, heaths are also vulnerable to invasion by trees and shrubs and the effects of large-scale heathland loss have been compounded by increased fragmentation of the remaining areas under heather (Webb & Haskins 1980). In order to combat the potential loss of heathland species, it may become necessary to manage remaining habitats more effectively, with reference to the requirements of invertebrates.

Finally, consideration is given to the capacity of caterpillars to make ecological and behavioural decisions that affect not only the survival of the larval stage, but fitness in the following pupal and adult phases. In a complex lifecycle, it is possible that while an animal in one life history stage must ultimately aim to transfer its genes to the next generation, there may be "life history trade-offs" which make it attempt to maximise its own performance, even at the expense of another phase (Reavey & Lawton 1991). For example, the length of time a larva feeds before pupation may be influenced by several considerations. In species where large body size is associated with higher adult fertility (*e.g.* Haukioja & Neuvonen 1985 in Reavey & Lawton 1991), increasing the larval feeding rate or feeding period may increase larval and adult body sizes and adult fecundity, but expose larvae to winter temperatures before they have entered a suitable form for overwintering *e.g.* larval diapause or pupae, or prolong the exposure of larvae to predators and parasites. In such cases it may benefit larvae to pupate or diapause as early as possible, forfeiting increased adult fertility. Some trends in the life history and feeding strategies of British "macro" and microlepidoptera appear to be related to larval size and other characteristics (Gaston & Reavey 1989; Gaston *et al.* 1991). These data suggest that larvae should be regarded as more than mere feeding machines (Reavey & Lawton 1991), since their behaviour may affect all other life history stages. Aspects of the foraging behaviour of heathland Lepidoptera larvae in the field and the degree to which certain species show a preference for some food-plants are examined in Chapter Eight.

Throughout this work *Calluna vulgaris* is also referred to as *Calluna* or by its common name heather. The use of the generic name alone follows convention as it is a monotypic genus. The terms macrolepidoptera and microlepidoptera are also used.

"Micro" and "macro" are arbitrary names given to moths of the groups whose size is small (*e.g.* Pyralidae, Tortricidae, Tineidae) or large (*e.g.* Geometridae, Noctuidae) respectively (Dickson 1976; Daly *et al.* 1981). The nomenclature of Lepidoptera species in this thesis follows Bradley and Fletcher (1979).

Chapter Two

The Study Areas and Sample Sites

2.1 The study areas

Five study areas were chosen in northern England and southern Scotland. All sites except Langholm-Newcastleton Hills S.S.S.I. lay east of the Pennine peaks. The study areas lay at altitudes between 220m and 470m above sea-level, but Waskerley Moor was the only location at which some of the sample sites were above 400m a.s.l. At all sites the vegetative assemblages were *Calluna vulgaris-Vaccinium myrtillus* heaths, mainly type H12 (Rodwell 1991), a habitat that Gimingham (1972) described as "northern heath". Gimingham's description of northern heaths comprised four categories. Two of these types are found in Britain. The type in this study was "*Calluna vulgaris-Vaccinium* heath", which is an assemblage of *Calluna* with *Vaccinium myrtillus*, *V. vitis-idaea* or *Empetrum nigrum* and abundant mosses on peaty podsols or shallow peats. Soils are acidic with high carbon/nitrogen ratios, often lie over base-poor rock and any periods of water stress are likely to be short (Gimingham 1972; Coulson 1988) as most areas have medium to high rainfall (although not as high as on blanket bog areas). At the sites in this study, the plants associated with *Calluna* were *Vaccinium myrtillus*, *Erica tetralix*, *Erica cinerea* and *Empetrum nigrum*. The terms "grouse moor" and "*Calluna* moor" are also used in this thesis. These are less specific and describe both northern heath and the higher altitude blanket bogs where *Calluna* is co-dominant with *Eriophorum* and *Sphagnum* species, soils are saturated with water for most of the year and the peat layer may be up to 2m deep (Pearsall 1950; Coulson 1988). When used in connection with the study areas grouse moor and *Calluna* moor refer only to the northern heath habitat to which this study was restricted.

The five field sites were chosen because all were actively managed by rotational burning. Regular burning creates a range of habitats for red grouse *Lagopus lagopus scoticus* and can maintain the *Calluna* in its most vigorous state, the building phase for sheep grazing. The net production of new shoots is higher in this life-history phase than in other stages of *Calluna* growth (Barclay-Estrup 1970). On heathlands where *Calluna* is managed for grouse, the width of the burned area is usually between 20-30m but on estates managed for sheep much wider strips are burned (Mowforth & Sydes 1989). Managed heathlands were valuable to this study because many *Calluna* stands with different ages and plant architectures could be found within a small area, in which other

environmental factors were likely to be similar. Heathlands managed for red grouse were preferred to those managed for sheep because a larger number of different-aged patches are usually available in a given area. Ease of access from Durham City was also considered when choosing locations for field work. In the description that follows, all altitude measurements refer to height above sea-level.

2.1.1 Waskerley Moor, near Edmundbyers, County Durham

Waskerley moor is an extensive area of *Calluna* heathland that covers approximately 35km^2 between 350m and 470m a.s.l. The site lies approximately 25km west of Durham City and the corners of the site are given by the grid references NZ0047, NZ0045 and NZ0445. Lambton estates, the owners of the land, burn narrow strips across the moorland to create a habitat suitable for red grouse, but sheep also have unrestricted access to the moor in the summer. The site lies on carboniferous coal measures. All the sample sites at this study area were located along the minor road that forms an east-west transect across the moor and links Castleside to Stanhope. An altitude gradient exists along this transect. Sample sites at the lower eastern end (stands WK23, WK24, WK25, WK26 and WK35) were 370-380m a.s.l., while those at the western end (WK1, WK2, WK7, WK8, WK10) were at 455-470m. The sample sites along this road faced north. Waskerley Moor is referred to as Waskerley throughout this thesis.

2.1.2 Winnowshill Farm, near Slaley, Northumberland

An area of heathland approximately 2km^2 on Winnowshill Farm (grid reference NY9853) is managed for red grouse. Light grazing by sheep occurs through part of the summer. The moor is a mosaic of small burned areas, and faces southwest. All sample sites were within 0.5km of each other and were located at 280-290m. The underlying geology is carboniferous namurian sandstone. This site is referred to as the Slaley site throughout this thesis. The Slaley site is approximately 30km northwest of Durham City.

2.1.3 Stuartfield Lodge, near West Butsfield, County Durham

Sampling sites were located at Stuartfield Lodge Plantation (grid reference NZ0744) and on other areas of *Calluna* on Stuartfield Lodge Farm. *Calluna* covers approximately 1.3km^2 at this site, and is managed for red grouse by burning. Sheep and cattle also graze the area. The sample sites on this farm are at 300-335m and lie on carboniferous westphalian sandstone. Aspect is northeast. The *Calluna* heath is bordered by a birch (*Betula* sp.) woodland, conifer plantations and pasture. Stuartfield

Lodge is approximately 20km west of Durham City and 4km south-east of Waskerley Moor.

2.1.4 Greenlaw Moor S.S.S.I., Berwickshire

This extensive *Calluna* heathland covers an area of approximately 12km^2 and is located at grid reference NT7050, approximately 120km north of Durham City. The moor is now managed for grouse but reflects a longer history of management for sheep, as many of the burned areas are very large (more than 30m wide by several hundred metres long). These large strips are separated by firebreaks that are created by mechanically cutting *Calluna*. All the sample sites were located on a southeast facing part of the moor, adjacent to the A6105 Polwarth to Greenlaw road, at 225 to 240m. The S.S.S.I. lies on upper old red sandstones. Greenlaw Moor has S.S.S.I. status because it is an important site for passage and wintering wildfowl and waders and because it is the only remaining extensive, mid-altitude shrub heath left in the Scottish Borders (Anon. 1987). Similar habitats below 300m have declined in the region since the 1940's.

2.1.5 Langholm-Newcastleton Hills S.S.S.I., Roxburghshire

The Langholm-Newcastleton Hills S.S.S.I. is another extensive area of *Calluna* heathland in southern Scotland and covers 77 km^2. Not all of the land within this area is under heather. Langholm Estates manage the area for grouse and consequently the *Calluna* is a mosaic of different-aged stands which are maintained by burning and recently also by cutting. All the sample sites were located along the Langholm-Newcastleton road in the area between Tarras Water and Middlemoss on a gradual south-east facing slope. Altitudes of the sample sites were in the range 220-250m. All the sample sites were created when *Calluna* plants regenerated from the burned stems of previous individuals or from seed. A range of Silurian and Carboniferous substrates lie below the S.S.S.I. The rocks beneath the part of the estate used as the study area are carboniferous limestone. The Langholm-Newcastleton Hills field site is the most westerly of the study areas, approximately 95km northwest of Durham City. Climate is described as intermediate between the extremely oceanic Galloway Hills and the drier Cheviots (Anon. 1985).

2.2 Sample sites

Sample sites were the specific places at a study area where Lepidoptera larvae were regularly collected during a monitoring programme that is described in section 5.2. Each sample site was a stand of *Calluna* that had been created by burning, a stand being a term used in vegetation classification to describe a plant association that may be

recognised elsewhere (Allaby 1992). The boundaries of sample sites could be recognised easily because all plants within a stand were in the same life-history phase and exhibited similar growth forms. These differed from the growth forms of plants in adjacent stands that had been burned at a different time. The width of a typical stand on heathland managed for grouse is usually 20-30m. The size of a sample site was set at approximately 25m by 25m. This choice was influenced by the characteristics of *Calluna* regeneration after a fire that were observed at some study areas. At study areas where regeneration was very patchy, pioneer stands larger than this often incorporated large areas of bare soil. This was not appropriate for the types of sampling methods that were used in this study (described in Chapter Four).

Stands were selected as sample sites on the basis of life-history phase and plant height, to represent the full range of architectures present at a study area. Stands were not selected if they contained drainage ditches, earthworks, or any features that made them otherwise atypical of stands of their height and life-history phase.

Chapter Three

The Vegetation at the Study Areas

3.1 Introduction

Most of the heaths in northwestern Europe comprise plant species that are low (less than 1m high) or dwarf (less than 25cm), the majority belonging to the family Ericaceae (Gimingham *et al.* 1979). Heather, *Calluna vulgaris* is often the dominant plant species in these heaths and on northern heath (Gimingham 1972) it grows on shallow, acidic, moist peats with ericaceous associates such as *Vaccinium myrtillus, V. vitis-idaea, Vaccinium uliginosum, Empetrum nigrum* and several mosses (Gimingham 1972; Gimingham *et al.* 1979).

Watt (1947, 1955) suggested that some plant communities, including *Calluneta,* pass through dynamic development cycles, the duration of which are dictated by the lifespan of the dominant species. Up to four phases may occur and these divide into "upgrade" and "downgrade" series. For *Calluna*, Watt's four phases were a pioneer phase in which *Calluna* established from seed or spread vegetatively from neighbouring plants and contributed little to total ground cover; a building phase in which *Calluna* established complete cover and suppressed the growth of other species; a mature phase during which gaps began to form in the canopy as some branches became less erect and a degenerate phase in which plants died, creating large gaps that were available for recolonisation by *Calluna* and other plants. Microclimate and plant species associations vary in different *Calluna* phases (Barclay-Estrup & Gimingham 1969; Barclay-Estrup 1971; Summers 1978; Gimingham *et al.* 1979). The duration of the cycle was similar to the lifespan of *Calluna.* Recent work has suggested that phases only re-establish repetitively when there is no opportunity for more permanent replacement by other species and that changes are often seral rather than cyclical (Diemont & Heil 1984; Marrs 1986; Gimingham 1988). The phases are still useful descriptions of morphological change in *Calluna.*

Calluna plants on northern heaths that are managed by regular burning rarely grow next to individuals of different chronological and physiological age (phase), because burning sets a common start point to regeneration. The burning regime produces a mosaic of stands in which individuals are in the same stage of development. Plants on burned heaths show the same range of phase characteristics described by Watt (1947, 1955), but because plants in individual stands are in the same stage of development, Watt's terms may be used to describe whole stands, rather than individual plants.

This chapter describes the vegetation at the different study areas and sample sites. The objectives were to measure features that could affect the Lepidoptera community. Heathland offers different resources to Lepidoptera adults, eggs, larvae and pupae. Plants may be regarded as potential oviposition sites, their leaves and flowers as food, their different physical structures as habitats with different microclimates or predation risks. Plant size, shape and degree of contrast against background features may influence the ability of adults and larvae to locate them (*e.g.* Bach 1980, 1981; MacGarvin 1982; Lawton 1983).

The height of *Calluna* plants and the density of leaves and flowers were examined in relation to stand age. The presence of other plant species was recorded and the relationship between several structural and floral composition variables was examined. In many plants, age and height are interchangeable. Part of this chapter examines the relationship between plant age and height, and other variables, to determine which of age or height was more useful for describing sample sites, and for further studies of Lepidoptera larvae.

3.2 Methods

3.2.1 The study areas

Vegetation was characterised at Slaley, Waskerley Moor, Greenlaw Moor S.S.S.I. and Langholm-Newcastleton Hills S.S.S.I. These study areas are described in Chapter Two. The *Calluna* stands investigated were the sample sites that were used during the 1992 and 1993 Lepidoptera sweepnet sampling programmes at Waskerley and Slaley and in visits to the two Scottish sites in the early summer and autumn of 1992 (section 5.2). Fifteen stands were studied at both Waskerley and Slaley, 20 at Greenlaw and Langholm. Three of the stands at Langholm were burned in the autumn of 1992 before all the vegetation variables could be measured.

3.2.2 Height of *Calluna* stands

The height of *Calluna* plants in each stand was measured at the end of the growing season in late September or early October 1992 and again at the same time in 1993. The mean height of each stand was calculated from 40 samples using a 40cm x 40cm quadrat that was also used in section 3.2.4. The quadrat was positioned at eight random locations within each stand, by using a random number grid. Five height measurements were taken in each quadrat by measuring the stem closest to the centre and each corner. Plant height was taken as the distance between the ground and the shoot tip nearest the ruler at these points, when the plant was standing in its natural position. Height was recorded to the

nearest 0.5cm. Stands L-O at Slaley and stands A-E at Waskerley were introduced in 1993. Their heights were measured in early October 1993.

3.2.3 Density of plant structures

The densities of different parts of the plants were measured in late September-early October 1992, using a 40 x 40cm quadrat and a pin that was 75cm long and 3mm diameter. The pin was marked at 2cm intervals between 0 and 10cm from its lowest point and above this at 10cm intervals up to 70cm. The pin was placed at five points in the frame, once at each corner and in the frame centre. Taking care to hold the pin vertical and to disturb the vegetation as little as possible, the number of times the pin touched different plant components in each height interval was recorded. The plant structures recorded were *Calluna* green shoots and flowers. Current and previous year's leaves of *Calluna* were not separated and were referred to only as green shoots. One person recorded the number of times the pin touched plants and measurements were not taken on windy days when it was difficult to record accurately.

Data were analysed by totalling the number of touches of each structure at all levels of the pin. The number of touches per five pins was summed and a mean value was calculated for each stand.

3.2.4 Floristic composition

Floristic composition was assessed when the densities of plant structures were measured, by modifying the method described in section 3.2.3 to record only the presence or absence of species. A species was recorded as present if the pin touched it at any of the marked intervals and was recorded only once at each position. Several plants expected on northern heaths were recorded at species level *e.g. Calluna, V. myrtillus, Erica tetralix, E. cinerea, Empetrum nigrum* and *Juncus squarrosus.* Plants that were not easy to identify to species were recorded at a more general taxonomic level *e.g.* bryophytes, lichens and grasses and plants that did not belong to any of these categories were called "others". The proportion of pins that touched each species was calculated as a percentage and was used as an estimate of cover.

Classification of some species into type *e.g.* grasses loses information. The survey aimed only to identify the presence of plants that represented alternative food sources to Lepidoptera larvae and to indicate stands where different soil or environmental conditions might be suspected. A technique capable of producing data with a higher degree of accuracy was not required.

3.2.5 Age of *Calluna* stands

At each stand, ten *Calluna* plants were selected at random, using a random number grid. The main stem of each plant was traced to its lowest point where an approximately 3cm long portion was removed using secateurs. Stems of plants in the degenerate phase may lie flat on the ground and start to grow small roots (a process known as "layering"), making it difficult to distinguish stems from roots. In this situation, wood with rootlets bordering more than 50% of the circumference was presumed to be root, while that with rootlets bordering less than 50% of the circumference was taken to be stem (Forrest 1971).

Stem pieces were preserved and softened in a solution of equal parts 70% alcohol and glycerol. Thin sections were prepared using a microtome. The annual growth rings in each stem section were counted using a light microscope and a mean value of age was calculated for each stand. Stand age was only estimated at Waskerley and Slaley because although harvesting stem sections and counting rings from prepared specimens could be performed quickly, the preparation of thin sections was time consuming.

Physiological age or "phase" was assessed by eye, using the characters described in Watt (1947, 1955), and Gimingham (1972). Although Chapman *et al.* (1975) prefer the term "post-burn" for *Calluna* that has newly regenerated from rootstocks after a fire, many other studies do not make this distinction. In this study all stands referred to as "pioneer" comprised plants that grew after an area was burned.

3.2.6 Statistical analyses

Statistical analyses in this thesis follow the procedures of Zar (1984). Several conventions apply throughout this study. Results are regarded as statistically significant if the probability (P) of their occurrence by chance in less than 0.05. In regression equations, ± values in parentheses represent ± 1SE, unless otherwise stated. NS denotes non-significance at the 0.05 probability level.

3.3 Results

3.3.1 The relationship between stand age and stand height

The mean age of *Calluna* stands at Slaley and Waskerley, and the mean height of stands at Slaley, Waskerley, Greenlaw and Langholm are shown in Appendices A.1-A.4. These tables also show estimates of stand life history phase (Watt 1947, 1955).

The range of stand ages was similar at Slaley and Waskerley (stand ages 2-23 years at Slaley, 4-23 years at Waskerley). The height of *Calluna* stands increased with age at both

study areas and the increase was most rapid in stands younger than 12 years-old. There were highly significant linear correlations between stand height and the logarithm of stand age ($P<0.001$, Figures 3.1a-b) and regression equations accounted for a high proportion of the variance in the data (94% at Slaley, 90% at Waskerley). The slope of the regression line was significantly steeper at Slaley ($t=2.48$, $df=26$, $P<0.05$) and this implies that *Calluna* grew more rapidly at this site.

3.3.2 The relationship between stand age and density of *Calluna* parts

3.3.2.1 Green shoot density

The number of green shoots touched by pins, green shoot density, increased with stand age at both study area. The nature of the relationship was difficult to define because of large variation in shoot density in older stands, especially at Slaley where fewer data were available for stands that were older than twelve years. When data for stands older than twenty years were excluded at both sites, there were significant positive linear relationships between shoot density and stand height at Slaley ($r=0.92$, $df=12$, $P<0.001$, Figure 3.2a) and at Waskerley ($r=0.76$, $df=12$, $P<0.001$, Figure 3.2b). More data are required to estimate the nature of the relationship in older heather.

3.3.2.2 Flower density

At both Slaley and Waskerley there was a positive curvilinear relationship between the stand age and flower density. Approximately 80% of variance was explained by second degree polynomial equations (Slaley $r=0.90$, $df=12$, $P<0.001$, Waskerley $r=0.90$, $df=12$, $P<0.001$, Figures 3.3a and 3.3b respectively). These equations imply that flower density increases with age but decreased in very old *Calluna* stands.

3.3.3 The relationship between stand height and density of *Calluna* parts

3.3.3.1 Green shoot density

The relationship between stand height and green shoot density were similar at Slaley, Waskerley and Greenlaw Moor. Data from these study areas were combined to give a general description of the trend. There was a significant positive linear relationship between stand height and green shoot density ($r=0.75$, $df=47$, $P<0.001$, Figure 3.4a). The relationship between *Calluna* height and shoot density did not follow this pattern at Langholm where greater densities of green shoots were recorded in 15-25cm tall *Calluna* than at any other sites. At Langholm, the relationship between the height and green shoot density appeared curvilinear, but no simple equation fitted the data well (Figure 3.4b).

Figure 3.1a

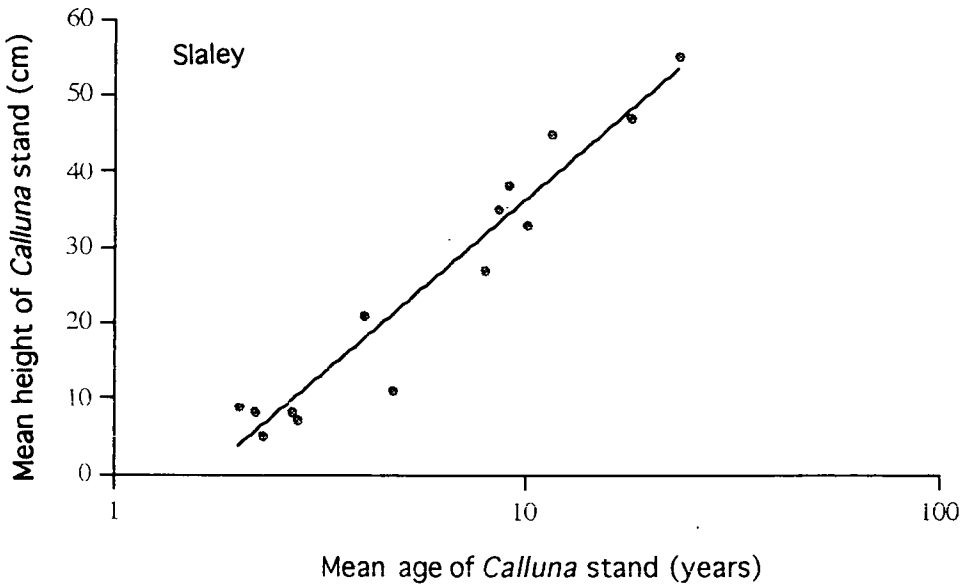
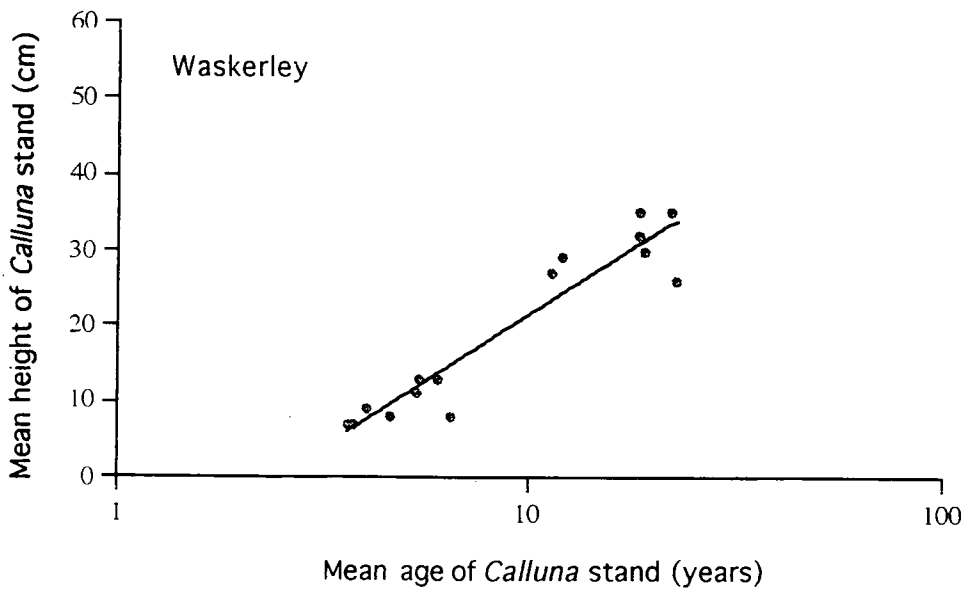


Figure 3.1b



Figures 3.1a and 3.1b. The relationship between the mean age of *Calluna* stands and their mean height at a) Slaley and b) Waskerley. Data recorded in 1992 and 1993 have been combined. The mean age was determined by counting annual growth rings using a sample of ten stems. The mean height was calculated from a sample of 40 plants at each stand. The *X*-axis of each plot is shown on a logarithmic scale. Regression analysis of 3.1a gives $Y = 46.7(\pm 3.3)\lg X - 10.3(\pm 2.7)$, r=0.97, df=13, P<0.001. Regression analysis of 3.1b gives $Y = 35.2\ (\pm 3.2)\lg X - 13.7(\pm 3.2)$, r=0.95, df=13, P<0.001. *X* is the mean age of the *Calluna* stand (years) and *Y* is the mean height of *Calluna* (cm).

Figure 3.2a

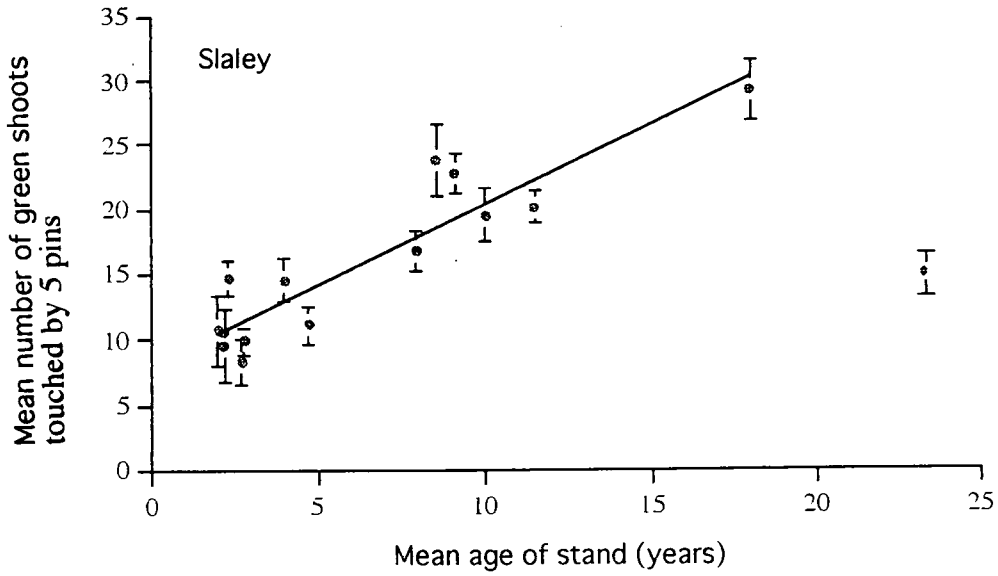
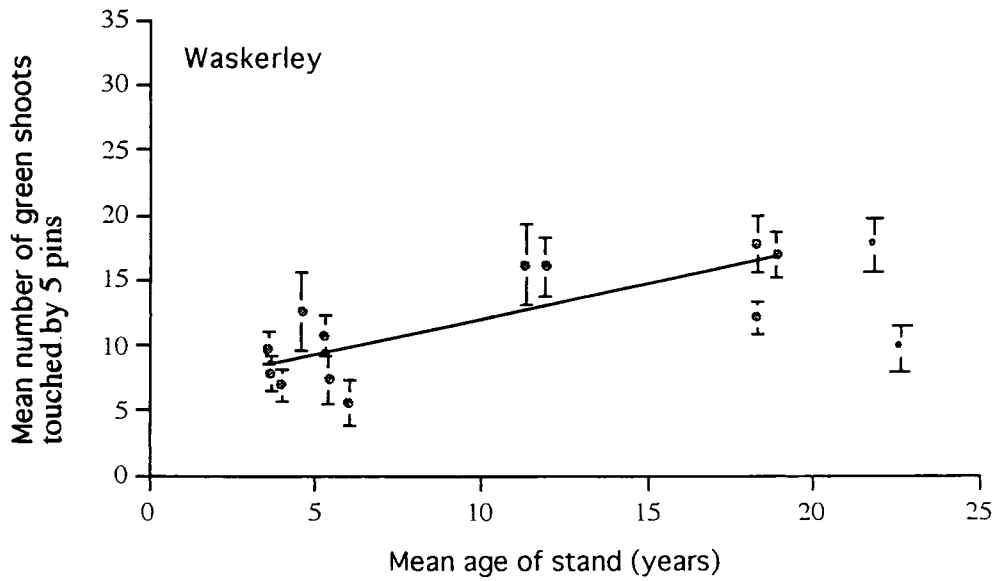


Figure 3.2b



Figures 3.2a and 3.2b. The relationship between the mean age of *Calluna* stands and the density of green shoots at a) Slaley and b) Waskerley. Data recorded in 1992 and 1993 have been combined. The mean green shoot densities are shown ±1SE and were calculated from eight samples of five pins. Data for stands less than 20 years-old were used to calculate regressions. Regression analysis of 3.2a gives $Y = 0.922(\pm 0.116)X + 9.0(\pm 1.1)$, $r=0.92$, $df=12$, $P<0.001$. Regression analysis of 3.2b gives $Y = 0.451(\pm 0.120)X + 6.8(\pm 1.5)$, $r=0.76$, $df=10$, $P<0.01$. X is the mean age of *Calluna* (years) and Y is *Calluna* green shoot density (the mean number of green shoots touched by five pins).

Figure 3.3a

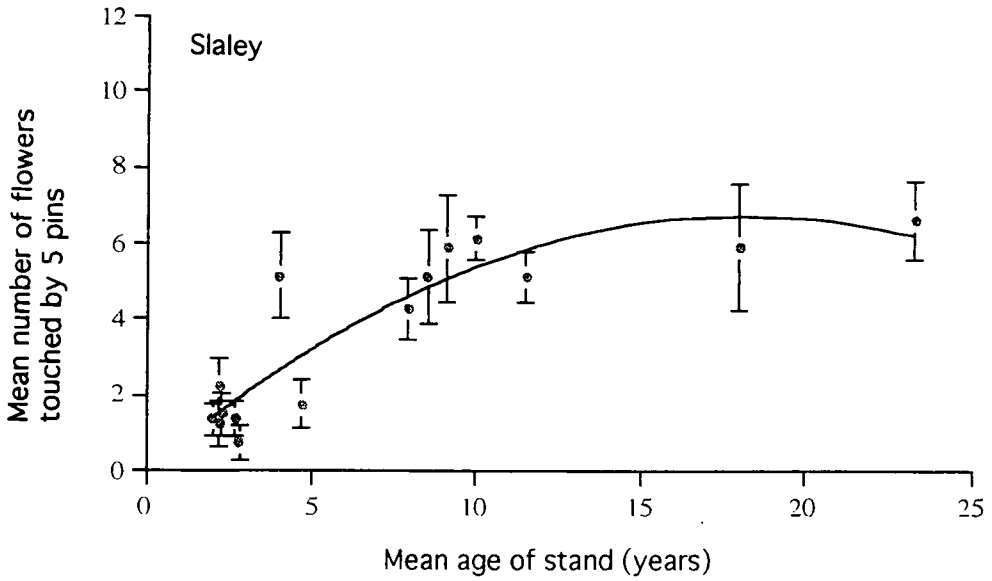


Figure 3.3b

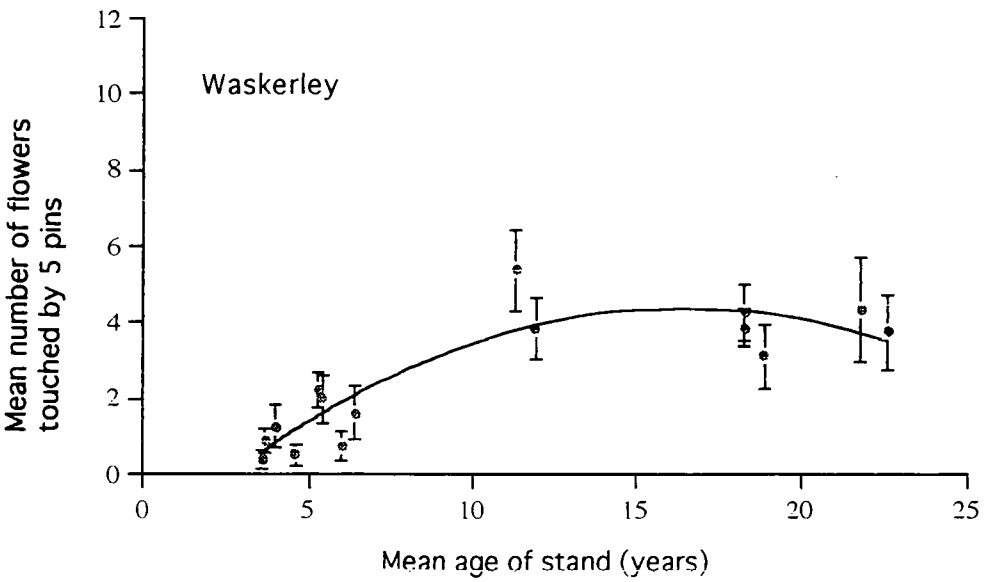


Figure 3.3a and 3.3b. The relationship between the mean age of *Calluna* stands and the density of flowers at a) **Slaley** and b) Waskerley. Data recorded in 1992 and 1993 have been combined. The mean age was determined by counting annual growth rings using a sample of ten stems. The mean flower densities are shown ±1SE and were calculated from eight samples of five pins. Regression analysis of 3.3a gives Y = 0.739(±0.154)X -0.020(±0.007)X^2+0.05(±0.64), r=0.90, df=12, P<0.001. Regression analysis of 3.3b gives Y = 0.765(±0.182)X -0.023(±0.007)X^2-1.86(±0.84), r=0.90, df=12, P<0.001. X is the mean age of *Calluna* (years) and Y is flower density (the mean number of green shoots touched by five pins).

Figure 3.4a

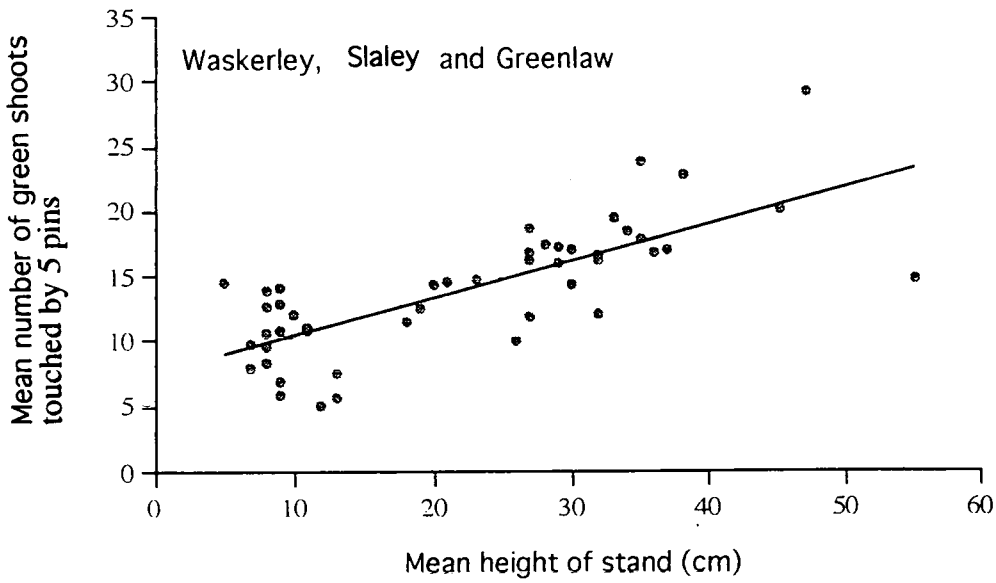


Figure 3.4b

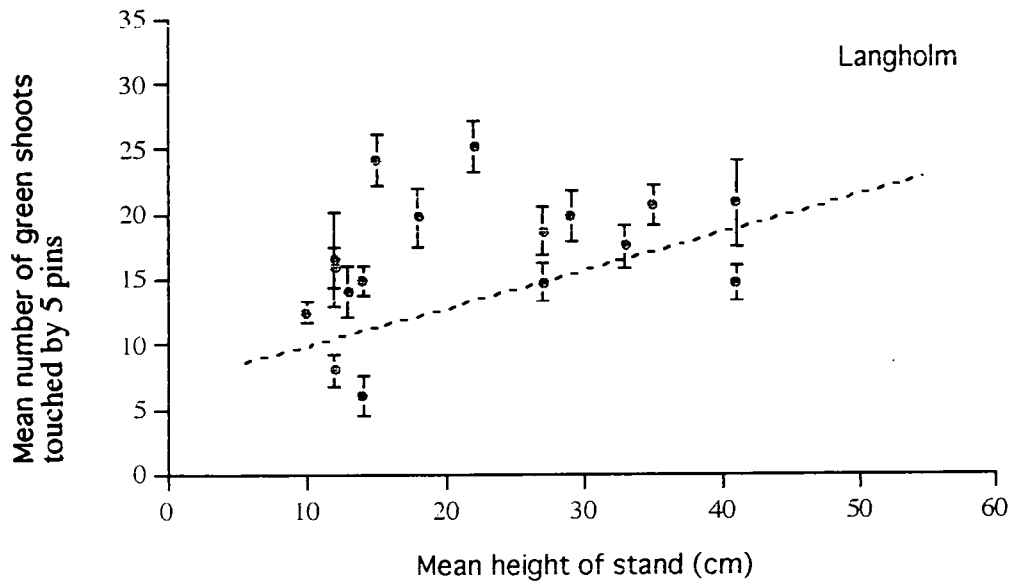


Figure 3.4a and 3.4b. The relationship between the mean height of *Calluna* stands and the density of green shoots at a) Slaley, Waskerley and Greenlaw and b) Langholm. At Slayley and Waskerley data recorded in 1992 and 1993 have been combined. The mean height was calculated from a sample of 40 plants at each stand. The mean green shoot densities are shown ±1SE and were calculated from eight samples of five pins. Regression analysis of 3.4a gives Y=0.285(±0.036)X+7.7(±0.9), r=0.75, df=47, P<0.001. X is the mean height of *Calluna* (cm) and Y is green shoot density (mean number of green shoots touched by five pins). Regression analysis of 3.4b gave no significant correlation. The trend line from 3.4a is superimposed on this graph to demonstrate the different relationships at these sites.

3.3.3.2 Flower density

Similar relationships between *Calluna* height and flower density were found at Slaley, Waskerley and Greenlaw, so data from these sites were combined. There was a significant, positive linear association between height and flower density ($r=0.91$, $df=48$, $P<0.001$, Figure 3.5a). Data at Langholm may have followed the same pattern because the equation (in Figure 35.b) was not significantly different to that of the grouped study areas (Figure 3.5b). However, the high variance associated with flower density over the small range of heights studied at Langholm, justified the separate treatment of this data.

3.3.4 The relationship between the densities of green shoots and flowers

Regressions of flower density against green shoot density were not significantly different at all four sites, so data were combined. There was a significant positive linear correlation between these variables ($r=0.73$, $df=63$, $P<0.001$, Figure 3.6). When shoot density doubled, flower density increased by a factor of approximately 2.4.

3.3.5 Floristic composition

Appendices A.5-A.8 show the floristic composition of individual stands at Slaley, Waskerley, Greenlaw and Langholm.

The cover of most species varied in different stands, but none was significantly correlated with *Calluna* height or green shoot density. Table 3.1 shows the average cover of each species at the four sites, when data from stands of all heights and ages were combined. The vascular plant most frequently associated with *Calluna* was *Erica tetralix*. *Empetrum nigrum* was recorded at Waskerley and *Erica cinerea* occurred in several stands at Slaley. Bryophytes were recorded in all study areas and achieved almost complete cover at ground level in some stands.

Calluna cover increased with stand height. The relationship was curvilinear and cover increased very little when *Calluna* was more than 25cm tall. Ground cover was significantly positively correlated with the decadic logarithm of *Calluna* height ($r=0.86$, $df=12$, $P<0.001$, Figure 3.7). This graph combined data from all field sites.

Figure 3.5a

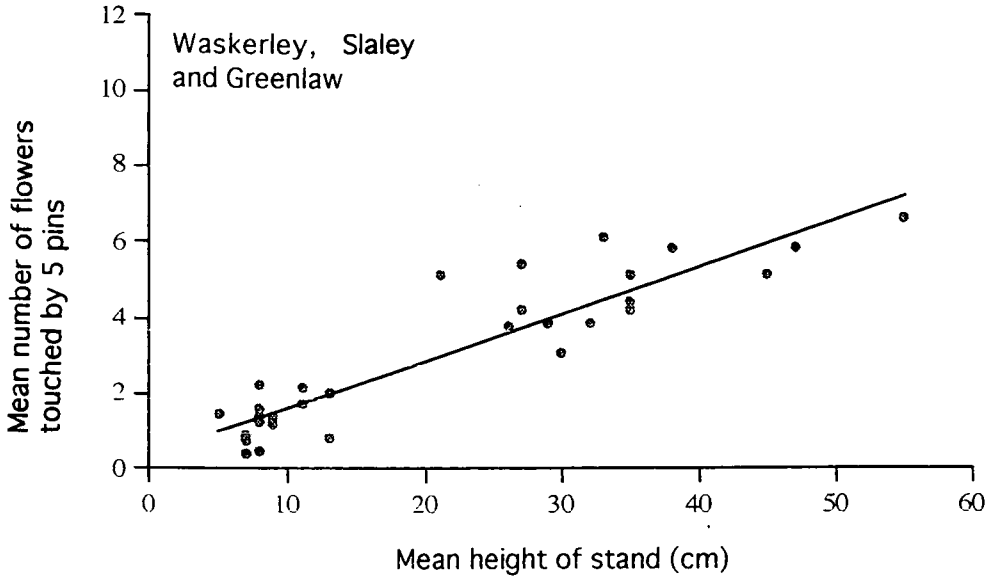


Figure 3.5b

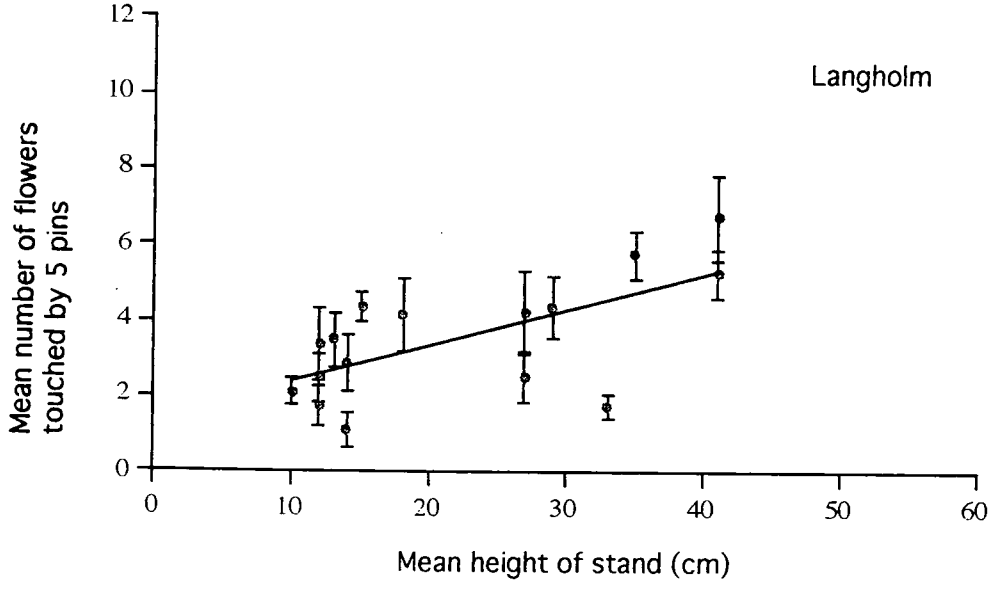


Figure 3.5a and 3.5b. The relationship between the mean height of *Calluna* stands and the density of flowers at a) Slaley, Waskerley and Greenlaw and b) Langholm. At Slayley and Waskerley data recorded in 1992 and 1993 have been combined. The mean flower densities are shown ±1SE and were calculated from eight samples of five pins. Regression analysis of 3.5a gives $Y = 0.121(\pm 0.011)X + 0.47(\pm 0.28)$, r=0.84, df=48, P<0.001. Regression analysis of 3.5b gives $Y = 0.097(\pm 0.030)X + 1.40\ (\pm 0.73)$, r=0.65, df=14, P<0.01. X is the mean height of *Calluna* (cm) and Y is green shoot density (mean number of green shoots touched by five pins)

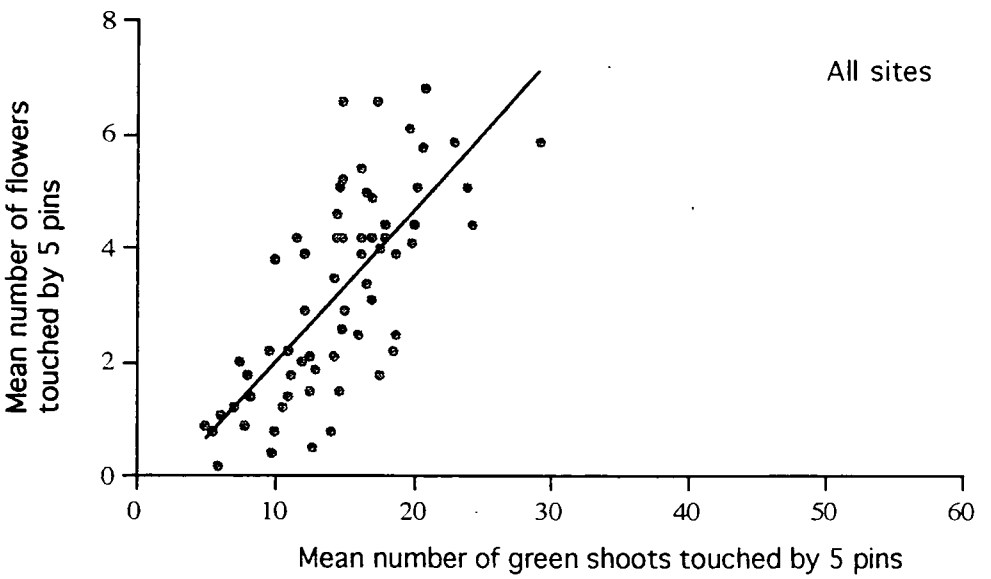


Figure 3.6. The relationship between *Calluna* green shoot density and flower density. Data from all sites have been combined. At Slaley and Waskerley data recorded in 1992 and 1993 have been combined. Regression analysis gives $Y = 0.258(\pm 0.031)X - 0.58(\pm 0.47)$, r=0.73, df=63, P<0.001. X is green shoot density (mean number of green shoots touched by five pins) and Y is flower density (mean number of flowers touched by five pins). Both green shoot density and flower density were calculated from eight samples of five pins at each stand.

Plant species % cover (± 1SD)										
Site	*Calluna vulgaris*	*Vaccinium myrtillus*	*Erica tetralix*	*Erica cinerea*	*Empetrum nigrum*	*Juncus squarrosus*	Bryophytes	Lichens	Grasses	Others
Slaley	91	0	6	1	0	0	20	3	3	0
(15 stands)	(11)	(0)	(11)	(3)	(0)	(1)	(14)	(4)	(5)	(0)
Waskerley	83	1	1	0	2	0	45	2	4	0
(15 stands)	(17)	(2)	(2)	(0)	(3)	(0)	(27)	(2)	(9)	(1)
Greenlaw	89	0	2	0	0	0	50	7	1	0
(20 stands)	(18)	(0)	(3)	(0)	(0)	(0)	(29)	(17)	(3)	(0)
Langholm	91	0	10	0	0	8	62	0	3	0
(17 stands)	(13)	(0)	(10)	(0)	(0)	(13)	(21)	(1)	(4)	(1)

Table 3.1. The average cover values of plants found at four study areas. Cover was estimated using 40 point quadrats at each stands. Species were recorded as present if they touched a vertical pin and cover values were calculated from 40 pin samples at each stand. The values in the table are the average cover values for all the stands sampled in each study area, These were calculated by combining data from all the different-aged stands at a study area. At Slaley and Waskerley data collected in 1992 and 1993 have been combined. The value in parentheses is ± 1SD.

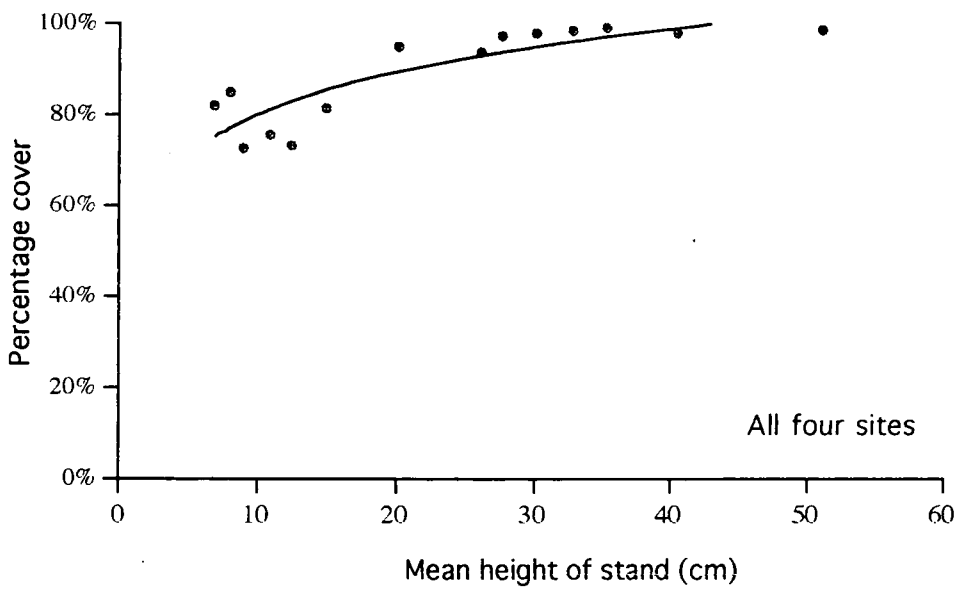


Figure 3.7. The relationship between mean stand height and *Calluna* cover. Data from all sites have been combined. At Slaley and Waskerley data collected in 1992 and 1993 have been used. The points on the graph were average values calculated from sets of five data points, when data was arranged in order of ascending height. Regression analysis gives $Y = 31.0(\pm 5.4)\lg X + 49.5(\pm 7.0)$, r=0.86, df=12, P<0.001. X is the mean height of *Calluna* (cm) and Y is the percentage of ground covered by *Calluna*.

3.4 Discussion

3.4.1 Age and height as descriptions of stand vegetation

At Slaley and Waskerley, *Calluna* height was significantly correlated with the logarithm of stand age, as less vertical extension was observed in older stands. This result is predictable. Most plants grow as they become older, but growth cannot be sustained indefinitely because of the species lifespan, which in *Calluna* is approximately 25-40 years (Watt 1955; Barclay-Estrup & Gimingham 1969; Gimingham 1972, 1988). Barclay-Estrup (1970) recorded that *Calluna* was shortest in the pioneer phase, taller in the building and mature phases and shorter in the degenerate than in the mature. Barclay-Estrup noted that phase-related changes in *Calluna* height were less marked than similar changes in biomass.

Although in this study of managed northern heaths, *Calluna* height increased with *Calluna* age, *Calluna* does not behave in this way in all circumstances. On blanket bog *Calluna* exists in a steady state of production because factors including snow weight and strong winds restrict canopy height, the bog surface grows upwards, and buried stems gradually die (Forrest 1971).

The slopes of the regression equations describing the relationship between stand age and height were significantly different at Slaley and Waskerley. Environmental factors such as altitude, soil nutrition, water supply and exposure could influence *Calluna* growth rate and maximum height. Marked differences in *Calluna* growth characteristics can occur where there are large regional or altitudinal differences between sites. For example, *Calluna* plants from high altitude or high exposure sites tend to have a prostrate growth form, while those from less exposed or lower altitude sites are more erect (Grant & Hunter 1962). Since plants in Grant and Hunter's studies were grown from seed collected at different sites, it is clear that plant structure is partially inherited.

The maximum age displayed in Appendices A.1-A.2 gives the minimum time between the date of sampling and the date on which the stand was burned, assuming immediate regeneration of *Calluna*. However, since speed of regeneration depends on a number of factors, including the phase of the plant when burned, the burning season and the temperature of the fire (Whittaker 1961; Miller & Miles 1970; Hobbs & Gimingham 1987) is it not usually possible to accurately estimate the time since the stand was burned. Mean stand age was the time that has elapsed since most plants in the stand had began to regenerate from rootstocks after a fire.

It was decided that even though the relationship between *Calluna* age and height is not linear throughout the whole of the *Calluna* lifecycle, height was more useful for discriminating between different stands than stand age for the purpose of this study. Although Watt (1955) noted certain associated difficulties with the use of annual growth rings to determine stand age, the main problem with the technique in this study was not accuracy, but the length of time required to obtain results. *Calluna* height could be measured quickly at each stand. Also because the relationship between age and height differed between sites, age *per se* was less useful for examining other variables because data from different sites could not be combined. The main disadvantage associated with height as a description of the stand is its potential to change during the growing season.

3.4.2 Variation in the density of *Calluna* green shoots

The point quadrat technique provided a relative measure of the density of plant structures. Other studies of *Calluna* heathland have used absolute measures of vegetation variability *e.g.* biomass to describe differences in structure or estimate the productivity of different *Calluna* ages, plant species or sites (*e.g.* Chapman *et al.* 1975).

Calluna vulgaris is an evergreen, woody, perennial shrub that may retain the leaves produced in any growth season for up to four years (Gimingham 1960; Chapman *et al.* 1975; Gimingham *et al* 1979). In this study, green shoots were not separated into current and previous year's growth categories. Therefore data do not constitute an index of production, but results from this study may be compared with those of studies that have measured leaf biomass.

The rate of increase of green shoot density with stand age was significantly higher at Slaley than at Waskerley ($t=2.82$, $df=22$, $P<0.01$, Figures 3.2a and 3.2b). However, stand height and the logarithm of stand age were also significantly correlated ($P<0.001$), as were stand height and green shoot density. It was not possible to determine whether green shoot density increased because of increased age, or increased height because of the intercorrelations between these variables.

The significant, positive linear relationship between *Calluna* height (X) and green shoot density (Y) $Y = 0.285(\pm0.036)X + 7.65(\pm0.922)$, $r=0.75$, $df=47$, $P<0.001$, was common to the Slaley, Waskerley and Greenlaw study areas. This equation did not explain the relationship between these variables at Langholm (Figure 3.4b). This site lay further west than the other three and may have had a warmer, wetter climate that promoted denser, more vigorous growth. Alternatively other environmental factors *e.g.* edaphic nutrition or the grazing regime could have affected the relationship between height and green shoot density.

Published work describes a decrease in canopy density as *Calluna* ages because branches and plants die (Miller & Miles 1970; Forrest 1971). In Forrest's study of a high altitude North Pennines blanket bog, this decrease began after eight years. Plants that grew more slowly due to heavy grazing, poor soil or cold climate remained short, dense and vigorous for longer than fast growing plants (Miller 1980). *Calluna* biomass increased with seral age and was lowest in the pioneer and degenerate phases and highest in the building and mature phases (Barclay-Estrup 1970). The greatest part of the increase in biomass that occurred in the building and mature phases was due to the formation of wood (Miller 1979). Net production of young *Calluna* shoots was highest in the building phase, intermediate in the mature and lowest in the degenerate (Barclay-Estrup 1970). Miller and Watson (1978) disputed these results, finding no evidence for decrease in production until the degenerate stage. Year to year variation in green shoot production has been related to mean air temperature between mid April and late August (Miller 1979). Exposure reduced production (Summers 1978).

3.4.3 Variation in the density of *Calluna* flowers

The significant positive linear correlation between flower and green shoot density ($r=0.73$, $df=63$, $P<0.001$, Figure 3.6) is expected when the growth pattern of *Calluna* is considered, because flower shoots arise from the currents year's leaf-bearing long shoots. Flower production has been correlated positively with April temperature (Miller 1979) and negatively with altitude (Miller & Watson 1978). Results from studies of production under different grazing regimes have not proved consistent (Hewson 1962; Grant 1971; Moss & Hewson 1985) and Miller (1979) found that his measure of flower production was not related to stand age.

3.4.4 Development of *Calluna* cover

Calluna usually exceeded 90% ground cover when its height was approximately 23cm of more (Figure 3.7). The time required to achieve this level of cover would have been different at Slaley and Waskerley because of the significant difference in *Calluna* growth rates at these sites (section 3.3.1). Other authors have estimated that it may take five to ten years to establish a *Calluna* cover of 80-90% (Chapman *et al.* 1975; Miller & Watson 1978; Miller 1979; Gimingham *et al.* 1979). *Calluna* cover is maximal in the late building and early mature phases (Watt 1947, 1955; Barclay-Estrup & Gimingham 1969).

3.4.5 The relationship between *Calluna* height, green shoot density and other species

In this study there were no significant correlations between *Calluna* height or shoot density and the proportion of ground covered by other species. *Calluna* can dominate the

canopy even when density of the plant is low at ground level (Barclay-Estrup & Gimingham 1969). Plants that exist below the canopy must be able to tolerate shade. Barclay-Estrup and Gimingham (1969) found that *Calluna* cover in the canopy was negatively correlated with the cover of dwarf shrubs, grasses, bryophytes and lichens, and other vascular plants. Cover by other vascular plants was lowest in the building phase, and highest when *Calluna* was establishing in the early pioneer (Barclay-Estrup & Gimingham 1969). The lack of correlation between *Calluna* height or density and the cover of other species may have resulted from a lack of sensitivity in the survey method. If too few pins are used rarer species and plants with little horizontal spread may go unrecorded.

3.4.6 The flora at the study areas

The vascular plant found most often with *Calluna* in the study was *Erica tetralix*, with several records of *Empetrum nigrum* at Waskerley and *Erica cinerea* at Slaley. Bryophytes were recorded at all sites. European heaths are not usually floristically rich (Gimingham *et al.* 1979). Plant composition within a region may be affected by the soil nutrition (Moss 1969), the burning regime (Pearsall 1950; Gimingham *et al.* 1979) and different grazing practices (Pearsall 1950; Welch 1984). Examples are the association of *E. tetralix* with damper areas of moorland (Pearsall 1950; Gimingham 1972) and the promotion of ericoids and lichens, graminoids and forbs by light and heavy grazing regimes respectively (Welch 1984).

3.4.7 Evaluation of methodologies

The number of point quadrats used in this study was small compared to studies by other authors (Barclay-Estrup 1969; Miller & Watson 1978; Welch 1984). Some studies have used up to 1000 pins m^{-2} (*e.g.* Barclay-Estrup & Gimingham 1969). It took between 15-40 minutes to record touches at 40 points. Tall, dense stands were particularly time consuming to survey. The homogeneity of stands that have been managed by regular burning allowed the use of a relatively low number of samples per stand, at least when recording plant structure.

Chapter Four

Methods of Sampling Lepidoptera Larvae

4.1 Introduction

This chapter describes the methods that were used to capture Lepidoptera larvae and assess their density at the different sample sites during this study. Estimates of animal density may be 'absolute' or 'relative'. Absolute estimates express density as the number of animals per unit area, relative estimates describe density as the number of animals per unit sampling effort (Morris 1955). The distinction between absolute and relative sampling techniques is not always clear because absolute techniques do not often operate with complete efficiency, and relative methods may be corrected to give estimates of absolute density (Southwood 1978). In this study the ideal sampling method was required to provide an absolute population estimate, or a relative estimate that could be calibrated by an absolute technique. The perfect method would operate with equal efficiency in *Calluna* stands with different heights and densities, sample all species effectively, be portable and non-destructive to the vegetation, and collect data rapidly so that a number of *Calluna* stands could be studied on the same date.

This work attempts to study the complete heathland Lepidoptera community. This required the identification of larvae to species. It was important to identify techniques that did not sample some species effectively. To this end, experiments examined the sampling efficiency of different techniques with different species and a number of comparisons were made between methods.

4.2 The identification of Lepidoptera larvae

The larvae of some Lepidoptera species occur in a variety of colour forms. Distinguishing marks are not always clear and the appearance of individuals may change dramatically as they grow through a series of instars before pupation. However, few of the published works that are currently available facilitate the correct identification of unknown specimens collected in the field. Carter and Hargreaves (1986) and Brooks (1991) do not describe all the British species. Those guides that are more comprehensive *e.g.* South (1961) and Stokoe (1948) do not combine a descriptive text with illustrations of larvae in different instars. None of these books include dichotomous identification keys. Due to this lack of information, it was necessary to

rear unknown species of larvae to the adult stage, since adults could be more easily identified from colour photographic plates in text books (*e.g.* Skinner 1984; Brooks 1991).

Features of macrolepidopteran larvae were easily learned and most species could be identified in the field. Microlepidoptera larvae were difficult to recognise. Only one species, *Ambylyptilla acanthodactyla* was distinctive as a larva. Few microlepidoptera larvae were successfully reared to the adult stage. Those that did survive are detailed in a species list (Chapter Five, Table 5.2). Microlepidoptera larvae found during the monitoring programme were not identified to species, and were referred to as microlepidoptera.

It was practical to identify larvae alive, as dead specimens, whether fresh or preserved in alcohol, soon lost colour and other features that aided their identification.

4.3 Description of the methods used to sample Lepidoptera larvae

4.3.1 Two-stage sampling method: jarring the vegetation followed by extraction in Berlese-Tullgren funnel

This technique collected larvae in two stages. The first stage captured larvae in the field and was followed by a longer period of laboratory extraction to collect animals that had been missed in stage one. Absolute estimates of population density could be calculated from these data.

4.3.1.1 Stage one: Jarring the vegetation

Jarring has been used to locate a variety of invertebrates. With some species of weevils, chrysomelids and Lepidoptera larvae the technique is so effective that it provides absolute population estimates (Gibb & Betts 1963; White 1975; Southwood 1978).

The sample unit was a quadrat of either 35cm by 35cm ($0.12m^2$), or 50cm by 50cm ($0.25m^2$). Large quadrats were used except where ground cover by *Calluna* was sparse and occupied less than 50% of a randomly located $0.25m^2$ quadrat. In these circumstances, the $0.12m^2$ quadrats were used. Ten quadrats of one size were used at each *Calluna* stand.

Each quadrat was placed at a random location within the stand and a white tray was placed under the plants in the quadrat. Where stems were particularly dense, plants from the delimited area were bent over the tray. *Calluna* inside the quadrat was shaken vigorously and tapped with a stick for a period of approximately one minute. Both the

tray and the surface of the litter were searched thoroughly for larvae that had been knocked from the foliage. Searching proved most effective when a period of five minutes was left after jarring, to allow animals that were hidden in litter to emerge. All larvae found at this stage were identified and recorded in the field.

Calluna from each quadrat was harvested for the second phase of laboratory extraction. All vegetation within the quadrat frame was clipped to ground level and placed in a sealed plastic bag. The top 2cm of litter within the quadrat was removed separately.

A period of 15-20 minutes was required to jar, search and harvest vegetation at each quadrat.

4.3.1.2 Stage two: Extraction by Berlese-Tullgren funnel

Berlese-Tullgren funnels as described by Southwood (1978) extract invertebrates from soil or litter samples. They exploit the tendency of animals to move away from heat to avoid desiccation.

Funnel dimensions were cylinder height 22cm, cylinder diameter 40cm, cone height 21cm. The heat source was a 100W electric light bulb. A total of 24 funnels was available in the first year of the study, 1991, and 52 in 1992. In 1992, 22 smaller funnels with cylinder height 15cm, cylinder diameter 15cm, cone height 10cm and a 100W light bulb heat source were available for the extraction of larvae from litter. Plant material and litter collected from quadrats (section 4.3.1.1) was placed in the funnels on the evening of harvesting or the morning after. The contents of each quadrat were placed in separate funnels. Separate extraction from litter did not yield more larvae, so the litter layer from each quadrat was included in the funnel with other vegetation. Southwood (1978) recommends that humidity within funnels be maintained above 90% for animals that are not resistant to desiccation. The funnels did not have a humidity regulation system so they were sealed as tightly as possible, both to prevent animals escaping at the top and to maximise humidity by retaining moisture that had evaporated from the vegetation inside the funnel. Animals were extracted live into dry collecting jars that were checked every day. Funnels were run for a period of ten days or until no animals had been extracted from any of the funnels for three consecutive days.

The number of funnels available and the time required for extraction prevented more than five stands from being examined by this method in the same week.

4.3.2 Sampling with a sweep net

In this technique a net is brushed rapidly across the top of the vegetation, collecting a proportion of the invertebrates that have not flown or dropped off at the approach of the operator. Relative estimates of population density can be calculated. The technique has been used extensively for the collection of pest species in agricultural systems. It is not suitable for all insects. Efficiency may vary in different habitats, with different species and age classes of insect, and with different weather conditions including wind speed, wind direction, temperature, humidity and wetness of the vegetation (Carpenter & Ford 1936; Romney 1945; Hughes 1955; Johnson *et al.* 1957; Saughstad *et al.* 1967; Southwood 1978; Schotzko & O'Keeffe 1986b). Since only the top of the vegetation is swept, a progressively smaller fraction of the foliage is sampled as vegetation becomes taller (Southwood 1978). This causes the technique's effectiveness to vary with time of day and microclimate within the plant for species that exhibit vertical movement patterns that are regulated by a diel cycle or environmental conditions (Davidson & Shackleford 1929; Poinar & Gyrisco 1960; Fewkes 1961).

The sweep net used in this study had a circular frame of diameter 50cm, attached to a 40cm long handle. The bag was 70cm deep and was made from fine mesh white polyester, strengthened at the rim with canvas.

Each sample comprised ten brisk strokes across the vegetation. Each stroke was separated by a pace as the operator walked forward, and the net was swept in alternating directions in front of the operator's feet, so that each stroke collected from untouched vegetation. At the end of each set of ten strokes the bag was searched for larvae. These were identified in the field and released. In the early part of 1991, ten samples of ten strokes were collected at each stand but this was later changed to 20 samples per stand to increase the precision of the population estimate. Approximately 15-25 minutes were required to collect 20 samples from a *Calluna* stand by this technique.

4.3.3 Direct searching

The larvae of two lasiocampid species, the fox moth *Macrothylacia rubi* and the northern eggar *Lasiocampa quercus callunae* could be located by moving carefully through the stand and searching visually for individuals. Larvae of these species are large (up to 8-10cm long) and could be observed at all levels of the plant. The method was inappropriate for smaller species *e.g.* noctuids and geometrids, because their small size promoted observer bias. For example, small species would be found more easily in

the canopy than at ground level. Brightly coloured larvae would be more obvious than cryptic species.

Searching provided a relative estimate of population density. Quantitative searches were performed by searching a stand thoroughly for a period of five minutes, after Fielding (unpublished Ph.D. thesis 1992).

4.3.4 Blow-Vac

The Blow-Vac is a hand-held petrol driven suction machine. Machines of this type are sold for garden use, but are easily adapted for collecting insects. The machine is converted for sampling by placing a fine mesh nylon bag inside the collecting nozzle, to collect invertebrates and debris, and a wire grid further into the tube to prevent the bag being sucked into the engine. Wilson *et al.* (unpublished manuscript quoted in Wright and Stewart 1992) and Wright and Stewart (1992) have described the early use of this machine for sampling invertebrates.

The Blow-Vac was used to sample stands where *Calluna* was less than 10cm tall. Each sample was taken from an area of $1m^2$, that was delimited by a circular metal frame quadrat. The nozzle of the Blow-Vac was pressed systematically over the vegetation until the whole of the quadrat had been sampled. This took approximately five minutes. The contents of the mesh bag were emptied into a plastic bag and returned to the laboratory for sorting. Five $1m^2$ quadrat samples were collected at each stand.

4.3.5 D-Vac

Suction samplers may be highly efficient (Johnson *et al.* 1957; Ellington *et al.* 1984), so the number of animals collected from a known area is often taken to represent the absolute density. For high extraction rates windspeed at the nozzle must be greater than 96km/h and the vegetation should not be damp (Southwood 1978). This D-Vac suction sampler was described by Dietrick (1961). The nozzle diameter was 36cm .

A circular metal quadrat frame was used to enclose an area of $1m^2$. The nozzle of the D-vac was pressed systematically over the vegetation until the whole quadrat had been sampled, taking a time period of approximately 5 minutes. The collecting bag was emptied into a plastic bag which was sealed and returned to the laboratory for sorting. Five $1m^2$ samples were taken at each stand.

4.4 Evaluation of Methods

The merits of the sampling methods were examined by experiments to test efficiency, and by comparing the results of two or more techniques used to sample the same site on

the same day. Appraisal considered the number of larvae and species collected, evidence that species were collected selectively, operation time, the range of vegetation heights that could be sampled, ease of use and portability. Table 4.1 summarises the properties of the different techniques.

4.4.1 A comparison of sweepnet sampling with jarring followed by extraction in Berlese-Tullgren funnels

4.4.1.1 Method

During the 1991 and 1992 field seasons, 31 *Calluna* stands were sampled both by sweepnetting (section 4.3.2) and by a combination of jarring and extraction in Berlese-Tullgren funnels (section 4.3.1) on the same date. The mean height of the stands ranged between 8cm and 40cm. At each stand the vegetation in ten quadrats was jarred, clipped and removed for extraction in Berlese-Tullgren funnels. The stand was then sampled using a sweepnet. Quadrat samples were always collected before the area was sampled by sweepnet, to reduce interference between the techniques.

The mean number of larvae of each species collected per sample was calculated for each method and densities of larvae were derived.

4.4.1.2 Results

Table 4.2 shows the number of larvae collected by each method and the proportion of microlepidoptera and macrolepidoptera in the catches. Data for the combined jarring and Berlese-Tullgren extraction method are shown for the combined process and for the component jarring and extraction stages. Table 4.3 lists the 29 macrolepidoptera species found during the three year study, gives the number of individuals of each species that were taken by different methods and shows the proportion of each species in the catches. Table 4.4 gives a relative variability measure $SD^{1.7}/x$, which was calculated for each of the species from data collected by each method. x was the mean number of animals per sample, and SD the standard deviation of the mean. The variability measure $SD^{1.7}/x$ was calculated in place of the coefficient of variation or other measures of variability because all these were found to be significantly correlated with the mean.

The number of Lepidoptera larvae collected by sweepnetting was approximately 1.3 times greater than the number collected by jarring followed by Berlese-Tullgren extraction (Table 4.3). However, the proportions of macrolepidoptera and microlepidoptera in the catches were similar for all methods and ranged between 91-94% for macrolepidoptera and 6-9% for microlepidoptera (Table 4.2).

Property	Sampling Method					
	Jarring	**Berlese-Tullgren**	**Sweepnet**	**Direct searching**	**Blow-Vac**	**D-Vac**
Sampling unit	Quadrat ($0.25m^2$ or $0.12m^2$)	Quadrat ($0.25m^2$ or $0.12m^2$)	10 strokes (approx. $4.2m^2$)	5 minutes	Quadrat ($1m^2$)	Quadrat ($1m^2$)
No. of samples at each stand	10	10	20	1	5	5
Time to collect all samples from stand	3.5 hours to jar, search, clip and pack vegetation	Jarring time + 10 days	15-25 minutes	5 minutes	30 minutes	30 minutes

Table 4.1. A summary of the various methods used to locate Lepidoptera larvae during this study. The number of species recorded * refers to the number of species found at the stands that were sampled by both sweepnet, jarring and Berlese-Tullgren extraction on the same day. The number of species recorded by Blow-Vac was the total number of species from all sites sampled by that method in 1993. † denotes that these data are quoted from Wright and Stewart (1992). **(Continued overleaf)**.

Property	Sampling Method					
	Jarring	**Berlese-Tullgren**	**Sweepnet**	**Direct searching**	**Blow-Vac**	**D-Vac**
No. of macrolepidoptera species recorded	11 * 6 * Total by both methods = 12 *		13	Appropriate for *M.acrothylacia rubi*, *Pavonia pavonia*, *Lasiocampa quercus callunae*)	7	0
Destructive to vegetation?	Yes	Yes	No	No	No	No
Portability	Beating tray weight 1.1kg. Good.	Poor, requires transportation of bulky samples	Good (weight 0.8kg)	Excellent (No equipment required)	Good (weight approximately 8kg) †	Poor (weight approximately 30kg) †
Calluna height range sampled in trials	8cm - 40cm	8cm - 40cm	5cm - 40cm	All *Calluna* heights	<10cm	<10cm
Limitations	Not for use in strong winds. Difficult where stems dense	Poor extraction of phototactic species or larvae with poor mobility. Mortality in funnels.	Samples only top of vegetation	Observer bias	Low extraction efficiency in test (section 4.4.4)	Failed to extract larvae in test (section 4.4.4). Heavy and difficult to operate

Table 4.1. (Continued from previous page).

Lepidoptera Class	Sweepnet		Jarring		Berlese-Tullgren		Jarring + Berlese-Tullgren	
	No.	%	No.	%	No.	%	No.	%
Macrolepidoptera	1236	94%	738	94%	184	91%	922	93%
Microlepidoptera	80	6%	46	6%	19	9%	65	7%

Table 4.2. The relative proportions of macrolepidoptera and microlepidoptera larvae in catches by different methods. Data have been pooled from all stands that were sampled with a sweepnet and by a combination of jarring the vegetation followed by extraction in Berlese-Tullgren funnels on the same date. Each column lists the number of larvae found and re-expresses this value as a percentage of the total number of Lepidoptera individuals found by the same method.

Species	Sweepnet		Jarring		Berlese-Tullgren		Jarring + Berlese-Tullgren	
	No.	%	No.	%	No.	%	No.	%
Geometridae								
Dyscia fagaria	3	0.2%	0	0%	0	0%	0	0%
Ectropis bistortata	0	0%	0	0%	0	0%	0	0%
Ematurga atomaria	20	1.6%	2	0.3%	0	0%	2	0.2%
Entephria caesiata	21	1.7%	19	2.6%	1	0.5%	20	2.2%
Epirrita filigrammaria	98	7.9%	51	6.9%	1	0.5%	52	5.6%
Eulithis spp.	152	12.3%	116	15.7%	12	6.5%	128	13.9%
Early instars of *Eupithcia* spp.	15	1.2%	6	0.8%	0	0%	6	0.7%
Eupithecia goossensiata	92	7.4%	22	3.0%	0	0%	22	2.4%
Eupithecia nanata	440	35.6%	85	11.5%	3	1.6%	88	9.5%
Hydriomena furcata	224	18.1%	171	23.2%	41	22.3%	212	23.0%
Operophtera brumata	0	0%	0	0%	0	0%	0	0%
Perizoma didymata	0	0%	0	0%	0	0%	0	0%

Table 4.3. The macrolepidoptera larvae found by different sampling methods at the 31 stands that were sampled with a sweepnet and by a combination of jarring the vegetation followed by extraction in Berlese-Tullgren funnels on the same date. The Table lists all the species of macrolepidoptera that were found during the three years of the study by any method. *Eulithis populata* and *E. testata* are grouped together because it is difficult to separate the larvae of these species. Similarly, early instars of the *Eupithecia* species could not be identified to species and are not separated. Each column lists the number of each species found and re-expresses this value as a percentage of the total number of macrolepidoptera individuals found by the same method. **(Continued overleaf)**.

Species	Sweepnet		Jarring		Berlese-Tullgren		Jarring + Berlese-Tullgren	
	No.	%	No.	%	No.	%	No.	%
Noctuidae								
Anarta myrtilli	31	2.5%	9	1.2%	0	0%	9	1.0%
Aporophylla lueneburgensis	0	0%	0	0%	0	0%	0	0%
Autographa gamma	0	0%	0	0%	0	0%	0	0%
Blepharita adusta	0	0%	0	0%	0	0%	0	0%
Ceramica pisi	2	0.2%	0	0%	0	0%	0	0%
Diarsia mendica	0	0%	0	0%	0	0%	0	0%
Lycophotia porphyrea	119	9.6%	254	34.4%	126	68.5%	380	41.2%
Orthosia gothica	0	0%	0	0%	0	0%	0	0%
Papestra biren	0	0%	0	0%	0%	0%	0	0%
Phlogophora meticulosa	0	0%	0	0%	0	0%	0	0%
Xestia agathina	0	0%	0	0%	0	0%	0	0%
Lasiocampidae								
Lasiocampa quercus callunae	11	0.9%	1	0.1%	0	0	1	0.1%
Macrothylacia rubi	8	0.6%	1	0.1%	0	0	1	0.1%
Trichuria crataegi	0	0	0	0	0	0	0	0
Others								
Dicallomera fascelina	0	0	0	0	0	0	0	0
Pavonia pavonia	0	0	1	0.1%	0	0	1	0.1%
Phragmatobia fuliginosa	0	0	0	0	0	0	0	0

Table 4.3. (Continued from previous page).

Class / species	Mean $SD^{1.7}/x$ by sweepnet (n)	Mean $SD^{1.7}/x$ by jarring (n)	Mean $SD^{1.7}/x$ by Berlese-Tullgren (n)	Mean $SD^{1.7}/x$ by jarring and Berlese-Tullgren (n)
Macrolepidoptera excluding *L. porphyrea*	1.33 (30)	1.46 (26)	1.40 (12)	1.41 (27)
Microlepidoptera	1.38 (22)	1.28 (12)	1.54 (10)	1.34 (14)
Eulithis spp.	1.35 (10)	1.42 (11)	1.34 (7)	1.37 (12)
Eupithecia nanata	1.16 (20)	1.27 (15)	- -	1.27 (15)
Eupithecia goossensiata	1.46 (14)	1.40 (5)	- -	1.40 (5)
Hydriomena furcata	1.46 (10)	1.68 (8)	1.64 (6)	1.69 (9)
Lycophotia porphyrea	1.36 (16)	1.69 (16)	1.91 (13)	1.84 (16)

Table 4.4. The mean values of a relative variability measure $SD^{1.7}/x$ by diferent sampling methods. Data for the combined jarring and Berlese-Tullgren extraction method are shown for both the combined method and for its component stages. x is the mean number of larvae collected per sample, SD the standard deviation of the mean. n is the number of stands for which a variability measure could be calculated because the number of animals collected was greater than zero. The mean value of the variability measure was calculated only where n was greater than or equal to 5.

Similar numbers of species were collected by sweepnetting and by the combined Berlese-Tullgren extraction methods (13 and 12 species respectively). There is an 86% overlap between the species that were located by these techniques. Only six species were extracted by Berlese-Tullgren funnel. All species found by heat extraction were also recorded by sweeping and jarring.

If all species are considered in the analysis, correlation between the proportion of each species in the combined jarring and Berlese-Tullgren catch and its proportion in the sweepnet catch is not significant (r=0.45, df=13, NS). Much of the variation in the data is associated with the two most abundant species, the geometrid *Eupithecia nanata* and the noctuid *Lycophotia porphyrea*. *E. nanata* is strongly represented in the sweepnet catch (36%) but poorly in the two-stage sampling method (10%). Conversely, *L. porphyrea* occurs more frequently in the two-stage method catch (41%) than in the sweepnet samples (10%). If these species are removed from the dataset, there is a highly significant positive linear relationship between the proportions of the remaining species found by the two techniques (r=0.96, df=11, P<0.001, Figure 4.1), and 92% of variation is explained by the equation $Y = 0.699\ (\pm 0.064)X + 2.33\ (\pm 0.99)$ where Y is the proportion of each species in the sweepnet catch and X is the proportion of each species in the sample collected by jarring and Berlese-Tullgren extraction.

4.4.2 Calibration of sweepnet data against data collected by the two-stage jarring and Berlese-Tullgren extraction technique

4.4.2.1 Method

Densities of larvae calculated from data collected by the two-stage sampling method were considered to be absolute and were used to calibrate the relative densities derived from sweepnet data. Larvae densities from sweepnet data were regressed against densities from the two-stage sampling method data, with the jarring and Berlese-Tullgren estimate as the independent variable.

The ratio of the two density estimates (number of animals per sweepnet sample / number of animals per m^2) was regressed against *Calluna* stand height, to determine whether the relationship between the two methods changed with *Calluna* height.

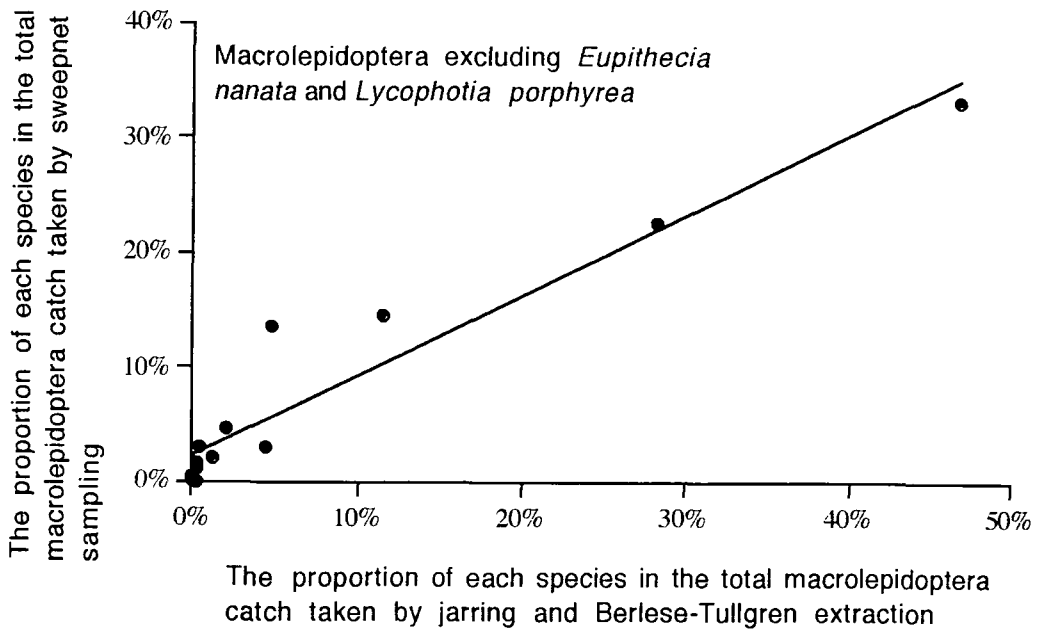


Figure 4. 1. The relationship between the proportions of each macrolepidoptera species in the total sweepnet catch and the corresponding proportions of each species in the samples taken by jarring and Berlese-Tullgren extraction. The exclusion of the geometrid *Eupithecia nanata* and the noctuid *Lycophotia porphyrea* is discussed in the text. Regression analysis gives $Y = 0.699(\pm 0.064)X + 2.33(\pm 0.99)$, r=0.96, df=11, P<0.001. Y is the proportion of each species in the sweepnet catch. X is the proportion of each species in the sample collected by jarring and Berlese-Tullgren extraction. Data are pooled from the 31 *Calluna* stands that were sampled by both techniques on the same date in 1991 and 1992.

Regressions were calculated only for Lepidoptera classes or macrolepidoptera species where a minimum of five data points were available for analysis. Logarithmic transformation of both axes was found to improve the normality of some calibration graphs. However, because the regression lines were unchanged by this transformation, figures and regression data are shown in the untransformed state.

4.4.2.2 Results

Examples of calibration graphs are given in Figures 4.2-4.4. Regressions for the relationships between densities estimated by different sampling techniques for different Lepidoptera classes and species are given in Table 4.5. Table 4.6 uses the regression equations in Table 4.5 to give the number of sweepnet samples that would be required to remove the number of larvae found on $1m^2$ of *Calluna*. Table 4.7 shows the correlations between the ratio of the two density estimates and *Calluna* stand height.

For most of the macrolepidoptera species examined, significant positive relationships existed between the population estimates calculated from the sweepnet data and those provided by jarring combined with Berlese-Tullgren extraction. Calibration data for a geometrid species *Hydriomena furcata* should be treated with caution. Since of the eleven data points, nine are for animals at low density (<10 per m^2) and two show larvae at very high density (>20 per m^2), the regression line is strongly influenced by the two high values.

Density of *L. porphyrea* estimated by jarring and Berlese-Tullgren extraction data did not correlate with the density calculated from sweepnet data ($r=0.15$, $df=17$, NS, Figure 4.2). The relationship was so poor that a 37% increase in the proportion of variation explained by the regression equation occurred if, when calculating a common calibration line for all macrolepidoptera species, data for *L. porphyrea* were excluded. Data for this species were therefore excluded when calculating a general calibration line for macrolepidoptera (Figure 4.3) because it behaved so differently to the majority of the macrolepidoptera species. Estimates of microlepidoptera density by sweepnet sampling also failed to correspond with estimates calculated from combined jarring and Berlese-Tullgren data ($r=0.15$, $df=29$, NS, Figure 4.4).

The relationship between the two population estimates was not affected by *Calluna* height (Table 4.7). However, it should be noted that for two species (the *Eulithis* group and *H. furcata*) data were available for only a limited range of *Calluna* heights.

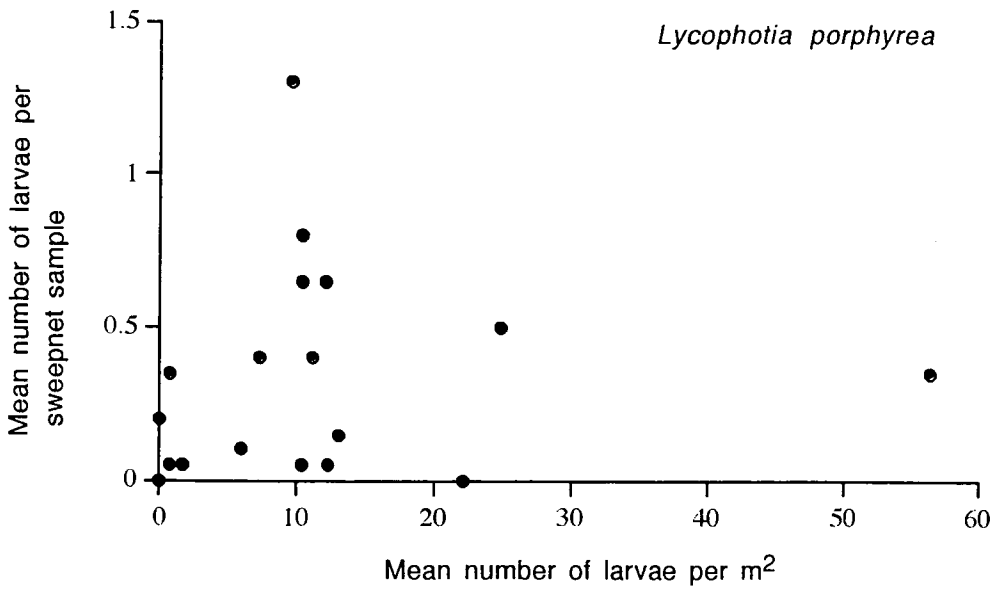


Figure 4.2. The relationship between the relative density estimates calculated from sweepnetting data and the absolute densities calculated from combined jarring and Berlese-Tullgren extraction for the noctuid *Lycophotia porphyrea.* Data were collected from 31 *Calluna* stands where both techniques were applied on the same date in 1991 and 1992. Regression analysis gives r=0.15, df=17, NS. One sweepnet sample constitutes ten strokes of the net. There was no significant relationship between the densities of larvae calculated from sweepnet data and those calculated from combined jarring and Berlese-Tullgren data.

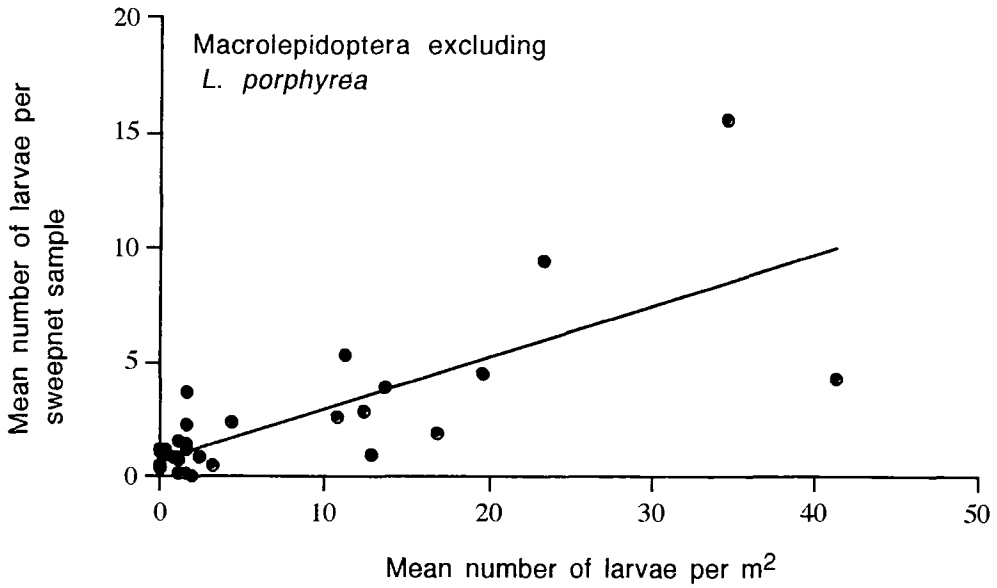


Figure 4.3. The relationship between the relative densities calculated from sweepnetting data and the absolute densities calculated from combined jarring and Berlese-Tullgren extraction for the macrolepidoptera species. Data were collected from 31 *Calluna* stands where both techniques were applied on the same date in 1991 and 1992. Sweepnet population estimates for *Lycophotia porphyrea* did not correlate with estimates from jarring and Berlese-Tullgren extraction (Figure 4.2) and were excluded from this regression. Regression analysis gives $Y = 0.225(\pm 0.037)X + 0.78(\pm 0.46)$, $r=0.75$, $df=29$, $P<0.001$. Y is the mean number of larvae per sweepnet sample. X is the number of larvae per m^2 estimated by jarring and Berlese-Tullgren extraction. One sweepnet sample constitutes ten strokes of the net.

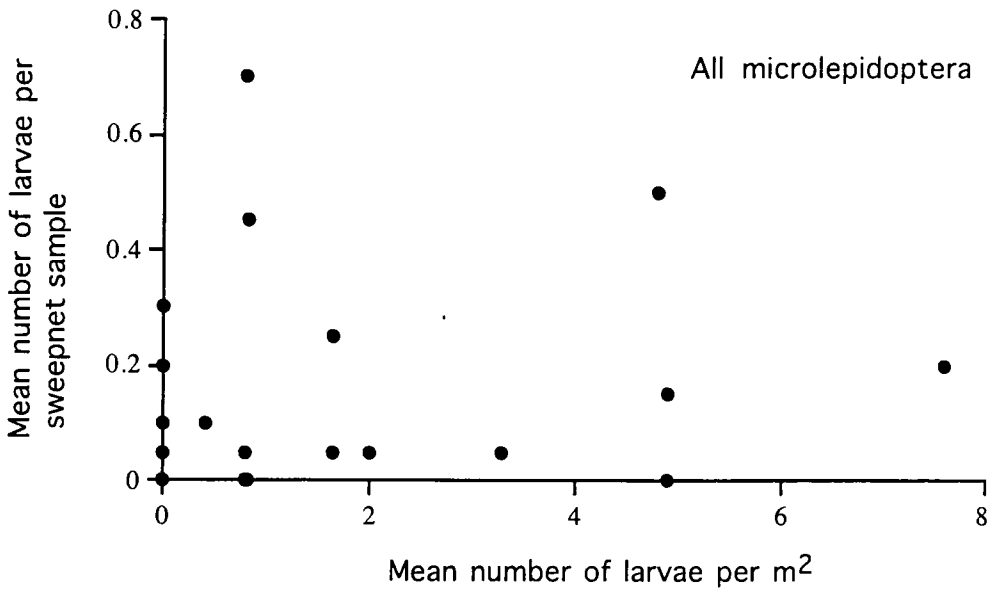


Figure 4.4. The relationship between the relative densities calculated from sweepnetting data and the absolute densities calculated from combined jarring and Berlese-Tullgren extraction for the microlepidoptera species. Data were collected from 31 *Calluna* stands where both techniques were applied on the same date in 1991 and 1992. Regression analysis gives r=0.15, df=29, NS. One sweepnet sample constitutes ten strokes of the net. There was no significant relationship between the densities of larvae calculated from sweepnet data and those calculated from combined jarring and Berlese-Tullgren data.

Class / Species	Regression coefficient B (± SE)	constant (±SE)	df	r	P
All macrolepidoptera	0.104 (±0.038)	1.15 (±0.74)	29	0.45	<0.02
Macrolepidoptera excluding *L. porphyrea*	0.225 (±0.037)	0.78 (±0.46)	29	0.75	<0.001
All microlepidoptera	0.013 (±0.016)	0.13 (±0.04)	29	0.15	NS
Eupithecia nanata	0.256 (±0.071)	0.61 (±0.23)	18	0.65	<0.01
Eupithecia goossensiata	0.325 (±0.078)	0.09 (±0.10)	14	0.75	<0.001
Eulithis spp.	0.238 (±0.025)	-0.05 (±0.09)	29	0.87	<0.001
Hydriomena furcata	0.163 (±0.051)	0.54 (±0.67)	9	0.73	<0.02
Lycophotia porphyrea	0.004 (±0.006)	0.27 (±0.11)	17	0.15	NS

Table 4.5. The regressions describing the relationships between the relative density estimates of larvae calculated from sweepnet data (*Y* larvae per sweepnet sample) and the absolute densities calculated from data collected by jarring followed by Berlese-Tullgren extraction (*X* larvae per m^2). *Eulithis populata* and *E. testata* have been grouped together because it is difficult to separate the larvae of these species. One sweepnet sample constitutes ten strokes of the net. NS indicates non-significance at the 0.05 probability level.

Lepidoptera class / species	**Number of sweepnet samples required to collect the number of larvae in $1m^2$ (95% confidence intervals)**
All macrolepidoptera	5.4 (3.5 - 7.3)
Macrolepidoptera excluding *Lycophotia porphyrea*	3.0 (1.4 - 4.6)
All microlepidoptera	-
Eupithecia nanata	1.8 (0.8 - 2.8)
Eupithecia goossensiata	2.1 (0.1 - 4.0)
Eulithis spp.	4.8 (1.3 - 8.3)
Hydriomena furcata	4.3 (0.6 - 8.0)
Lycophtia porphyrea	-

Table 4.6. The number of sweepnet samples required to collect the mean number of larvae present in a $1m^2$ area at the same stand. Results were calculated using data for the regressions in Table 4.5, that calibrated the number of larvae found in sweepnet catches with animals calculated by jarring and Berlese-Tullgren extraction. One sweepnet sample constitutes ten strokes of the net. The number of sweepnet samples required to collect the number of larvae in $1m^2$ was not estimated for the microlepidoptera or *Hydriomena furcata* because there were no significant relationships between the densities of these species calculated from sweepnet data and those obtained from the combined jarring and Berlese-Tullgren extraction technique.

Class / Species	r	df	P
Macrolepidoptera excluding *Lycophotia porphyrea*	-0.23	24	NS
All microlepidoptera	-0.02	9	NS
Eupithecia nanata	0.26	13	NS
Eupithecia goossensiata	0.42	5	NS
Eulithis spp.	-0.31	7	NS
Hydriomena furcata	-0.66	6	NS
Lycophotia porphyrea	-0.28	13	NS

Table 4.7. Linear correlations between the ratio of the density estimates calculated from sweepnet data and data collected by jarring and heat extraction in Berlese-Tullgren funnels (no. of larvae collected per sweep sample / no. of larvae per m^2) and the height of *Calluna* in the stand. r is the correlation coefficient. Data are shown for several classes and species of Lepidoptera larvae. *Eulithis populata* and *E. testata* have been grouped together because it is difficult to separate the larvae of these species. NS indicates non-significance at the 0.05 probability level.

4.4.3 The efficiency of Berlese-Tullgren extraction with different species of Lepidoptera larvae

4.4.3.1 Method

The ability of Berlese-Tullgren funnels to extract three common species of Lepidoptera larvae, the spring geometrid *H. furcata*, the autumn geometrid *Eupithecia nanata* and the autumn noctuid *L. porphyrea* was examined. Marked larvae were introduced into known quantities of *Calluna* in funnels and the number of animals extracted was recorded. Experiments on *E. nanata* and *L. porphyrea* took place in September 1991. The test of Berlese-Tullgren performance with *H. furcata* was begun on 6 July 1993.

Animals were marked dorsally with small quantities of pink or red cellulose paint (*Lycophotia porphyrea* and *H. furcata* respectively) or black indelible ink (*E. nanata*). Tests on all species showed good survival and mobility after being marked, and the majority retained the marks for at least a week.

Ten identical Berlese-Tullgren funnels, equipped with a 100W light bulb heat source were filled with weighed *Calluna* (five with wet mass 600g and five with wet mass 1200g). The two volumes were used to simulate extraction of larvae from different life-history phases of *Calluna*. The 1200g samples represented the volume of *Calluna* that might be expected from 0.25m^2 quadrats in mature *Calluna* of height 36-40cm, while 600g samples were similar to 0.25m^2 quadrats placed in early building phase *Calluna* with height 20-25cm. In September 1991 each funnel was seeded with ten marked final instar *E. nanata* and seven marked final instar *L. porphyrea*. In July 1993, twelve marked final instar *H. furcata* larvae were introduced to each of the ten funnels. All animals were extracted live into dry collecting jars that were checked at 0900 hours each day, until ten days after the last animal had been found.

For the autumn species, *Calluna* in each funnel was searched by hand after the extraction period, to locate larvae that had not moved into the collecting jars. As hand searching proved difficult and time consuming, a control was operated for the spring species *H. furcata*. Twelve larvae were placed inside nylon mesh bags filled with *Calluna* and placed in the centre of funnels that contained 600g and 1200g wet mass *Calluna* respectively. The larvae in these bags were checked on the second, fourth and tenth day of the experiment, to determine the number that had died or pupated in each volume of *Calluna*.

4.4.3.2 Results

The proportions of each species that were extracted from each mass of *Calluna* are shown in Table 4.8, together with the time periods during which extraction occurred. The median average number of days for larvae to leave the funnels and the last day on which larvae were recorded are given. No attempt was made to remove any larvae that were accidentally introduced with the weighed *Calluna*, so animals that had lost their marks by ecdysis or wear could not be distinguished from accidental introductions. Several unmarked larvae were collected but only animals with marks were used to calculate the proportion of larvae that were extracted. Unmarked animals of the same species were included in the calculation of the median and final dates of extraction. A median average was calculated because data were skewed toward low values and a mean would not have represented the number of days required for most larvae to leave the funnels.

Some animals were extracted as late as ten days after the start. However, most individuals were collected much earlier, usually within the first two days (*E. nanata*, *Hydriomena furcata* and *L. porphyrea* in the smaller volume of *Calluna*) or within the first five days (*L. porphyrea* in 1200g *Calluna*). No animals were extracted after ten days.

The extraction efficiency was very different between species. The funnels extracted the majority of individuals of two species, *L. porphyrea* and *H. furcata* and were especially effective for the extraction of the latter species. In the 600g samples the average proportion of *H. furcata* larvae extracted was 87%. The proportion of *E. nanata* larvae extracted was almost negligible, not more than 6% in either volume of *Calluna*.

There were no significant differences between the proportions of larvae extracted from the two volumes of *Calluna* (Table 4.9). Except for *L. porphyrea*, where individuals in the 1200g samples took longer to leave the funnels, the median and final number of days of extraction were similar for both volumes.

Hand searches recovered a further 11% and 3% of *L. porphyrea* in the 600g and 1200g samples respectively. All animals found by this method were dead. Hand searches for *E. nanata* increased the proportion of individuals accounted for to 16% (600g samples) and 12% (1200g samples). Of the nine animals recovered by hand, three had pupated and six were dead. *H. furcata* larvae that were prevented from moving away from the centre of the funnels by being held in mesh bags survived longer in the 1200g samples. By the fourth day of extraction all larvae in the 600g sample were dead, but only three

Species	No. of funnels in each weight class	No. of larvae per funnel	Mean % larvae extracted from 600g *Calluna* (95% C.I.)	Mean% larvae extracted from 1200g *Calluna* (95% C.I.)	Median day of extraction from 600g *Calluna* (95% C.I.)	Median day of extraction from 1200g *Calluna* (95% C.I.)	Last day larva extracted from 600g *Calluna*	Last day larva extracted 1200g *Calluna*
Eupithecia nanata	5	10	6% (1% - 11%)	4% (0% - 9%)	2 (‡)	1.5 (‡)	5	2
Hydriomena furcata	5	12	87% (80% - 93%)	65% (44% - 86%)	1 (1 - 2)	1 (1 - 1)	7	8
Lycophotia porphyrea	5	7	60% (35% - 85%) *	57% (33% - 81%) **	2 (2 - 3)	5 (4 - 5)	5	10

Table 4.8. The table shows the proportion of Lepidoptera larvae extracted from Berlese-Tullgren funnels and the duration of extraction in a test of Berlese-Tullgren funnel efficiency. Extraction rates in two masses of *Calluna* (600g and 1200g) were examined to determine whether volume of *Calluna* in the sample affected the efficiency of extraction. The median day of extraction is the median average number of days that larvae took to leave the funnels. The attachment of 95% confidence intervals to median values follows the method of Zar (1984). ‡ indicates that the number of larvae extracted was too small to attach a 95% confidence interval to the median day of extraction. Unmarked larvae of *L. porphyrea* were extracted from the 600g and 1200g *Calluna* samples marked * and ** respectively. The mean number of unmarked larvae extracted per funnel (95% confidence intervals) was 2.0 (0.0-4.0) in the 600g samples and 3.4 (1.7-5.1) in the 1200g samples. No unmarked *E. nanata* or *Hydriomena furcata* larvae were recorded.

Species	No. of larvae extracted from 600g *Calluna*	No. of larvae extracted from 1200g *Calluna*	χ^2 with Yates' correction for continuity	df	P
Eupithecia nanata	3	2	‡	-	-
Hydriomena furcata	52	39	1.87	1	NS
Lycophotia porphyrea	21	20	0	1	NS

Table 4.9. The difference between the total number of larvae that were extracted from 600g and 1200g *Calluna* samples in a test of Berlese-Tullgren extraction efficiency. Three species of larvae were used in the experiments. ‡ denotes that the number of larvae extracted was too small to calculate the χ^2 statistic. NS denotes non-significance at the 0.05 probability level.

had died in the larger sample, while one had pupated and eight remained alive. All animals were dead by the tenth day.

4.4.4 The efficiency of the Blow-Vac and D-Vac suction methods for the extraction of Lepidoptera larvae

4.4.4.1 Method

The ability of the Blow-Vac and D-Vac suction methods to remove larvae from short stands of *Calluna* was tested using a marked population of the spring geometrid *Hydriomena furcata*. The test took place at stand L at the Slaley field site on 29 June 1993. On this date, *Calluna* was approximately 5cm tall. A series of point quadrats taken at the end of the field season, in October 1993 (section 3.2.5), estimated that 93% of the ground was covered by *Calluna*.

Ten quadrats were placed at random positions within the stand. Each quadrat was a continuous strip of "Darvic" plastic approximately 15cm high that delimited a circle with area $1m^2$. The quadrats were sunk into the ground by cutting a narrow trough with the sharp edge of a spade, to ensure that there were no gaps below the quadrat through which animals could escape. The smooth, shiny sides of the plastic aimed to prevent animals climbing over the edge.

Ten final instar *H. furcata* larvae, marked dorsally with red cellulose paint were introduced to each of the five quadrats to be sampled by Blow-Vac and five quadrats to be sampled by D-Vac. Animals were allowed 15 minutes to settle down. Each quadrat was then sampled every 15 minutes by one method for one hour. The quadrats used to test efficiency of Blow-Vac extraction were sampled once more by Blow-Vac two hours after the start of the experiment.

4.4.4.2 Results

The number of *H. furcata* larvae extracted at each time interval and the proportion of the marked population that was extracted by each method are given in Table 4.10.

Neither method was effective at extracting *H. furcata* larvae from short *Calluna*. The D-Vac failed to remove any larvae. The Blow-Vac recorded the presence of marked larvae but the proportion of the population recovered was extremely low (6%). In addition to the animals from the marked population, the Blow-Vac also collected single specimens of the geometrid *Ematurga atomaria* and the noctuid *Anarta myrtilli*.

Method	No. of quadrats	No. of marked larvae per quadrat	No. marked larvae found in all quadrats at 15 mins.	No. marked larvae found in all quadrats at 30 mins.	No. marked larvae found in all quadrats at 45 mins.	No. marked larvae found in all quadrats at 1 hour	No. marked larvae found in all quadrats at 2 hours	Total extracted in first hour from all quadrats	Mean % extracted per quadrat (95% C.I.)
Blow-Vac	5	10	2	0	1	0	0	3	6% (0% - 14%)
D-Vac	5	10	0	0	0	0	n/a	0	0%

Table 4.10. The number of *Hydriomena furcata* larvae extracted by two suction methods. Quadrats contained a $1m^2$ area of *Calluna*. Figures shown at each time interval are the total number of larvae extracted from all five quadrats.

4.5 Discussion

None of the sampling methods fulfilled all the criteria that were set at the beginning of the investigation. Most methods operated with some restrictions *e.g.* direct searching could be used only for certain species and the extraction rates of the Blow-Vac and D-Vac suction devices were very low (Table 4.10). Other studies have shown that suction sampling devices extract Lepidoptera larvae less effectively than other invertebrate groups (Johnson *et al.* 1957; Shepard 1974), but the efficiency of some other techniques in this study was probably affected by the *Calluna* habitat itself. For example, the efficiency of searching may be less in dense *Calluna* stands, while *Calluna* that is less than 10cm tall is more difficult to jar and sweep.

No technique worked perfectly in all conditions. The methods that were used most often during the three year study were sweepnetting and jarring combined with Berlese-Tullgren extraction. Sweepnetting was used for the main Lepidoptera monitoring programme (described in Chapter Five, section 5.2) and was only replaced by other techniques such as Blow-Vac, where exceptional conditions *e.g. Calluna* less than 10cm tall necessitated experimentation with other techniques. The use of the two-stage sampling method was restricted to 31 stands in the first two years, as a device for calibrating the relative sweepnet data. The chief factors precluding the wider use of this technique were the time required to perform the field and laboratory work, the number of funnels available and the destruction caused to the stands.

Sweepnetting is an appealing sampling method because it is quick, easy to operate, cheap, non-destructive and capable of extracting animals that occur at low density. For these reasons it is often the method of choice for studying pest densities in agricultural systems (Schotzko & O' Keeffe 1986a) where it can provide good approximation to absolute population estimates (Schotzko & O' Keeffe 1986a; Rudd & Jensen 1977). Other studies have found drawbacks, where the net was unable to penetrate the plant canopy (Byerley *et al.* 1978; Ellington *et al.* 1984) or because the estimates it presented were less reliable than those of other techniques (Johnson *et al.* 1957; Southwood 1978; Ellington *et al.* 1984), or were affected by conditions such as vegetation height, weather, or the individual operator (Carpenter & Ford 1936; Romney 1945; Hughes 1955; Johnson *et al.* 1957; Saughstad *et al.* 1967; Southwood 1978; Schotzko & O' Keeffe 1986b). In some instances, more efficient techniques were also more rapid (Ellington *et al.* 1984). The extensive use of sweepnetting in this study was justified, on the grounds that for most of the common macrolepidoptera species and the macrolepidoptera class, highly significant correlations were obtained between sweepnet

density estimates and those from jarring and Berlese extraction that were taken to be absolute.

The estimates calculated from data collected by combined jarring and Berlese-Tullgren extraction were taken as absolute, but it is more correct to say that they were closer to absolute than the estimates of any other techniques. In any direct method of sampling animals, size of the population may be underestimated because individuals are likely to be missed during extraction (Morris 1955). Used independently, it is clear that jarring (Table 4.3) did not extract all Lepidoptera larvae, because additional animals were found when vegetation was treated in the Berlese-Tullgren funnels. Some larvae would also have been knocked into the litter during jarring and would not have been captured. The experiments testing the efficiency of the Berlese-Tullgren funnels showed that when operated alone, this technique also failed to extract a large proportion of the individuals of some species *e.g. E. nanata*. Fielding (unpublished Ph.D. thesis 1992) used Berlese-Tullgren funnels extensively to study moorland Lepidoptera and reported that in three years *E. nanata* was never found in Berlese-Tullgren samples even though the species was well-represented in sweepnet catches. Evidence in Table 4.3 suggests that several other species may also have low extraction rates in Berlese-Tullgren funnels. For example, while 33% of the total number of *Lycophotia porphyrea* and 19% of *Hydriomena furcata* found in the combined method were extracted by Berlese-Tullgren funnels, heat extraction took much smaller proportions of the *Eulithis* species, *Entephria caesiata* and *Eupithecia nanata* (9%, 5% and 3% respectively). Even though heat extraction was not used independently, and more efficient removal of these species by jarring could also have explained the result, such low extraction rates must indicate these species experience higher mortality between clipping the vegetation and extraction, or in the funnels. Six species were extracted in Berlese-Tullgren funnels. This was approximately half the number of species collected by either jarring or sweepnet (Table 4.1). While this again is affected by the removal of animals at the jarring stage, the number of species extracted is still extremely low. Used together, with a knowledge of their individual limitations the jarring and Berlese-Tullgren techniques extract higher numbers of animals than either used separately.

A strong positive correlation between density estimates calculated from sweepnet data and those calculated from jarring combined with Berlese-Tullgren extraction occurs if the sweepnet collects a constant proportion of individuals in the vegetation, if the distribution of a species is not highly aggregated and where both methods sample the population from similar locations in the vegetation. Sweepnet population estimates of the microlepidoptera and one macrolepidoptera species *Lycophotia porphyrea* did not correlate with the absolute data. Population estimates of the microlepidoptera may

have been less reliable than those of the macrolepidoptera both because of the comparative scarcity of this group and because animals may have been less available to extraction techniques, because many of these species tie leaves together or inhabit cases. Low density may affect the accuracy of a density estimate, because more animals are sometimes overlooked at low densities (Morris 1955).

The relative variances associated with the jarring and Berlese-Tullgren technique were larger than those associated with sweepnetting (Table 4.4). Greater aggregation in the jarring and Berlese-Tullgren data, observed because samples cover a smaller area than sweepnetting, may affect the precision of the absolute population estimate for this species. There was also evidence that *L. porphyrea* occurred in different parts of the *Calluna* bush to other species. Although larvae were also found in the canopy, many *Lycophotia porphyrea* were found in the litter when the *Calluna* was clipped. The litter layer was not accessible to the sweepnet, so animals in the litter were recorded only by the two-stage sampling method. Southwood (unpublished Ph.D. thesis 1955) quoted in Johnson *et al.* (1957) described a similar situation in which three species of Mirid (Heteroptera) nymphs were recorded at different densities by suction sampling and sweepnetting, because they utilised different height zones of the grasses *Dactylis glomerata* and *Holcus lanatus*. In suction samples the three species *Leptopterna dolobrata*, *Stenotus binotatus* and *Capsus ater* were equally abundant, but sweepnetting found only *L. dolobrata* and *S. binotatus* in large numbers and recorded few individuals of *C. ater*. *C. ater* were found in the matted bases of the grasses that were inaccessible to the sweepnet, but *L. dolobrata* and *S. binotatus* occurred in the flower-heads and could be taken easily. Use of different height zones within vegetation is recorded for different species, for different sexes and ages of the same species and occurs in the Lepidoptera (Romney 1945; Johnson *et al.* 1957; Gross & Fritz 1982). Stratification patterns can change with time, when species make diel vertical movements (Davidson & Shackleford 1929; Poinar & Gyrisco 1960; Fewkes 1961). For this reason, *Calluna* was swept during the day and during the night to determine whether the density of *L. porphyrea* larvae in the canopy changed at different times of day (section 8.4).

The ratio of the density estimates provided by sweepnet sampling and combined jarring and Berlese-Tullgren extraction was not related to *Calluna* height (Table 4.7). This validates the use of the sweepnet in this habitat, since other studies have shown that vegetation height can be one of the most important factors to affect the population estimate obtained by the sweepnet (Saughstad *et al.* 1967). This usually occurs when, as vegetation grows taller, the sweepnet penetrates a smaller proportion of the plant and hence collects a smaller proportion of the fauna. Southwood (1978) maintains this is

most likely to occur when vegetation is more than 30cm tall. The effect may have been avoided in this study due to a combination of features of *Calluna* structure and the type of equipment used. Perennial *Calluna* retains the same leaves for up to four years (Gimingham 1960; Chapman *et al.* 1975; Gimingham *et al.* 1979) but has a natural lifespan of 25-40 years (Watt 1955; Barclay-Estrup 1969; Gimingham 1971, 1988). New growth sprouts from the previous year's end of season short-shoots (Gimingham 1972) and the region between the tip of the current year's shoot and the lower limit of leaves on the stem is usually no greater than 30cm, with woody stems below that zone. While *Calluna* height may vary greatly between stands, the depth of green foliage varies less and is often a similar layer of leaves raised to different heights above the ground. The sweepnet used had a wide diameter of 50cm, and would have been capable of penetrating the top 25cm of most *Calluna* stands. In all stand heights some of the larvae would have been knocked into the litter by the net and not caught.

Significant correlation between the proportion of each of the species in the total sweepnet catch and the proportion of each species in the combined jarring and Berlese-Tullgren extraction only occurred if *E. nanata* and *L. porphyrea* were removed from the analyses (Figure 4.1). This does not invalidate the use of the sweepnet technique because reasons for differential extraction of these species are known. These two species were from different genera and related species were more available to both sampling techniques. This illustrates that availability to a sampling method may be different even for closely related species, and can be a function of individual species' behaviour (Johnson *et al.* 1957). The departure of the slope of the regression line from one (B=0.699±0.064, Figure 4.1), may occur because sweepnetting not only collects a slightly higher number of species than combined jarring and Berlese-Tullgren extraction (Table 4.3), but the number of species where more than one individual was recorded was also larger in the sweepnet catch (sweepnet 13 species, jarring and Berlese-Tullgren nine species). The division of the sweepnet catch between a larger number of species reduces the proportion of each species in the total catch.

Chapter Five

An Introduction to the Lepidoptera Larvae Found During the Study

5.1 Introduction

This chapter lists the species of macrolepidoptera and microlepidoptera that were found at five sites during this study. The results are compared with those of another study and literature review (Fielding unpublished Ph.D. thesis 1992). The composition of the macrolepidoptera communities at five study areas are compared. Seasonal variations in the abundance of Lepidoptera larvae and the composition of the Lepidoptera communities are described.

5.2 Sampling regime

5.2.1 Durham and Northumberland study areas

Between 5 May and 5 November 1992 and between 29 April and 2 August 1993, the sweepnet technique was used to monitor population changes of Lepidoptera larvae in different-aged *Calluna* stands. Three study areas, Waskerley, Slaley and Stuartfield Lodge (described in Chapter Two) were monitored at intervals of approximately 10-14 days throughout the 1992 season. The number of sampling sites swept during the monitoring programme was ten, ten and three at Waskerley, Slaley and Stuartfield Lodge respectively.

Between 5 and 26 May 1992, access to Waskerley was restricted because of red grouse breeding. Sampling initially took place at three stands and the number of sampling sites was increased gradually as access improved. Between 4 June and 7 July 1992 nine stands were sampled and all ten stands were monitored regularly from 16 July 1992. The Slaley site was not introduced to the study until 26 June 1992 and all ten stands at this site were sampled regularly from 10 July 1992.

In 1993 the 20 stands sampled at Waskerley and Slaley in 1992 were sampled every 16-20 days between 29 April and 2 August, to obtain information corresponding to the period of restricted access in the spring of 1992. The Stuartfield Lodge sample sites were not monitored in 1993. Five stands where *Calluna* was less than 10cm tall (A-E at Waskerley and K-O at Slaley) were introduced to the study in 1993. They were sampled by sweepnet and Blow-Vac on 2 and 4 June 1993. Since Blow-Vac sampling proved to

be inefficient (section 4.4.4), subsequent sampling of these very short stands was completed using the sweepnet technique and was timed to coincide with high densities of larvae at taller stands.

Appendices B.1, B.2a and B.2b list the sampling dates at the Durham sites and Northumberland sites in 1992 and 1993.

5.2.2 Scottish study areas

Two Scottish field sites at Greenlaw Moor S.S.S.I. and Langholm-Newcastleton Hills S.S.S.I. (described in Chapter Two) were the subjects of two visits in the early summer and autumn of 1992. The summer visit occurred between 14 and 16 June 1992 (Greenlaw Moor) and between 18 and 20 June 1992 (Langholm). On these occasions 20 *Calluna* stands of different heights were sampled at each site. The autumn visits occurred between 23 and 25 September 1992 and between 26 and 27 September 1992 at Greenlaw Moor and Langholm respectively. On these dates the 20 stands sampled at each site in the summer were again sampled by sweepnetting.

5.3 The Lepidoptera species found during the study

5.3.1 Methods

Lists of Lepidoptera species were compiled using data collected by any sampling method during the period April 1991-September 1993. These data were compared with the results of another field study and literature review (Fielding unpublished Ph.D. thesis 1992). For the purpose of comparisons in this chapter the site at Slaley is regarded as a Durham site, although it is just across the county boundary in neighbouring Northumberland.

5.3.2 Results

Lists of the species of Lepidoptera recorded at the five study areas are given in Tables 5.1a-c and Table 5.2. Macrolepidoptera were recorded in the larval stage to assess the breeding community at these sites. Tables 5.1a-c list species from the Geometridae, Noctuidae and other macrolepidoptera families that were recorded as larvae. Species of microlepidoptera could not be identified as larvae and only a few individuals were reared successfully to the adult stage. However, microlepidoptera larvae were regularly taken in sweepnet samples, so were known to contribute to the community of Lepidoptera. Therefore adult specimens are also included in the microlepidoptera species list (Table 5.2), because some of the larvae that were not identified may have belonged to these species.

Table 5.3a records the number of macrolepidoptera species found as larvae by any sampling method at the five study areas during the period April 1991-September 1993. Table 5.3b lists the number of macrolepidoptera species found as larvae by sweepnet sampling during the spring and autumn periods described in section 5.4.1.1c. A total of 29 species (11 Geometridae, 11 Noctuidae and 7 species from other families) were recorded during the three year study (Table 5.3a). A high proportion (83%) of these species were recorded from more than one study area and nine species (31% of the total number of species) were recorded at all five study areas in Durham, Northumberland and southern Scotland. The largest number of macrolepidoptera species was recorded at Slaley (23 species) while the smallest total number of species was recorded at Langholm-Newcastleton Hills S.S.S.I. (12 species). Three microlepidoptera species from two families were recorded as larvae (Table 5.2).

Table 5.4 compares the list of macrolepidoptera species found in County Durham during this study with the results of another study and literature review (Fielding unpublished Ph.D. thesis 1992). The results of this study strongly support the findings of Fielding (unpublished Ph.D. thesis 1992). The number of species of macrolepidoptera, Geometridae, Noctuidae and other families found as larvae were very similar (Table 5.4). The two studies also found similar proportions of the group Fielding classed as "potential" species *i.e.* species that were associated with *Calluna vulgaris* and had a distribution that included County Durham according to literature sources. Both authors found several "extra" species, larvae that were collected from *Calluna* during the field studies but for which *Calluna* was not listed as a food-plant in Fielding's (unpublished Ph.D. thesis 1992) literature review. These extra species constituted approximately one third of the total number of macrolepidoptera species that were recorded in each study.

Table 5.5 lists potential species (Fielding unpublished Ph.D. thesis 1992) that were not found as larvae during this study.

Table 5.1a. The geometrid species found as larvae at the five study areas. The Table records species collected by any method during the period April 1991 - September 1993. The symbols '*' , '†' and '√' indicate that no more than one, no more than five, or more than five individuals respectively were found at a study area in any year. *Eulithis testata* and *E. populata* could not be separated as larvae and have been grouped.

Geometrid species	Waskerley	Slaley	Stuartfield	Greenlaw	Langholm
Dyscia fagaria	*	†	†	†	
Ectropis bistortata	*	†	*		
Ematurga atomaria	√	√	√	*	√
Entephria caesiata	√	√	*	†	
Epirrita filigrammaria	√	√			
Eulithis species	√	√	√	√	√
Eupithecia goossensiata	†	√	√	√	√
Eupithecia nanata	√	√	√	√	√
Hydriomena furcata	√	√	√	*	√
Operophtera brumata		*			
Perizoma didymata	*	*	†		

Table 5.1b. The noctuid species found as larvae at the five study areas. The Table records species collected by any method during the period April 1991 - September 1993. The symbols '*' , '†' and '√' indicate that no more than one, no more than five, or more than five individuals respectively were found at a study area in any year.

Noctuid species	Waskerley	Slaley	Stuartfield	Greenlaw	Langholm
Anarta myrtilli	√	√	√	†	√
Aporophyla lueneburgensis			†	*	
Autographa gamma		*			
Blepharita adusta	*	√			
Ceramica pisi	*	√	*		
Diarsia mendica		*			
Lycophotia porphyrea	√	√	√	√	√
Orthosia gothica			*		*
Papestra biren			√		†
Phlogophora meticulosa				*	
Xestia agathina	*	√	†		

Table 5.1c. The species from macrolepidoptera families other than the Geometridae and Noctuidae that were found as larvae at the five study areas. The Table records species collected by any method during the period April 1991 - September 1993. The symbols '*' , '†' and '√' indicate that no more than one, no more than five, or more than five individuals respectively were found at a study area in any year.

Other species	Waskerley	Slaley	Stuartfield	Greenlaw	Langholm
Lasiocampidae					
Lasiocampa quercus callunae	†	†	†	*	√
Macrothylacia rubi	√	†	†	√	√
Trichiura crataegi			*	*	
Arctiidae					
Parasemia plantaginis plantaginis	*				
Phragmatobia fuliginosa	*	†		√	
Lymantriidae					
Dicallomera fascelina	†	√		†	
Saturniidae					
Pavonia pavonia	√	†		√	√

FAMILY	SPECIES	NOTES
Gelechiidae		
	Bryotropha terella (D. & S.)	WK
	Mirificarma mulinella (Zell.)	SL
Pyralidae		
	Scoparia ambigualis (Treit.)	WK
Pterophoridae		
	Ambylyptilia acanthodactyla (Hb.)	SL *
Tortriciidae		
	Acleris hyemana (Haw.)	WK *, SL
	Exapate congelatella (Cl.)	WK *
	Olethreutes palustrana (Lien & Zell)	WK
Yponomeutidae		
	Yponomeuta padella (Linn.)	WK

Table 5.2. The microlepidoptera species that were found as larvae or adults at Waskerley and Slaley during the period April 1991-September 1993. Species names are followed by a code identifying the study area from which they were recorded (WK = Waskerley, SL = Slaley). An asterisk indicates that the species was known to breed at a study area, because a record was obtained by rearing a larva to the adult stage.

Family	Waskerley	Slaley	Stuartfield	Greenlaw	Langholm	All sites
Geometrid species	10	11	9	7	5	11
Noctuid species	5	7	7	4	4	11
Other species	6	5	3	6	3	7
Total	21	23	19	17	12	29

Table 5.3a. Summary of the total number of macrolepidoptera species found as larvae at five study areas in Durham, Northumberland and southern Scotland. The table records species collected by any method during the period April 1991-September 1993. The "Other" species category comprises records from the families Arctiidae, Lasiocampiidae, Lymantriidae and Saturniidae.

Site and time period	Geometrid species	Noctuid species	Other species	Total species
Greenlaw Summer	5	2	2	9
Langholm Summer	4	3	2	9
Waskerley Summer	4	0	2	6
Stuartfield Summer	4	3	0	7
Greenlaw Autumn	3	2	2	7
Langholm Autumn	2	2	2	6
Waskerley Autumn	1	2	2	5
Stuartfield Autumn	2	2	1	5
Slaley Autumn	3	3	3	9

Table 5.3b. Summary of the number of macrolepidoptera species found as larvae in 1992 by sweepnet sampling at the five study areas in the summer and autumn periods (section 5.4.1). The "Other" species category comprises records from the families Arctiidae, Lasiocampiidae, Lymantriidae and Saturniidae.

	Macrolepidoptera	Geometridae	Noctuidae	Others
Maximum potential number of species (Fielding 1992)	42	18	17	7
No. of potential species recorded as larvae	20 (19)	9 (8)	6 (6)	5 (5)
Proportion of potential species recorded as larvae	48% (45%)	50% (44%)	35% (35%)	71% (71%)
Extra species found as larvae	9 (7)	3 (3)	4 (1)	2 (3)
Total number of species recorded as larvae	29 (26)	12 (11)	10 (7)	7 (8)
Extra species as proportion of total species recorded	31% (27%)	25% (27%)	40% (14%)	29% (38%)
Combined total no. of species found by this study and Fielding (1992)	34	14	11	9
Proportion of potential species recorded by combined studies	52%	56%	41%	71%
Proportion of combined total that were extra species	35%	29%	36%	44%
Number of species in common with Fielding (1992)	21	9	6	6
Proportion of species in common with Fielding (1992)	62%	64%	55%	67%

Table 5.4. A comparison of data from this study with the results of Fielding (unpublished Ph.D. thesis 1992). The maximum potential number of species was the number of macrolepidoptera species that are associated with *Calluna* and have a distribution that includes County Durham according to literature sources (Fielding unpublished Ph.D. thesis 1992). Extra species were those that were not stated to feed on *Calluna* in the literature, but were found on the plant in this study or in Fielding's study. Figures in parentheses are the results of Fielding (unpublished Ph.D. thesis 1992). "Others" comprises records from the families Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae.

Table 5.5. Table prepared after Fielding (unpublished Ph.D. thesis 1992) The status of 22 macrolepidoptera species that are associated with *Calluna vulgaris* and occur in County Durham (Fielding unpublished Ph.D. thesis 1992), but were not found as larvae during the present study. Status of these species in County Durham follows Dunn and Parrack (1986). Species were (a) rare or uncommon in County Durham (b) found in habitats not sampled by this study (c) common and widespread in County Durham. The results of Fielding (unpublished Ph.D. thesis 1992) are displayed in parentheses.

Species	**(a)**	**(b)**	**(c)**
Callophrys rubi			X
Scopula ternata			X
Idaea straminata	X		
Scotopteryx mucronata	X		
Chloroclysta citrata		X	
Chloroclysta truncata			X
Eupithecia satyrata			X
Alcis repandata			X
Gnophos obscuratus		X	
Perconia strigillaria	X		
Diacrisia sannio	X		
Noctua comes			X
Paradiarsia glareosa			X
Xestia alpicola alpina	X		
Xestia castanea	X		
Aporophyla nigra			X
Lithomia solidaginis	X		
Agrochola macilenta			X
Agrochola helvola			X
Acronicta menyanthidis	X		
Acronicta rumicis			X
Syngrapha interrogationis	X		
Total number of species	9	2	11
Proportion of missing species	41% (39%)	9% (9%)	50% (52%)

5.4 The composition of the Lepidoptera larvae community at different study areas

5.4.1 Methods

5.4.1.1 Analysis of community composition using similarity matrices

The similarity of the macrolepidoptera communities at different study areas were compared using binary data (species lists) and quantitative data (relative abundance of species). Data were analysed using two similarity indices, measures which assessed the degree of similarity in the faunal composition between two samples.

5.4.1.1a Sorensen's similarity coefficient

Sorensen's similarity coefficient (Sorensen 1948) compares two samples using a binary data set *e.g.* a species list. It considers the number of species that are unique to each of two samples, or common to both using the equation:

$$Ss = \frac{2a}{2a + b + c}$$

where Ss = Sorensen's similarity coefficient
a = number of species in sample A and sample B (joint occurrences)
b = number of species in sample B but not in sample A
c = number of species in sample A but not in sample B.

The use of a binary dataset gives equal weighting to all species. Sorensen's index weights matches more heavily than mismatches (Krebs 1989).

5.4.1.1b Percentage similarity index

The percentage similarity index or Renkonen index (Renkonen 1938) is weighted to consider the scarcity of species by examining the proportion of each species in each sample. The index is calculated according to the equation:

$$PS = \sum \text{minimum } (p_{1i}, p_{2i})$$

where PS = Percentage similarity between samples 1 and 2
p_{1i} = Percentage of species in community sample 1
p_{2i} = Percentage of species in community sample 2

5.4.1.1c General methods

To compare all the study areas, only samples collected just before and after the visits to the Scottish sites were used. An early summer period comprised the sampling week before and after the Scottish visits of 14-20 June 1992 (12 and 28 June at Stuartfield, 10 and 24 June at Waskerley). An autumn period comprised Durham data collected close to the Scottish visits of 25-29 September 1992 (15 September and 6 October at Stuartfield, 17 September and 8 October at Waskerley, 18 September and 5 October at Slaley). Similarity matrices were also prepared for the Durham sites for the part of 1992 when the sites were sampled at similar intervals (14 July-5 November 1992).

5.4.1.2 Chi-square contingency tests

The proportions of macrolepidoptera and microlepidoptera larvae, and larvae from the Geometridae, Noctuidae and "Other" macrolepidoptera families at the different study areas were compared using chi-square contingency tests. The Noctuidae and "Others" categories were grouped together if samples were small to ensure that all expected values were equal to or greater than five. The time periods examined were the summer and autumn periods described in section 5.4.1.1c, 14 July-5 November 1992 and 29 April-2 August 1993.

5.4.1.3 Rank of macrolepidoptera species

Graphs of species rank against the logarithm of species abundance (Tokeshi 1993) were prepared for Waskerley and Slaley (16 July-5 November 1992) and Greenlaw and Langholm (June and September 1992), marking the identity of the five most abundant species at each site during these periods.

5.4.2 Results

5.4.2.1 Analysis of community composition using similarity matrices

Tables 5.6a and b show matrices calculated using the Sorensen similarity coefficient for data from the summer and autumn periods in 1992 respectively. Table 5.6c gives the values of the Sorensen's similarity coefficient for comparison between pairs of Durham sites (14 July-5 November 1992). Tables 5.7a-c show matrices for the same sites and time periods calculated using quantitative data and the percentage similarity index.

Four sites Waskerley, Stuartfield, Greenlaw and Langholm were compared in the summer period as Slaley was not sampled until after the summer visit to the Scottish sites. According to Sorensen's similarity coefficient, which considered species presence, the most similar sites were Waskerley and Greenlaw (Ss=0.667) while the most

dissimilar were Stuartfield and Greenlaw (*Ss*=0.250). Species lists at Stuartfield and Langholm were also very similar (*Ss* =0.625). Using quantitative data, the percentage similarity index also ranked Waskerley and Greenlaw as the most similar sites (*PS*=59.9%) and Stuartfield and Langholm were the most dissimilar (*PS*=4.2%). Langholm and Greenlaw however, were more alike than Langholm and Stuartfield.

In the autumn, Sorensen's coefficient identified the most similar sites to be Stuartfield and Langholm (*Ss*=0.909). Slaley and Greenlaw were also very similar (*Ss*=0.875). The least similar pair were Slaley and Langholm (*Ss*=0.667). The percentage similarity index chose a different order. The most similar pair of sites was Waskerley and Langholm (*PS*=90.2%), the least similar pair Waskerley and Slaley (*PS*=18.5%). Study areas were significantly more similar in the autumn than in the summer (Paired t-test for pairs of Sorensen's values t=4.54, df=5, P<0.01; Paired t-test for pairs of percentage similarity index values t =5.36, df=5, P<0.01).

Comparisons for the Durham study areas during the main sampling period in 1992 (16 July-5 November 1992) gave a discrepancy between the percentage similarity index and Sorensen's index. Sorensen's index considered Waskerley and Slaley to be most similar, but the percentage similarity index considered Stuartfield and Waskerley to be approximately 14 percentage points more similar than any other pair (Table 5.7c). The fact that Waskerley and Slaley were more similar to Stuartfield than they were to each other suggests that the overlap occurred with different components of the Lepidoptera community at Stuartfield Lodge.

When values of Sorensen's similarity coefficient and the percentage similarity index were considered on a scale of 0-1, values of Sorensen's coefficient were higher than the corresponding values of the percentage similarity index.

5.4.2.2 Chi-square contingency tests

The proportions of macrolepidoptera and microlepidoptera found in the total catch were significantly different at the different study areas in the spring and autumn periods (Tables 5.8a-b) but not at the Durham sites over a more prolonged period *e.g.* 14 July-5 November 1992 or 29 April-2 August 1993. The proportions of individuals from the Geometridae, Noctuidae and Others were significantly different at the different study areas in the spring, autumn and 29 April-2 August time periods (Tables 5.9a, b, d).

5.4.2.3 Rank of macrolepidoptera species

Figures 5.1a-b show graphs of species rank against the logarithm of species abundance at Waskerley and Slaley (16 July-5 November 1992).

At Waskerley and Slaley, four of the five most abundant species found at one site were also among the five most abundant species at the other. The ranks of these species were not the same. *Eupithecia goossensiata* and *Macrothylacia rubi*, both species that were among the five most abundant species at Slaley and Waskerley respectively, were ranked between positions 8-11 and 8-9 at the other site. Similar results were obtained when rank abundance plots for Greenlaw and Langholm (June and September 1992) were compared. Four of the five most abundant species at Greenlaw were also in ranks one to five of the abundance list at Langholm. *Eupithecia nanata* was the most abundant species at both Scottish sites.

The geometrid *E. nanata* and the noctuid *Lycophotia porphyrea* were among the five most abundant species at all four study areas, despite the difference in the sampling periods.

5.5 General phenology of the macrolepidoptera species found during the study

Figures 5.2-5.4 (a) illustrate seasonal variation in the number of macrolepidoptera and microlepidoptera larvae recorded at the three Durham study areas during the 1992 and 1993 sweepnet sampling programmes. The number of larvae recorded has been expressed as the average number per stand, because it was not possible to sample the same number of stands at all times of the year at Waskerley. Figures 5.2-5.4 (b) show seasonal variation in the proportions of macrolepidoptera and microlepidoptera larvae in the catch at the three Durham study areas.

Two peaks of macrolepidoptera larvae abundance were observed at Waskerley, the first in May and early June, the second in late August and September. The May-June peak was observed in both the 1992 and 1993 datasets, but the amplitude of the 1993 peak was smaller. There are no samples for the earliest part of the 1992 season at Slaley, but abundance of macrolepidoptera also appears to peak in September-October, and a small May-June peak was apparent in 1993. At Stuartfield in the 1992 season only the autumn peak was apparent. The number of macrolepidoptera larvae recorded decreased at all sites in late June-early July.

The proportions of macrolepidoptera and microlepidoptera larvae changed appreciably throughout the year at all three sites (Figures 5.2b, 5.3b and 5.4b). This was caused by the abrupt change in late June from a community dominated by macrolepidoptera to one dominated briefly by microlepidoptera. The proportion of microlepidoptera larvae in the Stuartfield Lodge Lepidoptera community was also higher than expected in the October-November period.

Table 5.6a

	Stuartfield	Waskerley	Greenlaw
Waskerley	0.308		
Greenlaw	0.250	0.667	
Langholm	0.625	0.533	0.556

Table 5.6b

	Stuartfield	Waskerley	Slaley	Greenlaw
Waskerley	0.800			
Slaley	0.714	0.714		
Greenlaw	0.833	0.833	0.875	
Langholm	0.909	0.727	0.667	0.769

Table 5.6c

	Stuartfield	Waskerley
Waskerley	0.667	
Slaley	0.640	0.857

Tables 5.6a-c. Matrices comparing the similarity of the macrolepidoptera larvae communities at different study areas using Sorensen's similarity coefficient (Sorensen 1948). a) The Durham and Scottish sites summer 1992 (section 5.4.1). b) The Durham and Scottish sites autumn 1992 (section 5.4.1). c) The Durham sites 14 July-5 November 1992.

Table 5.7a

	Stuartfield	Waskerley	Greenlaw
Waskerley	4.4%		
Greenlaw	4.2%	59.9%	
Langholm	25.8%	46.4%	56.0%

Table 5.7b

	Stuartfield	Waskerley	Slaley	Greenlaw
Waskerley	51.5%			
Slaley	65.4%	18.5%		
Greenlaw	69.2%	78.4%	36.6%	
Langholm	56.6%	90.2%	22.0%	78.8%

Table 5.7c

	Stuartfield	Waskerley
Waskerley	73.2%	
Slaley	58.9%	33.9%

Tables 5.7a-c. Matrices comparing the similarity of the macrolepidoptera larvae communities at different study areas using the percentage similarity index (Renkonen 1938). a) The Durham and Scottish sites summer 1992 (section 5.4.1). b) The Durham and Scottish sites autumn 1992 (section 5.4.1). c) The Durham sites 14 July-5 November 1992.

Table 5.8a

	Waskerley	Stuartfield	Greenlaw	Langholm	χ^2	df	P
Macros	68% (140)	73% (27)	87% (48)	78% (199)	11.3	3	<0.03
Micros	32% (65)	27% (10)	13% (7)	22% (56)			

Table 5.8b

	Waskerley	Slaley	Stuartfield	Greenlaw	Langholm	χ^2	df	P
Macros	99% (265)	95% (1536)	86% (92)	91% (556)	93% (366)	28.0	4	<0.001
Micros	1% (4)	5% (88)	14% (15)	9% (52)	9% (28)			

Table 5.8c

	Waskerley	Slaley	Stuartfield	χ^2	df	P
Macros	92% (1168)	90% (3527)	91% (546)	5.81	2	NS (<0.10)
Micros	8% (101)	10% (398)	8% (52)			

Table 5.8d

	Waskerley	Slaley	χ^2	df	P
Macros	86% (717)	90% (587)	5.71	1	<0.03
Micros	14% (114)	10% (62)			

Tables 5.8a-d. The numbers and proportions of macrolepidoptera and microlepidoptera larvae in the total catch at different study areas. Data have been analysed for several time periods during the sweepnet sampling programmes of 1992-1993. a) Durham and Scottish sites summer 1992 b) All sites autumn 1992 c) Durham sites 14 July-5 November 1992 d) Durham sites 29 April-2 August 1993. Figures in parentheses are the numbers of larvae that were caught.

Table 5.9a

	Waskerley	Greenlaw	Langholm	χ^2	df	P
Geometrids	94% (132)	79% (38)	59% (118)	48.0	2	<0.001
Noctuids / Others	6% (8)	21% (10)	41% (81)			

Table 5.9b

	Waskerley	Slaley	Stuartfield	Greenlaw	Langholm	χ^2	df	P
Geometrids	60% (158)	94% (1447)	84% (77)	80% (446)	60% (219)	388	4	<0.001
Noctuids / Others	40% (107)	6% (89)	16% (15)	20% (110)	40% (147)			

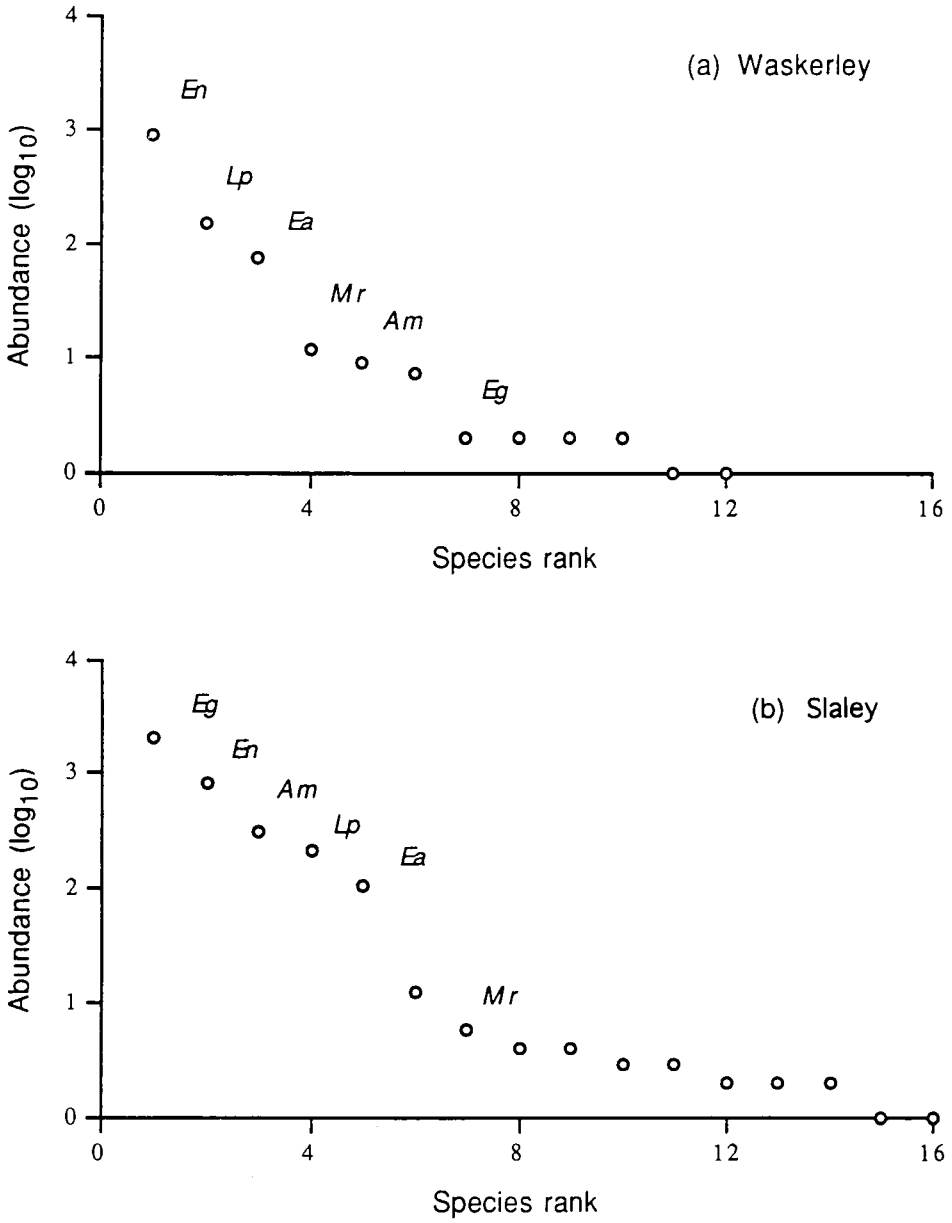
Table 5.9c

	Waskerley	Slaley	Stuartfield	χ^2	df	P
Geometrids	86% (987)	85% (2968)	87% (472)	2.49	2	NS
Noctuids	14% (162)	15% (541)	13% (72)			

Table 5.9d

	Waskerley	Slaley	χ^2	df	P
Geometrids	99% (697)	85% (476)	86.8	1	<0.001
Noctuids	1% (9)	15% (86)			

Tables 5.9a-d. The numbers and proportions of geometrid and noctuid larvae in the total catch at different study areas. Data have been analysed for several time periods during the sweepnet sampling programmes of 1992-1993. a) Durham and Scottish sites summer 1992 b) All sites autumn 1992 c) Durham sites 14 July-5 November 1992 d) Durham sites 29 April-2 August 1993. Figures in parentheses are the numbers of larvae that were caught. Stuartfield was not included in (a) because sample sizes were too small. In (a) and (b) the Noctuids have been combined with the "Others" to increase sample sizes.



Figures 5.1a and b. Rank abundance graphs for the Lepidoptera species found by sweepnet sampling at a) Waskerley and b) Slaley during the period 14 July-5 November 1992. The identities of the five most abundant species at each site are marked on each graph. Abbreviations are as follows: *En Eupithecia nanata*, *Lp Lycophotia porphyrea*, *Ea Ematurga atomaria*, *Mr Macrothylacia rubi*, *Am Anarta myrtilli*, *Eg Eupithecia goossensiata*. The ranks of species with equal abundances are interchangeable.

Figures 5.5-5.7 (a) show seasonal variation in the numbers of macrolepidoptera larvae recorded from the Geometridae, Noctuidae and the group "Others" which incorporated species from the Arctiidae, Lasiocampidae, Lymantriidae and Saturniidae. Figures 5.5-5.7 (b) show the proportions of the macrolepidoptera individuals that belonged to the Geometridae, Noctuidae and other families.

The large spring and autumn peaks in the number of macrolepidoptera larvae were mainly due to changing numbers of geometrid larvae. This group comprised approximately 85% of the Lepidoptera community, while the Noctuidae, the second largest group contributed approximately 15% of individuals. Seasonal variation in the proportion of the noctuids in the Lepidoptera community was different at the three sites. At Waskerley the proportion of noctuids in the community was negligible in the spring and summer months before August, but increased to approximately 60% when the number of noctuid individuals peaked in October. At Slaley the majority of noctuid individuals were found between mid-July and September. Stuartfield was intermediate between these two sites, noctuids making a larger contribution to the community between mid June-mid August and again in October-November.

5.6 Discussion

5.6.1 The Lepidoptera species found during the study

This study raised the total number of macrolepidoptera species taken as larvae on *Calluna* in County Durham from 26 to 34 (Table 5.4). This figure comprised 14 Geometridae, 11 Noctuidae and nine "Others". Five of the new species found in this study were animals that did not appear in Fielding's list of potential species *i.e.* species that were associated with *Calluna* and had a distribution in County Durham according to literature sources (Fielding unpublished Ph.D. thesis 1992). For this reason the increase in the proportion of the potential species that were actually found was very small. Although the addition of the results from this three-year study to those of Fielding's three-year study effectively doubled the sampling effort, the proportion of the potential number of species of macrolepidoptera, Geometridae, Noctuidae and Others that were found increased by only 7, 10, 6 and 0 percentage points respectively.

Fielding (unpublished Ph.D. thesis 1992) suggested three explanations for the discovery of species not usually reported as *Calluna* feeders. Single specimens could be "accidental tourists", while other species may be known to feed on plants that grow in the same habitat as *Calluna e.g. Vaccinium myrtillus*. The third group could comprise species of larvae that are regarded as widely polyphagous, because complete food-plant

Figure 5.2a

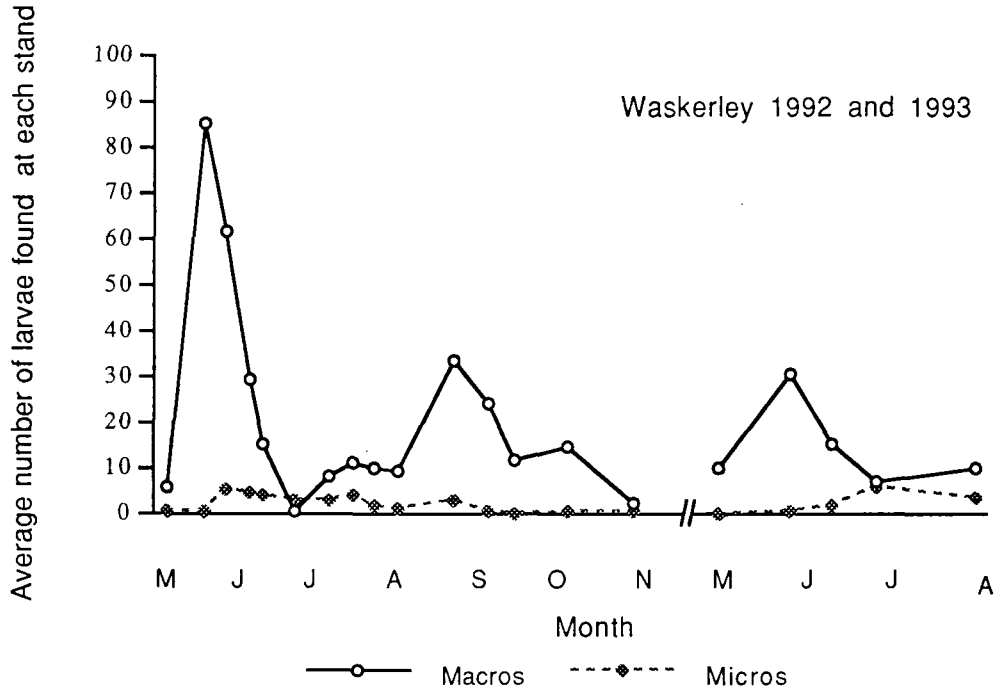
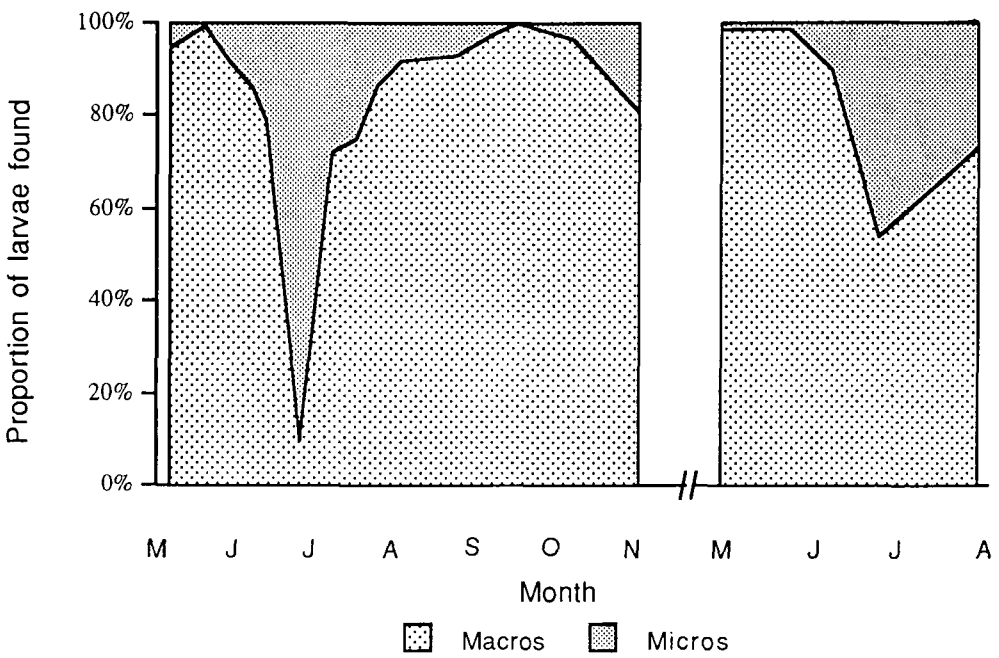


Figure 5.2b



Figures 5.2a and 5.2b. Seasonal variation in the number of Lepidoptera larvae recorded at Waskerley during the 1992 and 1993 sweepnet sampling programme described in section 5.2.1. Figure 5.2a shows the average number of macrolepidoptera and microlepidoptera larvae found per stand on each sampling date. Figure 5.2b expresses these data as proportions of the total Lepidoptera catch on each date. Twenty samples of ten sweepnet strokes were taken at each stand on each sampling date.

Figure 5.3a

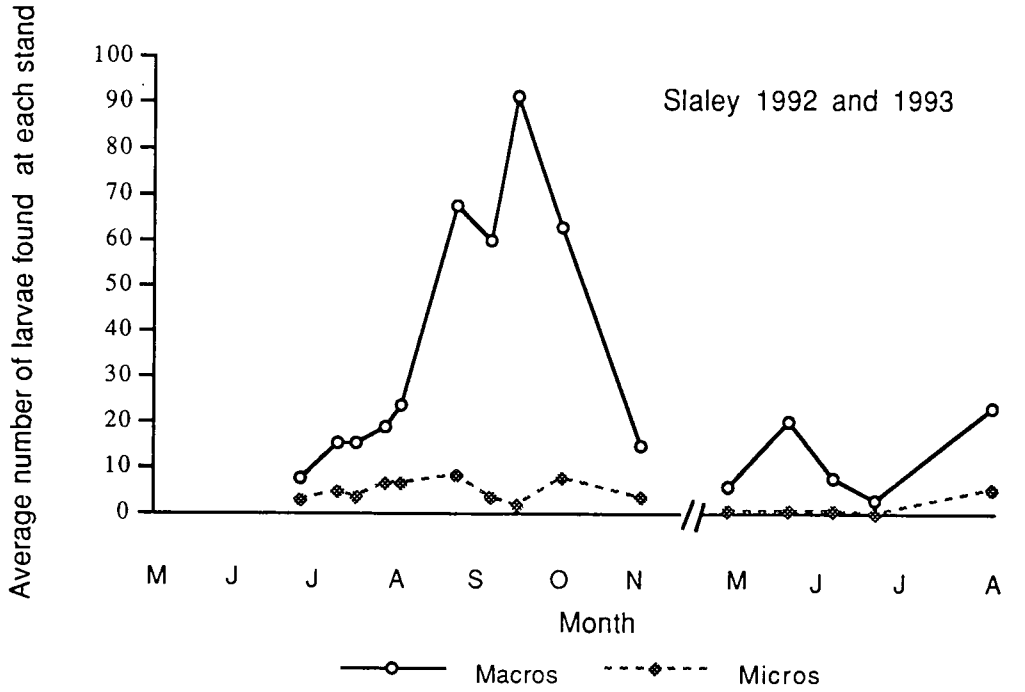
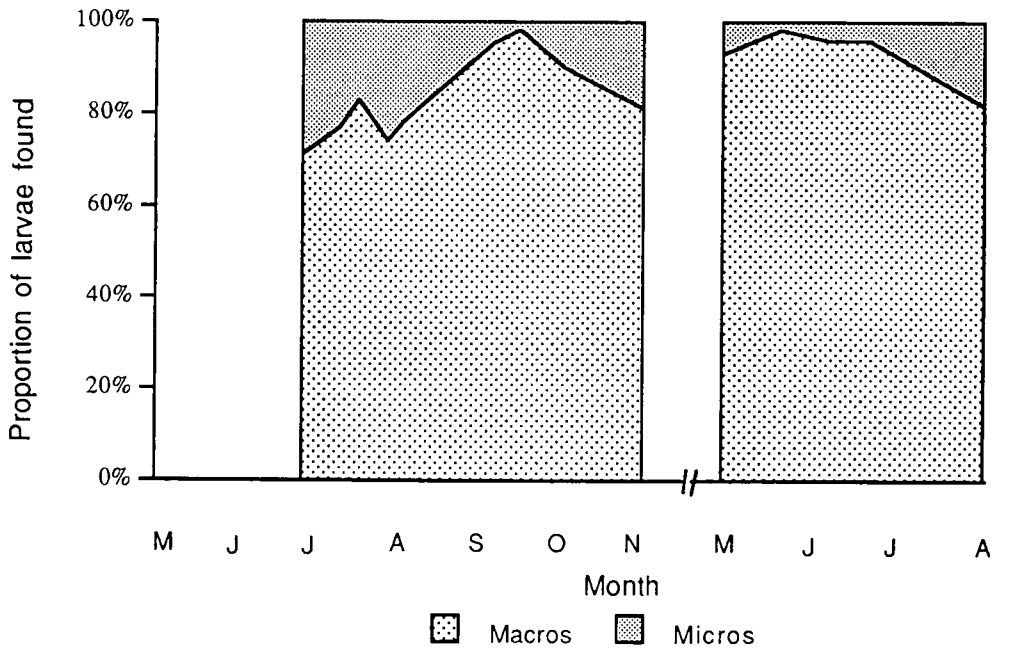


Figure 5.3b



Figures 5.3a and 5.3b. Seasonal variation in the number of Lepidoptera larvae recorded at Slaley during the 1992 and 1993 sweepnet sampling programme described in section 5.2.1. Figure 5.3a shows the average number of macrolepidoptera and microlepidoptera larvae found per stand on each sampling date. Figure 5.3b expresses these data as proportions of the total Lepidoptera catch on each date. Twenty samples of ten sweepnet strokes were taken at each stand on each sampling date.

Figure 5.4a

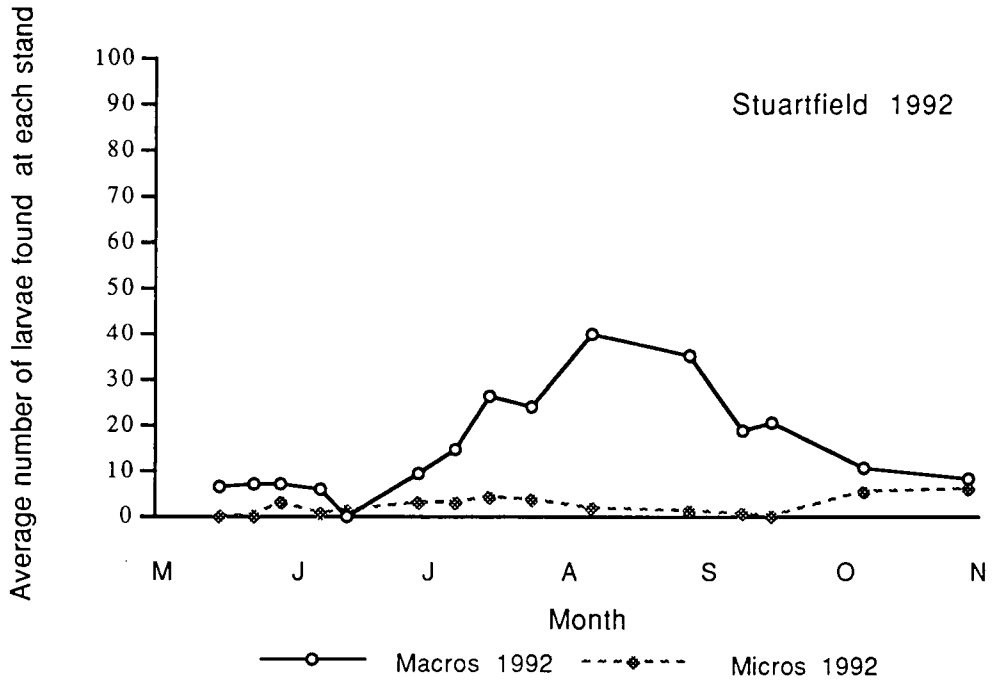
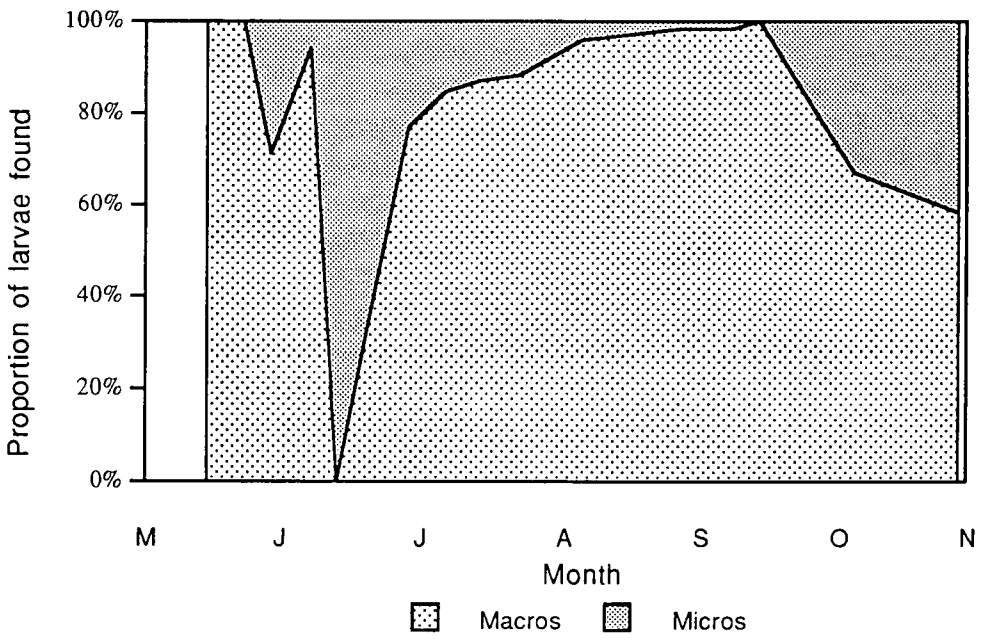


Figure 5.4b



Figures 5.4a and 5.4b. Seasonal variation in the number of Lepidoptera larvae recorded at Stuartfield Lodge during the 1992 sweepnet sampling programme described in section 5.2.1. Figure 5.4a shows the average number of macrolepidoptera and microlepidoptera larvae found per stand on each sampling date. Figure 5.4b expresses these data as proportions of the total Lepidoptera catch on each date. Twenty samples of ten sweepnet strokes were taken at each stand on each sampling date.

Figure 5.5a

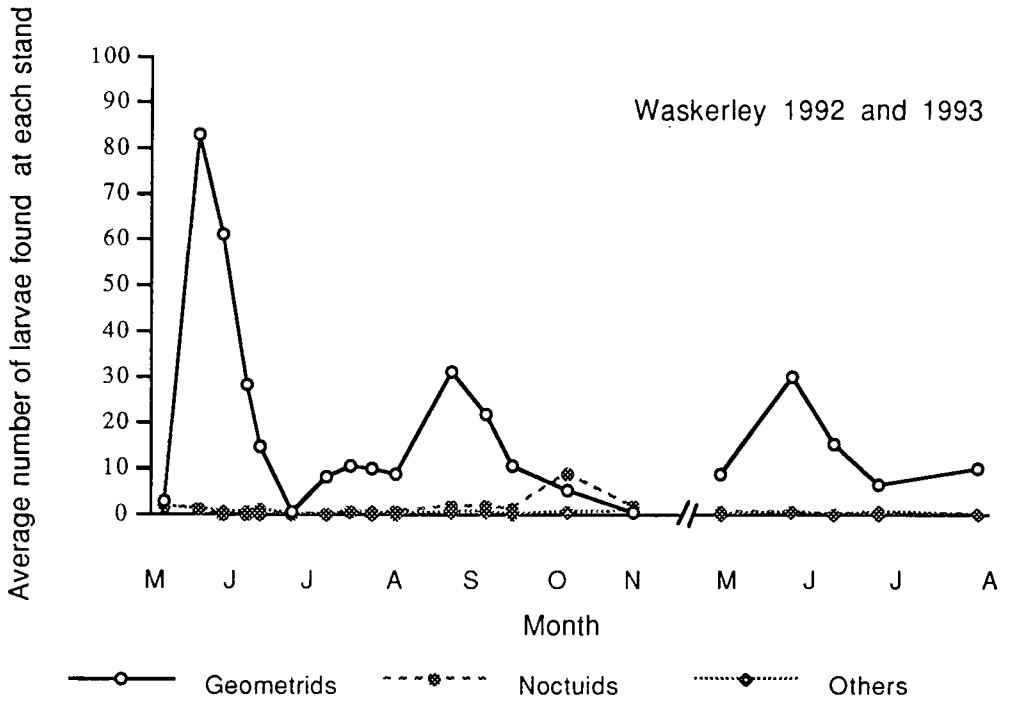
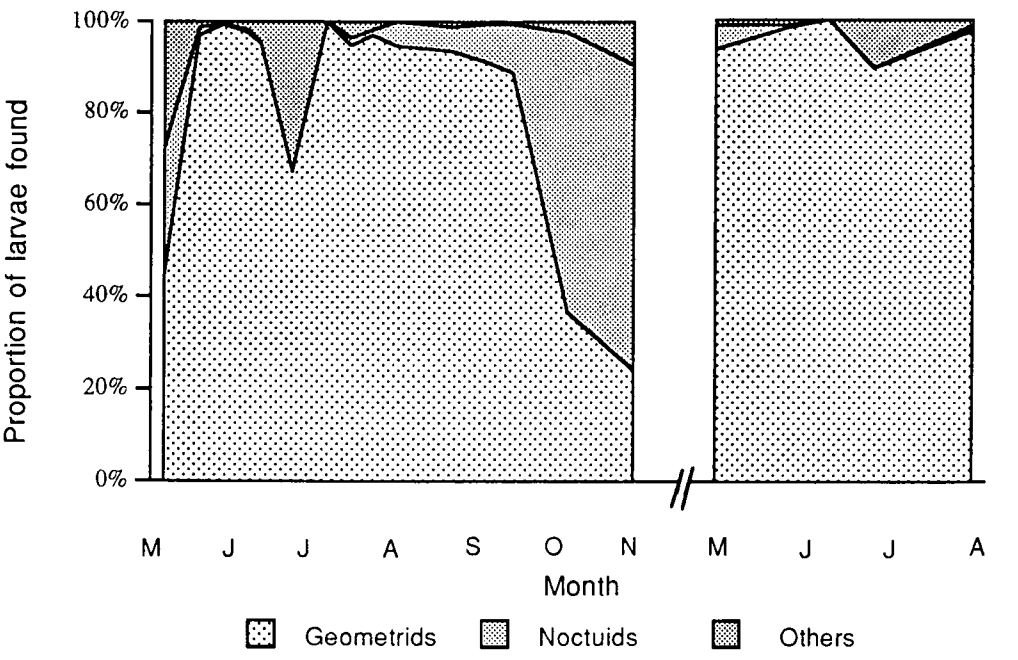


Figure 5.5b



Figures 5.5a and 5.5b. Seasonal variation in the number of larvae of the Geometridae, Noctuidae and 'Other' macrolepidoptera families recorded at Waskerley during the 1992 and 1993 sweepnet sampling programme described in section 5.2.1. Figure 5.5a shows the average number of geometrids, noctuids and other larvae found per stand on each sampling date. Figure 5.5b expresses these data as proportions of the total Lepidoptera catch on each date. Twenty samples of ten sweepnet strokes were taken at each stand on each sampling date.

Figure 5.6a

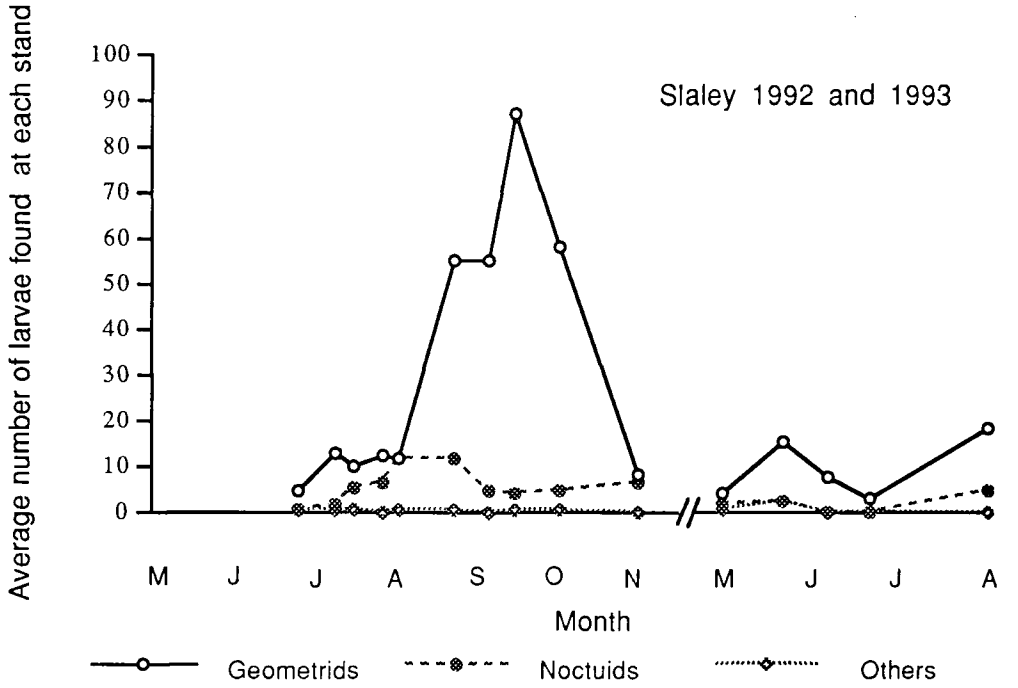
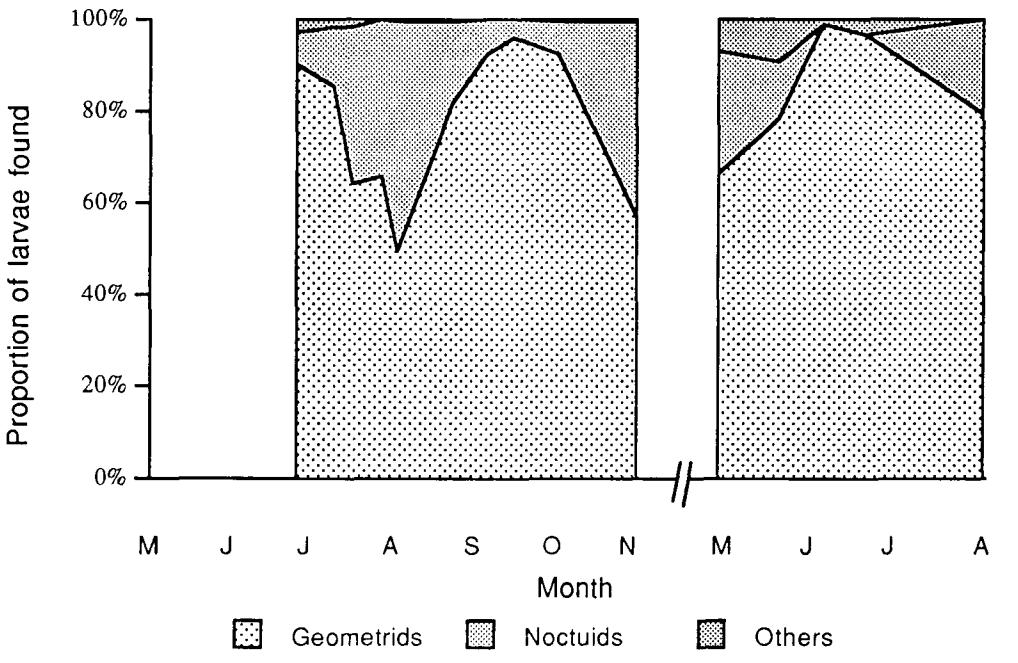


Figure 5.6b



Figures 5.6a and 5.6b. Seasonal variation in the number of larvae of the Geometridae, Noctuidae and 'Other' macrolepidoptera families recorded at Slaley during the 1992 and 1993 sweepnet sampling programme described in section 5.2.1. Figure 5.6a shows the average number of geometrids, noctuids and other larvae found per stand on each sampling date. Figure 5.6b expresses these data as proportions of the total Lepidoptera catch on each date. Twenty samples of ten sweepnet strokes were taken at each stand on each sampling date.

Figure 5.7a

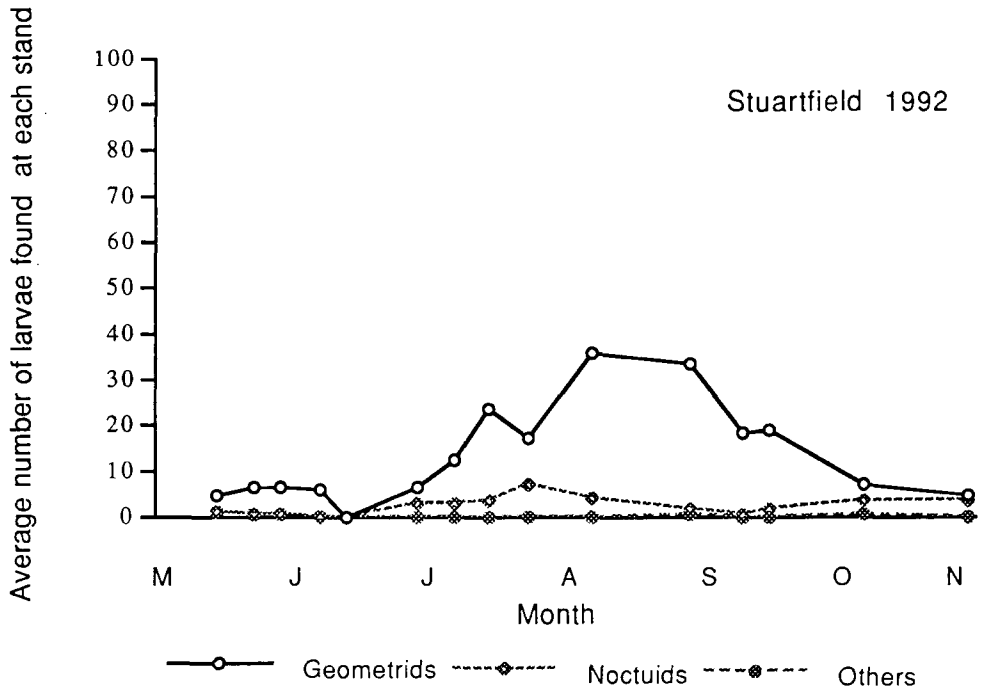
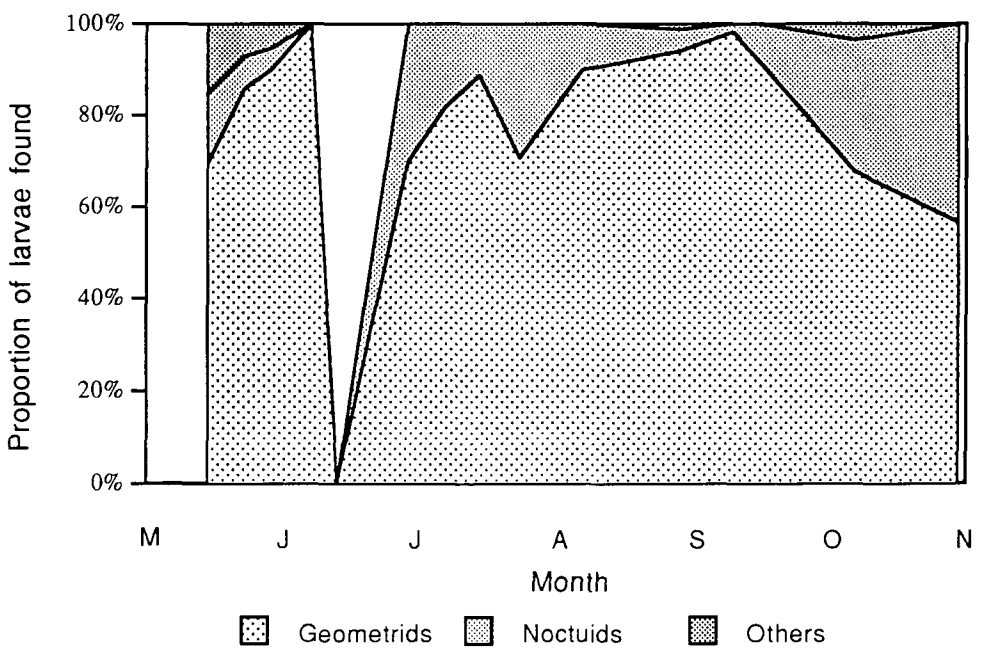


Figure 5.7b



Figures 5.7a and 5.7b. Seasonal variation in the number of larvae of the Geometridae, Noctuidae and 'Other' macrolepidoptera families recorded at Stuartfield Lodge during the 1992 sweepnet sampling programme described in section 5.2.1. Figure 5.7a shows the average number of geometrids, noctuids and other larvae found per stand on each sampling date. Figure 5.7b expresses these data as proportions of the total Lepidoptera catch on each date. Twenty samples of ten sweepnet strokes were taken at each stand on each sampling date.

lists are not usually given for such species (Fielding unpublished Ph.D. thesis 1992). In this study, eight of the nine species recorded that were not expected (*Ectropis bistortata*, *Perizoma didymata*, *Blepharita adusta*, *Orthosia gothica*, *Autographa gamma*, *Ceramica pisi*, *Phragmatobia fuliginosa* and *Parasemia plantaginis plantaginis*) were classified as widely polyphagous by two texts (Skinner 1984; Emmet & Heath 1991) and one species *Eulithis populata* was said to feed only on *Vaccinium myrtillus*. The major reason for the recognition of extra species appears to be the failure of texts to recite food-plant lists in full.

Fielding (unpublished Ph.D. thesis 1992) concluded that the total number of species associated with *Calluna vulgaris* in Great Britain (86 species) was probably an underestimate and predicted the actual number to be 25% greater at over 100 species. When the present study was combined with Fielding's work, 35% of the 34 macrolepidoptera species found were not on the list of potential species, and on this basis the number of macrolepidoptera species predicted to have an association with *Calluna* in Great Britain might be in the order of 115.

Of potential species not found by this study, 50% were listed as common and widespread in the county by Dunn and Parrack (1986), 41% as rare or uncommon and 9% from habitats not sampled by the study (Table 5.5). The proportions of the species in each of these categories were almost the same as Fielding's study, despite small differences in the identities of the species in each category. The field sites in this study covered only a small part of the area surveyed by Dunn and Parrack (1986) and it is likely that a much larger area would have to be sampled to find all the common species listed in their study.

Most of the species found in this study (62%) were also found in Durham study areas by Fielding (unpublished Ph.D. thesis 1992). Of the species found in this study, but not by Fielding, *Dyscia fagaria*, *Ectropis bistortata*, *Papestra biren*, *Orthosia gothica*, *Blepharita adusta* and *Autographa gamma* occurred in very low numbers or at study areas not visited by Fielding. *Epirrita filigrammaria* was found in higher numbers at Slaley and Waskerley but at Waskerley, the only study area also used by Fielding, the species was local to several of the higher altitude stands and was present for only a few weeks in April-May. Species that are relatively uncommon, local or appear as larvae for a brief time period may be encountered only by chance, so it is not surprising that they do not appear on Fielding's list. Of the species found by Fielding (unpublished Ph.D. thesis 1992) but not by this study, *Orgyia antiqua* has a local distribution in County Durham that includes Waldridge Fell (Dunn & Parrack 1986), a site sampled by Fielding but not by this study. The adults of *Arctia caja* are not regarded as common in County Durham except in areas of rough grassland with mixed vegetation (Dunn &

Parrack 1986), and *Noctua comes* though common as an adult (Dunn & Parrack 1986) was found by Fielding only in blanket bog, a habitat not sampled by this study. Larvae of *Eupithecia satyrata* may have been located in this study, but misidentified as the related *E. goossensiata*. This species has several colour forms, some of which resemble *satyrata*. Several thousand specimens of *E. goossensiata* were recorded during this study and it was not feasible to rear all to the adult stage. Of those reared successfully, all were *E. goossensiata*.

It seems that in the majority of cases, species found in one study but not the other were uncommon and would have been encountered only by chance. It is also possible that the abundance of some species changed between 1988-90 (Fielding's study) and 1991-1993 (this study). Fielding's (unpublished Ph.D. thesis 1992) study sampled six study areas at altitudes between 290-650m. Two study areas were on blanket bog, a habitat type not used in this study. Only one site, Waskerley Moor, was common to both studies, so it is the overall similarity of the species encountered that is most interesting.

Only one new species was found by visiting Scottish sites. This was a single larva of *Phlogophora meticulosa* and must be regarded as a chance encounter. The different total numbers of species found at the five study areas (Table 5.3a), clearly owe more to variations in the sampling intensity than actual species richness values, as the number of species recorded at each site were more similar over a short time period when sampling regimes were similar (Table 5.3b).

5.6.2 Composition of the Lepidoptera community at different study areas

Caution should be used when comparing values of two indices because the maximum value possible for some coefficients can vary for different sample sizes (Krebs 1989). Maximum values of Sorensen's similarity coefficient may be much less than 1.0 when sample sizes are small, but the percentage similarity index is not affected greatly by sample size or species diversity (Krebs 1989). On a 0-1 scale, values of Sorensen's coefficient were much higher than values of the percentage similarity index. Comparison between these indices may be valid in this case because the difference between the two indices was fairly large (5-50%). This suggests that the same common species were present at most of the sites but the relative abundance of species was not consistent between study areas. This was supported by the rank abundance plots for pairs of Durham sites (Figures 5.1a-b), which showed that four of the five most abundant species at one site were also among the five most abundant species at the other, although the rank order was not the same.

The degree of similarity in species composition was not related to the geographic distance between the study areas. The indices found greater similarity between combinations of Durham and Scottish sites, than between pairs of Durham sites, even though none of the Durham sites were more than 14km apart while the distance between the Durham and Scottish sites could be as much as 120km.

Values of the Sorensen's similarity coefficient and the percentage similarity index were significantly higher in the autumn than in the summer. The longer periods of larval development found in autumn larvae (Fielding unpublished Ph.D. thesis 1992) may be partly responsible for this effect. If spring species spend less time as larvae, slight differences in sampling dates at different study areas could result in failure to detect the species at all the sites at which they occur, particularly if the dates of the larval periods are not highly synchronised at different locations. Longer larval periods could increase the probability of detection. Whatever the underlying cause, it appears that more species are common to the different sites in the autumn.

Values of the two indices based on data from a longer time period (14 July-5 November 1992), grouped Waskerley and Slaley more closely than either site with Stuartfield, although this contradicted results for the summer and autumn periods considered separately. This may have been caused by differences in the sampling intensity (ten stands at Waskerley and Slaley, three stands at Stuartfield).

Significant differences were observed in the proportions of both macrolepidoptera and microlepidoptera larvae and larvae from the Geometridae, Noctuidae and "Other" families at different sites. This suggests that data from different study areas should not be combined to examine ecological effects, without first determining whether composition of the communities is similar, since even sites that are geographically close may host different species or show different organisation of the community.

5.6.3 Phenology of the species at the study areas

There was a heterogeneous distribution of Lepidoptera larvae throughout the season. The strongest trends were the greater abundance of macrolepidoptera than microlepidoptera larvae throughout the year, except for a short period in June-July and two peaks of macrolepidoptera abundance in May-June and August-September. The May-June peak comprised geometrid species and the August-September peak both geometrid and noctuid species.

Such a scheme is much simplified however, because of differences in species composition between study areas. For example, at Stuartfield Lodge there was no spring peak and at Slaley, the main period of noctuid abundance occurred between mid

July and September, because of the density of *Anarta myrtilli*. Fielding (unpublished Ph.D. thesis 1992) examined patterns in the species richness of Lepidoptera associated with *Calluna vulgaris* and found similar spring and autumn peaks in the species richness of macrolepidoptera. Fielding stated that seasonal variation in the proportion of geometrid and noctuid larvae was an exaggeration of seasonal trends in species richness. Her results emphasised the dominance of noctuid species throughout the autumn period, a trend that was not so strong at any of the areas in this study. Differences between the two studies appear to derive from different lists of species that were considered very common. While Fielding's interpretation of the relative abundance of individuals belonging to the geometrid and noctuid families provides a general scheme it was probably inappropriate to combine the data of two sampling techniques, three years and six study areas. Year to year variation in abundance of the groups could not be identified and the pattern was probably not representative of all her study areas. The use of combined data from two sampling techniques is also confusing because unless the techniques are used in parallel at a consistent intensity throughout a survey, changes in the relative abundance of a taxonomic group could be caused by the bias of the dominant sampling method.

Seasonal patterns of species richness and abundance of herbivores have been related to seasonal changes in plant defence mechanisms (Feeny 1970), nutritional resources (*e.g.* Hill 1982), leaf toughness (Feeny 1970; Stamp & Bowers 1990), parasitism pressure (Myers 1981), and plant structure (Lawton 1978, 1983). Some plants *e.g.* trees, have a structure that is in place at the beginning of the growing season. The structural complexity of others *e.g.* herbs increases through the year. The former allows early colonisation by herbivores, while in the latter case the herbivore community may increase as the season progresses (Lawton 1978). Some plants have a short flush of new growth that is nutritious or lacks quantitative chemical defences *e.g. Quercus robur* (Feeny 1970; Niemelä & Haukioja 1982), while other species *e.g. Populus* sp. (Niemelä & Haukioja 1982) produce new leaves throughout the plant growing season. The distribution of the species richness patterns of the herbivores associated with such plants may be skewed to the early or late season respectively (Niemelä & Haukioja 1982). Fielding (unpublished Ph.D. thesis 1992) noted the similarity in the seasonal species richness pattern of *Calluna* species with that of the bimodal pattern of Lepidoptera species richness on oak (Feeny 1970). The abundance peaks in this study coincide with the beginning of the periods of new growth of *Calluna* leaves in the spring and flowers in August and September. As *Calluna* is evergreen and retains leaves for up to four years (Gimingham 1960; Chapman *et al.* 1975; Gimingham *et al.* 1979), foliage is always available but its suitability to Lepidoptera throughout the year is unknown.

Study areas that were sampled for more than one year, showed peaks in macrolepidoptera abundance at the same time of year, but peaks often differed in amplitude. Varley (1947) considered fluctuations of density from year to year to be caused by different weather conditions and the relative population levels of individual species to be under the control of density dependent effects such as parasitism. Fluctuations in the abundance of different species in different years could also have contributed to the greater emphasis that Fielding (unpublished Ph.D. thesis 1992) placed on the abundance of the Noctuidae in the autumn.

Chapter Six

The Effects of Plant Architecture on the Lepidoptera Larvae Associated with Northern Heath

6.1 Introduction

Ecologists have made many attempts to determine the number of invertebrate species in different habitats and to define patterns of the distribution of species and individuals on single plant species (Lawton 1978, 1983; Southwood 1978; Strong *et al.* 1984). One of the most important factors to influence the total number of invertebrate species that feed on a plant species is the extent of the host-plant's geographic range (Lawton & Schröder 1977; Neuvonen & Niemelä 1981; Fowler & Lawton 1982). Widely-distributed plant species tend to have larger invertebrate faunas than plants with small geographic ranges (Lawton & Schröder 1977; Banerjee 1981; Neuvonen & Niemelä 1981; Fowler & Lawton 1982). A similar approach is to consider the number of vegetation communities a plant species occurs in. A species that occurs in many different assemblages will be exposed to a wider variety of generalist herbivores and may consequently accumulate a larger herbivore fauna than a species that is restricted to a few habitat types (Fowler & Lawton 1982).

The number of invertebrate species encountered tends to increase as larger areas of host plant are sampled (Lawton 1978; Strong *et al.* 1984), because of new species in different geographic locations and because of the greater probability of finding rare species in larger samples of individuals (Krebs 1985). Small patches of host-plant may hold the full regional complement of species (Lawton 1978). For example, swards of bracken *Pteridium aquilinum* (Rigby, quoted in Lawton 1978) and juniper *Juniperus communis* (Ward & Lakhani 1977) hosted all the species known in the area, while still many orders of magnitude smaller than the geographical region (Lawton 1978).

Even at the scale of an individual plant, many factors influence the number of species, and the abundance of individuals. Various hypotheses cite vegetation diversity, habitat successional stage, plant defence strategy, disturbance, the area of the plant "island" or vegetation characteristics *e.g.* plant height, plant structure, number of different resources as key factors determining the subsequent size and richness of the hosted invertebrate community (MacArthur & Wilson 1967; Root 1973; Feeny 1976;

Rhoades & Cates 1976; Lawton 1978, 1983; Lawton & McNeill 1979; Petraitis *et al.* 1989). Some of these hypotheses share common features and two or more mechanisms may act together to influence the number of individuals and species present. Some of the hypotheses are described below.

Invertebrate abundance and species richness may be affected by vegetation diversity. Root (1973) predicted higher absolute densities of herbivores in monocultures than polycultures, but greater species richness in polycultures than single-crop systems. This theory was the foundation of many subsequent experiments to reduce the effects of pest species in agricultural systems, by manipulating crop diversity (*e.g.* Tahvanainen & Root 1972; Bach 1980, 1981; Latheef & Ortiz 1983; Thomas 1986; Andow 1991). Root suggested that two mechanisms, the "resource concentration hypothesis" and the "natural enemies hypothesis" could cause these effects, either by working alone or in concert. Greater densities of invertebrates would occur in a host-plant monoculture if herbivores located a concentrated resource more easily, (perhaps because of stronger chemical and visual cues), and then exhibited longer tenure times and greater reproduction. The high densities of some invertebrate species in pure stands would lower overall diversity. The resource concentration hypothesis may be reversed to explain lower densities of herbivores in polycultures. Competition for nutrients between different plant species may reduce quality of the host-species, while scent or appearance of non-host plants may reduce the ability of invertebrates to locate host-plants. This could result in lower colonisation and reproduction rates and shorter tenure times in polycultures (Root 1973).

In the natural enemies hypothesis, higher densities of predators and parasitoids occur in polycultures and suppress herbivore densities. Higher densities of both specialised and generalist predators were predicted because of a richer herbivore fauna associated with the non-host plants and a greater variety of refuges for prey (Root 1973). The relative importance of the two hypotheses has been examined (Russell 1989; Andow 1991). The "resource concentration hypothesis" may be the best explanation of herbivore abundance and species richness, but the relative importance of the two theories also depends on whether annual or perennial systems are studied (Andow 1991).

Some theories predicting levels of species richness and abundance apply to specific habitat types or stages. In habitats that undergo periodic disturbance, the "intermediate disturbance hypothesis" (Petraitis *et al.* 1989) gives the disturbance process a role in controlling species diversity. Greatest species richness is predicted at intermediate levels of disturbance. In successional habitats, the abundance of individuals may be related to the life-history strategies of the species that utilise each stage. Lawton and

McNeill (1979) predicted that insect species which attack early successional herbs and weeds or ephemeral plants would have higher *r* (rate of increase) values (Pianka 1970) than those that exploit long-lived or late successional species. From this Lawton and McNeill (1979) calculated that population sizes of insects on early succession or non-apparent plants (Feeny 1976) would be larger than those of insects attacking the apparent plants of late climax-stages. On islands, or areas of habitat that are physically isolated from others of the same type, species richness may be determined by the rates of immigration and extinction (MacArthur & Wilson 1967). Islands nearer the shore may have more species through greater immigration rates, while extinction may be higher on small islands and species number smaller because fewer niches are available for colonisation.

Theories concerning the role of plant architecture in controlling the number of species and abundance of individuals apply to a wider range of habitats. The structure of the vegetation itself influences insect distribution. Architecture refers to vegetative characteristics such as size, growth form, pattern of seasonal development and the persistence and variety of above-ground parts (Lawton 1983). Across the range of plant life forms, the total number of invertebrate species associated with different plants decreases in the order trees > shrubs > perennial and woody plants > herbs (Lawton & Schröder 1977; Lawton 1983). Lawton (1983) interpreted this as the effect of plant height. Taller plants were predicted to have more associated insect species, because they are more apparent in space and time and because they offer greater structural complexity and a larger number of resources. Neuvonen and Niemelä (1981) objected to the application of this hypothesis across different growth forms because the theory does not consider the antiherbivore strategies possessed by different plant types (Feeny 1976; Rhoades & Cates 1976). The effects of plant chemical defence systems on insect populations are discussed in Chapter Seven.

Within a growth form, plant height may account for much of the variation in the number of insect species associated with different plants, after host-plant range has been accounted for (Lawton & Price 1979; Neuvonen & Niemelä 1981). At the time of Lawton's (1983) review little work had been done on single species, but there is now evidence that the number of associated insect species and the number of individuals is sometimes related to plant height (*e.g.* Bach 1981; Cornell 1986; Tenow & Larsson 1987). Lawton (1983) proposed a "zonation hypothesis". This predicted that herbivore assemblages would differ on different size classes of a host tree-species and that the faunal composition of upper and lower canopy levels of an individual tree would differ to some extent. Separation of different insect species into upper and lower canopies is termed "vertical zonation" while the selection of certain sizes of tree is "horizontal

zonation". Other architectural variables known to have influenced invertebrate density and species richness include plant density (Pimentel 1961; Price *et al.* 1980; Horton & Capinera 1987; Segarra-Carmona & Barbosa 1990), plant patch size (Price *et al.* 1980; Cain 1985; Bach 1988a; Schoener 1988) and degree of taxonomic isolation (Neuvonen & Niemelä 1981). Lawton (1983) also explained seasonal changes in species richness on host plants in terms of changing architectural complexity and resource quality.

Variation in the density and heterogeneity of the Lepidoptera larvae associated with *Calluna vulgaris* might be explained by several of these hypotheses. For example, on managed northern heath the process of repeated burning creates pieces of land in different successional stages. There is a period of disturbance associated with each fire. Lepidoptera species richness at different stages of succession and disturbance could be compared with the theories of Lawton and McNeill (1979) and Petraitis *et al.* (1989). Similarly, *Calluna* is a virtual monoculture in the building and mature phases of the life-cycle but other plant species are also common in the pioneer and degenerate stages (Barclay-Estrup & Gimingham 1969; Gimingham 1972). The relevance of the resource concentration and natural enemies hypotheses to *Calluna* systems could therefore be explored.

Calluna plants exist in a range of structural forms across their latitudinal and altitudinal ranges (Gimingham 1960; Grant & Hunter 1962). The architectural complexity and number of resources also changes with plant age and season (Barclay-Estrup 1970; Gimingham 1972; Miller 1979). The plant is therefore a good subject for examining the effects of architectural variation on an invertebrate fauna. This chapter examines whether vegetation structure affects the density and heterogeneity of the Lepidoptera larvae associated with *Calluna*. The study aimed to determine whether different species of Lepidoptera made individual responses to vegetation characteristics such as plant age and whether the same factors influenced the Lepidoptera communities at different study areas.

6.2 Methods

6.2.1 Sampling of Lepidoptera larvae

Data on the distribution of Lepidoptera larvae in stands of *Calluna* with different ages and different vegetation characteristics were collected by sweepnet sampling, according to the regime in section 5.2.

6.2.2 Description of vegetation characteristics

The vegetation characteristics examined at each sampling site in 1992 were the average age of *Calluna* plants, plant height, green shoot density, flower density and *Calluna* cover. Plant age was determined at the two main study areas, Waskerley and Slaley but not at the Scottish sites, because the process was too time-consuming to repeat at many stands. The methods used to quantify the vegetation characteristics are described in Chapter Three (section 3.2). All measurements of plant height, refer to the average height of plants at the end of the growing season. Green shoot density, flower density and *Calluna* cover were not measured in 1993, except at the new sampling sites A-E at Waskerley and L-O at Slaley. Values of these variables at other stands in 1993 were represented by their 1992 estimates.

6.3 The effects of plant architecture on the density of Lepidoptera larvae in *Calluna*

6.3.1 Method

The effects of plant architecture on the density of Lepidoptera larvae were examined using two regression analysis techniques. The architectural variables considered were the average height of *Calluna* plants in each stand, plant age, green shoot density, flower density and *Calluna* cover. The measure of Lepidoptera larval density at each *Calluna* stand on any sampling date was the total number of Lepidoptera larvae caught in 20 sweepnet samples of ten strokes.

Data for different sites were analysed separately. Data collected on different sampling dates were pooled for several time periods. The time periods were: Waskerley 4 June-7 July 1992, 16 July-5 November 1992, 29 April-2 August 1993; Slaley 16 July-5 November 1992, 29 April-2 August 1993; June and September visits in 1992 were combined at both Greenlaw and Langholm. The reasons for the allocation of these time periods are given in Chapter Five.

In the first regression technique, vegetation variables and the total number of larvae collected during each period were offered to a stepwise multiple regression program (SPSS 1990). The program selected the vegetation character that explained most variation in the density of larvae. The values of the *Probability of F-to-enter* and the *Probability of F-to-remove* were set at 0.05 and 0.10 respectively. The maximum number of steps allowed was twice the number of independent variables.

The squares, square roots and decadic logarithms of each vegetation characteristic were also offered as independent variables to the stepwise program, in case

relationships between larvae density and *Calluna* were non-linear. If the program selected the square, square root or logarithm of a vegetation character, the correlation values were examined, to determine whether these explained a significantly higher proportion of variation in the data than the simpler alternative. If the difference between the character and its more complex square, square root or logarithm was minimal, the variables were offered to the stepwise multiple regression program again, omitting the more complex vegetation characters.

Multiple stepwise regressions were computed for the macrolepidoptera, microlepidoptera, geometrids, noctuids and each of the more common geometrid and noctuid species. Regressions were performed only if larvae that occurred in at least half of the stands sampled at a site, to restrict analysis to common species. Regressions were not performed if no more than five larvae were found in any stand at a site. Stands with missing data for one of the vegetation characteristics were excluded from the stepwise program. Flower density was only included in the analysis in periods that included the months in which *Calluna* flowers, August and September.

The stepwise multiple regression programme could select different vegetation characteristics to explain variations in the density of different groups of larvae. To compare the relationship between plant architecture and the density of one group of larvae at different sites and time periods, it was necessary to regress larvae density against a single independent variable. The vegetation characteristic most frequently found to explain variation in larvae density was chosen.

The slope of the regression line between larvae density and the independent variable, may be influenced by the actual density of individuals. To determine whether the relationships between larvae density and the common independent variable were the same at different sites and times, the regression slope data were converted into units that were independent of actual density. This conversion was achieved by using the regression equation to estimate the density of larvae Y at a given value of the independent variable X_1. Division of the regression coefficient B and the standard error of B by Y_{X1} converted both into units of proportional change in larvae density, for a given change in the value of the independent variable.

6.3.2 Results

The stepwise multiple regression program most frequently selected *Calluna* height to explain variation in the density of different groups of larvae. *Calluna* height was therefore used as the independent variable against which the densities of different groups of larvae were regressed at all sites and time periods. Tables 6.1-6.6 show

regression data for the relationships between *Calluna* height and the densities of macrolepidoptera, microlepidoptera, geometrids, noctuids and individual geometrid and noctuid species respectively. The densities of most Lepidoptera larvae were correlated positively and significantly with *Calluna* height. An asterisk indicates that *Calluna* height was not the independent variable selected by the stepwise program. Table 6.7 shows the alternative variables selected by the stepwise program and gives data for the regressions between these variables and larvae density.

Regression coefficients for the relationship between *Calluna* height and larvae density could be significantly different at different sites and times. For example, the slope of the regression between macrolepidoptera density and *Calluna* height at Slaley (16 July-5 November 1992, Table 6.1) was significantly different to the slope of the same regression at Waskerley for the same time period ($t=2.61$, $df=12$, $P<0.03$). For this comparison, examination of the regression slopes was restricted to similar ranges of *Calluna* height *i.e.* stand heights less than 38cm.

The steepest regression gradient occurred at Slaley (16 July-5 November 1992) between *Calluna* height and the density of macrolepidoptera larvae ($B=13.7$, SE of $B=0.80$). The regression coefficient B, when converted to a measure of proportional change in larvae density per cm change in height (Table 6.8) was not significantly different to any of the other values of proportional change shown in Table 6.8. This indicated that when the actual values of density were taken into account, the underlying trend in the relationship between *Calluna* height and the density of macrolepidoptera larvae was similar at all sites and time periods. The trend was an increase in the density of macrolepidoptera larvae by 2-9% for every cm increase in *Calluna* height. Conversions of the regression coefficients between *Calluna* height and the densities of the other groups of larvae into units of proportional change in density per cm increase in *Calluna* height are shown in Tables 6.9-6.12. All values lie within the range for the macrolepidoptera larvae, except for *Ematurga atomaria* (Langholm 1992). This species showed a significant decrease in larval density as *Calluna* height increased ($r=-0.52$, $df=18$, $P<0.02$, Table 6.5). This change was in the same order as positive changes recorded for other larvae.

For those groups of larvae for which another variable explained variation in the data more thoroughly than height (Table 6.7), no single *Calluna* variable consistently accounted for variation in the data. Plant age, green shoot density, the square of *Calluna* height, flower density and *Calluna* cover were all selected as independent variables for at least one group of larvae, site or time period.

Site and time period	Dependent variable	Independent variable	Regression coefficient (B)	SE of B	Constant	SE of constant	r	df	P
Waskerley 4 June-7 July 1992	Macrolepidoptera	Height	3.69	1.02	-45	28	0.81	7	<0.01
Waskerley 16 July-5 November 1992	Macrolepidoptera	Height	5.53	1.86	-22	49	0.73	8	<0.02
Waskerley 29 April-2 August 1993	Macrolepidoptera	Height*	4.60	2.16	-53	63	0.60	8	NS
Slaley 16 July-5 November 1992	Macrolepidoptera	Height	13.7	0.798	-85	28	0.99	8	<0.001
Slaley 29 April-2 August 1993	Macrolepidoptera	Height*	1.73	0.468	2.11	17	0.79	8	<0.01
Greenlaw June and September 1992	Macrolepidoptera	Height	2.06	0.425	-16	10	0.75	18	<0.001
Langholm June and September 1992	Macrolepidoptera	Height	1.62	0.173	-12	4.83	0.91	18	<0.001

Table 6.1. Data for the regression of macrolepidoptera larvae density against *Calluna* height at a series of sites and time periods. Macrolepidoptera is the total number of macrolepidoptera larvae recorded by sweepnet sampling during the time period. An asterisk indicates that *Calluna* height was not the first vegetation character selected as an independent variable by a stepwise multiple regression program.

Site and time period	Dependent variable	Independent variable	Regression coefficient (B)	SE of B	Constant	SE of constant	r	df	P
Waskerley 4 June-7 July 1992	Microlepidoptera	Height*	0.130	0.926	11.6	25.7	0.05	7	NS
Waskerley 16 July-5 November 1992	Microlepidoptera	Height*	0.418	0.165	-0.299	4.39	0.67	8	<0.05
Waskerley 29 April-2 August 1993	Microlepidoptera	Height*	0.403	0.387	0.490	11.4	0.35	8	NS
Slaley 16 July-5 November 1992	Microlepidoptera	Height*	1.18	0.560	6.51	19.7	0.60	8	NS
Slaley 29 April-2 August 1993	Microlepidoptera	Height*	0.137	0.088	1.72	3.15	0.48	8	NS
Greenlaw June and September 1992	Microlepidoptera	Height	0.233	0.051	-2.28	1.26	0.73	18	<0.001
Langholm June and September 1992	Microlepidoptera	Height*	0.222	0.046	-1.35	1.27	0.75	18	<0.001

Table 6.2. Data for the regression of microlepidoptera larvae density against *Calluna* height at a series of sites and time periods. Microlepidoptera is the total number of microlepidoptera larvae recorded by sweepnet sampling during the time period. An asterisk indicates that *Calluna* height was not the first vegetation character selected as an independent variable by a stepwise multiple regression program.

Site and time period	Dependent variable	Independent variable	Regression coefficient (B)	SE of B	Constant	SE of constant	r	df	P
Waskerley 4 June-7 July 1992	Geometridae	Height	3.57	1.00	-43.3	27.7	0.80	7	<0.01
Waskerley 16 July-5 November 1992	Geometridae	Height	4.47	1.59	-13.5	42.3	0.71	8	<0.05
Waskerley 29 April-2 August 1993	Geometridae	Height*	4.53	2.20	-52.9	64.4	0.59	8	NS
Slaley 16 July-5 November 1992	Geometridae	Height	13.6	0.798	-85.0	28.1	0.99	8	<0.001
Slaley 29 April-2 August 1993	Geometridae	Height*	1.36	0.472	3.20	16.8	0.71	8	<0.05
Greenlaw June and September 1992	Geometridae	Height*	1.60	0.354	-11.8	8.67	0.73	18	<0.001
Langholm June and September 1992	Geometridae	Height	0.992	0.144	-7.99	4.02	0.85	18	<0.001

Table 6.3. Data for the regression of geometrid larvae density against *Calluna* height at a series of sites and time periods. Geometridae is the total number of geometrid larvae recorded by sweepnet sampling during the time period. An asterisk indicates that *Calluna* height was not the first vegetation character selected as an independent variable by a stepwise multiple regression program.

Site and time period	Dependent variable	Independent variable	Regression coefficient (B)	SE of B	Constant	SE of constant	r	df	P
Waskerley 4 June-7 July 1992	Noctuidae	Few noctuid larvae found in spring sampling period.							
Waskerley 16 July-5 November 1992	Noctuidae	Height*	0.892	0.308	-6.19	8.19	0.72	8	<0.02
Waskerley 29 April-2 August 1993	Noctuidae	Height*	0.022	0.025	0.313	0.736	0.29	8	NS
Slaley 16 July-5 November 1992	Noctuidae	Height	1.84	0.249	-4.53	8.77	0.93	8	<0.001
Slaley 29 April-2 August 1993	Noctuidae	Height*	0.255	0.096	0.250	3.41	0.69	8	<0.05
Greenlaw June and September 1992	Noctuidae	Height	0.410	0.125	-4.06	3.07	0.61	18	<0.01
Langholm June and September 1992	Noctuidae	Height	0.406	0.071	-3.43	1.99	0.80	18	<0.001

Table 6.4. Data for the regression of noctuid larvae density against *Calluna* height at a series of sites and time periods. Noctuidae is the total number of noctuid larvae recorded by sweepnet sampling during the time period. An asterisk indicates that *Calluna* height was not the first vegetation character selected as an independent variable by a stepwise multiple regression program.

Site and time period	Dependent variable	Independent variable	Regression coefficient (B)	SE of B	Constant	SE of constant	r	df	P
Waskerley 4 June-7 July 1992	*Eulithis* species	Height	1.85	0.709	-25.4	19.6	0.70	7	<0.05
	Hydriomena furcata	Height*	1.19	0.530	-14.5	14.7	0.65	7	NS
Waskerley 16 July-5 November 1992	*Ematurga atomaria*	Height	0.639	0.251	-8.43	6.68	0.67	8	<0.05
	Eupithecia nanata	Height	3.76	1.40	4.05	37.2	0.69	8	<0.05
Waskerley 29 April-2 August 1993	*Ematurga atomaria*	Height	0.289	0.082	-2.92	2.39	0.78	8	<0.01
	Eulithis species	Height*	0.643	0.338	-5.62	9.92	0.56	8	NS
Slaley 16 July-5 November 1992	*Ematurga atomaria*	Height*	0.427	0.105	-3.27	3.68	0.82	8	<0.01
	Eupithecia goossensiata	Height	9.18	0.606	-90.3	21.3	0.98	8	<0.001
	Eupithecia nanata	Height*	2.22	0.404	11.1	14.2	0.89	8	<0.001

Table 6.5. Data for the regression of the density of individual species of geometrid larvae against *Calluna* height at a series of sites and time periods. The dependent variable is the total number of larvae from of the species that were recorded by sweepnet sampling during the time period. An asterisk indicates that *Calluna* height was not the first vegetation character selected as an independent variable by a stepwise multiple regression program. **(Continued overleaf).**

Site and time period	Dependent variable	Independent variable	Regression coefficient (B)	SE of B	Constant	SE of constant	r	df	P
Slaley 29 April-2 August 1993	*Ematurga atomaria*	Height*	0.396	0.194	3.16	6.91	0.59	8	NS
	Eulithis species	Height*	0.500	0.223	5.16	7.96	0.62	8	NS
	Hydriomena furcata	Height*	0.337	0.110	-5.51	3.92	0.74	8	<0.02
Greenlaw June and September 1992	*Eulithis* species	Height	0.093	0.042	-0.580	1.02	0.47	18	<0.05
	Eupithecia goossensiata	Height*	0.370	0.103	-3.40	2.53	0.65	18	<0.01
	Eupithecia nanata	Height*	1.09	0.262	-7.30	6.41	0.70	18	<0.001
Langholm June and September 1992	*Ematurga atomaria*	Height	-0.073	0.028	3.23	0.79	0.52	18	<0.02
	Eulithis species	Height	0.243	0.062	-2.53	1.72	0.68	18	<0.01
	Eupithecia nanata	Height	7.49	0.101	-7.97	2.80	0.87	18	<0.001

Table 6.5. (continued from previous page)

Site and time period	Dependent variable	Independent variable	Regression coefficient (B)	SE of B	Constant	SE of constant	r	df	P
Waskerley 4 June-7 July 1992		Few noctuid larvae of any one species found in this sampling period							
Waskerley 16 July-5 November 1992	*Lycophotia porphyrea*	Height*	0.822	0.149	-4.90	5.25	0.89	8	<0.001
Waskerley 29 April-2 August 1993		Few noctuid larvae of any one species found in this sampling period							
Slaley	*Anarta myrtilli*	Height	0.924	0.217	1.63	7.63	0.83	8	<0.01
16 July-5 November 1992	*Lycophotia porphyrea*	Height*	0.865	0.291	-6.51	7.74	0.73	8	<0.02
Slaley 29 April-2 August 1993	*Xestia agathina*	Height*	0.172	0.069	-2.04	2.46	0.66	8	<0.05
Greenlaw June and September 1992	*Lycophotia porphyrea*	Height	0.388	0.116	-3.87	2.85	0.62	18	<0.01
Langholm	*Lycophotia porphyrea*	Height	0.364	0.055	-3.31	1.53	0.84	18	<0.001
June and September 1992	**Other families**								
	Pavonia pavonia	Height	0.185	0.062	-1.13	1.72	0.58	18	<0.01

Table 6.6. Data for the regression of the density of individual species of noctuid larvae against *Calluna* height at a series of sites and time periods. The dependent variable is the total number of larvae of a species that were recorded by sweepnet sampling during the time period. An asterisk indicates that *Calluna* height was not the first vegetation character selected as an independent variable by a stepwise multiple regression program.

Site and time period	Dependent variable	Independent variable	Regression coefficient (B)	SE of B	Constant	SE of constant	r	df	P
Waskerley	Microlepidoptera	No variable	fulfilled	stepwise	criteria				
4 June-7 July 1992	*Hydriomena furcata*	Age	1.77	0.653	-9.60	10.54	0.72	7	<0.05
Waskerley	Microlepidoptera	*Calluna* cover	0.223	0.079	-8.97	6.97	0.71	8	<0.05
16 July-5 November	Noctuids	*Calluna* cover	0.471	0.148	-24.3	13.0	0.75	8	<0.02
1992	*Lycophotia porphyrea*	*Calluna* cover	0.445	0.144	-23.1	12.6	0.74	8	<0.02
Waskerley	Macrolepidoptera	No variable	fulfilled	stepwise	criteria				
29 April-2 August	Microlepidoptera	No variable	fulfilled	stepwise	criteria				
1993	Geometrids	No variable	fulfilled	stepwise	criteria				
	Noctuids	No variable	fulfilled	stepwise	criteria				
	Eulithis species	No variable	fulfilled	stepwise	criteria				
Slaley	Microlepidoptera	Age	6.20	1.08	-6.42	10.3	0.91	7	<0.001
16 July-5 November	*Ematurga atomaria*	Age	1.05	0.240	-0.091	2.80	0.84	8	<0.01
1992	*Eupithecia nanata*	Flower density	19.4	3.36	-9.86	16.9	0.90	8	<0.001
	Lycophotia porphyrea	*Calluna* cover	1.33	0.194	-103	18.2	0.92	8	<0.001

Table 6.7. Data for the regression of the density of Lepidoptera larvae against different vegetation characters. For these species a stepwise multiple regression program selected a vegetation character other than *Calluna* height as the independent variable. The dependent variable is the total number of larvae collected by sweepnet sampling during each time period. **(Continued overleaf).**

Site and time period	Dependent variable	Independent variable	Regression coefficient (B)	SE of B	Constant	SE of constant	r	df	P
Slaley									
29 April-2 August 1993	Macrolepidoptera	Green shoot density	4.73	0.754	-31.1	14.7	0.92	7	<0.001
	Microlepidoptera	Green shoot density	0.587	0.106	-4.17	2.06	0.90	7	<0.001
	Geometrids	Green shoot density	4.08	0.759	-29.4	14.8	0.90	7	<0.01
	Noctuids	Height^2	0.004	0.001	2.95	1.94	0.79	8	<0.01
	Hydriomena furcata	Age	0.954	0.173	-4.96	2.16	0.89	8	<0.001
	Ematurga atomaria	Green shoot density	1.33	0.353	-8.88	6.87	0.82	7	<0.01
	Eulithis species	*Calluna* cover	1.038	0.227	-75.3	21.3	0.85	8	<0.01
	Xestia agathina	No variable	fulfilled	stepwise	criteria				
Greenlaw									
June and September 1992	Geometrids	Flower density	9.94	2.06	-7.05	7.28	0.75	18	<0.001
	Eupithecia nanata	Flower density	6.97	1.48	-4.68	5.24	0.74	18	<0.001
	Eupithecia goossensiata	Flower density	2.36	0.593	-2.51	2.10	0.68	18	<0.001
Langholm									
June and September 1992	Microlepidoptera	1. Height	0.274	0.043	3.10	1.76	0.94	2, 13	<0.001
		2. Green shoot density	-0.346	0.108			-0.47		

Table 6.7. (Continued from previous page)

Site and time period	Regression coefficient (B)	SE of B	Estimated no. of larvae in 20 sweepnet samples of 30cm tall *Calluna* (y_{30})	B/y_{30}	SE/y_{30}
Waskerley 4 June-7 July 1992	3.69	1.02	65.8	5.6%	1.5%
Waskerley 16 July-5 November 1992	5.53	1.86	144	3.8%	1.3%
Waskerley 29 April-2 August 1993*	No significant relationship between density of macrolepidoptera larvae and *Calluna* height				
Slaley 16 July-5 November 1992	13.68	0.798	325	4.2%	0.2%
Slaley 29 April-2 August 1993*	1.73	0.468	54.0	3.2%	0.9%
Greenlaw June and September 1992	2.06	0.425	45.8	4.5%	0.9%
Langholm June and September 1992	1.62	0.173	48.6	3.3%	0.4%

Table 6.8. Conversion of the regression coefficients given in Table 6.1 to units of proportional change in density of macrolepidoptera larvae per cm increase in *Calluna* height. The number of macrolepidoptera larvae found in sweepnet samples of 30cm tall *Calluna* was estimated from regression data in Table 6.1 and is referred to as y_{30}. An asterisk indicates that *Calluna* height was not the vegetation character selected by a stepwise multiple regression program as the independent variable.

Site and time period	Regression coefficient (B)	SE of B	Estimated no. of larvae in 20 sweepnet samples of 30cm tall *Calluna* (y_{30})	B/y_{30}	SE/y_{30}
Waskerley 4 June-7 July 1992	3.57	0.998	63.8	5.6%	1.6%
Waskerley 16 July-5 November 1992	4.47	1.59	121	3.7%	1.3%
Waskerley 29 April-2 August 1993*	No significant relationship between density of geometrid larvae and *Calluna* height				
Slaley 16 July-5 November 1992	13.7	0.798	325	4.2%	0.2%
Slaley 29 April-2 August 1993*	1.36	0.472	43.9	3.1%	1.1%
Greenlaw June and September 1992*	1.60	0.354	36.3	4.4%	1.0%
Langholm June and September 1992	0.992	0.144	21.8	4.6%	0.7%

Table 6.9. Conversion of the regression coefficients given in Table 6.3 to units of proportional change in density of geometrid larvae per cm increase in *Calluna* height. The number of geometrid larvae found in sweepnet samples of 30cm tall *Calluna* was estimated from regression data in Table 6.3 and is referred to as y_{30}. An asterisk indicates that *Calluna* height was not the vegetation character selected by a stepwise multiple regression program as the independent variable.

Site and time period	Regression coefficient (B)	SE of B	Estimated no. of larvae in 20 sweepnet samples of 30cm tall *Calluna* (y_{30})	B/y_{30}	SE/y_{30}
Waskerley 4 June-7 July 1992	–	–	–	–	–
Waskerley 16 July-5 November 1992*	0.892	0.308	20.6	4.3%	1.5%
Waskerley 29 April-2 August 1993*	No significant relationship between density of noctuid larvae and *Calluna* height				
Slaley 16 July-5 November 1992	1.84	0.249	50.5	3.6%	0.5%
Slaley 29 April-2 August 1993*	0.255	0.096	7.9	3.2%	1.2%
Greenlaw June and September 1992	0.410	0.125	8.2	5.0%	1.5%
Langholm June and September 1992	0.406	0.071	8.8	4.6%	0.8%

Table 6.10. Conversion of the regression coefficients given in Table 6.4 to units of proportional change in density of noctuid larvae per cm increase in *Calluna* height. The number of noctuid larvae found in sweepnet samples of 30cm tall *Calluna* was estimated from regression data in Table 6.4 and is referred to as y_{30}. An asterisk indicates that *Calluna* height was not the vegetation character selected by a stepwise multiple regression program as the independent variable.

Site and time period	Geometrid species	Regression coefficient (B)	SE of B	Estimated no. of larvae in 20 sweepnet samples of 30cm tall *Calluna* (y_{30})	B/y_{30}	SE/y_{30}
Waskerley 4 June- 7 July 1992	*Eulithis* species *Hydriomena furcata**	1.85 1.19	0.709 0.530	30.3 21.1	6.1% 5.6%	2.3% 2.5%
Waskerley 16 July-5 November 1992	*Ematurga atomaria* *Eupithecia nanata*	0.639 3.76	0.251 1.40	10.7 109	6.0% 3.5%	2.3% 1.3%
Waskerley 29 April-2 August 1993	*Ematurga atomaria* *Eulithis* species	0.289 0.643	0.082 0.338	5.8 13.7	5.0% 4.7%	1.4% 2.5%
Slaley 16 July-5 November 1992	*Ematurga atomaria** *Eupithecia nanata** *Eupithecia goossensiata**	0.427 2.22 9.18	0.105 0.404 0.606	9.5 77.7 185	4.5% 2.9% 5.0%	1.1% 0.5% 0.3%
Slaley 29 April-2 August 1993	*Hydriomena furcata**	0.337	0.110	4.6	7.3%	2.4%
Greenlaw June and September 1992	*Eulithis species* *Eupithecia nanata** *Eupithecia goossensiata*	0.093 1.09 0.370	0.042 0.262 0.103	2.2 25.5 7.7	4.2% 4.3% 4.8%	1.9% 1.0% 0.3%
Langholm June and September 1992	*Eulithis* species *Ematurga atomaria* *Eupithecia nanata*	0.243 -0.073 7.49	0.062 0.028 0.101	4.8 1.0 217	5.1% -7.3% 3.5%	1.3% 2.8% 0.05%

Table 6.11. Conversion of the regression coefficients in Table 6.5 to units of proportional change in the density of individual species of geometrid larvae per cm increase in *Calluna* height. The number of larvae in 30cm tall *Calluna* was estimated from regression data in Table 6.5 and is referred to as y_{30}. An asterisk in the species column indicates that *Calluna* height was not the vegetation variable selected by the stepwise multiple regression program.

Site and time period	Noctuid species	Regression coefficient (B)	SE of B	Estimated no. of larvae in 20 sweepnet samples of 30cm tall Calluna (y_{30})	B/y_{30}	SE/y_{30}
Waskerley 4 June- 7 July 1992	–	–	–	–	–	–
Waskerley 16 July-5 November 1992	*Lycophotia porphyrea* *	0.822	0.149	19.8	4.2%	0.8%
Waskerley 29 April-2 August 1993	–	–	–	–	–	–
Slaley 16 July-5 November 1992	*Anarta myrtilli* *Lycophotia porphyrea* *	0.924 0.865	0.217 0.291	29.4 19.4	3.1% 4.4%	0.7% 1.5%
Slaley 29 April-2 August 1993	*Xestia agathina* *	0.172	0.069	3.1	5.5%	2.2%
Greenlaw June and September 1992	*Lycophotia porphyrea* *	0.388	0.116	7.8	5.0%	0.3%
Langholm June and September 1992	*Lycophotia porphyrea* **Other** *Pavonia pavonia*	0.364 0.185	0.055 0.062	7.6 4.4	4.8% 4.2%	0.7% 1.4%

Table 6.12. Conversion of the regression coefficients in Table 6.6 to units of proportional change in the density of individual species of noctuid larvae per cm increase in *Calluna* height. The number of larvae in 30cm tall *Calluna* was estimated from regression data in Table 6.6 and is referred to as y_{30}. An asterisk in the species column indicates that *Calluna* height was not the vegetation variable selected by the stepwise multiple regression program.

Site and time period	Age	Green shoot density	Flower shoot density	*Calluna* cover
Waskerley 4 June-7 July 1992	r=0.82 df=7 P<0.01	r=0.79 df=7 P<0.02	-	r=0.73 df=7 P<0.05
Waskerley 16 July-5 November 1992	r=0.86 df=8 P<0.002	r=0.83 df=8 P<0.005	r=0.80 df=8 P<0.01	r=0.79 df=8 P<0.01
Waskerley 29 April-2 August 1993	r=0.92 df=8 P<0.001	r=0.77 df=8 P<0.01	-	r=0.77 df=8 P<0.01
Slaley 16 July-5 November 1992	r=0.89 df=7 P<0.001	r=0.93 df=7 P<0.001	r=0.86 df=7 P<0.005	r=0.90 df=7 P<0.002
Slaley 29 April-2 August 1993	r=0.91 df=7 P<0.001	r=0.89 df=7 P<0.002	r=0.79 df=7 P<0.02	r= 0.85 df=7 P<0.005
Greenlaw June and September 1992	-	r=0.69 df=18 P<0.001	r= 0.68 df=18 P<0.001	r=0.59 df=18 P<0.01
Langholm June and September 1992	-	r=0.65 df=14 P<0.01	r=0.65 df=14 P<0.01	r=0.56 df=14 P<0.05

Table 6.13. A summary of the intercorrelations between *Calluna* height and other vegetation variables.

	Sweepnet sampling	Combined jarring and Berlese-Tullgren method
Mean no. larvae per sample in short stands	1.33	6.24
Mean no. larvae per sample in long stands	2.7	16.9
Ratio of larvae in paired short stands: long stands	1 : 2.1	1 : 2.7
Mean rank of short stands	6.8	6.4
Mean rank of long stands	12.2	12.6
N	9	9
Z corrected for ties	2.17	2.25
P	< 0.05	< 0.02

Table 6.14. The results of Mann-Whitney U tests to compare the densities of macrolepidoptera larvae in a series of paired short and tall *Calluna* stands that were sampled by sweepnetting and combined jarring and Berlese-Tullgren extraction on the same day. The units of the sweepnet sampling method were larvae per sample of ten sweepnet strokes. The units of the combined jarring and Berlese-Tullgren extraction method were larvae per m^2. The mean heights of the short and long stands ± 2SE were 15 ± 6cm and 32 ± 4cm respectively.

It was difficult for the stepwise program to select between *Calluna* height and other vegetation characteristics because there were significant positive correlations between many of the *Calluna* variables. Table 6.13 lists the intercorrelations between *Calluna* height and other vegetation variables. At almost all sites and time periods, the correlations between *Calluna* height and the other vegetation variables plant age, green shoot density, flower density and cover were significant and positive.

In order to determine whether the relationship between larvae density and *Calluna* height was caused by the sweepnet sampling method, data provided by another technique, the combined jarring and Berlese-Tullgren extraction method (section 4.3.1) were examined. Nine pairs of adjacent *Calluna* stands comprising one short stand and one tall stand were sampled by both techniques on the same days in 1991 and 1992 (section 4.4.1). The difference in height between pairs of *Calluna* stands was not fixed. The densities of macrolepidoptera larvae in the long and short stands were compared using the Mann-Whitney U Test and each set of data. Both methods were expected to give similar results unless one technique was affected by other factors.

Table 6.14 shows the results of the Mann-Whitney U test that was used to compare differences in the density of macrolepidoptera larvae in the paired stands, as assessed by the sweepnet technique and the combined method of beating followed by extraction in Berlese-Tullgren funnels. Both techniques recorded significantly higher densities of macrolepidoptera larvae in the taller stands. The average order of the difference was similar for both sampling methods.

6.4 The effect of plant architecture on the diversity of Lepidoptera larvae in *Calluna*

6.4.1 Selection of an appropriate measure of heterogeneity

Figures 6.1a-b illustrate the importance of selecting the correct measure of Lepidoptera heterogeneity. Figure 6.1a shows the relationship between *Calluna* height and species richness, the number of species of macrolepidoptera larvae that were found at Langholm (June & September 1992). Figure 6.1b illustrates the relationship between species richness and the number of individual larvae found in each stand. Both regressions are highly significant (Figure 6.1a $r=0.70$, $df=18$, $P<0.001$; Figure 6.1b $r=0.71$, $df=18$, $P<0.001$). However since there is also a highly significant linear relationship between *Calluna* height and the density of macrolepidoptera larvae ($r=0.91$, $df=18$, $P<0.001$, Table 6.1), it is not possible to determine whether species

Figure 6.1a

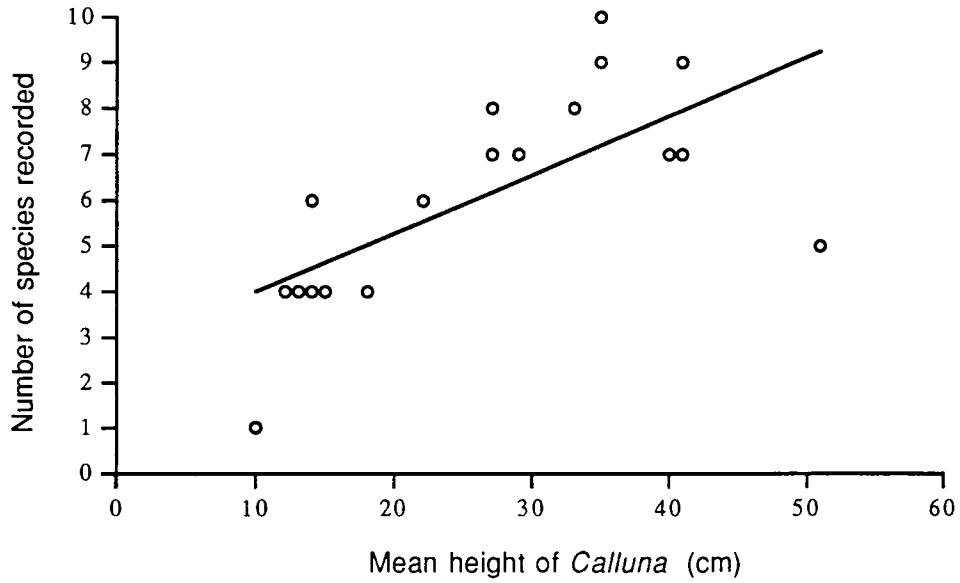
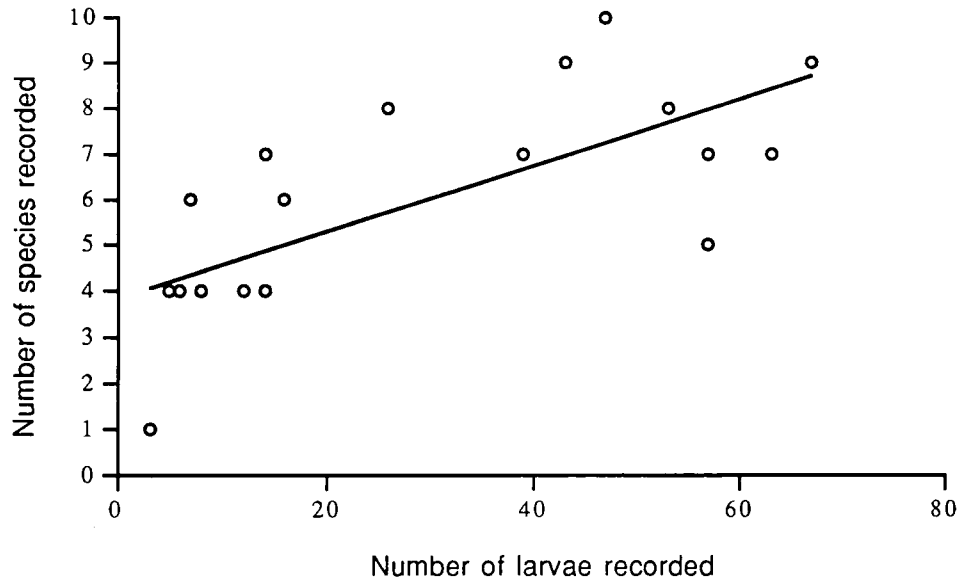


Figure 6.1b



Figures 6.1a and 6.1b. The relationships between *Calluna* height, the number of macrolepidoptera species recorded and the number of macrolepidoptera larvae recorded at Langholm (combined June and September 1992 data). Figure 6.1a shows the relationship between *Calluna* height and the number of species recorded. Regression analysis gives $Y = 0.128(\pm 0.031)X + 2.68(\pm 0.858)$, r=0.70, df=18, P<0.001. Figure 6.1b shows the relationship between the number of macrolepidoptera larvae and the number of species recorded at each stand. Regression analysis gives $Y = 0.073(\pm 0.017)X + 3.84(\pm 0.610)$, r=0.71, df=18, P<0.001. There is a possibility that these data are better described by a curve but the improvement in the variance explained does not increase significantly.

richness increases because of increased *Calluna* height, or because more larvae are found in taller stands. Species richness is an unsuitable measure of heterogeneity, because its value is inflated by any procedure that increases the number of individuals found, since in this situation there is a greater probability of encountering rare species (Lewis & Taylor 1974; Kempton 1979; Usher 1983; Krebs 1985; Magurran 1988).

Measures of diversity consider both species richness and the mixing of individuals in the community. Community organisation may be examined using graphical models of species abundance patterns, or diversity indices that summarise this information in a single figure (Tokeshi 1993). Since this study aimed to examine community heterogeneity in different heights of *Calluna*, at several sites and time periods, a diversity index was the most appropriate analysis tool.

A variety of diversity measures exist (Southwood 1978; Usher 1983; Magurran 1988; Tokeshi 1993) and are derived from statistical or biological models of species abundance patterns, probability hypotheses or information theory (Magurran 1988; Krebs 1989; Tokeshi 1993). Many indices are affected differently by sample size, have different powers of discrimination between similar sites, place different emphases on the species richness or evenness components of diversity and vary in precision, bias, ease of calculation and interpretability (Usher 1983; Giavelli *et al.* 1986; Magurran 1988; Tokeshi 1993).

6.4.1.1 Method

Two widely used diversity indices, Simpson's index (Simpson 1949) and α of the logarithmic series, were applied to one set of data (Slaley 16 July-5 November 1992) in an exploratory manner.

a) Simpson's index

Simpson's index is a non-parametric probability measure calculated from the formula:

$$D = \sum p_i^2$$

where D = Simpson's index

p_i = Proportion of species i in the community (Krebs 1989)

The index was used in the $1/D$ form (Williams 1964; MacArthur 1972), which is not a probability (Usher 1983) and varies on a scale of 1 (lowest diversity) to s the number of species in the sample (Krebs 1989).

b) α of the logarithmic series (Fisher *et al.* 1943)

This measure uses the number of species and the number of individuals in the sample and is calculated from:

$$S = \alpha \log_e (1 + \frac{N}{\alpha})$$

where S = Number of species in the sample
N = Number of individuals in the sample
α = Index of diversity

Random number tables were used to create a subset of the Slaley data, with equal number of individuals in each stand. Individuals in the original data were numbered and 46 random numbers (corresponding to the smallest number of individuals collected from a stand in the original data) were drawn to select the new subsample. Five replicate subsamples were created in this way for each stand. The average number of species in a sample of 46 individuals was calculated from the replicate subsamples. These data were regressed against *Calluna* height.

Values of Simpson's $1/D$ and α were calculated for both the original data and the average values of the replicate subsets. Index values were plotted against *Calluna* height. Values of each index for the original and derived data were compared using paired t-tests.

The preferred index was one that showed a relationship with *Calluna* height that was like a plot of the average number of species in 46 individuals against *Calluna* height, and which exhibited little difference between the index values calculated from the original and derived data.

6.4.1.2 Results

Figure 6.2 shows the relationship between *Calluna* height and the average number of species collected in a sample of 46 larvae. The average number of species found decreased in taller stands but this trend was not significant ($r = -0.46$, $df=8$, NS).

Figures 6.3a and 6.3b show the relationship between *Calluna* height and Simpson's $1/D$ and α respectively using both the original and derived data. Figure 6.3a shows two significant regressions between *Calluna* height and Simpson's $1/D$. Values of this index were not significantly different when calculated from the original and derived data ($t=1.23$, $df=8$, NS). Values of α were not significantly related to *Calluna* height (Figure 6.3b). However, values of α that were calculated from the derived data were

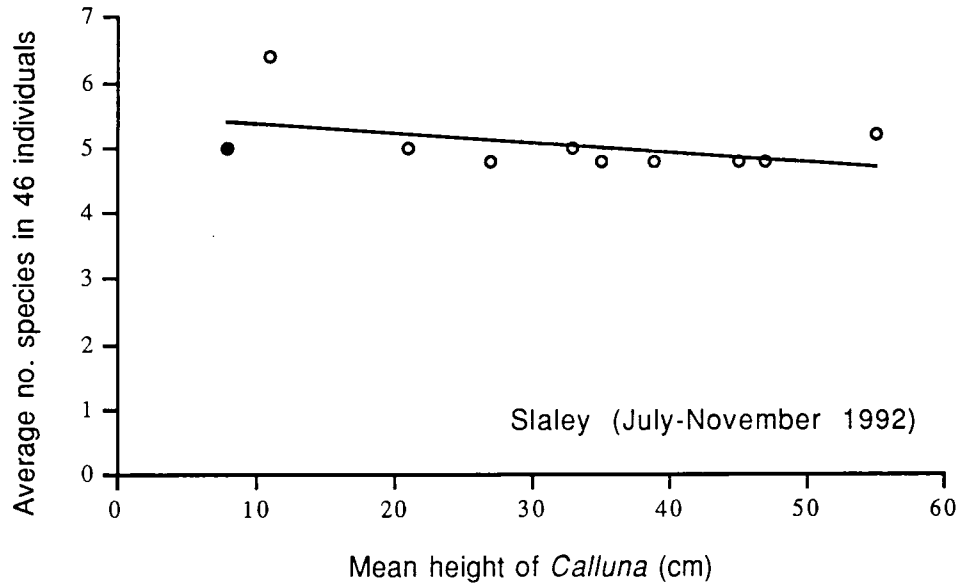


Figure 6.2. The relationship between *Calluna* height and the average number of species found in a sample of 46 larvae. Samples of 46 larvae were generated at random from original data. The dark point is the sample in the original data that comprised 46 individuals. All other points are average values calculated from five replicate random subsets of 46 larvae. The equation for the regression line is Y = -0.015(±0.010)X +5.53(±0.35), r=0.46, df=8 and so there is no significant relationship between *Calluna* height and species richness.

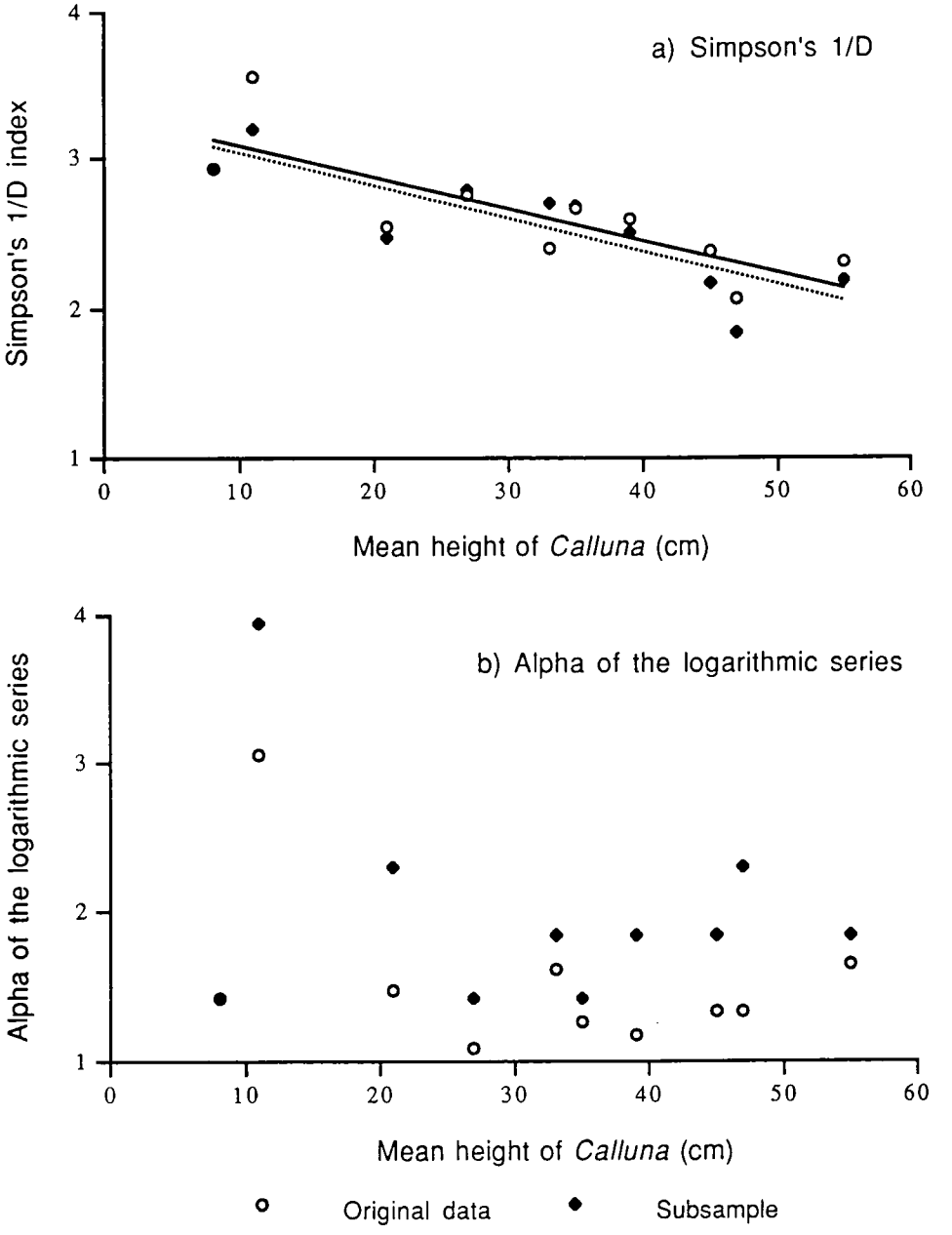


Figure 6.3a-b. The relationship between *Calluna* height and a) Simpson's 1/D and b) α of the logarithmic series at Slaley (16 July-5 November 1992). Indices were calculated for the original data and for a derived subsample of 46 larvae. Index values for the subsample were based on an average of five random replicates. The dark circle represents the sample of 46 larvae in the original data and has been included in both regressions. Regressions for the original data are shown by a solid line. Regression data are for a) original data Y = -0.021(± 0.006)X +3.31(± 0.197, r=-0.80, df=8, P<0.01; derived data Y = -0.022(± 0.005)X +3.26(± 0.18), r=-0.84, df=8, P<0.01 b) original data r=0.42, df=8, NS; derived data r=0.30, df=8, NS. Derived values of α in Figure 6.3b are higher than values calculated from the original data.

significantly higher than values calculated from the original data ($t=5.00$, $df=8$, $P<0.01$).

Simpson's $1/D$ was chosen to examine data at the remaining sites and time periods, because index values were not changed by differences in sample size.

6.4.2 Diversity of Lepidoptera larvae in different heights of *Calluna* according to Simpson's 1/D index

6.4.2.1 Methods

The diversity at other sites and sampling periods was calculated using Simpson's $1/D$. Values of Simpson's $1/D$ were regressed against *Calluna* height. Stands with fewer than ten larvae were combined with other stands of similar height before calculation of the index. This index value was plotted against an average height of the combined stands.

Results 6.4.2.2

Table 6.15 gives values of the correlations between *Calluna* height and the diversity index Simpson's $1/D$. The diversity of Lepidoptera larvae was related to *Calluna* height at some sites but no consistent trend occurred between different study areas. Of those sites and time periods at which the relationship between *Calluna* height and diversity was significant, regressions at two sites Greenlaw (1992) and Waskerley (16 July-5 November 1992) were positive. At Slaley (16 July-5 November 1992) there was a significant negative relationship between *Calluna* height and Simpson's $1/D$.

Even at the same site, trends in diversity were not the same in different sampling periods. At Waskerley, the significant positive relationship between *Calluna* height and Simpson's 1/D during the period 16 July-5 November 1992 was not observed at other times when the site was sampled (4 June-7 July 1992, 29 April-2 August 1993).

Few sites provided information about the diversity of larvae in stands that were taller than 40cm. Data for the Langholm site (June and September 1992, Figure 6.4) appear non-linear, diversity increasing from a low value in the shorter stands and then remaining constant in the medium *Calluna* heights. A significant polynomial equation to describe this relationship could not be found. Suggestion of a decrease in diversity at heights of 40cm and above cannot be supported without further data.

Site and time period	r	df	P
Waskerley 4 June -7 July 1992 *	0.414	6	NS
Waskerley 16 July-5 November 1992	0.830	8	<0.01
Waskerley 29 April-2 August 1993 *	-0.079	8	NS
Slaley 16 July-5 November 1992	-0.840	8	<0.01
Slaley 2 April-2 August 1993	0.499	8	NS
Greenlaw (June & September 1992)	0.597	17	<0.01
Langholm (June & September 1992)	Non-linear see Figure 6.4		

Table 6.15. Linear correlation data for the relationships between *Calluna* height and the diversity of Lepidoptera larvae that were recorded by sweepnet sampling at various sites and time periods. Diversity was measured using Simpson's $1/D$ index. An asterisk indicates that an outlier was removed from the data (see text).

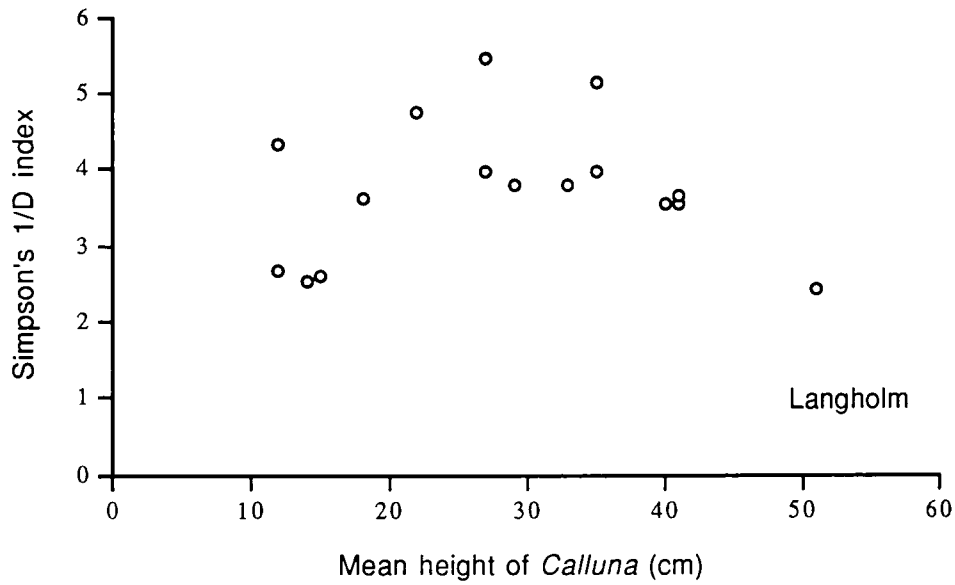


Figure 6.4. The relationship between *Calluna* height and the diversity of macrolepidoptera larvae at Langholm (June and September 1992). Diversity was measured using Simpson's 1/*D*. The relationship appears non-linear but a polynomial equation could not be found to describe the distribution of data.

6.5 Variation in the composition of the Lepidoptera larvae community in different heights of *Calluna*

Since diversity comprises both species richness and the evenness of the species distribution, change in diversity across a *Calluna* height gradient may be generated in two ways. Both the presence of additional species at one end of the height gradient and change in the dominance of species could cause this effect.

6.5.1 Methods

6.5.1.1 Analyses using similarity indices

Data were analysed using two similarity indices, measures which assessed the degree of similarity in the faunal composition between two samples. The indices used were the Sorensen similarity coefficient (Sorensen 1948) and the percentage similarity measure (Renkonen 1938), both described in Chapter Five (section 5.4.1). It was predicted that if community composition was related to *Calluna* height, sites with similar heights would have similar faunas. A negative relationship would be expected between the height difference between *Calluna* stands and the value of the similarity indices.

Values of Sorensen's coefficient were calculated at all sites and time periods, but because the percentage similarity index was calculated by hand, matrices were prepared at a selection of study areas. The sites chosen were those which showed the widest range of *Calluna* heights.

6.5.1.2 Analyses using chi-square contingency tests

Chi-square contingency tests were used to determine whether the proportions of different Lepidoptera classes, or macrolepidoptera species varied in different heights of *Calluna*. Data were divided into three height categories: *Calluna* stands less than 15cm tall, stands with heights in the 16-30cm range and stands taller than 30cm. Contingency tables considered changes in the proportions of a) macrolepidoptera and microlepidoptera and b) common macrolepidoptera species in the different height zones. Stand WK35 was excluded from the calculations at Waskerley (4 June-7 July 1992, 29 April-2 August 1993) because much larger numbers of a particular species of microlepidoptera larva were found there than at any other stand. Combinations of species were examined independently of other species to identify the species that made the largest changes.

6.5.2 Results

6.5.2.1 Analyses using similarity indices

Table 6.16 shows regression data for plots of the difference in height between pairs of *Calluna* stands and the corresponding values of Sorensen's similarity coefficient. There were significant negative relationships between these variables at Waskerley (16 July-5 November 1992 r=-0.490, df=43, P<0.001), Slaley 29 April-2 August 1993 (r=-0.411, df=43, P<0.01) and Langholm (r=-0.379, df=118, P<0.001). Negative trends at two other sites (Waskerley 29 April-2 August 1993 and Greenlaw 1992) reached only the 0.10 probability level. The slopes of all regression lines were shallow and no greater than $-0.010X$ (± 0.003).

Table 6.17 shows regression data for plots of the differences in height between pairs of *Calluna* stands and the corresponding values of the percentage similarity index. Figures 6.5a and 6.5b show graphs of these relationships at Waskerley and Slaley in the period 16 July-5 November 1992). Gradients of the regression line were shallow but significantly negative at all sites and time periods examined. Attention is drawn to Figure 6.5b. Although the trend was negative, the validity of this regression is questioned because the distribution of the data points is bimodal. This was caused by the greater dissimilarity of the fauna at the two shortest stands, SL1 and SL5 from all other sites. Almost all the points in the lower group were pairs of stands that included either SL1 or SL5. The composition of the macrolepidoptera fauna at stands SL1 and SL5 was very similar (percentage similarity index PS= 85%). There was no evidence of a bimodal distribution of data at the same site in the period 29 April-2 August 1993.

The range of percentage similarity index values was different at different sites and time periods. The similarity of stands at Waskerley (16 July-5 November 1992) ranged between 71%-97% and was high compared with the ranges of values at Langholm and Slaley. At these sites the similarity between some pairs of stands was as low as 40%.

6.5.2.2 Analyses using chi-square contingency tests

Table 6.18 shows the proportions of macrolepidoptera and microlepidoptera larvae in different heights of *Calluna*. Macrolepidoptera and microlepidoptera larvae occurred in the proportions 87-91% to 9-13% respectively but there were significant differences between the study areas (Chapter Five, section 5.4). At several sites the ratio changed significantly in at least one height class. At Waskerley (16 July-5 November 1992) the proportion of microlepidoptera larvae in the under 15cm height class was significantly larger than expected (15%), causing a highly significant difference in the composition of the fauna in the three height classes (χ^2=10.7, df=2, P<0.01). Results appeared

Site and time period	B	SE of B	Constant	SE of constant	r	df	P
Waskerley 16 July-5 November 1992	-0.010	0.003	0.774	0.040	0.49	43	<0.001
Waskerley 29 April-2 August 1993	-0.004	0.002	0.741	0.030	0.26	43	NS <0.10
Slaley 16 July-5 November 1992	-0.002	0.001	0.737	0.025	0.20	43	NS
Slaley 29 April-2 August 1993	-0.004	0.001	0.820	0.030	0.41	43	<0.01
Greenlaw June & October 1992	-0.004	0.002	0.650	0.025	0.18	103	NS <0.10
Langholm June & October 1992	-0.007	0.001	0.734	0.025	0.38	118	<0.001

Table 6.16. Regression data for the relationships between the difference in height between pairs of *Calluna* stands and the value of Sorensen's similarity coefficient. At Greenlaw and Langholm data from stands with fewer than ten larvae were pooled with other stands of similar height before the calculation of the coefficient.

Site and time period	B	SE of B	Constant	SE of constant	r	df	P
Waskerley 16 July-5 November 1992	-0.346	0.093	91.5	1.22	0.49	43	<0.001
Slaley 16 July-5 November 1992	-1.11	0.166	97.1	3.62	0.72	43	<0.001
Slaley 29 April-2 August 1993	-0.50	0.128	74.7	2.59	0.48	51	<0.001
Langholm June & October 1992	-0.261	0.130	63.2	2.20	0.18	118	<0.05

Table 6.17. Regression data for the relationships between the difference in height between pairs of *Calluna* stands and the value of the percentage similarity index at selected sites and time periods. At Greenlaw and Langholm data for stands with fewer than ten larvae were pooled with other stands of similar height before calculation of the index.

Figure 6.5a

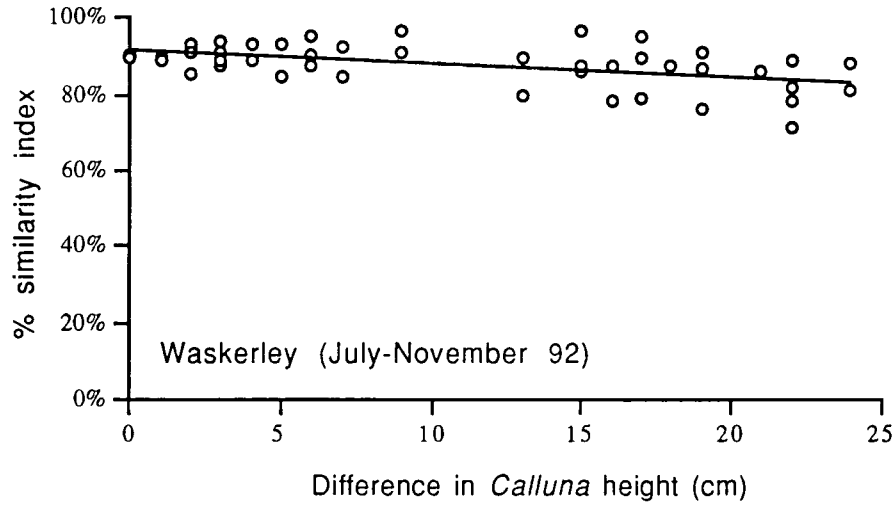
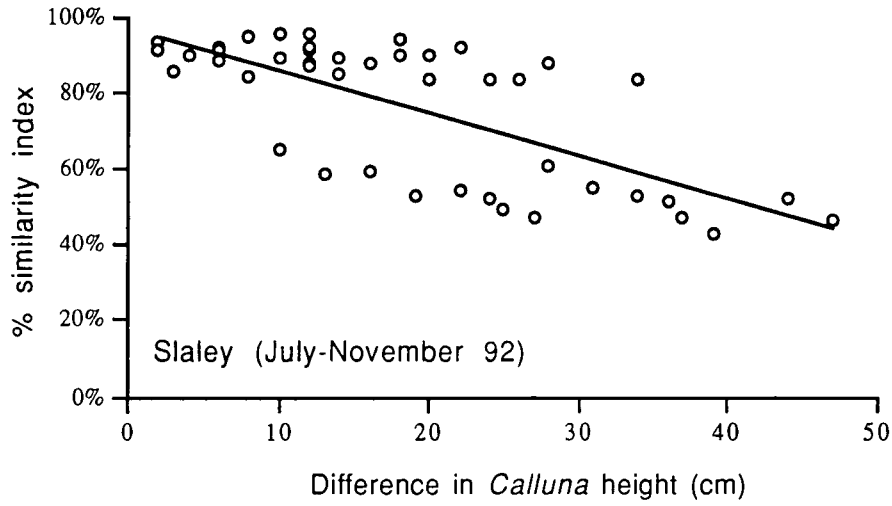


Figure 6.5b



Figures 6.5a and 6.5b. The relationship between the difference in height between pairs of *Calluna* stands and values of the percentage similarity index at a) Waskerley and b) Slaley during the period 16 July-5 November 1992. The scale of the *X*-axis in Figure 6.5a is smaller than in Figure 6.5b because a wider range of *Calluna* heights were available at Slaley. Regression data are for a) $Y = -0.346(\pm 0.093)X + 91.5(\pm 1.22)$, r=0.49, df=43, P<0.001 b) $Y = -1.114(\pm 0.166)X + 97.1(\pm 3.62)$, r=0.72, df=43, P<0.001. The distribution of data points in Figure 6.5b is bimodal.

similar in two other sampling periods (4 June-7 July 1992, 29 April-2 August 1993), but too few larvae were found to meet the condition of the chi-square contingency test that all expected values be equal to or greater than five. At Slaley (16 July-5 November 1992) the proportion of microlepidoptera in the 16-30cm height class was significantly larger than expected at 17% (χ^2=17.5, df=1, P<0.001). All other sites showed similar composition of the Lepidoptera fauna in different height classes.

Tables 6.19-6.22 show the proportions of several common species of macrolepidoptera in different height classes of *Calluna*. The proportions of some species *e.g. Ematurga atomaria* (Waskerley 16 July-5 November 1992, 29 April-2 August 1993; the *Eulithis* species (Waskerley 29 April-2 August 1993; Langholm 1992), *Eupithecia goossensiata* (Slaley 16 July-5 November 1992), *Lycophotia porphyrea* (Waskerley 16 July-5 November 1992; Slaley 16 July-5 November 1992; Greenlaw 1992, Langholm 1992) and *Hydriomena furcata* (Waskerley 29 April-2 August 1993) were larger in the taller stands. The proportions of other species *e.g. Eupithecia nanata* (Waskerley 16 July-5 November 1992, 29 April-2 August 1993, Slaley 16 July-5 November 1992, 29 April-2 August 1993) were highest in the shortest height class and decreased in the taller stands.

Change in the contribution of a common species to the community was more often associated with a shift in the dominance of another common species in certain height classes, than change in the number of rare individuals. For example at Slaley (16 July-5 November 1992), there was a highly significant change in the dominance of the two pug moth species *Eupithecia nanata* and *E. goossensiata* at different *Calluna* heights (χ^2=79.2, df=2, P<0.001, Table 6.20a). If these two species were considered in isolation, the proportion of *E. nanata* decreased from 71% in the less than 15cm height class to 26% in the over 30cm height class with a reciprocal increase in the proportion of *E. goossensiata*.

The behaviour of only a few pairs of species may be compared at different sites because species composition was not the same at the five study areas (Chapter Five, section 5.4). At Waskerley, (16 July-5 November 1993), the proportions of *Ematurga atomaria* and *Lycophotia porphyrea* changed significantly in different height classes. *Ematurga atomaria* increased to a maximum in the tallest heather while *L. porphyrea* decreased to a minimum in the shortest height class (χ^2=16.7, df=2, P<0.001). At Slaley during the same period, *E. atomaria* was dominant in the shortest height class and the largest proportion of *L. porphyrea* occurred in mid-height *Calluna*, although there were not enough individuals to perform a chi-square contingency test. At Langholm (1992) there was a highly significant change in the proportions of the two

Site and time period	Larvae class	*Calluna* height <15cm	*Calluna* height 16-30cm	*Calluna* height >30cm	χ^2	df	P
Waskerley	Macros	63% (22)	87% (112)	90% (298)	20.7	2	<0.001
4 June-7 July 1992	Micros	37% (13)	13% (17)	10% (34)			
Waskerley	Macros	85% (151)	92% (451)	92% (524)	10.7	2	<0.01
16 July-5 November 1992	Micros	15% (27)	8% (37)	8% (43)			
Waskerley	Macros	78% (31)	83% (66)	92% (524)			
29 April-2 August 1993	Micros	22% (9)	17% (14)	8% (43)	-	-	-
Slaley	Macros	87% (123)	83% (444)	90% (2960)	23.7	2	<0.001
16 July-5 November 1992	Micros	13% (18)	17% (92)	10% (332)			
Slaley	Macros	91% (31)	88% (80)	91% (266)	0.79	2	NS
2 April-2 August 1992	Micros	9% (3)	12% (11)	9% (25)			
Greenlaw	Macros	100% (18)	90% (320)	91% (266)			
(June & September 1992)	Micros	0% (0)	10% (34)	9% (25)	-	-	-
Langholm	Macros	84% (69)	87% (136)	88% (360)	0.72	2	NS
(June & September 1992)	Micros	16% (13)	13% (20)	12% (51)			

Table 6.18. The numbers and proportions of macrolepidoptera and microlepidoptera larvae that were found in the total catch in different height classes of *Calluna*. All larvae were caught by sweepnet sampling. An asterisk indicates that one stand (WK35) was excluded from the analysis because of the presence of large numbers of one species of microlepidoptera larva. Figures in parentheses are the numbers of larvae that were found. The value of χ^2 is left blank where the criteria for the test (all expected values equal or greater than five) could not be fulfilled.

Table 6.19a

Species	*Calluna* heights <15cm	*Calluna* heights 16-30cm	*Calluna* heights >30cm	χ^2	df	P
Ematurga atomaria	1% (2)	4% (17)	10% (57)	48.0	6	<0.001
Eupithecia nanata	89% (134)	78% (353)	73% (415)			
Lycophotia porphyrea	9% (13)	15% (68)	13% (71)			
Others	1% (2)	3% (13)	4% (23)			
Ematurga atomaria	13% (2)	20% (17)	45% (57)	16.7	2	<0.001
Lycophotia porphyrea	87% (10)	80% (68)	55% (71)			

Table 6.19b

Species	*Calluna* heights <15cm	*Calluna* heights 16-30cm	*Calluna* heights >30cm	χ^2	df	P
Eulithis spp.	27% (11)	21% (14)	15% (93)	45.8	4	<0.001
Hydriomena furcata	17% (7)	47% (31)	65% (397)			
Others	56% (23)	32% (21)	20% (120)			
Ematurga atomaria	21% (4)	42% (5)	65% (40)	11.6	2	<0.01
Eupithecia nanata	79% (15)	58% (7)	35% (22)			

Tables 6.19a and 6.19b. The numbers and proportions of common macrolepidoptera species that were found in the total catch in different height classes of *Calluna* at Waskerley. All larvae were found by sweepnet sampling a) 16 July-5 November 1992 b) 29 April-2 August 1993. Figures in parentheses are the numbers of larvae that were found. Species were sometimes grouped together *e.g.* "others" to fulfil the criteria of the χ^2 test that all expected values should be equal to or greater than five. Pairs of species that made large changes have been isolated.

Figure 6.20a

Species	*Calluna* heights <15cm	*Calluna* heights 16-30cm	*Calluna* heights >30cm	χ^2	df	P
Eupithecia nanata	43% (53)	29% (129)	22% (639)			
Eupithecia goossensiata	18% (22)	52% (232)	60% (1780)			
Anarta myrtilli	28% (35)	9% (40)	8% (237)	144	6	<0.001
Lycophotia porphyrea	1% (1)	7% (31)	6% (182)			
Others	10% (12)	3% (12)	4% (122)			
Eupithecia nanata	71% (53)	36% (129)	26% (639)	79.2	2	<0.001
Eupithecia goossensiata	29% (22)	64% (232)	74% (1780)			

Figure 6.20b

Species	*Calluna* heights <15cm	*Calluna* heights 16-30cm	*Calluna* heights >30cm	χ^2	df	P
Ematurga atomaria	29% (9)	23% (18)	28% (134)			
Eulithis spp.	16% (5)	58% (46)	34% (164)	23.0	4	<0.001
Others	55% (17)	20% (16)	37% (178)			
Ematurga atomaria	64% (9)	28% (18)	45% (134)	8.82	2	<0.03
Eulithis spp.	36% (5)	72% (46)	55% (164)			

Figures 6.20a and 6.20b. The numbers and proportions of common macrolepidoptera species that were found in the total catch in different height classes of *Calluna* at Slaley. All larvae were found by sweepnet sampling a) 16 July-5 November 1992 b) 29 April-2 August 1993. Figures in parentheses are the numbers of larvae that were found. Species were sometimes grouped together *e.g.* "others" to fulfil the criteria of the χ^2 test that all expected values should be equal to or greater than five. Pairs of species that made large changes have been isolated.

Table 6.21

Species	*Calluna* heights <15cm	*Calluna* heights 16-30cm	*Calluna* heights >30cm	χ^2	df	P
Eupithecia goossensiata	22% (4)	14% (44)	19% (50)			
Eupithecia nanata	78% (18)	57% (181)	56% (150)	-	-	-
Others	0% (0)	30% (95)	25% (66)			
Eupithecia goossensiata	22% (4)	20% (44)	25% (50)			
Eupithecia nanata	78% (14)	80% (181)	75% (150)	-	-	-

Table 6.22

Species	*Calluna* heights <15cm	*Calluna* heights 16-30cm	*Calluna* heights >30cm	χ^2	df	P
Eulithis spp.	6% (4)	10% (13)	15% (54)			
Eupithecia nanata	38% (26)	30% (41)	41% (149)			
Lycophotia porphyrea	13% (9)	19% (26)	23% (81)	66.0	8	<0.001
Pavonia pavonia	4% (3)	26% (35)	7% (26)			
Others	39% (27)	15% (21)	14% (50)			
Eulithis spp.	17% (4)	81% (13)	95% (53)	48.1	2	<0.001
Ematurga atomaria	83% (19)	26% (6)	5% (3)			
Ematurga atomaria	68% (19)	19% (6)	4% (3)	55.9	2	<0.001
Lycophotia porphyrea	32% (9)	81% (26)	96% (81)			

Tables 6.21 and 6.22. The numbers and proportions of common macrolepidoptera species that were found in the total catch in different height classes of *Calluna* at Greenlaw (Figure 6.21) and Langholm (Figure 6.22). All larvae were found by sweepnet sampling in the visits of June and September 1992. Figures in parentheses are the numbers of larvae that were found. Species were sometimes grouped together *e.g.* "others" to fulfil the criteria of the χ^2 test that all expected values should be equal to or greater than five. The χ^2 column is left blank where these criteria were not fulfilled. Pairs of species have been isolated.

species in different height classes (χ^2=55.9, df=2, P<0.001). *E. atomaria* was more abundant than *L. porphyrea* in the shortest *Calluna* stand (68%) and least abundant in the tallest *Calluna* (4%). Another example of a pair of species that failed to show the same dominance relationship at all the study areas was the occurrence of the two *Eupithecia* species at Greenlaw (1992). *Eupithecia nanata* was approximately four times more abundant than *E. goossensiata* in all *Calluna* height classes.

6.5.3 Species composition in *Calluna* stands less than 10cm tall

6.5.3.1 Method

Five stands where *Calluna* was less than 10cm tall (A-E at Waskerley and K-O at Slaley) were sampled by Blow-Vac and also by the sweepnet sampling programme described in section 5.2. The *Calluna* in stands A-E at Waskerley was too dense to be sampled by sweepnet effectively and all sampling at these stands stopped when the Blow-Vac was deemed to be inefficient. Sweepnet and Blow-Vac data were used to compile lists of the species that were found in *Calluna* less than 10cm tall at each study area.

On 2 August and 29 September 1993, the number of larvae found by sweepnet sampling in these short stands, was large enough to compare the proportions of the most abundant species with their proportions in the tallest stands where *Calluna* height was greater than or equal to 40cm. The comparisons were made using chi-square contingency tests.

6.5.3.2 Results

Four geometrid species (*Eulithis* sp., *Ematurga atomaria*, *Eupithecia nanata* and *Eupithecia goossensiata*) and three noctuid species (*Anarta myrtilli*, *Lycophotia porphyrea* and *Ceramica pisi*) and unidentified microlepidoptera larvae were found at Slaley in *Calluna* less than 10cm tall. A pupal case, thought to be that of *Lasiocampa quercus callunae* was also found tied to short stems at Slaley. This indicated that Lasiocampid species also occur in these short stands. Unidentified microlepidoptera larvae and the geometrid *Eulithis* sp. were also found in stands less than 10cm tall at Waskerley.

Tables 6.23a-b show the proportions of the most abundant species in stands less than 10cm cm tall and greater than 40cm tall at Slaley on two sampling dates. Different assemblages of species were present on the two dates. The relative proportions of

Table 6.23a 2 August 1993

Species	*Calluna* heights < 10cm	*Calluna* heights > 40cm	χ^2	df	P
Ematurga atomaria	53% (8)	71% (55)	1.22	1	NS
Anarta myrtilli	47% (7)	29% (23)			

Table 6.23b 22 September 1993

Species	*Calluna* heights < 10cm	*Calluna* heights > 40cm	χ^2	df	P
Eupithecia nanata	24% (16)	3% (6)			
Eupithecia	73% (49)	84% (187)	36.2	2	<0.001
goossensiata	3% (2)	13% (30)			
Anarta myrtilli					

Tables 6.23a and 6.23b. The numbers and proportions of the most abundant macrolepidoptera species that were found in the total catch in two height classes of *Calluna* at Slaley. All larvae were found by sweepnet sampling on a) 2 August 1993 b) 22 September 1993. Figures in parentheses are the numbers of larvae that were found.

Ematurga atomaria and *Anarta myrtilli* on 2 August 1993 did not differ in extremely short and tall *Calluna* (χ^2=1.22, df=1, NS). On 22 September 1993, the proportions of *Eupithecia nanata*, *E. goossensiata* and *A. myrtilli* were significantly different in the short and tall stands (χ^2= 36.2, df=2, P<0.001). The greatest change was a fall in the proportion of *E. nanata* from approximately 24% in very short *Calluna*, to approximately 3% in stands taller than 40cm.

6.6 Discussion

6.6.1 The effect of plant architecture on the density of Lepidoptera larvae in *Calluna*

The abundance of Lepidoptera larvae was significantly affected by changes in *Calluna* architecture. For most of the taxonomic groups and individual species studied, *Calluna* height was the variable that explained most variation in the density of larvae at different stands. Although the slopes of regressions that plotted density of larvae against *Calluna* height could be significantly different for the same species at different sites or time periods, conversion of regression data into units of proportional change in density per cm increase in height resulted in a common trend for most groups of larvae. This suggested that the differences seen in the initial regressions were due to variation in the absolute population sizes at different sites and time periods and implied that the same ecological factor influenced the density of larvae at all sites. This hypothesis is proposed with the caveat that, since the range of the proportional change in density per cm increase in height was large (2-9%), greater accuracy could show different rates of proportional change for different species, sites or time periods.

The greater density of larvae in taller *Calluna* stands could reflect a larger biomass of *Calluna* per unit area, since a larger biomass of plant might accommodate more larvae. *Calluna* biomass changes in different phases of the life-history cycle (Gimingham 1972). Plant biomass is minimal in the pioneer phase and increases with age to a maximum in the mature phase, after which the death of some branches in the degenerate causes biomass reduction (Barclay-Estrup 1970). *Calluna* biomass per unit area was not measured in this study. The density of green shoots may act to some extent as an index of the biomass of green material as Miller and Watson (1978) were able to calibrate a similar measure against biomass, at least within one life-history phase. It might be possible to distinguish between biomass and height *per se* as factors influencing the abundance of Lepidoptera larvae, by searching the same biomass of leaf material for larvae from *Calluna* stands of different heights. This would require a more

efficient and less species-biased extraction technique than the Berlese-Tullgren method used in section 4.4.3.

For several species, variables other than height were identified by the stepwise multiple regression program to explain variation in larvae density. High intercorrelation between the vegetation variables made it difficult to be certain which variables directly affected larvae density most. For example, it was plausible that the densities of *Eupithecia nanata* and *E. goossensiata,* both species that feed on flowers, were related to flower density (Table 6.7). Yet because flower density was also significantly correlated with *Calluna* height ($r=0.84$, $df=48$, $P<0.001$, Figure 3.5a), the relationships between the densities of these species and *Calluna* height were also significant. *Calluna* does not always flower in its first year of growth, so the absence of flower-feeding species from non-flowering stands would be more informative. Unfortunately literature sources (*e.g.* Skinner 1984; Emmet & Heath 1991) do not describe the relative importance of foliage and flowers in the diet of these species. Other authors have also found it difficult to separate the effects of related vegetation characters (Andow 1991; Harrison & Thomas 1991). For example, Andow (1991) noted the difficulty of distinguishing between the resource concentration and natural enemies hypotheses because change from monoculture to polyculture also affected host plant densities.

At most sites and time periods, the density of microlepidoptera larvae was not correlated significantly with any of the vegetation variables that were measured. The lower abundance of this group in comparison to the macrolepidoptera and the fact that many of these species tie nets or make cases, may make their capture by the sweepnet technique less predictable.

The results of this study are similar to those of Fielding (unpublished Ph.D. thesis 1992) who recorded that the density of some macrolepidoptera species *e.g. Macrothylacia rubi*, *Hydriomena furcata*, *Eupithecia nanata* and *Lycophotia porphyrea* were significantly correlated with *Calluna* age, time of sampling and altitude. She also found that the density of the Noctuidae was significantly higher in the building and mature phases than in the degenerate phase and suggested that some of these differences could be caused by variations in *Calluna* biomass. Gimingham (1985) found that Lepidoptera larvae and other invertebrates that feed on green shoots or *Calluna* sap were most abundant in building and mature phase stands. The distribution of invertebrates in different *Calluna* phases on moors and heathlands appears to vary for different groups. For example, taxa that live or feed on the ground are most abundant in the pioneer phase (Gimingham 1985) while Barclay-Estrup (1974) found that the highest numbers of most of the invertebrate groups he studied occurred in the pioneer and degenerate phases. According to Gimingham (1985), many invertebrate

taxa are more abundant in unmanaged stands that comprise different-aged bushes, but Gimingham's study does not give specific information about the Lepidoptera in unmanaged stands. Variation in the abundance and activity of invertebrates in different successional stages of *Calluna* have been attributed to changes in microclimate, *Calluna* biomass, food supply, the presence of a litter layer and architectural complexity of the vegetation (Barclay-Estrup 1974; Merrett 1976; Webb *et al.* 1984; Gimingham 1985; Fielding unpublished Ph.D. thesis 1992).

Few of these studies have examined change in the density of individual species and it is likely that studies that have examined only taxa (*e.g.* Barclay-Estrup 1974) have been misleading. The densities of different species of ant (Brian *et al.* 1976) and spiders (Merrett 1976; Usher & Smart 1988) varied in different stages of stand development. At least in the case of Merrett (1976), different conclusions would have been reached if only the taxon had been studied. Merrett found that the densities of different species peaked at different stages during the succession of burned ground to closed *Calluna* canopy, but the number of individuals and spider biomass peaked two years after burning, due to the extreme abundance of one species.

Variation in the density of animals in other habitats has also been related to plant height (and related architectural variables). For many species of plant, age and size are interchangeable variables. Some examples of the effect of plant height on invertebrate density are the higher densities of single insect species in taller Scots pines *Pinus sylvestris* (Tenow & Larsson 1987) and the relationship between age, height and reproductive index of tamaracks *Larix laricinia* and defoliation by the larch bud moth *Zeiraphera improbana* (Niemelä *et al.* 1980b). Bach (1981) found that a chrysomelid beetle *Acalymma vittata* was more abundant on same sized vertically grown than horizontally grown cucumbers and suggested beetle movement patterns could be a cause of the distribution. For species that show little variation in plant height, horizontal spread can be related to similar effects (MacGarvin 1982; Bach 1988a). Plant height, patch size, plant density, plant diversity and degree of clumping may all affect the ability of invertebrates to locate and remain on host-plants (*e.g.* Root 1973; Cromartie 1975; Jones 1977; Price *et al.* 1980; Bach 1981, 1988b; Cornell 1986; Tenow & Larsson 1987). Plant size may even affect invertebrate life-history strategy (Thompson 1983a, 1983b) or the evolution of body size (Niemelä *et al.* 1981).

6.6.2 The effect of plant architecture on the diversity of Lepidoptera larvae in *Calluna*

When choosing an appropriate diversity index, some authors (Southwood 1978; Magurran 1988; Krebs 1989) recommend that plots of the species abundance pattern

are made and compared with distributions predicted by models such as the logarithmic series (Fisher *et al.* 1943; Williams 1944), geometric series (Motomura 1932 in Tokeshi 1993), lognormal (Preston 1948, 1962 both in Tokeshi 1993) or "broken-stick' (MacArthur 1957), using chi-square goodness-of-fit tests. If the distribution of the data is similar to that of a model, an index derived from that model may be used for the analysis of diversity. The problem with this approach is that it is often difficult to decide which model best describes the distribution of the data. Data may fit more than one model (Gray 1987; Magurran 1988), samples of different size from the same community may fit different models (Whittaker 1975 in Tokeshi 1993), or the dataset may be too small to compare adequately with the model. For example, Tokeshi (1993) stated that frequency-distribution plots should only be used for assemblages that contain "well over 30 species".

Data collected during the sweepnet sampling programmes comprised relatively small species assemblages. Only 29 species of macrolepidoptera were found when data from all five study areas were combined (Chapter Five) and the largest number of macrolepidoptera species collected at a single study area during one of the sampling periods was 16 (Slaley 16 July-5 November 1992, Table 5.3b). These assemblages were too small to apply frequency-distribution plots (Tokeshi 1993), or to identify a descriptive model with certainty.

The application of α of the logarithmic series (Fisher *et al.* 1943) is said to have good discriminant ability and not to be strongly influenced by sample size (Taylor 1978 in Magurran 1988). Southwood (1978) advocated its use as a standard diversity index, to make different studies comparable, both for Taylor's reasons and because α has been studied more than many other indices. It has been used in studies of adult Lepidoptera using light-trap data (Kempton & Taylor 1974), but in this study of larvae, α was more strongly affected by changes in sample size than Simpson's $1/D$. The data may not fit the logarithmic series model, which predicts that a large number of rare species are represented by one individual. Figures 5.1a-b (Chapter Five) show that only a few of the species were represented by single specimens. The study's emphasis on the breeding community may eliminate many of the transients or migrants from other communities that can be encountered in light-traps. Simpson's $1/D$ is recommended for interpretability (Usher 1983) and for its precision and lack of bias (Giavelli *et al.* 1986). It has also been used satisfactorily with light-trap data (Giavelli *et al.* 1986). Its independence of species-abundance models appears to justify its use in this study.

The diversity of macrolepidoptera larvae changed in different heights of *Calluna,* but as no trend was consistent at different sites and time periods, it is unlikely that these changes are of major biological importance. Use of the Sorensen's and percentage

similarity indices confirmed that the composition of the fauna was most alike in stands with similar heights, but these data must be interpreted cautiously, because of the repeated use of the same stands within the data matrices. Variation of diversity in different *Calluna* heights occurred because both the species richness and evenness components changed.

More species were found in taller stands. The extra species were usually uncommon species that could have been detected by chance effects in the larger samples of larvae from the taller stands. None of the common Lepidoptera species were restricted to one height of *Calluna*. Changes were in the relative abundance of a species rather than strict presence or absence. This agrees with Fielding (unpublished Ph.D. thesis 1992), who examined the species present in building, mature and degenerate phase *Calluna*. In her study, the only species that were unique to a particular life-history phase were uncommon, and it is possible that a more intensive sampling programme may have found these in other phases.

These data suggest that the community of Lepidoptera larvae in *Calluna* is not arranged according to the "horizontal zonation hypothesis" (Lawton 1983), in which herbivore assemblages differ on large and small individuals of the same host species, with some species unique to certain size classes. A hierarchical association (Cornell 1986) would seem a better description. This predicts that large plants may have a richer herbivore fauna than small plants of the same species, but does not assume that the herbivores have definite preferences for certain height classes. According to this scheme, the invertebrate assemblage on a small plant may be a random or non-random subset of that on a larger individual. The absence from short *Calluna* of a species that contributes 20% of the individuals in taller stands, could occur by chance if a total of less than 25 Lepidoptera larvae of any species were found.

Eupithecia nanata and *E. goossensiata* showed complimentary change in their contribution to the community across *Calluna* height gradients (Slaley 16 July-5 November 1992). The diet of both these species includes flowers, but the distribution pattern is not direct evidence of competition. As many pairs of species did not show the same dominance relationships at different study areas, the dominance of individual species in different heights of *Calluna* cannot be predicted.

It is difficult to compare different studies of invertebrate communities on *Calluna* because different heterogeneity measures have been used. Fielding (unpublished Ph.D. thesis 1992) found no significant difference between the number of Lepidoptera species she recorded in building, mature and degenerate phase *Calluna*. Of 25 species she recorded on northern heath, 18 were found in each of these phases. Barclay-Estrup

(1974) found greatest species richness of spiders and Miller (unpublished Ph.D. thesis 1974 in Fielding unpublished Ph.D. thesis 1992) greatest invertebrate diversity in the pioneer and degenerate phases. Gimingham (1985) considered the invertebrate fauna to be most species rich in the late mature and degenerate *Calluna* phases, because these offered the greatest habitat diversity. Merrett (1976) found no clear change in the number of spider species during the first ten years after *Calluna* was burned. Usher and Smart (1988) found that the spider fauna was most diverse in unburned *Calluna* and in the margins of burned and unburned stands, because species characteristic of both burned and unburned areas were found together at the borders.

In other habitats, older taller or larger plants have often accumulated more herbivore species (*e.g.* Banerjee 1981; MacGarvin 1982; Cornell 1986). Lawton (1983) gives examples of species believed to exhibit "vertical" and "horizontal zonation. Some Lepidoptera larvae do show preference for certain height zones in a tree canopy and different sexes may be distributed at different heights (Gross & Fritz 1982). A distribution pattern cannot be assumed to indicate preference and a variety of mechanisms including plant apparency theory, the "natural enemies" and resource concentration" hypotheses (Root 1973) and adult flight and oviposition behaviour have been proposed to account for patterns of density and diversity.

Chapter Seven

The Effect of *Calluna* Age on Plant Chemistry

7.1 Introduction

Chapter Six described how the density and diversity of Lepidoptera larvae varied in different heights of *Calluna*. Density of the total macrolepidoptera larval fauna, and of several species was greater in older, taller heather than in the younger, shorter stands. This trend could be due to entirely physical factors. Older heather may provide a greater quantity of leaf shoots, a larger food resource, and the spatial area to accommodate more larvae. Alternatively, variations in microclimate, or the chemical composition of leaves in different aged *Calluna* stands could be responsible. For example, the presence of higher leaf nutrient concentrations in certain stands could encourage the immigration of ovipositing females and allow greater survival of larvae.

There are a number of factors that determine whether a larva will feed on a plant. The larva must satisfy certain nutritional demands. These requirements include quantities of protein, carbohydrate, water and certain vitamins and minerals that are essential for growth and metabolism. Most plant species provide nutrients in various quantities, but motivation to feed also depends on the presence of phagostimulants, which allow the larva to recognise a food source, while the presence of deterrents may discourage feeding (Chapman 1974). Such deterrents could be physical *e.g.* hairs, thorns, trichomes or leaf toughness, or chemical *e.g.* strong tastes and scents. Furthermore, mortality rate, feeding efficiency, or growth rate could be influenced by the ability of insects to overcome, or avoid, a wide variety of plant chemicals that have antiherbivore defensive properties (Feeny 1976; Rhoades & Cates 1976; Cates 1980). It was not possible, within the scope of this project, to analyse *Calluna* for all the compounds that might confer nutritive or defensive properties, because an extensive range of these exist in nature. It was decided to focus on one well-known "nutritive" element, one "defensive" compound group and water and to determine how the quantities of these in the leaves varied with the age of the plant.

The nutritive element considered was total nitrogen. Since animals use nitrogen based compounds as structural building blocks *e.g.* proteins, and plants use carbon *e.g.* carbohydrates, the limiting factor to animal fitness is more likely to be nitrogen than carbon (McNeill & Southwood 1978; Mattson 1980). Different plants exhibit a wide range of nutrient concentrations and some are unable to support herbivores (Kennedy

1953 in McNeill & Southwood 1978; Scriber & Slansky 1981). Heathlands are traditionally regarded as nitrogen poor (Davies *et al.* 1964) and it is possible that *Calluna* stands growing on different soil conditions, or different aged stands might have different concentrations of leaf nitrogen.

Choice of a "defensive" compound was more difficult. Two classes of plant secondary compound have defensive properties. The first class act as toxins, the second as digestibility reducing substances. Toxins tend to be small, lipophilic, molecules (molecular weight less than 500), which are able to cross animal cell membranes and cause internal damage (Rhoades & Cates 1976). They include cardiac glycosides, glucosinolates, alkaloids, coumarins, terpenes and many others. Although usually present in only low concentrations, (typically less than 2% dry weight) (Feeny 1976; Rhoades & Cates 1976), they are potent and tend to kill insects and other herbivores. Their effects are not related to their concentration but may be circumvented by specialists, that have coevolved closely with the plant. The digestibility reducing substances include the phenolic resins found in creosote bush *Larrea*, and the hydrolysable and condensed tannins (Rhoades & Cates 1976). The hydrolysable tannins are divided into two further subclasses: the gallic and elagic acid based tannins (Mole & Waterman 1987). These phenolic compounds are large molecules that do not cross the cell membranes of animals. Phenolic action is therefore believed to take place in the gut where they are supposed to act as generalised protein and starch complexing agents (Feeny 1969, 1970; Rhoades & Cates 1976). By forming complexes with proteins, starch, and digestive enzymes it is suggested that phenolics reduce digestive efficiency by lowering the amount of nitrogen available to insect herbivores (Feeny 1970; Rhoades & Cates 1976). Reduction in insect fitness may occur through slower growth rate or lower fecundity. Digestibility reducing substances are believed to be more difficult to overcome than toxins, because of their dosage dependent action (Feeny 1976; Cates & Rhoades 1977).

Phenolics are common in woody perennials. Approximately 79% of deciduous woody perennials and 87% of evergreen woody perennials are tanniniferous (Rhoades & Cates 1976). Plants that are "apparent" or "predictable" in space and time by virtue of long lifetime, large individual size, large clump size or dominance in their biome are easily discovered by many generalist herbivores. Since they must resist many herbivores, these plants should use dosage dependent defences *e.g.* digestibility reducing substances (Feeny 1976; Rhoades & Cates 1976). Plants that are "unapparent" or "unpredictable" by being rare, small, cryptic or ephemeral might escape location by all but specialised herbivores and should therefore invest fewer resources in antiherbivore defence *e.g.* low concentrations of toxins (Feeny 1976; Rhoades & Cates

1976). Plants that live in nitrogen poor environments often have carbon based defences *e.g.* phenolic compounds, rather than nitrogen based defences *e.g.* toxins (Mattson 1980). *Calluna* is an evergreen, woody perennial that occurs in extensive swards as the dominant plant on nitrogen poor northern heaths. It is "apparent" and for this reason and for others listed above, it might be predicted to contain antiherbivore phenolics. Jalal *et al.* (1982) have found *Calluna* to contain many phenolic substances. For these reasons, and because the compound analysed should act by occurring at a range of concentrations, phenolics are an appropriate group to examine.

It is also important to examine the water content of leaf tissue, because water is essential to all other metabolic functions, and the availability of water is intrinsically linked to uptake and metabolism of many other nutrients (Scriber 1979; Scriber & Slansky 1981). For many caterpillar species, moisture in plant tissues is their main or only source of water.

Concentrations of nitrogen, phenolics, or water in leaves can vary with season (Feeny 1970; Scriber & Slansky 1981; Hill 1982; Meyer & Montgomery 1987), with age of a given plant species (Rodin & Bazilevich 1967), or age of leaf (Feeny 1970; Schweitzer 1979; Coley 1983; Meyer & Montgomery 1987). As well as seasonal and ontogenetic factors, environmental effects such as water stress can change the nitrogen and secondary chemistry status of plants (Kennedy 1953 in McNeill & Southwood 1978; Bates 1971 in McNeill & Southwood 1978; Mattson 1980). The analysis of nutrient concentrations in different ages of *Calluna* is relevant to the study of Lepidoptera distribution patterns on heathland because some herbivore growth rates and fitnesses have been linked to variations in nitrogen, phenolics, or water concentration (Feeny 1969; Scriber 1979; Scriber & Slansky 1981; Meyer & Montgomery 1987).

The existing literature on the chemical composition of *Calluna* spans a century, but variation in aims, methodologies and plant part examined means that no study has been adopted as the definitive description of variation in heather chemistry. The earliest projects examined "crude protein content", fibre or "major ash constituents" (Wallace & Kind 1884 ; Godden 1933 in Thomas 1956). Studies which have examined the effects of heather age on different leaf nutrient concentrations include Thomas (1934), Lauder & Comrie (1936), Moss *et al.* (1972), and Miller (1979). The effect of season on nutrient concentration has also been researched (Lauder & Comrie 1936; Thomas 1937; Ulvesli & Nordbo 1945 in Thomas 1956; Miller 1979; Jalal *et al.* 1982). None of these studies provides the ultimate measure of an ageing effect, that is, the chemical analysis of marked plants through the lifespan of *Calluna*, a period of 25-40 years (Gimingham 1960, 1972, 1985). The choice of plant parts for study was determined, in many cases, by reference to the conjectured eating habits of animals and birds that graze on

heathland *e.g.* sheep *Ovis aries* and red grouse *Lagopus lagopus scoticus*. No study has been made with specific reference to heathland Lepidoptera.

7.2 Methods

7.2.1 Collection of *Calluna* samples

Samples of *Calluna* for chemical analysis were collected from the Slaley and Waskerley field sites. Three sampling months were chosen to collect heather at different stages of the growing season: mid May (the beginning of the growing season, prior to rapid shoot extension), mid June (the period of most vigorous shoot growth), and mid October (the end of the growing season). Whenever possible, samples were taken from one site within five days of the other. Dates of collection at Slaley and Waskerley were 22 and 24 May, 21 and 24 June, and 10 and 18 October respectively.

At each site, samples were collected from the 15 different aged stands used to monitor population density in 1992 and 1993 (section 5.2). The method used to age plants is described in section 3.2.5. A random number grid was used to select 20 points in each stand and the nearest bush to each point was clipped and placed in a polythene bag. Whole plants were collected in very young stands, while in tall stands only the top 20cm of the plant, the area that carried leaves, was removed. No attempt was made to keep material from each plant separate, so bulked material from the twenty plants chosen in each stand constituted one sample. The bags of vegetation were transported in an insulated box containing ice and placed immediately in a refrigerator at 0°C on return to the laboratory.

7.2.2 Preparation of samples for chemical analysis

Vegetation from each stand was sorted into current and previous years' growth. The current year's material comprised the long-shoots that grew in 1993. Previous years' material was older growth clipped from below the region of short-shoots that marked the end of growth in the season of 1992. Since the leaves formed in previous growing seasons may be retained for up to four years in *Calluna* (Gimingham 1960; Chapman *et al.* 1975; Gimingham *et al.* 1979), this sample probably included 2-4 year-old leaves. The clippings were placed in plastic tubes and rapidly frozen by flooding with liquid nitrogen. Frozen samples were ground to a powder using a pestle and mortar. All frozen, powdered samples were stored in a deep freeze at -20°C, prior to chemical analysis.

7.2.3 Chemical analyses

7.2.3.1 Analysis of total nitrogen

The concentration of total nitrogen in each sample was analysed using the indophenol-blue method. Technique details were modified from Allen (1972). This was a two day procedure requiring semi-digestion of leaves in a sulphuric acid-hydrogen peroxide solution prior to further reaction and spectrophotometric analysis. Due to the length of time required to run each batch and the small number of samples that could be run together, only samples collected in June, the time of most rapid shoot elongation were analysed. Results were expressed as a percentage of the dry matter.

7.2.3.2 Analysis of total phenolics

Measurement of total phenolics followed the Prussian-blue method. This spectrophotometric technique was described by Price & Butler (1977). Phenolics were first extracted using aqueous methanol. 0.3g samples of frozen powdered leaf material were placed in boiling tubes with 10ml of 50% aqueous methanol. The tubes were covered and boiled at 90°C for 10 minutes to extract phenolics. Each tube was centrifuged and 50µl of each extract was pipetted into test tubes. Reaction details then followed those of Price & Butler (1977). Total phenolics are expressed relative to +(-) catechin (Sigma, Dorset, UK). Results were expressed as a percentage of the dry matter.

7.2.3.3 Analysis of leaf water content

A sample of 0.5 g of frozen, powdered leaf sample was dried to constant mass at 80°C. The difference between wet and dry mass was the water content of the sample and was expressed as a percentage of the fresh mass.

7.2.4 Calculation and statistical analyses

All estimates of total nitrogen, phenolics and water content were based on two replicate analyses from the powdered sample for each stand and leaf age class. Where the standard error associated with the estimate was greater than 40% of the mean, estimates were discarded. Where the number of samples per sampling month was too large to analyse in one day, several batches were run over a period of days using fresh reagents each day. To maintain consistency between batches a standard sample was run each time, and all other estimates were adjusted to the mean value of this standard.

The linear correlation coefficient was used to test the relationships between total leaf nitrogen, phenolics, water content and heather age. Data were, however, examined for curvi-linear relationships but none were found. Relationships between nitrogen,

phenolic and water concentrations were also assessed. T-tests were used to compare the total nitrogen, phenolic and water content of current and previous years' leaves. Variables expressed as percentages were normalised using an arcsine transformation before t-tests were applied. Data from different months and different leaf age classes were examined separately.

7.3 Results

7.3.1 Trends with seral age of *Calluna*

Figures 7.1a to 7.13b show the total foliar concentrations of nitrogen, phenolics and water in *Calluna* plants between the ages of 2 and 24 years at the two field sites. Correlation statistics are given in Tables 7.1-7.3.

The concentrations of nitrogen and phenolics in current and previous years' leaves were not related significantly to plant age at any site or time of year (Tables 7.1 and 7.2). There were wide variations in the concentrations of both nitrogen and phenolics between similarly aged stands.

Concentration of water in the previous years' leaves of June samples (Slaley), and all October samples showed a significant ($P<0.05$ - $P<0.001$) linear decline with increasing stand age (Table 7.3). In October, concentrations in the oldest 24 year-old samples were approximately 75% of the youngest 2-year-old samples at Slaley. At Waskerley, the oldest 24-year-old stands had concentrations approximately 91% of 4-5 year-old stands. Except for the previous years' leaves sampled at Slaley in June, there were no other relationships between age of *Calluna* stand and water concentration.

7.3.2 Comparison of total nitrogen, phenolics and water concentration in current and previous years' leaves

The concentrations of total nitrogen, total phenolics and water were significantly higher ($P<0.03$ - $P<0.001$) in the current year's leaves (Tables 7.4-7.9). Results from both sites and all dates were similar, except heather samples taken from Waskerley in October, where there was no significant difference between phenolic concentration of current and previous year's leaves. The largest differences in concentration were between the nitrogen and phenolic concentrations of current and previous leaves, where concentrations in young leaves could be as much as 1.5-2 times greater than in old leaves. Water content was only marginally higher in younger leaves. The order of the difference in water concentration between current and previous years' leaves was remarkably consistent between sites (Table 7.6).

The order of the difference in chemical concentration in current and previous years' leaves was used to verify the absence of any trends related to the age of *Calluna* stands (Figures 7.14-7.16b). Concentration in the current year's leaves was divided by concentration in the previous years' leaves to obtain the order of the difference between young and old leaves in each stand. These values were plotted against age of *Calluna*. If trends with age were found in only the current or previous years' leaves, a positive or negative trend would be expected, as differences between current and previous concentrations grew larger at one end of the age scale. While the majority of points fell above 1, showing the concentration of current year's leaves to be higher than previous years' leaves, the difference did not change with age of heather stand. This was also true of the water content in October samples. Although leaf water content declined significantly with increasing age of stand ($P<0.01$ - $P<0.001$, Table 7.3) the order of the difference between current and previous years' leaves was a constant across all ages, because current and previous years' leaves behaved in the same manner.

7.3.3 Interrelation of total nitrogen, total phenolics and water concentrations

Data describing correlations between total nitrogen, total phenolics and total water concentrations are listed in Tables 7.10 a-c. Highly significant correlations ($P<0.05$ - $P<0.001$) were found between the current year's and previous years' leaf concentrations of nitrogen, phenolics or water at several sites and sampling periods. This was to be expected, since current and previous year classes constitute subdivisions of the same sample at each stand. Only one example of a chemical concentration being related to another was found. This occurred in the June Waskerley sample where nitrogen concentration in the current year's leaves was significantly positively correlated with the water content of previous years' leaves. This may be a spurious result, since at the 0.05 probability level, one in twenty correlations may be significant by chance. Twenty-eight correlations were examined, so one falsely significant result could be expected. The possibility that the concentrations of other nutrients might appear falsely related to *Calluna* age, through a stronger correlation with water content, was avoided by correcting concentrations to dry weights.

Figure 7.1a

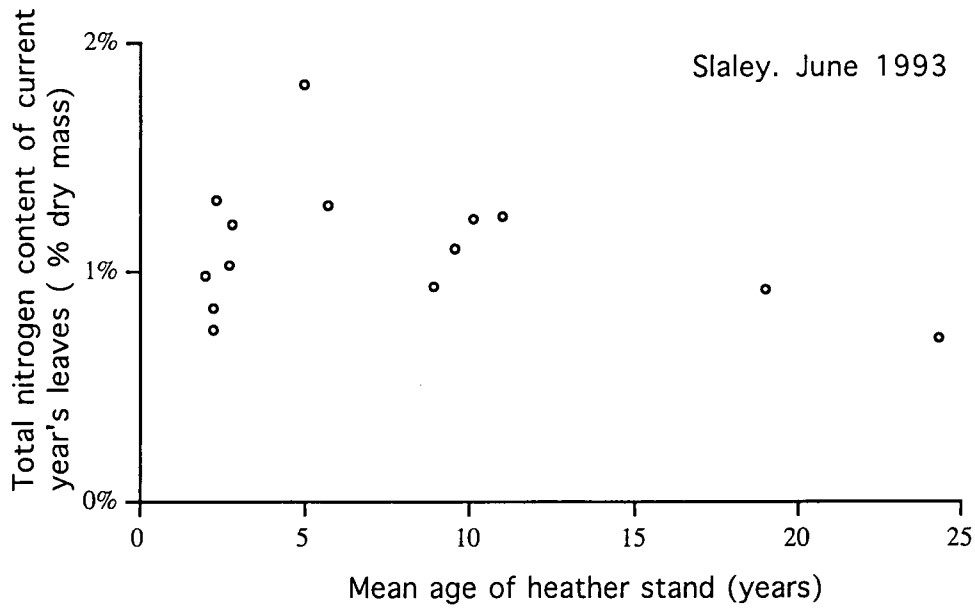
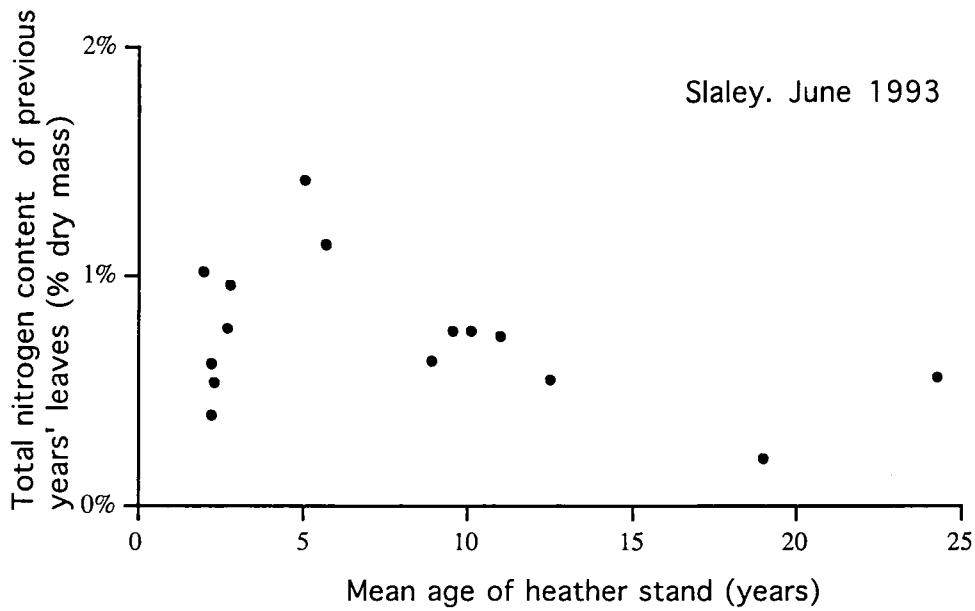


Figure 7.1b



Figures 7.1a and 7.1b. The total nitrogen content of *Calluna* samples taken from the 15 stands studied at the Slaley field site in 1993. Samples were derived from 20 plants collected in the field. Figure 7.1a shows the nitrogen content of current year's leaves, Figure 7.1b the nitrogen content of previous years' leaves. Estimates of total nitrogen content were based on two replicates from each stand and leaf class. There was no significant relationship between plant age and the concentration of leaf nitrogen. Linear correlation statistics are presented in Table 7.1.

Figure 7.2a

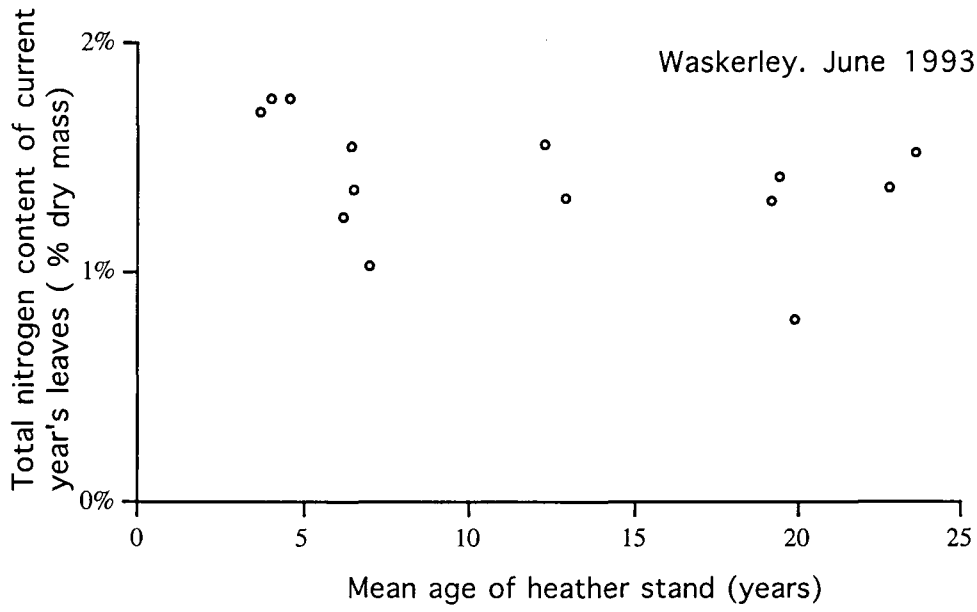
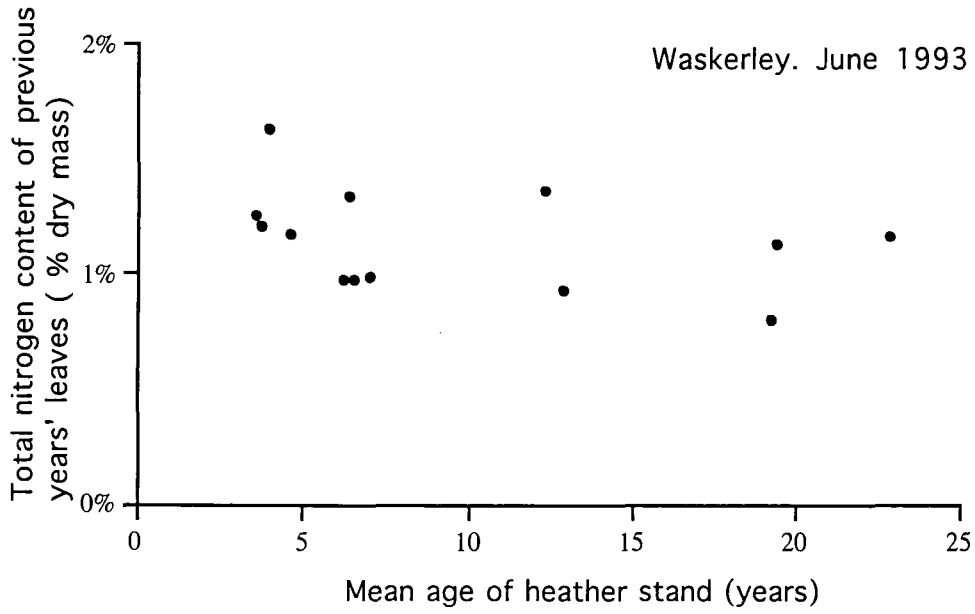


Figure 7.2b



Figures 7.2a and 7.2b. The total nitrogen content of *Calluna* samples taken from the 15 stands studied at the Waskerley field site in 1993. Samples were derived from 20 plants collected in the field. Figure 7.2a shows the nitrogen content of current year's leaves, Figure 7.2b the nitrogen content of previous years' leaves. Estimates of total nitrogen content were based on two replicates from each stand and leaf class. There was no significant relationship between plant age and the concentration of leaf nitrogen. Linear correlation statistics are presented in Table 7.1.

Figure 7.3a

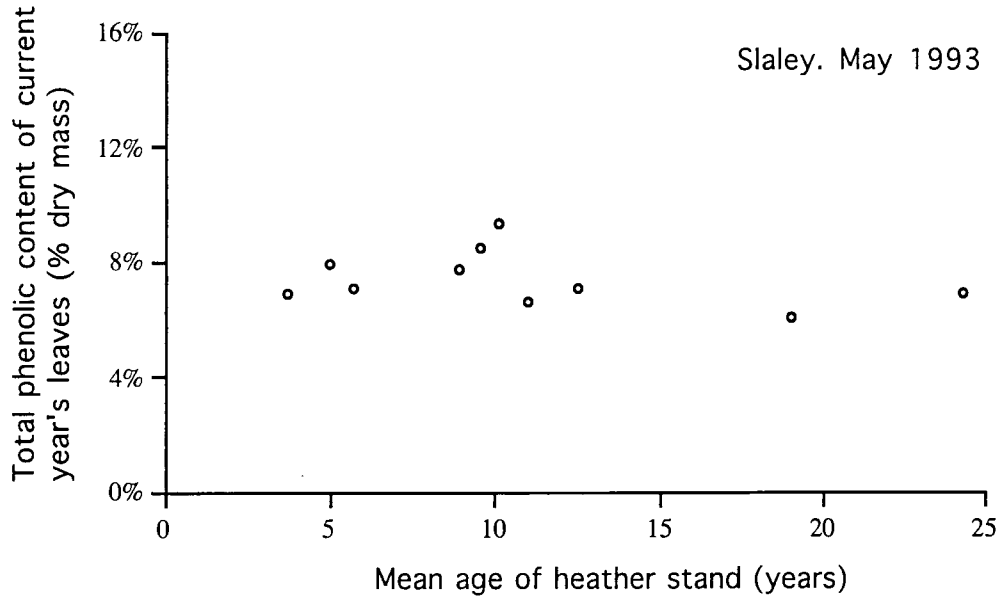
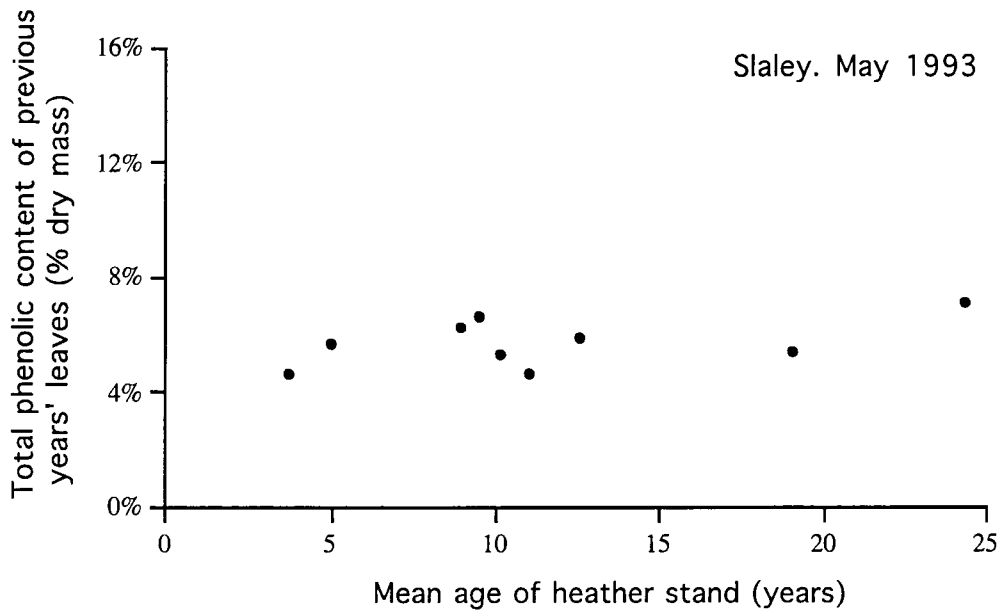


Figure 7.3 b



Figures 7.3a and 7.3b. The total phenolic content of *Calluna* samples taken from the ten stands studied at the Slaley field site in May 1993. Samples were derived from 20 plants collected in the field. Figure 7.3a shows the phenolic content of current year's leaves, Figure 7.3b the phenolic content of previous years' leaves. Estimates of total phenolic content were based on two replicates from each stand and leaf class. There was no significant relationship between plant age and the concentration of leaf phenolics. Linear correlation statistics are presented in Table 7.2.

Figure 7.4 a

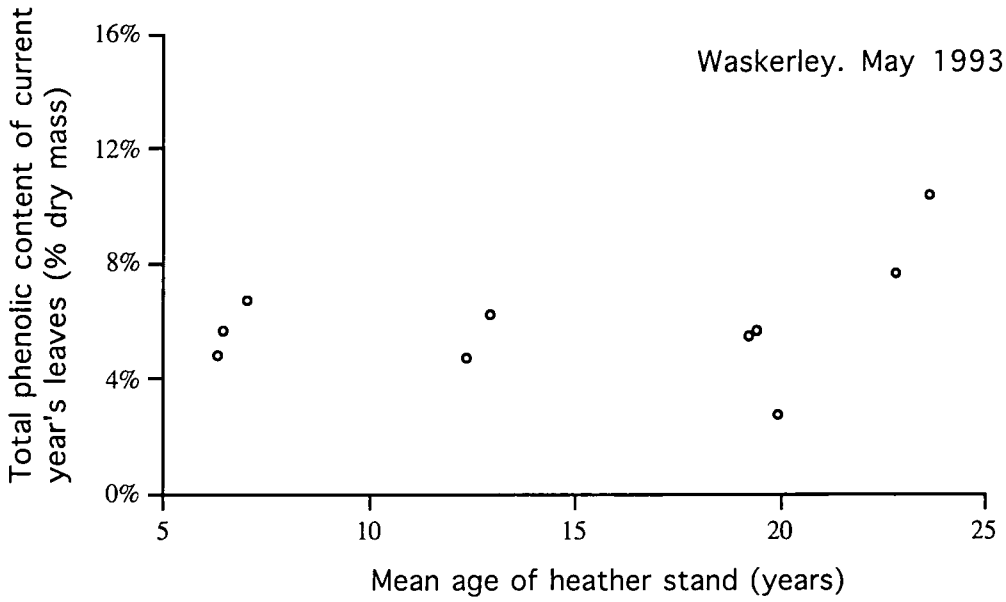
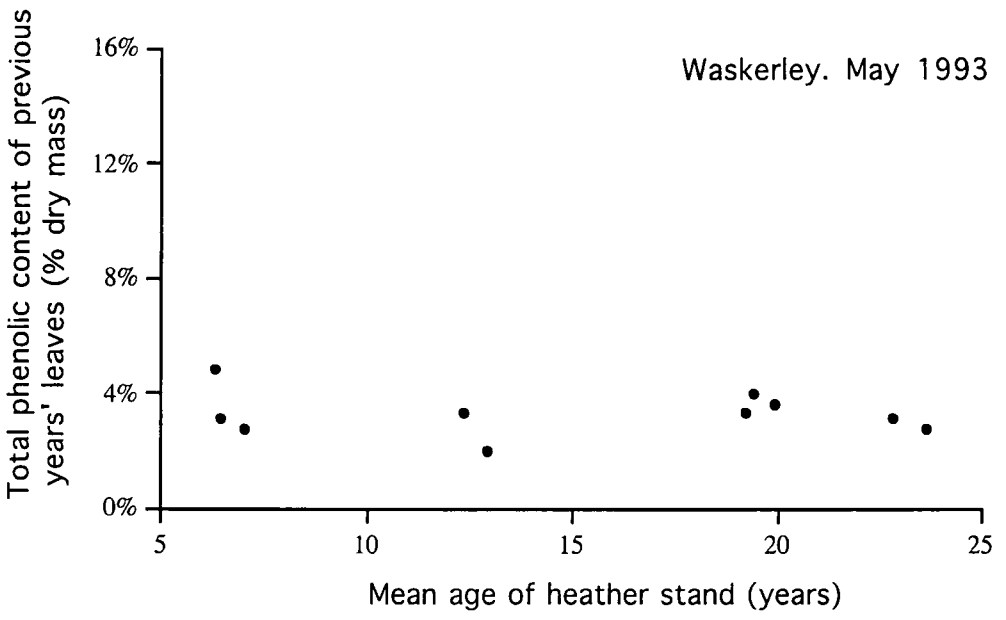


Figure 7.4b



Figures 7.4a and 7.4b. The total phenolic content of *Calluna* samples taken from the ten stands studied at the Waskerley field site in May 1993. Samples were derived from 20 plants collected in the field. Figure 7.4a shows the phenolic content of current year's leaves, Figure 7.4b the phenolic content of previous years' leaves. Estimates of total phenolic content were based on two replicates from each stand and leaf class. There was no significant relationship between plant age and the concentration of leaf phenolics. Linear correlation statistics are presented in Table 7.2.

Figure 7.5a

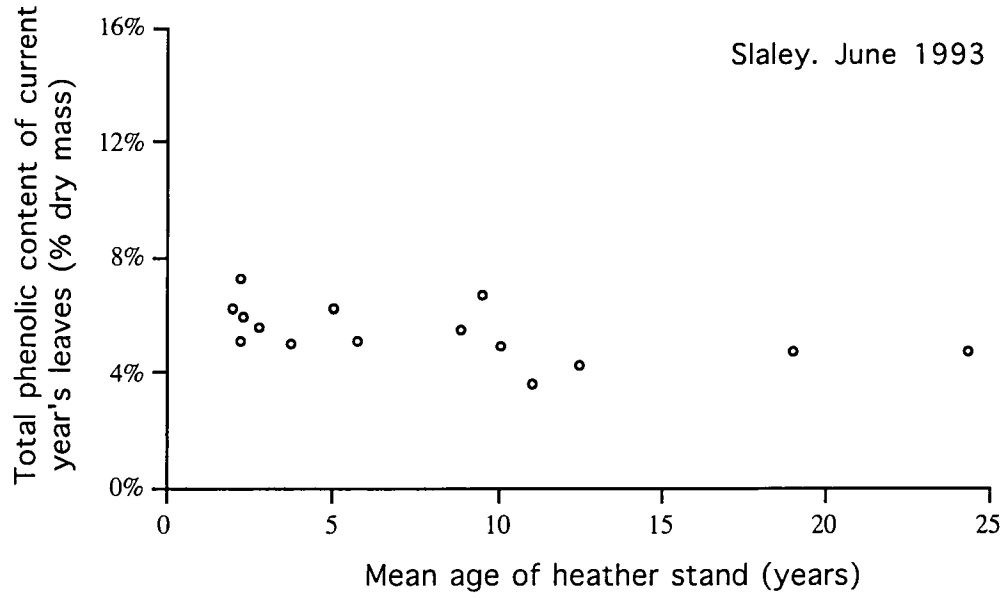
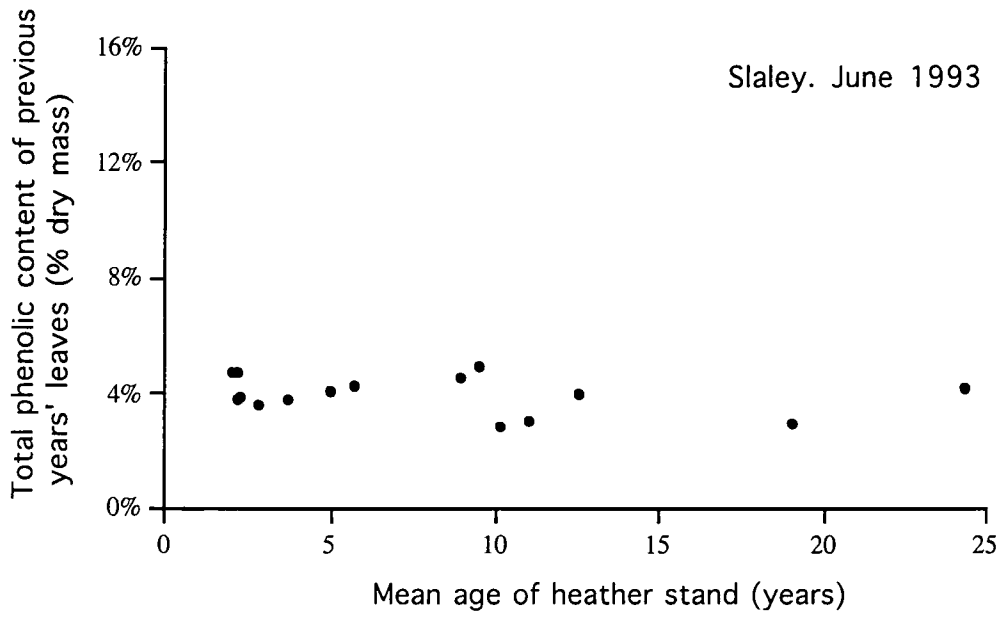


Figure 7.5b



Figures 7.5a and 7.5b. The total phenolic content of *Calluna* samples taken from the 15 stands studied at the Slaley field site in June 1993. Samples were derived from 20 plants collected in the field. Figure 7.5a shows the phenolic content of current year's leaves, Figure 7.5b the phenolic content of previous years' leaves. Estimates of total phenolic content were based on two replicates from each stand and leaf class. There was no significant relationship between plant age and the concentration of leaf phenolics. Linear correlation statistics are presented in Table 7.2.

Figure 7.6a

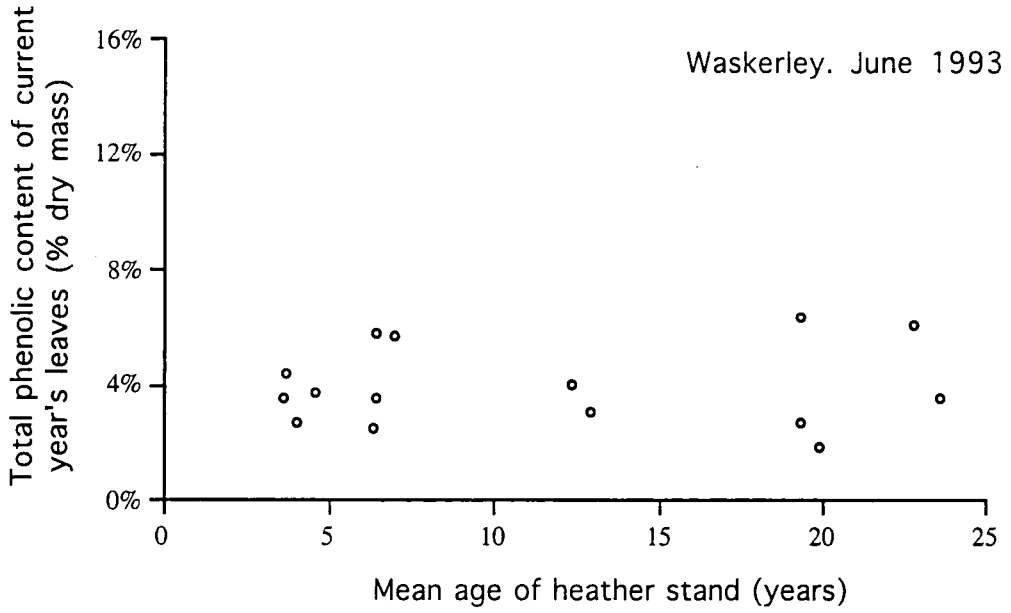
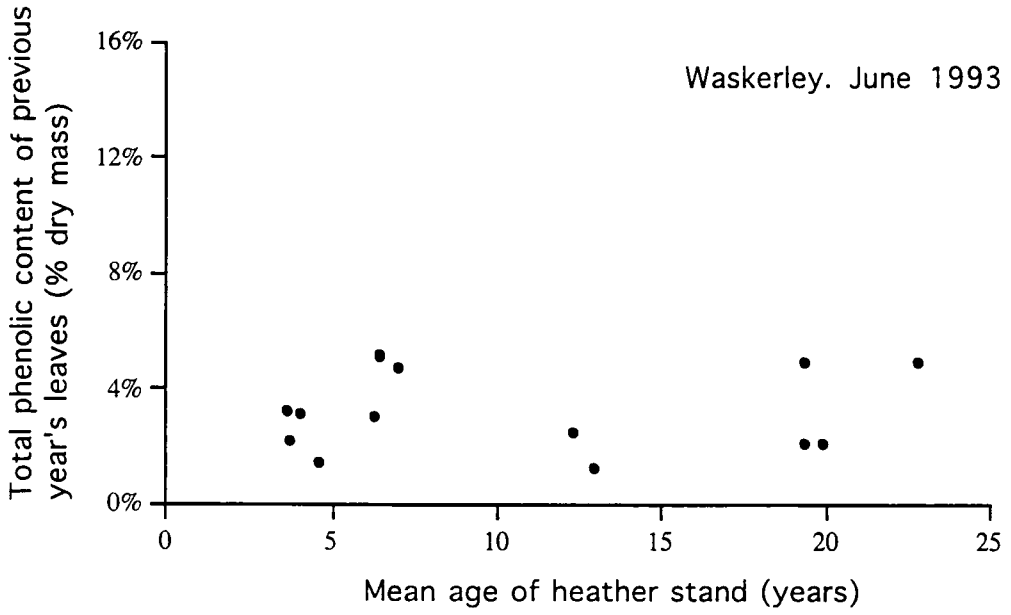


Figure 7.6b



Figures 7.6a and 7.6b. The total phenolic content of *Calluna* samples taken from the 15 stands studied at the Waskerley field site in June 1993. Samples were derived from 20 plants collected in the field. Figure 7.6a shows the phenolic content of current year's leaves, Figure 7.6b the phenolic content of previous years' leaves. Estimates of total phenolic content were based on two replicates from each stand and leaf class. There was no significant relationship between plant age and the concentration of leaf phenolics. Linear correlation statistics are presented in Table 7.2.

Figure 7.7a

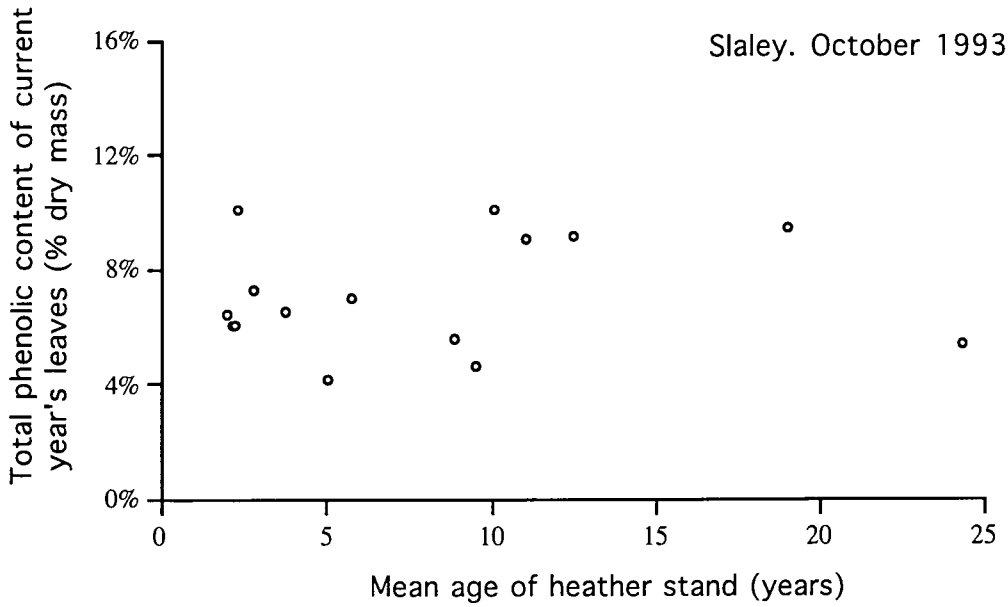
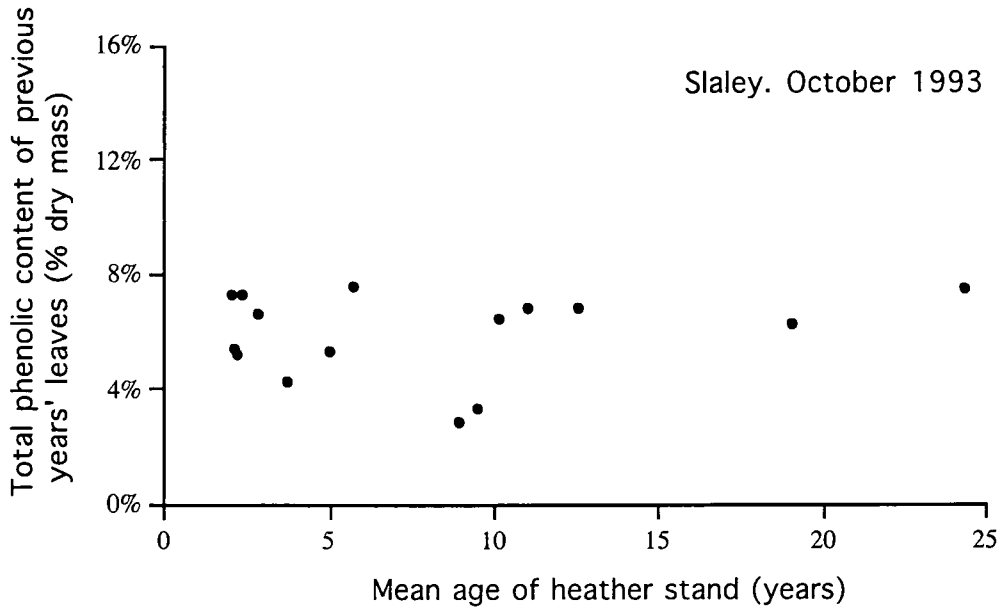


Figure 7.7b



Figures 7.7a and 7.7b. The total phenolic content of *Calluna* samples taken from the 15 stands studied at the Slaley field site in October 1993. Samples were derived from 20 plants collected in the field. Figure 7.7a shows the phenolic content of current year's leaves, Figure 7.7b the phenolic content of previous years' leaves. Estimates of total phenolic content were based on two replicates from each stand and leaf class. There was no significant relationship between plant age and the concentration of leaf phenolics. Linear correlation statistics are presented in Table 7.2.

Figure 7.8a

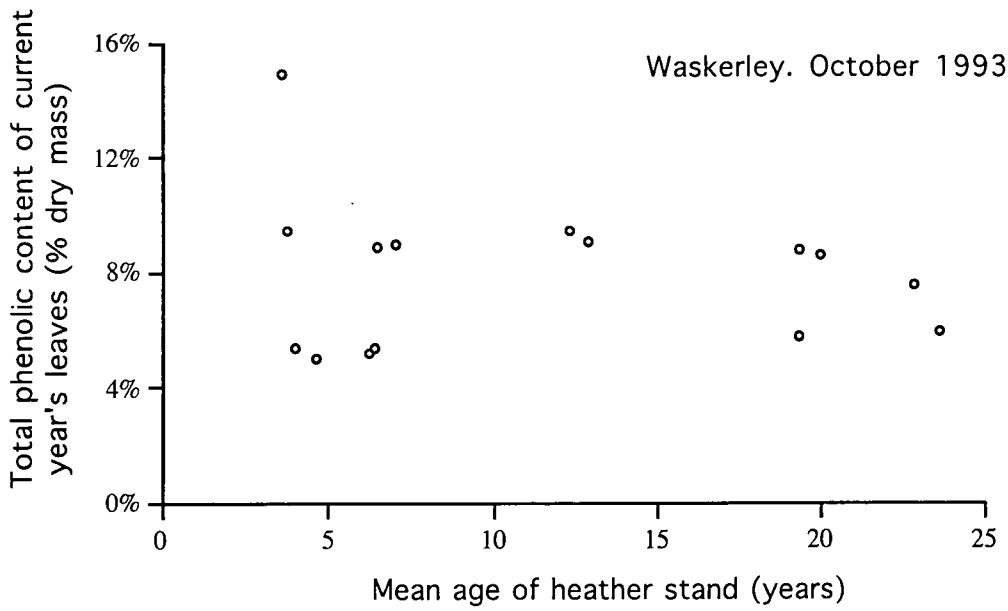
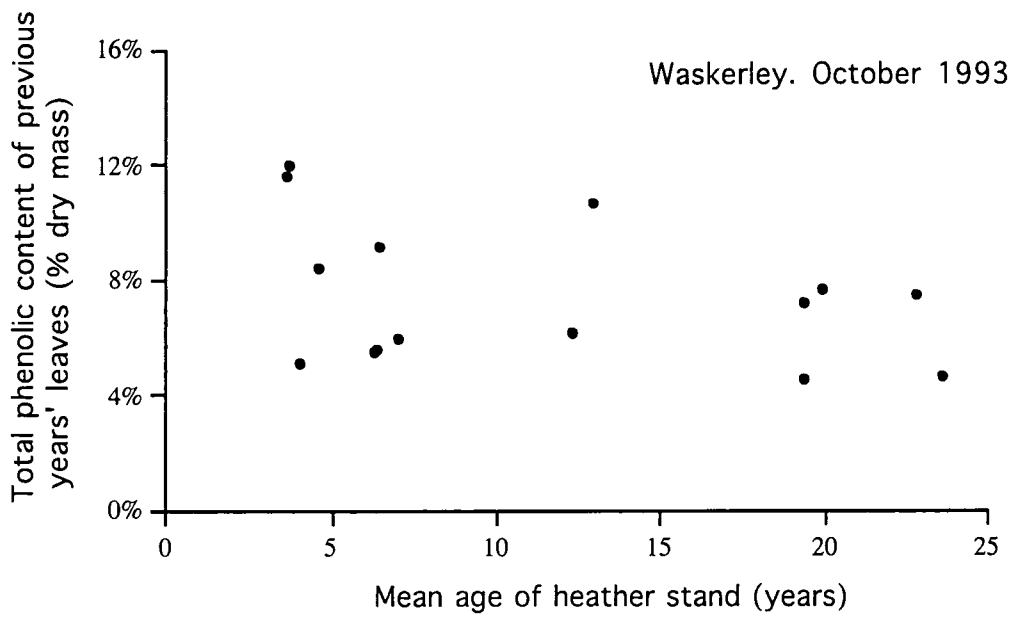


Figure 7.8b



Figures 7.8a and 7.8b. The total phenolic content of *Calluna* samples taken from the 15 stands studied at the Waskerley field site in October 1993. Samples were derived from 20 plants collected in the field. Figure 7.8a shows the phenolic content of current year's leaves, Figure 7.8b the phenolic content of previous years' leaves. Estimates of total phenolic content were based on two replicates from each stand and leaf class. There was no significant relationship between plant age and the concentration of leaf phenolics. Linear correlation statistics are presented in Table 7.2.

Figure 7.9a

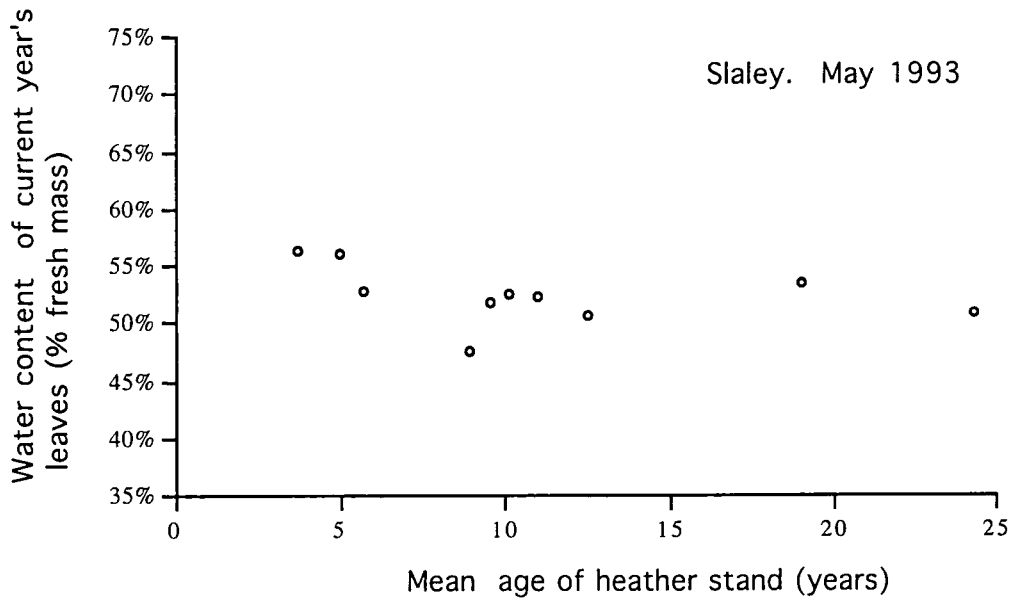
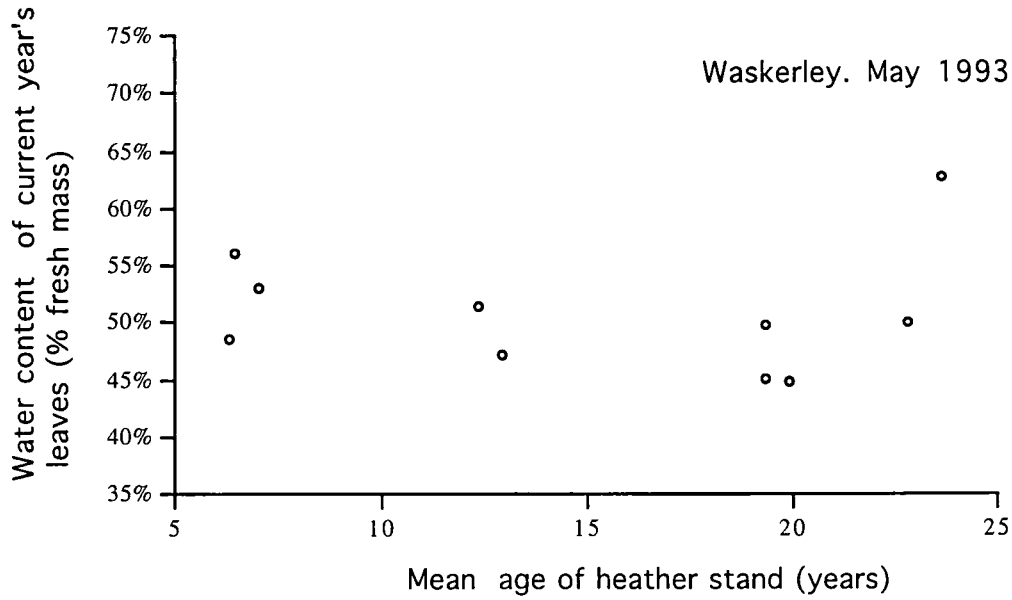


Figure 7.9b



Figures 7.9a and 7.9b. The water content of *Calluna* samples taken from the ten stands studied at the Slaley and Waskerley field sites in May 1993. Samples were derived from 20 plants collected in the field. Figure 7.9a shows the water content of current year's leaves, Figure 7.9b the water content of previous years' leaves. Estimates of water content were based on two replicates from each stand and leaf class. There was no significant relationship between plant age and leaf water content. Linear correlation statistics are given in Table 7.3.

Figure 7.10a

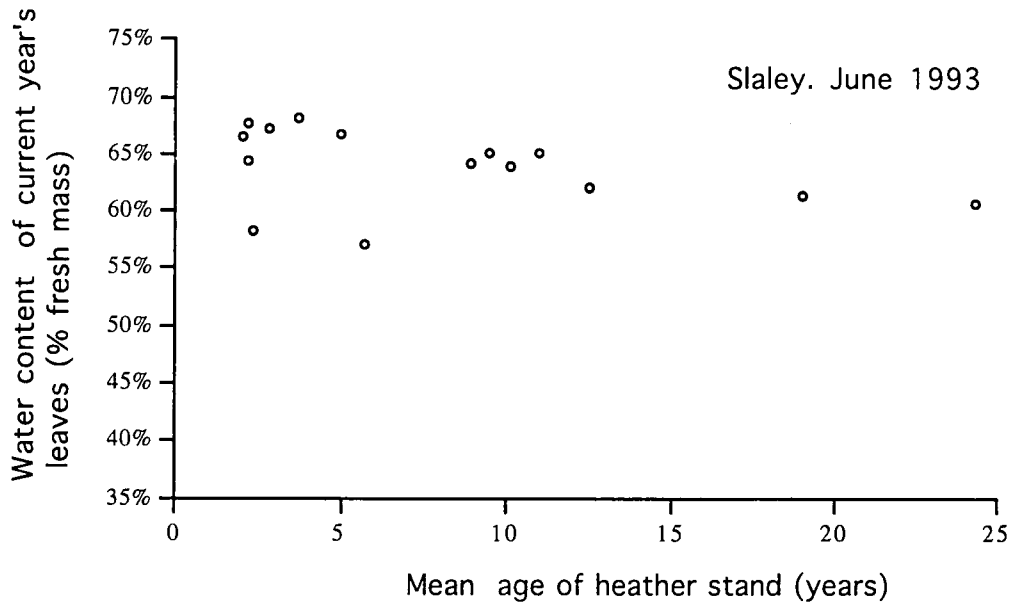
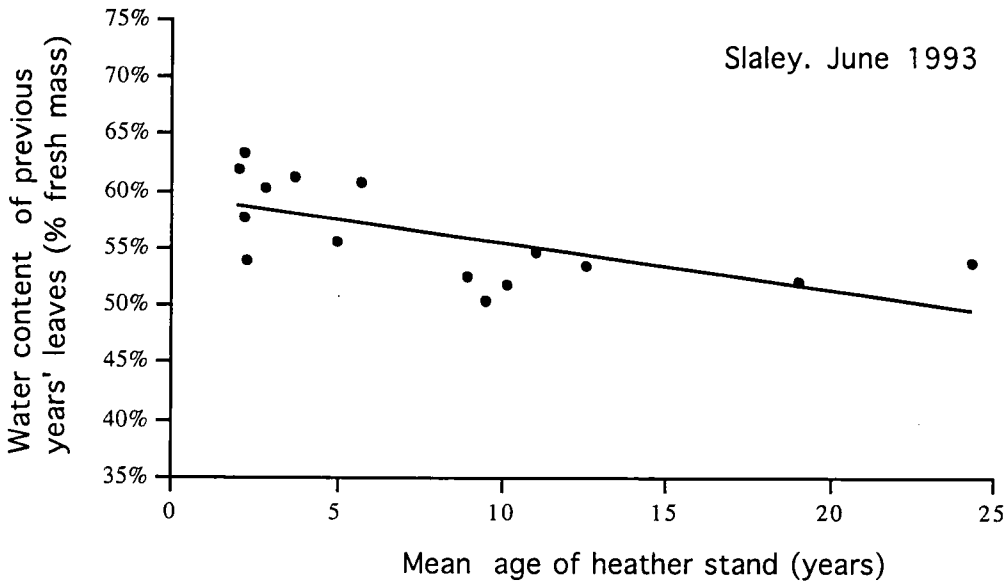


Figure 7.10b



Figures 7.10a and 7.10b. The water content of *Calluna* samples taken from the 15 stands studied at the Slaley field site in June 1993. Samples were derived from 20 plants collected in the field. Figure 7.10a shows the water content of current year's leaves, Figure 7.10b the water content of previous years' leaves. Estimates of water content were based on two replicates from each stand and leaf class. There was no significant relationship between plant age and leaf water content in Figure 7.10a and linear correlation statistics for this Figure are given in Table 7.3. Regression analysis of 7.10b gives $Y = -0.404(\pm 0.140)X + 59.5(\pm 1.4)$, df=13, r=0.63, P<0.02. Y is leaf water content (% fresh mass) and X is plant age (years).

Figure 7.11a

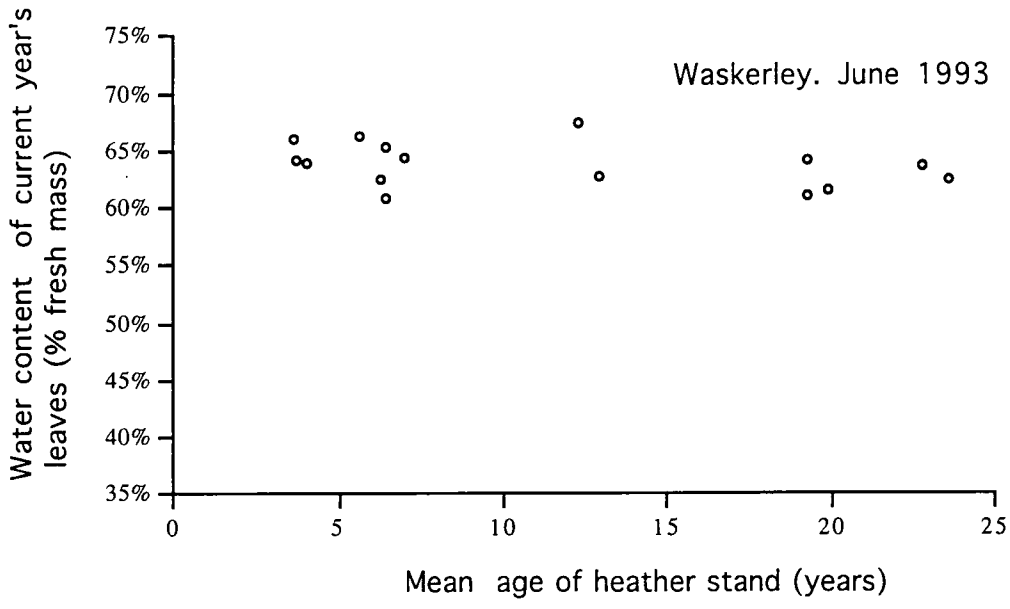
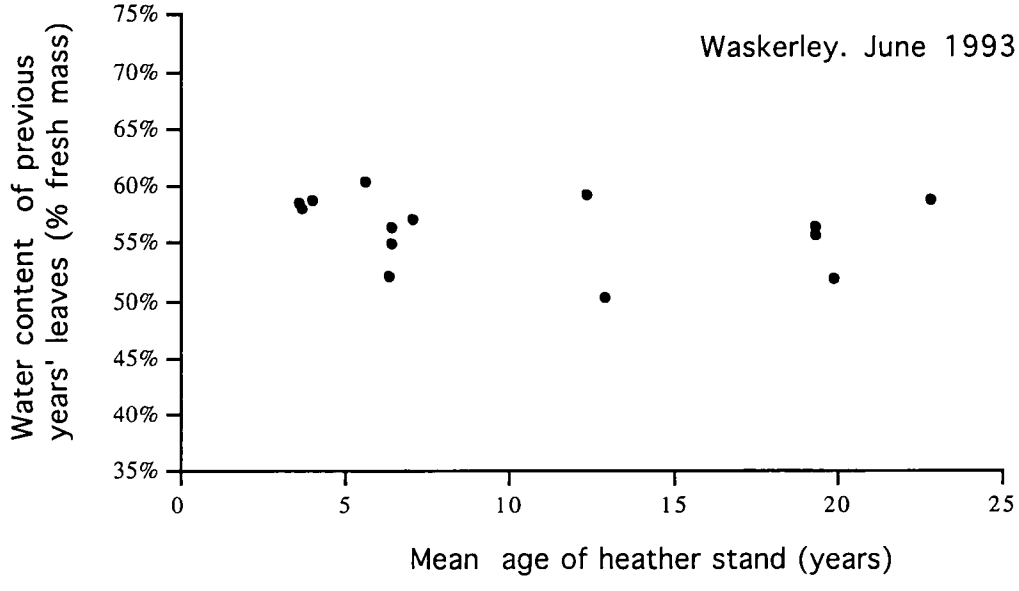


Figure 7.11b



Figures 7.11a and 7.11b. The water content of *Calluna* samples taken from the 15 stands studied at the Waskerley field site in June 1993. Samples were derived from 20 plants collected in the field. Figure 7.11a shows the water content of current year's leaves, Figure 7.11b the water content of previous years' leaves. Estimates of water content were based on two replicates from each stand and leaf class. There was no significant relationship between plant age and leaf water content. Linear correlation statistics are given in Table 7.3.

Figure 7.12a

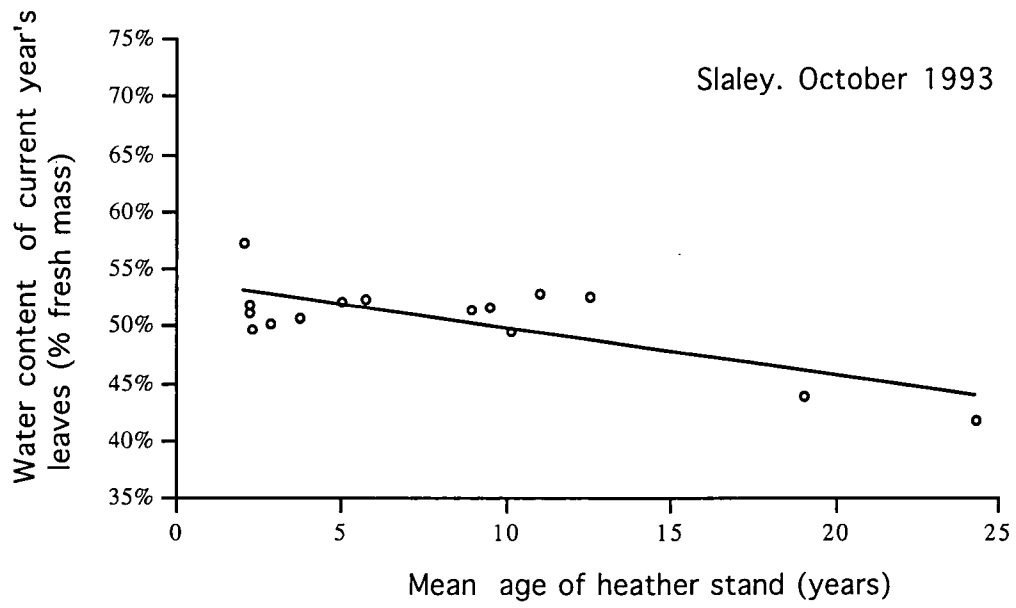
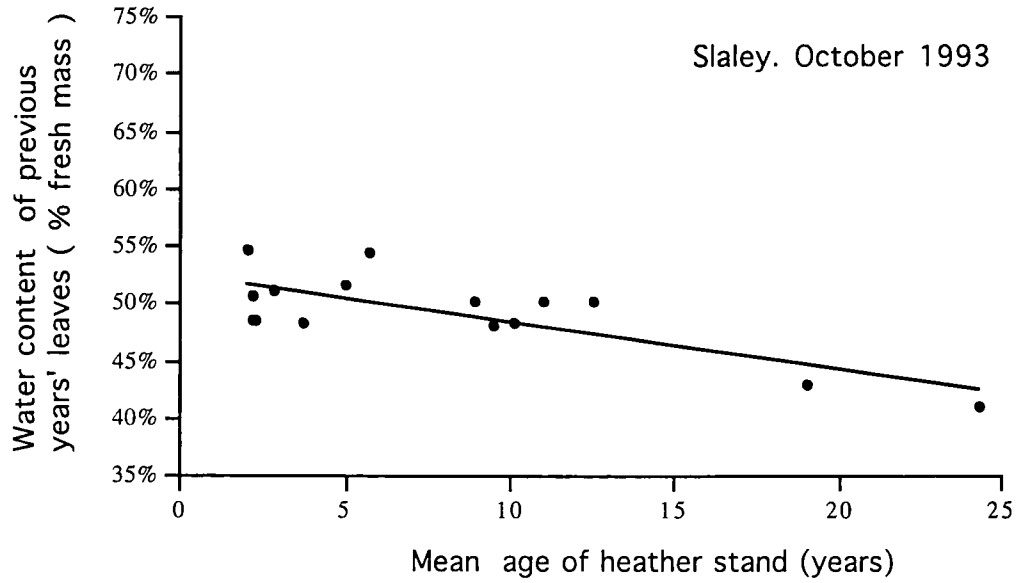


Figure 7.12b



Figures 7.12a and 7.12b. The water content of *Calluna* samples taken from the 15 stands studied at the Slaley field site in 1993. Samples were derived from 20 plants collected in the field. Figure 7.12a shows the water content of current year's leaves, Figure 7.12b the water content of previous years' leaves. Estimates of water content were based on two replicates from each stand and leaf class. Regression analysis of 7.12a gives $Y = -0.409(\pm 0.100)X + 53.9(\pm 1.0)$, df=13, r=0.75, P<0.01. Regression analysis of 7.12b gives $Y = -0.415(\pm 0.096)X + 52.6(\pm 1.0)$, df=13, r=0.77, P<0.001. Y is leaf water content (% fresh mass) and X is plant age (years).

Figure 7.13a

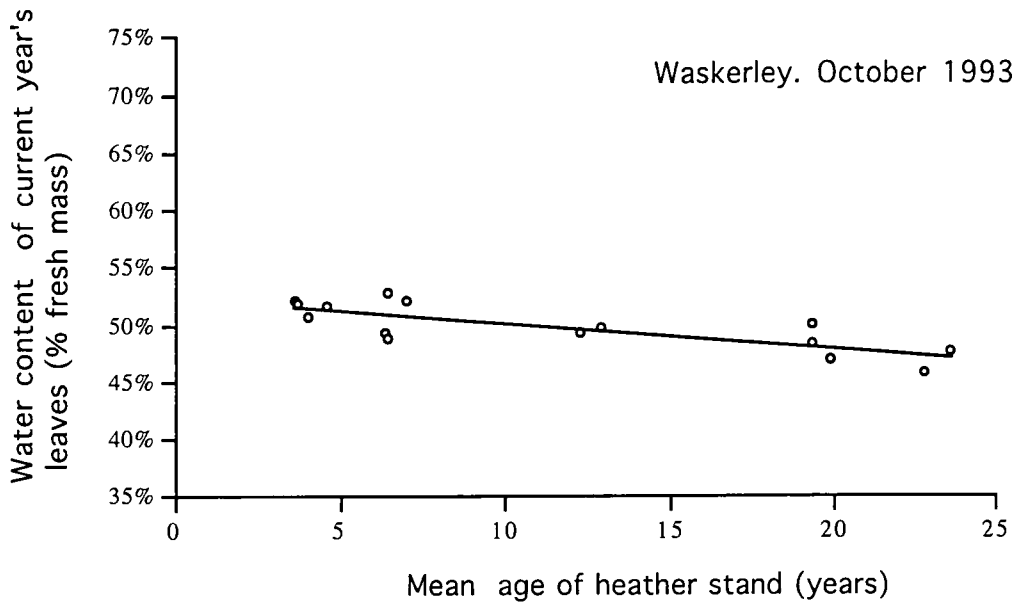
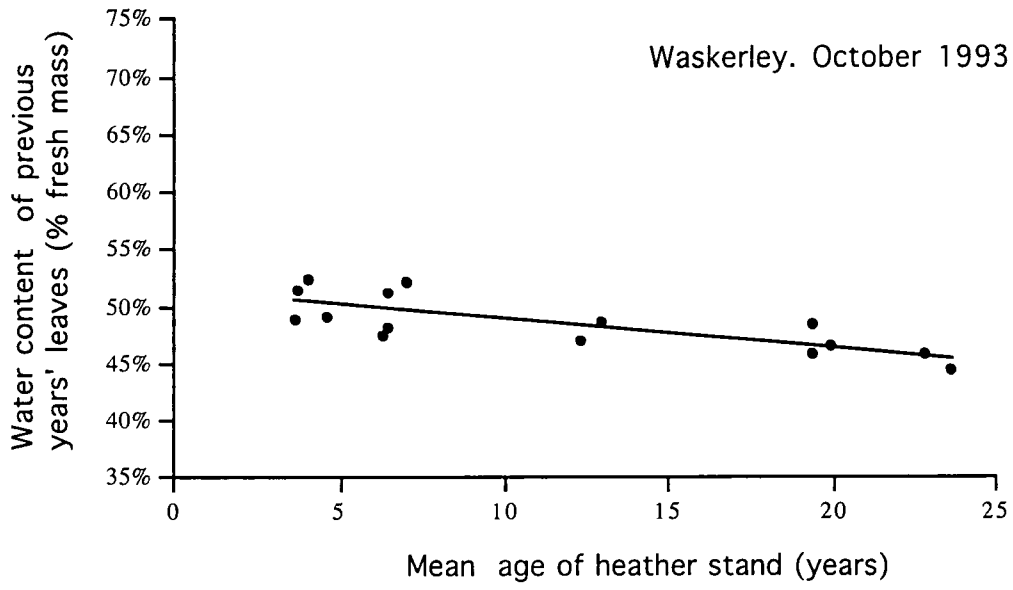


Figure 7.13b



Figures 7.13a and 7.13b. The water content of *Calluna* samples taken from the 15 stands studied at the Waskerley field site in October 1993. Samples were derived from 20 plants collected in the field. Figure 7.13a shows the water content of current year's leaves, Figure 7.13b the water content of previous years' leaves. Estimates of water content were based on two replicates from each stand and leaf class. Regression analysis of 7.13a gives Y = -0.226(± 0.046)X + 52.4(± 0.6), df=13, r=0.81, P<0.001. Regression analysis of 7.13b gives Y = -0.256(± 0.056)X + 51.4(± 0.8), df=13, r=0.78, P<0.001. Y is leaf water content (% fresh mass) and X is plant age (years).

Site	Date	Leaf Year Class	df	r	P
Slaley	June 1993	Current	12	-0.31	NS
Slaley	June 1993	Previous	13	-0.44	NS
Waskerley	June 1993	Current	12	-0.37	NS
Waskerley	June 1993	Previous	11	-0.37	NS

Table 7.1. The relationship between *Calluna* age and the concentration of total nitrogen in the leaves measured by linear correlation. Leaves were separated into current year's and previous years' growth. Concentrations were expressed as "% dry mass". NS denotes non-significance at the 0.05 probability level.

Site	Date	Leaf Year Class	df	r	P
Slaley	May 1993	Current	8	-0.36	NS
Slaley	May 1993	Previous	7	0.49	NS
Slaley	June 1993	Current	13	-0.51	NS
Slaley	June 1993	Previous	13	-0.29	NS
Slaley	October 1993	Current	13	0.13	NS
Slaley	October 1993	Previous	13	0.15	NS
Waskerley	May 1993	Current	8	0.28	NS
Waskerley	May 1993	Previous	8	-0.10	NS
Waskerley	June 1993	Current	13	0.05	NS
Waskerley	June 1993	Previous	12	0.04	NS
Waskerley	October 1993	Current	13	-0.10	NS
Waskerley	October 1993	Previous	13	-0.34	NS

Table 7.2. The relationship between *Calluna* age and the concentration of total phenolics in the leaves measured by linear correlation. Leaves were separated into current year's and previous years' growth. Concentrations were expressed as "% dry mass". NS denotes non-significance at the 0.05 probability level.

Site	Date	Leaf Year Class	df	r	P
Slaley	May 1993	Current	8	-0.38	NS
Slaley	May 1993	Previous	8	-0.23	NS
Slaley	June 1993	Current	13	-0.34	NS
Slaley	June 1993	Previous	13	-0.63	<0.02
Slaley	October 1993	Current	13	-0.75	<0.01
Slaley	October 1993	Previous	13	-0.77	<0.001
Waskerley	May 1993	Current	8	0.01	NS
Waskerley	May 1993	Previous	8	0.01	NS
Waskerley	June 1993	Current	13	-0.39	NS
Waskerley	June 1993	Previous	12	-0.25	NS
Waskerley	October 1993	Current	13	-0.81	<0.001
Waskerley	October 1993	Previous	13	-0.78	<0.001

Table 7.3. The relationship between *Calluna* age and the water content of leaves measured by linear correlation. Leaves were separated into current year's and previous years' growth. Water contents were expressed as "% fresh mass". NS denotes non-significance at the 0.05 probability level.

Site	Date	Number of stands	Mean value of current year's / previous years' concentration	SD	SE
Slaley	June 1993	13	1.48	0.39	0.11
Waskerley	June 1993	13	1.29	0.17	0.05

Table 7.4. The order of the difference in concentration of nitrogen between current and previous years' leaves. Values were calculated by dividing the concentration in the current year's leaves by that of the previous years' leaves in each stand, and computing the mean of these values for each site.

Site	Date	Number of stands	Mean value of current year's / previous years' concentration	SD	SE
Slaley	May 1993	9	1.33	0.23	0.08
Slaley	June 1993	15	1.37	0.19	0.05
Slaley	October 1993	15	1.25	0.34	0.09
Waskerley	May 1993	10	1.98	0.95	0.30
Waskerley	June 1993	14	1.40	0.62	0.17
Waskerley	October 1993	15	1.09	0.26	0.07

Tables 7.5. The order of the difference in concentration of phenolics between current and previous years' leaves. Values were calculated by dividing the concentration in the current year's leaves by that of the previous years' leaves in each stand, and computing the mean of these values for each site and month.

Site	Date	Number of stands	Mean value of current year's / previous years' concentration	SD	SE
Slaley	June 1993	15	1.14	0.09	0.02
Slaley	October 1993	15	1.03	0.03	0.01
Waskerley	June 1993	14	1.14	0.05	0.01
Waskerley	October 1993	15	1.03	0.03	0.01

Table 7.6. The order of the difference in water content between current and previous years' leaves. Values were calculated by dividing the concentration in the current year's leaves by that of the previous years' leaves in each stand, and computing the mean of these values for each site and month.

Site	Date	t	df	P
Slaley	June 1993	5.32	13	<0.001
Waskerley	June 1993	6.21	11	<0.001

Table 7.7. The difference between the nitrogen contents of current and previous years' *Calluna* leaves measured by paired t-tests. Samples were collected from two sites in three months in 1993. Concentrations were expressed as "% dry mass" and were normalised by arcsine transformation before t-tests were applied.

Site	Date	t	df	P
Slaley	May 1993	4.62	8	<0.01
Slaley	June 1993	8.62	14	<0.001
Slaley	October 1993	2.65	14	<0.02
Waskerley	May 1993	3.60	9	<0.01
Waskerley	June 1993	2.49	13	<0.05
Waskerley	October 1993	0.76	14	NS

Table 7.8. The difference between the phenolic contents of current and previous years' *Calluna* leaves measured by paired t-tests. Samples were collected from two sites in three months in 1993. Concentrations were expressed as "% dry mass" and were normalised by arcsine transformation before t-tests were applied.

Site	Date	t	df	P
Slaley	June 1993	6.16	14	<0.001
Slaley	October 1993	3.28	14	<0.01
Waskerley	June 1993	11.81	13	<0.001
Waskerley	October 1993	3.79	14	<0.01

Table 7.9. The difference between the water contents of current and previous years' *Calluna* leaves measured by paired t-tests. Samples were collected from two sites in three months in 1993. Concentrations were expressed as "% fresh mass" and were normalised by arcsine transformation before t-tests were applied.

Figure 7.14

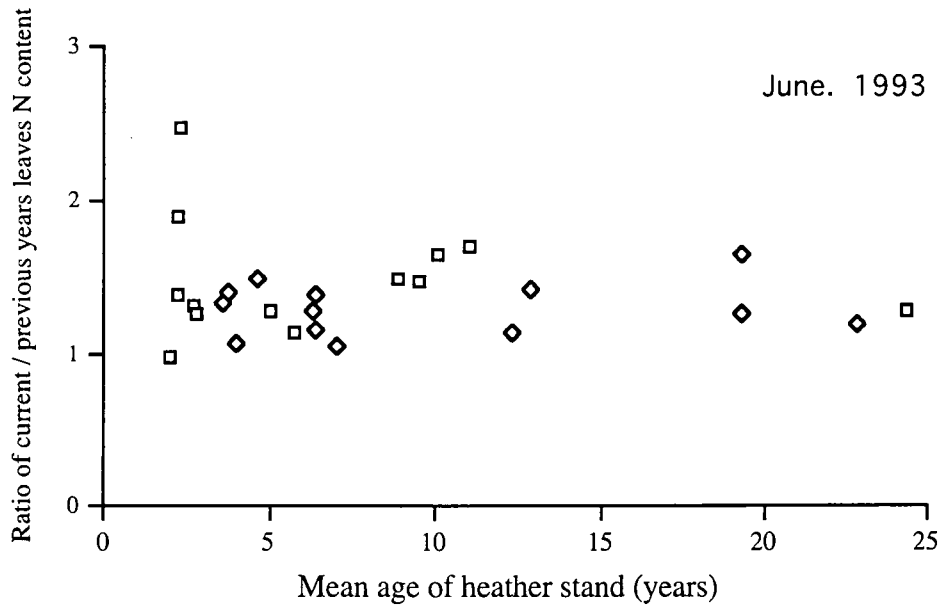
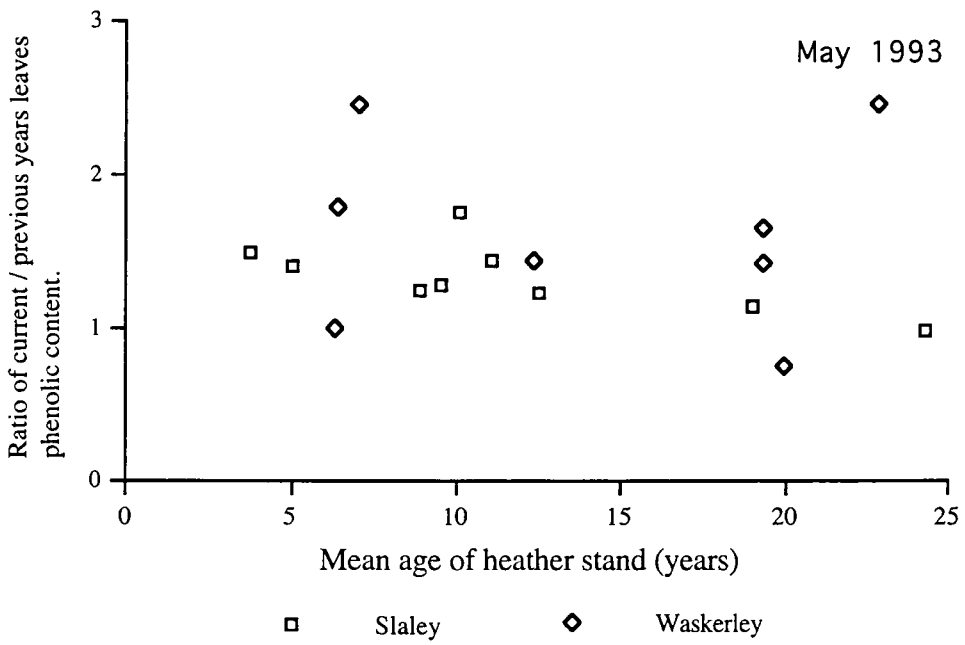


Figure 7.15a



Figures 7.14 and 7.15 a. The order of the difference in chemical concentration between current and previous years' leaves. Results from both Slaley and Waskerley have been combined. Figure 7.14 shows the difference in nitrogen concentration, Figure 7.15a the difference in phenolics between current and previous years' leaves. Results of t-tests are presented in Tables 7.7 and 7.8.

Figure 7.15b

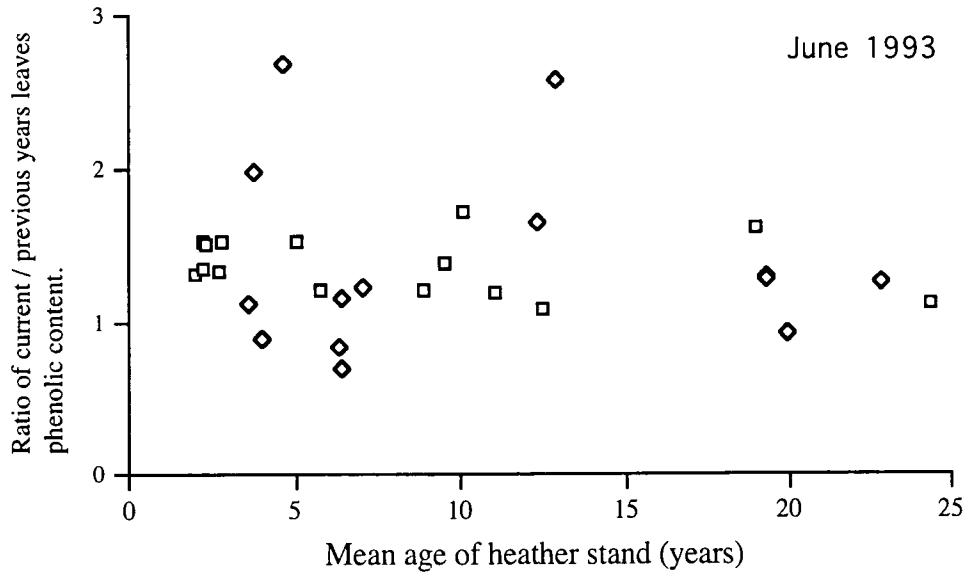
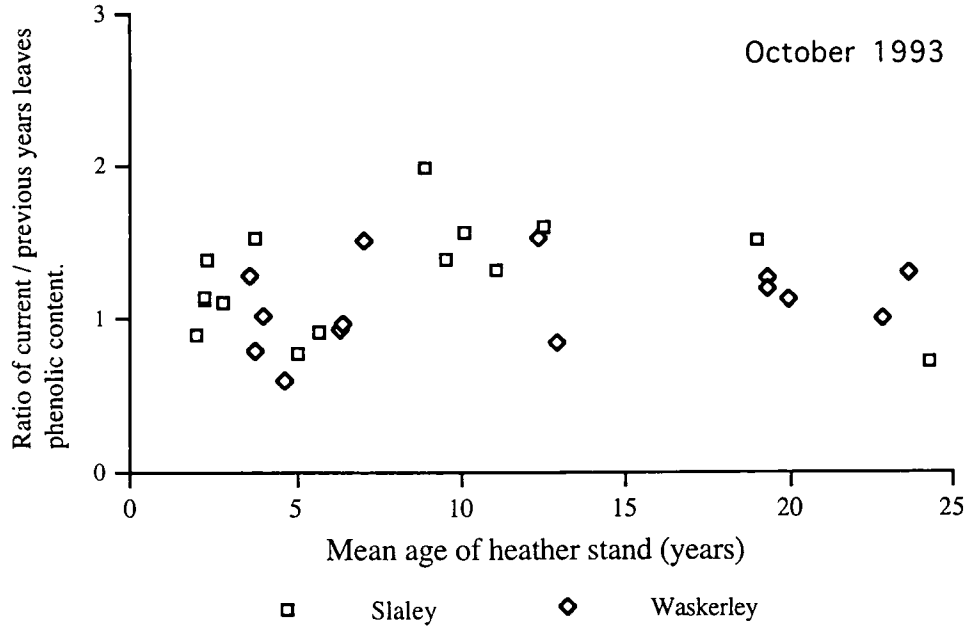


Figure 7.15c



Figures 7.15b and 7.15c. The order of the difference in total phenolics concentration between current and previous years' leaves. Results from both Slaley and Waskerley have been combined. Figure 7.15b shows results from June samples, Figure 7.15c those from October samples. Results of t-tests are presented in Table 7.8.

Figure 7.16a

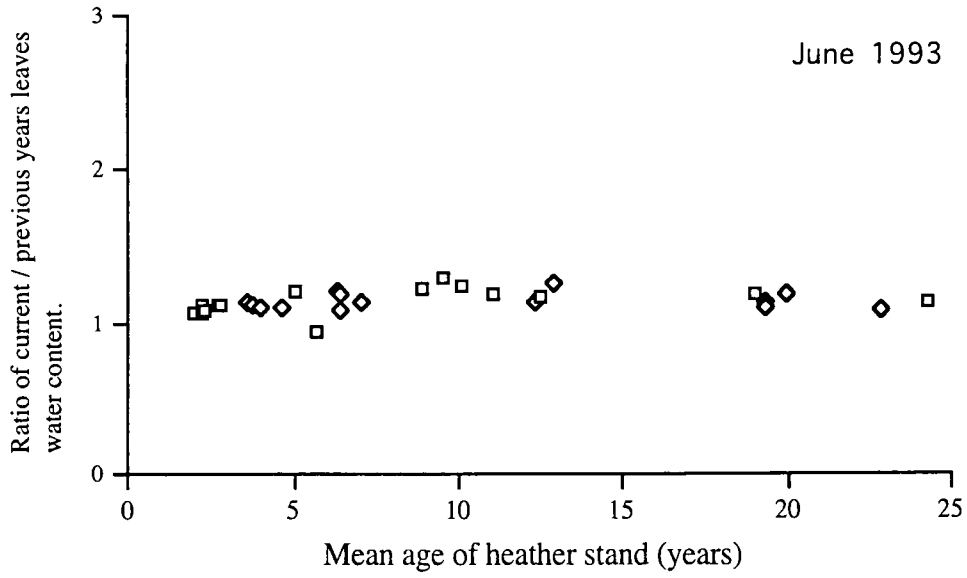
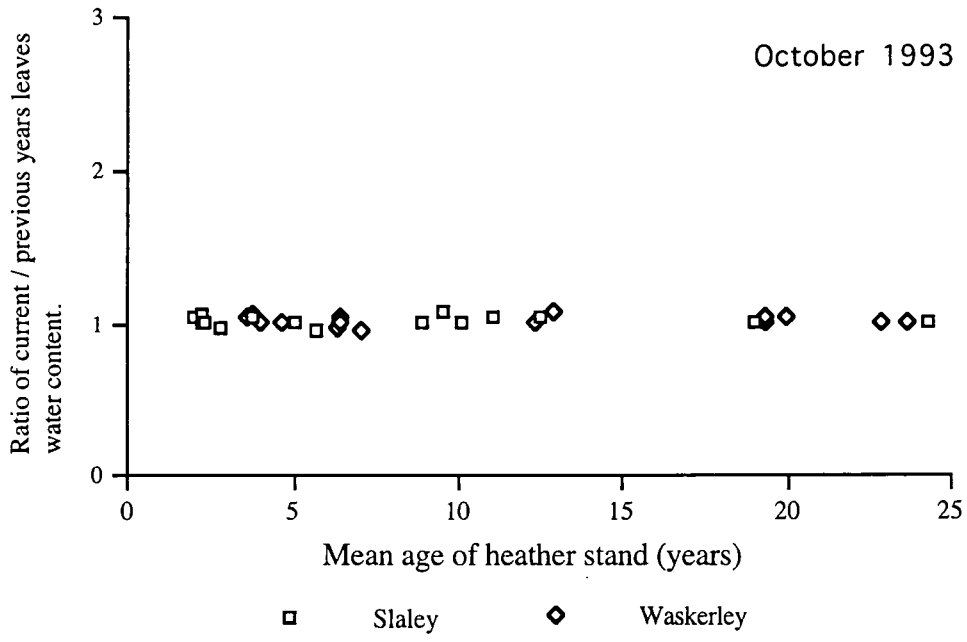


Figure 7.16b



Figures 7.16a and 7.16b. The order of the difference in water content between current and previous years' leaves. Results from both Slaley and Waskerley have been combined. Figure 7.16a shows the difference in June samples, Figure 7.16b the difference in October samples. Results of t-tests are presented in Table 7.9.

Site	Variable 1	Variable 2	df	r	P
No significant correlations at either site					

Table 7.10a. The relationships between the chemical constituents analysed in the *Calluna* samples in May 1993, measured by linear correlation. Only significant correlations between variables are shown.

Site	Variable 1	Variable 2	df	r	P
Slaley	current N	previous N	12	0.68	<0.01
Slaley	current phenolics	previous phenolics	13	0.71	<0.01
Waskerley	current N	previous N	10	0.72	<0.01
Waskerley	current N	previous water	11	0.61	<0.05
Waskerley	current water	previous water	12	0.61	<0.02
Waskerley	current phenolics	previous phenolics	12	0.65	<0.02

Table 7.10b. The relationships between the chemical constituents analysed in the *Calluna* samples in June 1993, measured by linear correlation. Only significant correlations between variables are shown.

Site	Variable 1	Variable 2	df	r	P
Slaley	current water	previous water	13	0.91	< 0.001
Slaley	current phenolics	previous phenolics	13	0.52	<0.05
Waskerley	current water	previous water	13	0.83	< 0.001
Waskerley	current phenolics	previous phenolics	13	0.69	<0.01

Table 7.10c. The relationships between the chemical constituents analysed in the *Calluna* samples in October 1993, measured by linear correlation. Only significant correlations between variables are shown.

7.3.4 Trends with season

There are insufficient data to make detailed comments on changes in the chemical concentration of nitrogen, phenolics and water in leaves through the season, and this was not a priority of the study. Nitrogen was examined only in June, and concentrations of phenolics in leaves are not directly comparable between months. This was because although a test sample was analysed to check the consistency of results through every batch, the test sample maintained consistent results within a sampling month, but changed between months. The water content of younger leaves was higher in June, the peak of the growing season, than in May or October (Figures 7.17a-b). The difference between water content in the current and previous years' leaves was also greater in June at both sites (Table 7.6).

7.4 Discussion

7.4.1 The effect of plant age on leaf chemical composition

The total nitrogen concentration in different plant tissues varies between 0.03% and 7.0% of dry weight, but the highest concentrations (3-7%) are found in young actively growing, or storage tissues such as meristems and seeds (Mattson 1980). On this scale, the nitrogen levels found in *Calluna* leaves in June were low. Values in this study ranged between minimum 0.20% to maximum 1.81%. Valid comparisons with absolute concentrations quoted in other studies of *Calluna* cannot be made because of differences in harvest date and extraction techniques but nitrogen concentrations ranging between 0.03% and 2.85% (Miller 1979) and 1.15% to 2.05% (Moss *et al.* 1972) can be similarly regarded as low. Studies investigating crude protein content in *Calluna* have also found this to be less than the average 13.4% dry weight calculated from 400 plant species (Russell 1947 in McNeill & Southwood 1978). Estimates of crude protein concentration in *Calluna* include ranges of 6.9-11.9% and 6.6-9.7% (Thomas 1934; Milne 1974) respectively.

Quantities of total phenolics in the *Calluna* samples cannot be compared with other published work. Different techniques tend to extract different phenolic components and although the results from some total phenolic extraction methods *e.g.* the Folin-Denis and Hagerman & Butler techniques, correlate closely, many others do not (Mole & Waterman 1987). So only the trends produced in this study, not absolute concentrations may be compared with other work.

None of the other studies investigating *Calluna* has tabulated the concentration of water in either current or previous years' leaves, so again no comparisons can be drawn.

Figure 7.17a

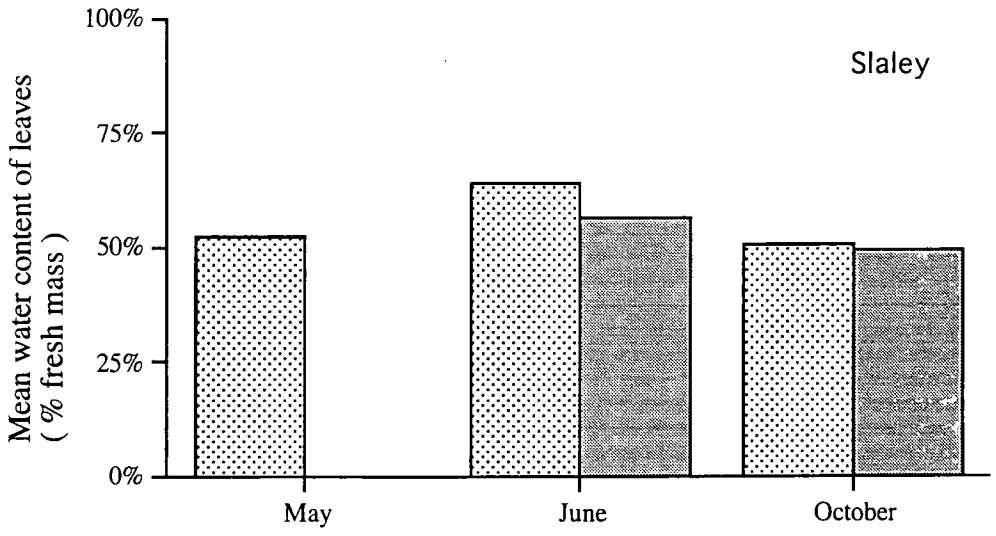
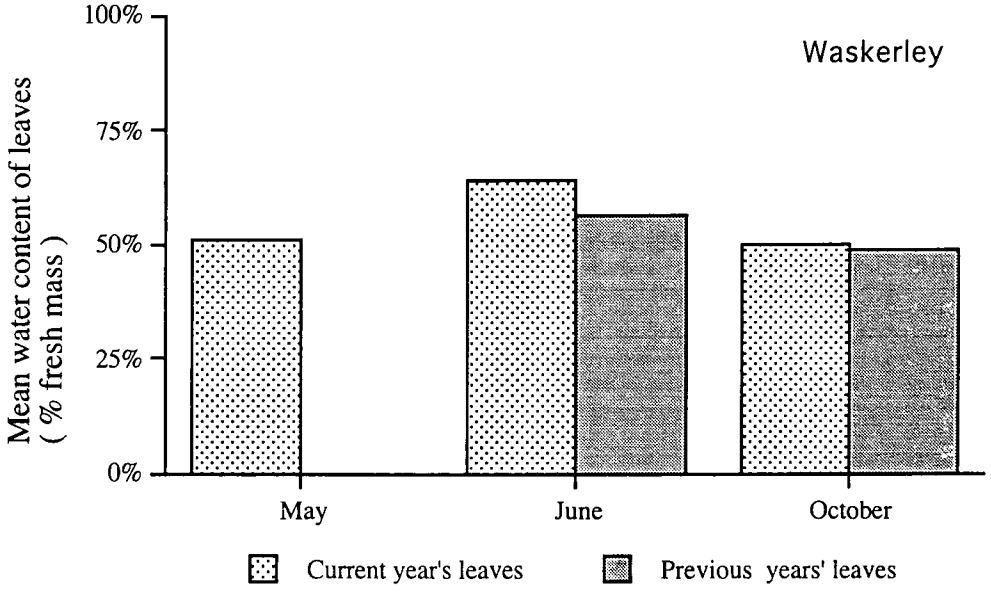


Figure 7.17b



Figures 7.17a and 7.17b. The mean water content of leaves from the different aged stands at Slaley and Waskerley during May, June and October 1993. Ten stands were sampled at each site in May, 15 stands in June and October. Leaf tissue has been separated into current year's and previous years' growth.

The total concentrations of nitrogen, phenolics and water in current and previous years' leaves were examined with respect to the seral age of *Calluna* stands. Only the water content of all October samples and the previous years' leaves from Slaley in June, showed a significant relationship with stand age ($P<0.05$ - $P<0.001$) with water content decreasing linearly with increasing stand age. This contrasts with several other studies of *Calluna* where concentrations of nutrients, particularly nitrogen and phosphorus, change with plant age. Generally, the concentration of leaf nitrogen has been found to decline as *Calluna* grows older, and is highest in the young *Calluna* that grows back in an area of burned moorland (Thomas 1934; Lauder & Comrie 1936; Moss *et al.* 1972). Age-related changes in *Calluna* chemistry vary in different plant parts. If concentrations of nitrogen, sodium, potassium, calcium, magnesium, phosphorus and soluble carbohydrate of whole stands including stems were analysed, nutrient concentration increased with age until stands were 15-20 years old, but concentrations in the shoot tips fell annually to the fourth year after burning (Miller 1979). Where nutrient decreases were observed, the steepest declines in nitrogen or protein occurred when heather was 2-4 years old (Thomas 1934; Moss *et al.* 1972; Miller 1979). This may explain why no significant relationship between leaf nitrogen concentration and plant age was found in this study. The youngest stands at Slaley were approximately 2 years-old, but at Waskerley it was difficult to find any stands younger than 3-4 years. Had younger stands been included, further trends in nutrient concentration may have been observed. Leaves from 2-year-old stands at Slaley did not, however, show extremely high nitrogen concentrations. Differences in the soil nutrient concentrations below Waskerley and Slaley stands could have outweighed any age related effects.

Moss *et al.* (1972) found soluble tannin concentrations that varied between stands, but these were not related to seral age. This study also showed large variations in total phenolic concentrations between stands, that were not correlated with plant age. Although the phenolic components measured were not identical, the two studies appear to agree.

In other plant species, changes in foliar nitrogen concentration with plant age are well documented. Nitrogen requirements and concentrations are often highest in juvenile stages, and total nitrogen decreases with the addition of nitrogen poor tissues (Mattson 1980). Although studies describing nitrogen changes with leaf age are more common, nitrogen and other nutrients can decline with plant age (Rodin & Bazilevich 1967) or factors related to age *e.g.* plant size. Competition from other plants can also cause a decline in leaf nitrogen (Mitchell & Chandler 1939). This could be particularly relevant to *Calluna* stands, where plants colonise the gaps created by fire and as stand density increases, individual *Calluna* plants may compete with neighbours for soil nutrients.

The studies reviewed focused on the role of leaf age, rather than plant age on foliar water concentration. Studies describing changes in the defensive chemistry of a single ageing plant species, apart from *Calluna*, could not be found.

7.4.2 The effect of leaf age on leaf chemical composition

In all except one sample (Waskerley, October) the total concentrations of nitrogen, phenolics and water were significantly higher in the current year's leaves ($P<0.03$ - $P<0.001$, Tables 7.4-7.9). As previous years' leaves may be retained on *Calluna* for up to four years (Gimingham 1960; Chapman *et al.* 1975; Gimingham *et al.* 1979), the difference in leaf age to cause this effect was between 1 and 3 years. The average order of the difference was up to 1.5 times greater for nitrogen, up to 2 times greater for phenolics but no more than 1.14 times greater for water. Other studies imply that current shoots are nutritionally richer, but only Miller (1979) quantified these differences. Miller described the amounts (gm^{-2}) of mineral nutrients in different components of *Calluna* stands. Since the concentrations of nutrients in the current and previous years' leaves were incorporated with a measure of plant abundance, his results cannot be compared with this study. Most other *Calluna* studies have focused on one tissue type in order to relate work to the voluntary dietary intake of moorland animals or birds. Hence Moss *et al.* (1972) selected the top 1cm current year's shoots believed to be eaten by grouse, while Godden (reported in Thomas 1956) "took only the parts sheep were presumed to eat". This study examined both current and previous shoots because the feeding preferences of *Calluna* feeding caterpillars are largely unknown.

In other plants, foliar nitrogen concentration is frequently higher in young leaves than mature leaves (Feeny 1970; McNeill & Southwood 1978; Scriber 1977; Scriber & Feeny 1979; Mattson 1980; Scriber & Slansky 1981; Damman 1987; Meyer & Montgomery 1987; Stamp & Bowers 1990). Water content is also often higher in younger leaves (Woodwell 1974; Scriber 1977; Schweitzer 1979; Scriber & Slansky 1981; Stamp & Bowers 1990).

Depending on plant species, phenolics can be present in higher concentrations in either young or old leaves. The oak *Quercus robur* (Feeny 1970, 1976), the bracken fern *Pteridium* and toyon *Heteromeles* (Rhoades & Cates 1976) all have greater tannin concentrations in the mature leaves. This phenomenon has been recorded for many other plant species (Orians & Janzen 1974 in Coley 1983; McKey 1979). In other species *e.g.* cottonwood tree *Populus deltoides* (Meyer & Montgomery 1987), creosote bush *Larrea* (Rhoades & Cates 1976), eucalypts (Macauley & Fox 1980 in Mattson 1980) and many rainforest trees (Coley 1983) concentrations of phenolic resins or tannins are much higher in young leaves. The difference in age between "young leaves"

and "old leaves" is set by phenology and lifeform. Plants like the oak have a single, synchronous flush of leaf growth each year (Feeny 1970). The leaf primordia are preformed during the previous season and leaf growth is completed within a few weeks of budburst. This is fixed or determinate growth (Meyer & Montgomery 1987) and because all the young leaves mature together, the degree of leaf maturity is determined by season. In free or indeterminate growth, leaves arise from primordia formed during the course of the growing season. Leaf growth continues late into the year and at any point immature and mature leaves may be present together on one bush. The "predictable", "apparent" plant versus "unpredictable", "unapparent" hypothesis (Feeny 1976; Rhoades & Cates 1976) can be adapted to the leaf resource so that fixed or determinate plants *e.g.* oak with one short burst of leaf growth, can effectively avoid some herbivores in space and time and reduce the "expense" of utilising generalised defensive compounds *e.g.* tannins in their young, unpredictable stages. The indeterminate, free growth plants such as *Larrea* have a predictable young leaf resource throughout the season and should benefit by the use of digestibility reducing substances (Rhoades & Cates 1976). The long shoots of *Calluna* expand through a growing season that begins in late May and ends in October. Like *Larrea*, the youngest shoots are retained longer than the oldest leaves in times of stress. Hence the plant apparentness hypothesis could predict higher levels of phenolic compounds in the youngest leaves of this species, although because of its dominant, evergreen lifeform one would expect phenolic compounds to be present in all leaves. It should also be recognised that tannins may be more readily extracted from young leaves than mature leaves, because they are not bound into permanent plant structures (Bate-Smith 1973; Oates *et al.* 1980). This has been countered by Coley (1983) in instances where differences seem too large (2-3 times) to be explained in this way.

7.4.3 The effect of season on leaf chemical composition

Although plant samples were collected at three stages of the growing season, it was not a primary objective of this study to quantify changes in concentration of chemical components with time. However, some seasonal differences were apparent. Water concentration was greater in both leaf ages at the peak of the growing season in June. This may reflect the increased metabolic demands on tissues at this time. Phenolic concentrations were difficult to compare between months for reasons described earlier. The number and quantity of phenolic substances in *Calluna* shoots does fluctuate seasonally, peaking in the summer and becoming minimal in January and February (Jalal *et al.* 1982). Seasonal fluctuation in foliar nitrogen and other nutrients has been reported in *Calluna* (Lauder & Comrie 1936; Thomas 1937; Miller 1979). In other plants, decreases in nitrogen concentration (Myers 1981) or nitrogen and water content

(Stamp & Bowers 1990) have been observed through the growing season. Changes in phenolic concentration as a function of season have also been described (Meyer & Montgomery 1987).

7.4.4 The effect of leaf chemical composition on Lepidoptera larvae

Some insects have been shown to reach greater densities, or achieve higher rates of survival or growth on plants, or plant parts that have higher nitrogen and water concentrations (Schweitzer 1979; Scriber & Slansky 1981; Stamp & Bowers 1990). Leaf water is of particular importance and if suboptimal may affect the efficient utilisation of food materials. In experiments with excised leaves, larval growth of 16 species of Lepidoptera was suppressed unless leaf water content was maintained near saturation level via high humidities and leaf water supplementation via the petiole (Scriber 1979).

If leaf water concentration played a key role in the survival or growth rate of caterpillars on heathland, one might expect to find higher densities of larvae in the shorter, younger *Calluna* stands where water concentration was greatest, at least in the autumn when this trend was observed. As density trends actually occurred in the opposite direction, it seems improbable that water content alone determines the distribution of Lepidopteran larvae among the different aged stands. It is possible that other factors *e.g.* predation or parasitism prevent the expression of these trends in the field. For example, the need for shelter against predators was more important than utilisation of the richest nutritional resources for caterpillars of a pyralid moth *Omphalocerca munroei* feeding on papaw *Asimina* (Damman 1987). Experiments manipulating the water and nitrogen concentrations of *Calluna* in the laboratory, and monitoring their effects on larval survival could produce different results to field feeding-trials.

Reduced survival and slower growth rates have also been linked to higher concentrations of phenolics in food-plants (Feeny 1969, 1970; Meyer & Montgomery 1987). It is usually assumed that phenolics lower growth rate by lowering the availability of nitrogen from digestion (Feeny 1970; Rhoades & Cates 1976) or by causing animals to reduce their voluntary intake of tanniniferous foods (Bryant & Kuropat 1980; Robins *et al.* 1987). The role of phenolic substances as dosage dependant antiherbivore defences is now controversial. Insects may be able to block the formation of tannin-protein complexes by maintaining gut pH above 8.5 and possibly by possessing surfactants able to interfere with protein precipitation at lower pH (Martin & Martin 1984). It may also be unwise to generalise about the relationships between insects and tannins since the effects of an individual hydrolysable tannin,

tannic acid, and the condensed tannin, quebracho were different on several related Acridids (Bernays 1978, 1981). Furthermore, in low concentration tannic acid acted as a phagostimulant when used to coat food offered to eight species of Lepidoptera larvae (Bernays 1981).

Analyses of "total nitrogen" and "total phenolics" may have been too crude to relate to trends of Lepidoptera larval distribution across heathland. This has been a problem in other studies. Not all the nitrogen in the plant may be available to the insect or the balance of amino acids present might be unsuitable (McNeill & Southwood 1978). For example, correlation of the population density of the whitefly *Aleurotrachus jelinekii* with total nitrogen of foodplant *Viburnum tinus* was not significant, but density was related to the distribution of ten essential amino acids (McNeill and Southwood 1978). Similarly, since the maxillary sensilla of different insects respond to different phenolic compounds, and sensitivity varies (Den Otter 1992) a blanket measure of total phenolics might not show genuine trends related to more specific compounds (Vicari & Bazely 1993). In 6 species of oak, there was no correlation between protein-precipitating capacity and either total phenolic or proanthocyanidin content (Martin & Martin 1982). In a study of this kind it may therefore be prudent to include a protein-precipitation assay in addition to measures of phenolic quantity.

The large variation in the concentration of phenolics in stands of similar age obscured any other trend that may have been related to seral age. Greater precision may have been obtained had more time been available to obtain and analyse more replicates. The spectrophotometric techniques applied relied on precise timing, and timing and dilution inaccuracies could both have increased "noise" in the results.

However, although only water concentration was seen to vary with age of *Calluna* during one month, and this could not account for the larva distributions observed, the larger differences in concentration of nitrogen, phenolics and water in current and previous years' leaves might determine the local feeding patterns of larvae on a bush.

Chapter Eight

Aspects of the Behaviour of Some Species of Heathland Lepidoptera Larvae

8.1 Introduction

This chapter is in three parts and examines several aspects of lepidopteran larval behaviour. The first two sections investigate whether some larvae prefer to feed on certain plant species or plant parts. The third section considers whether the density of some autumn species changes at different times of day.

With a few exceptions (*e.g.* Hodkinson 1973) most of the existing behavioural studies of animals that graze on heathlands have focused on mammalian herbivores *e.g.* red deer *Cervus elaphus*, sheep *Ovis aries*, mountain hares *Lepus timidus*, or avian herbivores *e.g.* red grouse *Lagopus lagopus scoticus* and ptarmigan *Lagopus mutus*. Studies have identified animals that selectively graze certain plant species (Nicholson *et al.* 1970; Grant & Hunter 1968; Watson 1964), particular plant parts (Thomas 1956), certain heights of *Calluna* (Moss *et al.* 1972) or different-aged *Calluna* plants (Miller & Miles 1969; Moss *et al.* 1972; Savory 1983). However, very little is known about the foraging behaviour of heathland Lepidoptera larvae. Fielding (unpublished Ph.D. thesis 1992) found that larvae of the July highflyer *Hydriomena furcata* were located more frequently on the tallest stems in mature phase *Calluna* stands and were most often found near the apex of the *Calluna* stems. Two colour forms of another geometrid, *Entephria caesiata*, preferred different ericaceous plants (Niemelä *et al.* 1980a).

This study exposed three common species of heathland Lepidoptera larvae to combinations of choices of three ericaceous plants, to determine whether some plants were consistently preferred. Two Lepidoptera species were monitored on *Calluna*, to investigate whether selection between leaves grown in current or previous seasons occurred.

Study animals were chosen from the three main families of Lepidoptera present on *Calluna* heath. They were the July highflyer *Hydriomena furcata* (Geometridae), the northern eggar *Lasiocampa quercus callunae* (Lasiocampidae) and the beautiful yellow underwing *Anarta myrtilli* (Noctuidae).

H. furcata has a one-year lifecycle. It overwinters as an egg, hatches in early May and feeds until June when it pupates. Early instar larvae are believed to feed at night (Carter & Hargreaves 1986; Emmet & Heath 1991). The caterpillar reaches a maximum length of approximately 20mm and feeds on sallow and willow *Salix*, poplar *Populus* hazel *Corylus*, bilberry *Vaccinium myrtillus* and *Calluna* (South 1961; Carter & Hargreaves 1986; Emmet & Heath; 1991).

The northern eggar *L. quercus callunae* has a two-year lifecycle and is widely regarded as a subspecies of the oak eggar *L. quercus quercus*, which has a one-year lifecycle. Subspecies status is debated, as larvae in some regions show phenotypic features of *callunae* but have a one-year lifecycle (Emmet & Heath 1991). *L. quercus callunae* adults lay eggs in June. These hatch in July and larvae feed until they enter diapause in October. The following May, larvae become active and feed until pupation in September. Larvae may exceed 80mm in length (Emmet & Heath 1991) and feed on *Calluna* and *V. myrtillus* (South 1961; Carter & Hargreaves 1986; Emmet & Heath 1991) or in captivity on *Salix* (Emmet & Heath 1991).

Adults of *A. myrtilli* have an extended flight and laying period, which lasts from April to August. Larvae may be found in most months of the year. Larvae which hatch in the summer feed until November, before they pupate or enter a larval diapause to overwinter. Individuals that overwinter as larvae become active in March and pupate between May and July. Larvae are up to 30mm long (Carter & Hargreaves 1986) and feed on *Calluna* and *Erica* spp. (South 1961; Carter & Hargreaves 1986; Emmet & Heath 1991) and possibly hawthorn *Crataegus monogyna* (South 1961).

The plant species that were offered to larvae were *Calluna* and two of its most common associates, *V. myrtillus* and cross-leaved heath *Erica tetralix*. All three are dwarf shrubs in the family Ericaceae and have similar growth forms. *Calluna* is a bushy, evergreen shrub which may reach 60cm tall. It has microphyllous leaves that are just 1-2mm long (Rose 1981). *E. tetralix* is shorter than *Calluna*. It grows up to 30cm tall and has a less erect, branched structure, which tends to straggle in competition with other species. The leaves are greyish and microphyllous and usually about 2-5mm long (Rose 1981). *V. myrtillus* is the only one of the three species to have macrophyllous and deciduous leaves. Its flat, oval, finely-toothed leaves are 1-3cm long and grow on bright green angled stalks (Rose 1981). *V. myrtillus* may be 20-60cm tall (Rose 1981). *Calluna* is the dominant plant on heathland (Pearsall 1950; Gimingham 1972). *Erica tetralix* may be found on the damper areas of heath and *V. myrtillus*, which is more shade tolerant, may occur below trees or form an understorey beneath the canopy of the less dense *Calluna* phases *i.e.* the pioneer and degenerate stages (Pearsall 1950; Gimingham 1972). After *Calluna* heathland has been burned, *V. myrtillus* and *Erica*

tetralix may be dominant to *Calluna* for several years because they recolonise burned ground more quickly (Gimingham 1972). Both *V. myrtillus* and *E. tetralix* initiate growth earlier in the year than *C. vulgaris* (Woolhouse & Kwolek 1981).

Studies of the spatial and temporal behaviour of heathland Lepidoptera larvae may benefit management and research practices. If larvae prefer foodplants other than *Calluna*, the addition of these species could provide extra food resources. Knowledge of temporal behaviour may be useful when interpreting data provided by different sampling methods.

8.2 Laboratory food preference tests

8.2.1 Methods

8.2.1.1 Preliminary experiments and design of the choice chamber

Choice chambers present study animals with two or more different foods simultaneously. Typically, herbivorous invertebrates are presented with leaf discs of equal area from several plant species (Jermy *et al.* 1968; Cates & Orions 1975). The area of leaf eaten from each species is measured, and these values are used to determine preference. The microphyllous leaf structure of *Calluna*, *E. tetralix* and several other species makes this an inappropriate technique for comparisons involving the Ericaceae. Equal leaf masses of different plants were therefore offered in place of equal leaf areas.

A preliminary investigation was required to determine the mass ratio of combinations of shoots from the different species, that would offer equal leaf mass to caterpillars. Ten 7cm shoots were cut from each plant and the wet mass of each shoot was recorded. The leaves of each shoot were removed and the shoots were reweighed. Leaf mass was calculated as a percentage of whole shoot mass. To test whether the mass ratio of shoots of different species required to present equal leaf mass was different on a dry weight basis, shoots were dried at 80°C until they reached constant mass before leaves were removed and the shoots were reweighed as before. For each species, values of leaf mass were calculated as a percentage of shoot mass. Average values were used to estimate the mass ratio in which whole shoots were offered to present equal leaf mass (Table 8.1).

A second investigation decided which of three prototype chambers minimised the loss of water from plant leaves. A design that minimised water loss was preferred so

Plant	Average leaf mass as a percentage of whole shoot mass	Coefficient of variation
Calluna vulgaris	73%	7%
Vaccinium myrtillus	54%	17%
Erica tetralix	66%	4%

Table 8.1. Leaf mass as a percentage of whole shoot mass for three plant species. Figures represent the average value calculated for each plant species after examining ten plant shoots.

Date	Caterpillar Species	Plant Species A	Plant Species B	Approximate mass ratio of whole shoots of A:B	No. of larvae per chamber
26.6.93	*Hydriomena furcata*	*C. vulgaris*	*V. myrtillus*	1:1.4	3
26.7.93	*Lasiocampa quercus callunae*	*C. vulgaris*	*V. myrtillus*	1:1.4	1
6.8.93	*Lasiocampa quercus callunae*	*C. vulgaris*	*V. myrtillus*	1:1.1	1
6.10.93	*Anarta myrtilli*	*C. vulgaris*	*V. myrtillus*	1:1.4	1

Table 8.2. Details of experimental conditions in four feeding-trials. The mass ratio of plant A to plant B is the approximate ratio in which whole shoots must be offered, in order to present larvae with equal leaf masses from each plant. This mass ratio was calculated using data in Table 8.1.

that reduction in plant mass due to consumption by caterpillars would be greater than mass change through transpiration. It was important to maintain leaf turgor so that leaves remained suitable as food throughout the experiment. The masses of shoots in each type of chamber were recorded daily through a five day period, so that changes in plant water content could be monitored.

The favoured design of choice chamber comprised a circular plastic jar that was 9.5cm in diameter and 8cm high (Figures 8.1a-b). The jar was sealed with a plastic lid. Water supplementation for the excised leaf shoots was achieved by lining the base of the container with a 1cm deep layer of florists' "Oasis" foam, that was saturated with water. The "Oasis" foam was covered with a circle of blotting paper to prevent caterpillars from contacting a wet surface directly. Six shoots, three from each of two plant species were arranged in the chamber. Shoots were pressed into the foam base, so that they were supported in an upright position. Shoots from the two plant species were placed in two straight lines that were 1.5cm apart, and were arranged in ABA, BAB formation . This design meant that at "ground" level a caterpillar could not travel from one plant to another of the same species, without first encountering a plant of a different species. At "canopy" level, all shoots touched others of different species, so a larva that climbed the first shoot it encountered would not be isolated from other choices.

8.2.1.2 Experimental procedure

Plants used in the experiment were harvested from nature and stored at 4°C, before shoots were cut and placed in the chambers. As far as possible, plants were used within one day of harvesting. Larvae were collected from nature and kept on *Calluna* prior to the experiments. *A. myrtilli* were collected using a sweepnet. *H. furcata* were taken by sweepnet and by searching. *L. quercus callunae* were found by searching. *L. quercus callunae* were second season larvae. *H. furcata* and *A. myrtilli* were in their final instar.

Thirty experimental chambers were used in each feeding trial. Experimental chambers contained the two plant species arranged as above and a fixed number of larvae. Thirty control chambers contained plants but no larvae. At the start of the experiment, the mass of each plant species in every chamber was recorded to 0.01g. Caterpillars were then introduced into the centre of the experimental chambers. All chambers were sealed and maintained at 15°C in a light regime of 18 hours light to 6 hours dark for 48 hours. After 24 hours the containers were checked to see whether larvae were alive and feeding. At 48 hours the containers were opened and the position of each caterpillar (on plant A, B or elsewhere) was recorded. Presence of frass, indicating recent feeding was also noted. At 48 hours, plants were reweighed and the

Figure 8.1a

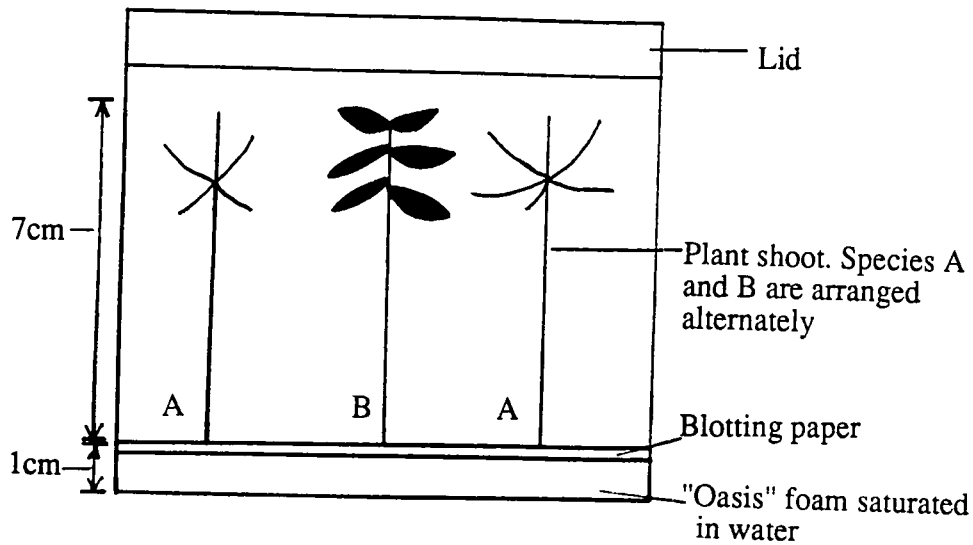
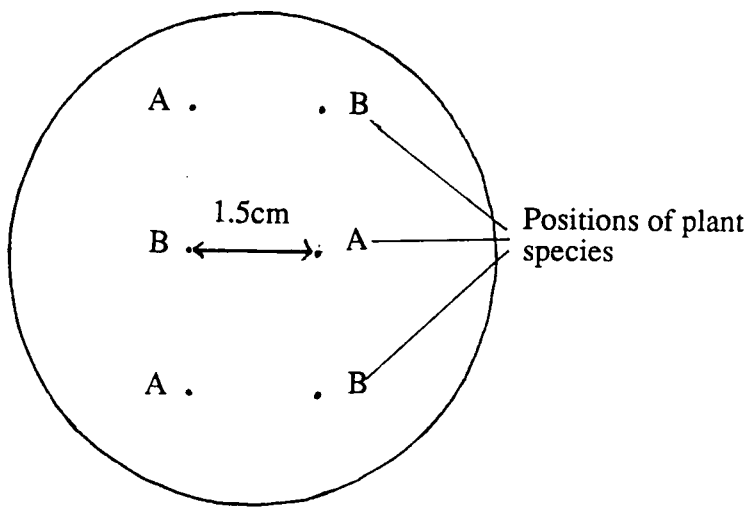


Figure 8.1b



Figures 8.1a and 8.1b. The choice chamber used in the feeding-trials. Figure 8.1a shows the choice chamber from side-view. Figure 8.1b shows the chamber in plan view. Plant shoots were 7cm tall and were arranged in two rows in order of alternate species.

presence of scars or holes in leaves was recorded. Exact details of conditions in each experiment are shown in Table 8.2.

8.2.1.3 Data analyses

Data were examined in two ways to interpret the foraging behaviour of larvae in the chambers. The first method utilised observations of caterpillar position and feeding damage. The second method determined the mass of each food plant consumed by larvae.

a) Comparison of food plant utilisation using observations of caterpillar position or feeding damage

The numbers of larvae on each plant species at the end of the experiment were compared using chi-square tests. Similarly, chi-square tests were used to compare the number of shoots of each plant type that were damaged by caterpillars, and the number of chambers in the *H. furcata* experiment that had damage to current or previous years' *Calluna* leaves. Yates' correction for continuity was used when there was one degree of freedom.

b) Comparison of food plant utilisation using changes in the mass of offered foods

Records of initial and final plant mass were used to calculate mass change. The change in mass was expressed as a percentage of the initial mass. Data from the 30 control jars were used to determine whether mass change was related to the initial mass of the shoots. This might be expected if a larger plant mass carries a larger leaf area for transpiration. If there was no relationship between the initial mass of the plant and its subsequent mass change (through dehydration or water uptake), the average percentage mass change was used to predict the final mass of each plant species in the 30 experimental chambers. If initial mass and percentage mass change were significantly correlated, the expected mass of plants in the experimental chambers was predicted using regression data.

The mass changes of plants in most experiments were normally distributed. For each plant species, the actual and predicted changes in mass were compared using paired t-tests. If actual mass changes differed significantly from predicted values, larvae were assumed to have eaten some of the foliage.

To discover whether caterpillars ate more of one plant than the other, a value was calculated to describe the percentage mass change of each plant species. This value was

corrected for changes in water content through adsorption and transpiration. The new figure was the percentage of plant mass eaten by larvae.

The amounts consumed from each plant species were compared using paired t-tests. The data from each chamber constituted a matched pair, the combined mass of the three type A shoots being paired against the combined mass of the three type B shoots. The amounts consumed from the two plant species were also correlated against each other, to determine whether these varied dependently.

8.2.2 Results

The positions of caterpillars at 48 hours are shown in Table 8.3. Observations of feeding-damage on different plant species, and on current and previous years' *Calluna* leaves are shown in Tables 8.4 and 8.5 respectively. Tests examining mass changes of plant material, and the percentage of plant mass consumed by larvae are shown in Tables 8.6-8.8. Figures 8.2a-8.2d are barcharts that show the average mass of each plant species that was consumed by larvae.

In all experiments, the final mass of plants in the test chambers was significantly smaller than the mass predicted by the controls ($P<0.01$-$P<0.001$, Table 8.6). Therefore larvae were assumed to have eaten some leaf tissue, in most of the chambers. The production of fresh frass in nearly all the chambers, showed that most larvae began to feed within the first 24 hours of the experiment.

8.2.2.1 Choice of *Calluna vulgaris* or *Vaccinium myrtillus* by *Hydriomena furcata* larvae

More *H. furcata* larvae were found on *Calluna* than *V. myrtillus*. but the difference was not significant ($\chi^2=2.21$, df=1, NS, Table 8.3). Although there was no significant difference between the number of *Calluna* and *V. myrtillus* shoots that incurred feeding damage (Table 8.4), a significantly larger mass of *Calluna* was consumed ($t=5.01$, df=27, $P<0.001$, Table 8.7). The quantities of *Calluna* and *V. myrtillus* consumed were not significantly correlated ($r=0.20$, df=28, NS, Table 8.8). Damage to the current year's leaves was seen in more chambers than damage to the previous years' leaves ($\chi^2=25.2$, df=1, Table 8.5).

8.2.2.2 Choice of *Calluna vulgaris* or *Vaccinium myrtillus* by *Lasiocampa quercus callunae* larvae

The numbers of larvae recorded on *Calluna* and *V. myrtillus* were not significantly different ($\chi^2=0.11$, df=1, NS, Table 8.3). A significantly larger number of *V. myrtillus*

shoots were damaged ($\chi 2$=12.0, df=1, P<0.001, Table 8.4) and indeed the consumption of *V. myrtillus* leaves was much greater than the consumption of *Calluna* (t=4.53, df=29, Table 8.7). The quantities of *Calluna* and *V. myrtillus* eaten were not significantly correlated (r=0.35, df=28, NS, Table 8.8).

8.2.2.3 Choice of *Calluna vulgaris* or *Erica tetralix* by *Lasiocampa quercus callunae* larvae

At the end of the experiment there were significantly more *L. quercus callunae* larvae on *E. tetralix* (χ^2=8.10, df=1, Table 8.3). However, both the number of shoots damaged, and the mass of plants consumed were similar (Tables 8.4 and Table 8.7). The mass of *C. vulgaris* was significantly correlated (B=0.364±0.173) with the mass of *E. tetralix* consumed (r=0.37, df=28, P<0.05, Table 8.8).

8.2.2.4 Choice of *Calluna vulgaris* or *Vaccinium myrtillus* by *Anarta myrtilli* larvae

This noctuid showed a strong selection for *Calluna*. There was a highly uneven distribution of larvae between the two plant species (χ^2=24.2, df=1, Table 8.3). The majority of larvae were observed on *Calluna*, and only one larva was found on *Vaccinium myrtillus*. Many more *Calluna* shoots than *V. myrtillus* shoots were damaged ($\chi 2$=40.1, df=1, P<0.001, Table 8.4) and a much larger mass of *Calluna* leaves was consumed (t=6.51, df=29, P<0.001, Table 8.7). The mass of *Calluna* consumed by *Anarta myrtilli* larvae was not significantly correlated with the mass of *Vaccinium myrtillus* consumed (r=0.06, df=28, NS, Table 8.8).

8.3 Field observations of the feeding behaviour of *Lasiocampa quercus callunae* larvae

8.3.1 Methods

8.3.1.1 Field procedure

This investigation took place at the Langholm field site on 11 and 12 July 1993. *Calluna* stands from the full range of available heights were systematically searched for the larvae of *L. quercus callunae*. A series of spot observations were compiled. Time of location, age of larva (first or second season larva), host plant, larva location (on current year's leaves, previous years' leaves or woody stem) and whether the larva was feeding were recorded. Where caterpillars were not actively feeding, but scars on leaf tissue showed the position of recent feeding sites, data on the position of leaf scars were recorded. For each caterpillar or leaf scar observation, the height of the plant, the length of the current year's shoot, the length of the previous years' growth and the distance of

Lepidoptera species	Plant A	Plant B	No. of larvae on plant A	No. of larvae on plant B	χ^2	df	P
H. furcata	*C. vulgaris*	*V. myrtillus*	23	14	2.21	1	NS
L. quercus callunae	*C. vulgaris*	*V. myrtillus*	10	9	0.11	1	NS
L. quercus callunae	*C. vulgaris*	*V. myrtillus*	4	17	8.10	1	<0.01
A. myrtilli	*C. vulgaris*	*V. myrtillus*	27	1	24.2	1	<0.001

Table 8.3. The positions of *Hydriomena furcata*, *Lasiocampa quercus callunae* and *Anarta myrtilli* larvae in choice chambers at the end of feeding trials. The differences in the number of larvae on plant A and plant B were compared using chi-square tests employing Yates' correction for continuity. NS indicates non-significance at the 0.05 probability level.

Lepidoptera species	Plant A	Plant B	No. damaged shoots of plant A	No. damaged shoots of plant B	χ^2	df	P
H. furcata	*C. vulgaris*	*V. myrtillus*	45	54	0.83	1	NS
L. quercus callunae	*C. vulgaris*	*V. myrtillus*	35	68	12.0	1	<0.001
L. quercus callunae	*C. vulgaris*	*V. myrtillus*	37	43	0.47	1	NS
A. myrtilli	*C. vulgaris*	*V. myrtillus*	43	1	40.1	1	<0.001

Table 8.4. The number of shoots of plants A and B that were damaged by larvae of *Hydriomena furcata*, *Lasiocampa quercus callunae* and *Anarta myrtilli* in feeding trials. The number of shoots of each species that were damaged were compared using chi-square tests employing Yates' correction for continuity. NS indicates non-significance at the 0.05 probability level.

Lepidoptera species	No. chambers with damage to current year's leaves	No. chambers with damage to previous years' leaves	χ^2	df	P
H. furcata	28	1	25.2	1	<0.001

Table 8.5. The number of chambers that showed damage to current year's or previous years' *Calluna* leaves in a feeding trial using *Hydriomena furcata* larvae. The number of chambers in each category was compared using chi-square tests, employing Yates' correction for continuity.

Lepidoptera species	Plant species	Average predicted final plant mass	Average actual plant mass	df	t	P
H. furcata	*C. vulgaris*	106.4%	96.0%	29	6.83	<0.001
	V. myrtillus	99.9%	97.7%	28	3.50	<0.01
L. quercus callunae	*C. vulgaris*	106.4%	94.0%	29	3.71	<0.001
	V. myrtillus	99.9%	72.8%	29	9.42	<0.001
L. quercus callunae	*C. vulgaris*	120.1%	103.0%	29	4.84	<0.001
	E. tetralix	112.7%	97.8%	29	4.55	<0.001
A. myrtilli	*C. vulgaris*	121.1%	101.4%	29	8.01	<0.001
	V. myrtillus	112.4%	109.6%	29	5.49	<0.001

Table 8.6. A comparison of the actual and predicted final masses of plants in the 30 experimental chambers. Masses are expressed as a percentage of the original plant mass. The predicted and final masses were compared using paired t-tests. Data from each chamber constituted a matched pair. The predicted final mass of plants was calculated using the average mass change of plants in the control chambers.

Lepidoptera species	Plant A	Plant B	Average mass of plant A eaten	Average mass of plant B eaten	df	t	P
H. furcata	*C. vulgaris*	*V. myrtillus*	9.8%	2.2%	28	5.01	<0.001
L. quercus callunae	*C. vulgaris*	*V. myrtillus*	11.6%	27.1%	29	4.53	<0.001
L. quercus callunae	*C. vulgaris*	*E. tetralix*	14.3%	13.2%	29	0.31	NS
A. myrtilli	*C. vulgaris*	*V. myrtillus*	16.2%	2.5%	29	6.51	<0.001

Table 8.7. A comparison of the masses of plants eaten by larvae in four feeding choice experiments. The average masses of plants that were eaten are expressed as a percentage of the original mass and have been compensated to take account of changes through adsorption and transpiration. Data were compared using paired t-tests. Data in each chamber constituted a matched pair. NS indicates non-significance at the 0.05 probability level.

Correlation	r	df	P
Correlation between the masses of *Calluna vulgaris* and *Vaccinium myrtillus* consumed by *Hydriomena furcata* larvae	0.20	27	NS
Correlation between the masses of *Calluna vulgaris* and *Vaccinium myrtillus* consumed by *Lasiocampa quercus callunae* larvae	0.35	28	NS
Correlation between the masses of *Calluna vulgaris* and *Erica tetralix* consumed by *Lasiocampa quercus callunae* larvae	0.37	28	<0.05
Correlation between the masses of *Calluna vulgaris* and *Vaccinium myrtillus* consumed by *Lasiocampa quercus callunae* larvae	0.06	28	NS

Table 8.8. Linear correlation data for the relationships between the masses of different food plants consumed in each of four feeding-trials. Correlations used the data from 30 experimental chambers. The masses of food plants that were eaten were expressed as a percentage of the original mass and were compensated for mass changes through adsorption and transpiration. NS indicates non-significance at the 0.05 probability level.

Figure 8.2a

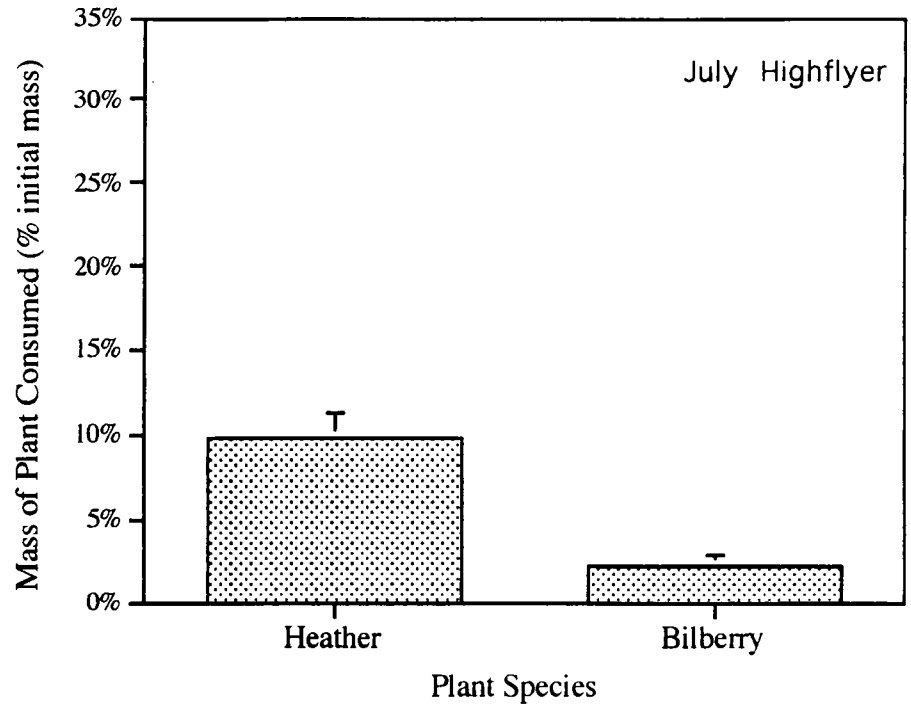
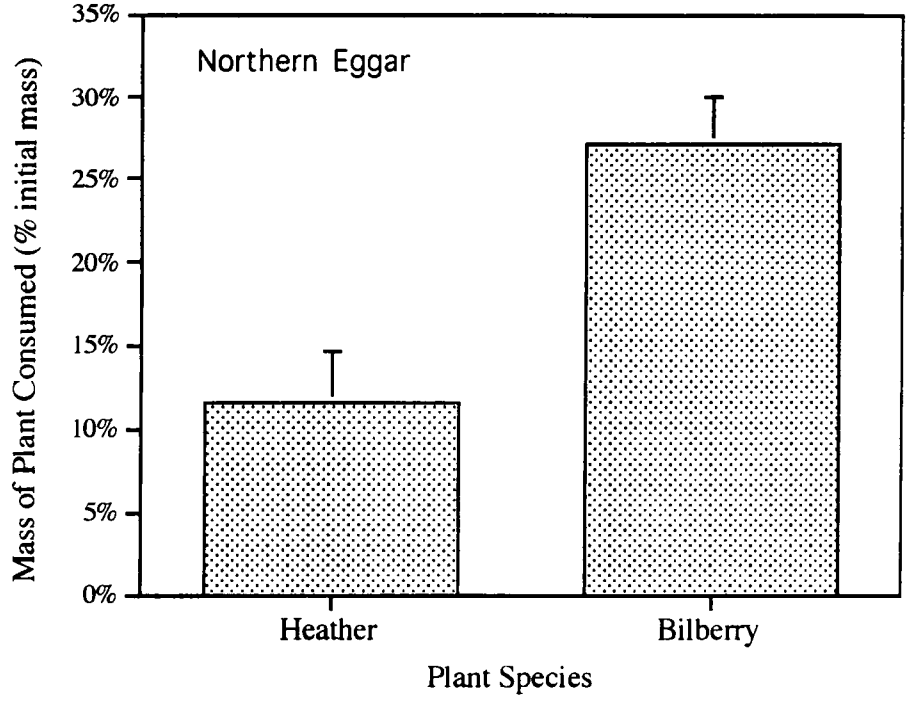


Figure 8.2b



Figures 8.2a and 8.2b. The average mass of plant material consumed in feeding choice experiments, expressed as a percentage of initial mass ±1SE. Figure 8.2a shows the relative amounts of heather *Calluna vulgaris* and bilberry *Vaccinium myrtillus* consumed by July highflyer *Hydriomena furcata* larvae. Figure 8.2b shows the amounts of the two plants consumed by northern eggar *Lasiocampa quercus callunae* larvae. Thirty choice chambers were used in each experiment.

Figure 8.2c

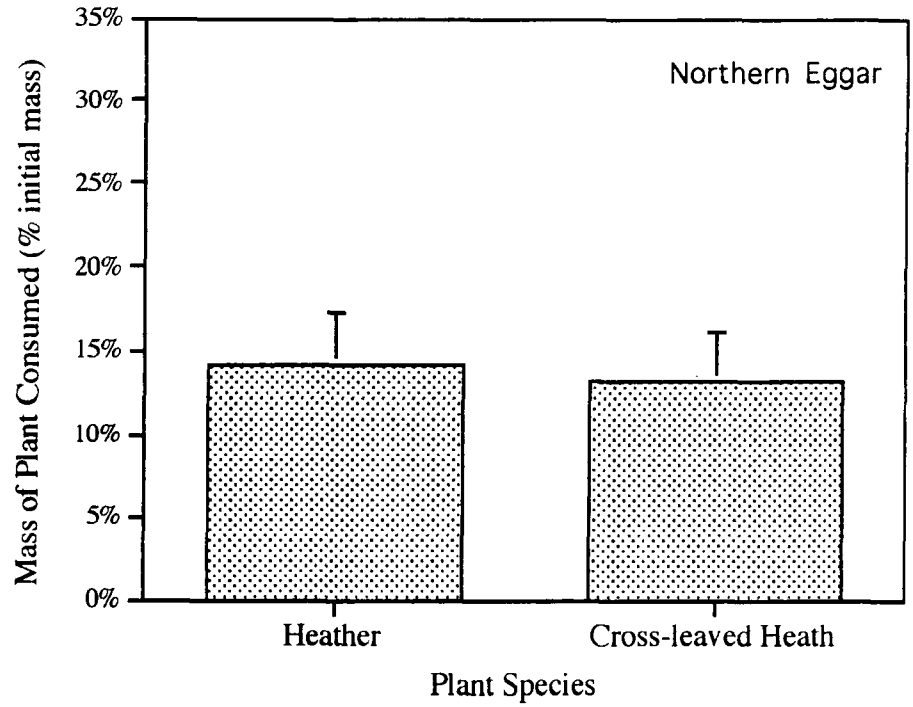
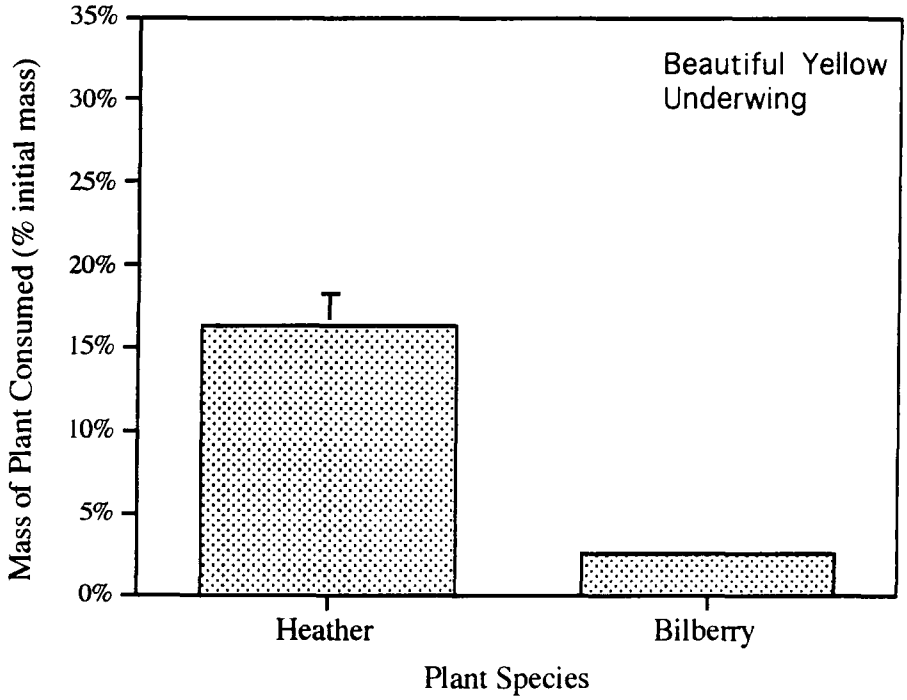


Figure 8.2d



Figures 8.2c and 8.2d. The average mass of plant material consumed in feeding choice experiments, expressed as a percentage of initial mass ±1SE. Figure 8.2c shows the relative amounts of heather *C. vulgaris* and cross-leaved heath *Erica tetralix* consumed by northern eggar *Lasiocampa quercus callunae* larvae. Figure 8.2d shows the amounts of heather and bilberry *Vaccinium myrtillus* eaten by beautiful yellow underwing *Anarta myrtilli* larvae. Thirty choice chambers were used in each experiment.

the larva's head or scar from the tip of the shoot were measured (Figure 8.3). Stem height was measured to the nearest 0.5cm. All other measurements were recorded to the nearest millimetre.

8.3.1.2 Data analyses

General observations regarding the location of larvae or scars and their behaviour were tabulated.

The numbers of larvae feeding on current or previous years' leaves were compared. Only records where larvae were actively feeding, or where there was evidence of recent feeding *e.g.* leaf-scars, were included in the analysis. Observations of larvae that were feeding on other plants, or on a *Calluna* stem that offered only one type of leaf, were also excluded. Data were compared using the chi-square test. The expected values were calculated by considering the total lengths of current and previous years' leaf shoot material examined.

The positions of feeding sites on leaf shoots were examined by comparing the frequency of different lengths of leaf shoot in the sample with the frequency of different feeding positions. Two analyses were completed. The first compared the frequency of different feeding positions with the frequency of different lengths of leaf shoot in the sample. For this, the total length of stem covered in leaf tissue was considered and was the distance between the shoot tip and the lowest point of continuous growth on the stem. Total leaf growth included leaves produced in both 1993 and earlier seasons. The feeding position was measured as the distance below the shoot tip that feeding or feeding damage was observed. The second analysis followed the same procedure, except that feeding position was compared against the frequency of lengths of current year's growth. The length of the current year's shoot was the distance between the shoot tip and the lowest point of current year's leaves on the stem.

The frequency distributions of current years' shoot lengths and total shoot lengths were grouped into 5mm and 1cm categories respectively. Chi-square goodness-of-fit tests compared the observed and expected feeding position frequency distributions . If expected frequencies were low, adjacent categories were grouped to ensure that expected values were greater than five.

Data combining observations of feeding larvae and recent feeding-scars, and data from feeding larvae only were analysed separately.

8.3.2 Results

Descriptive statistics for observations of second season *L. quercus callunae* larvae are given in Tables 8.9-8.12. Tables 8.13 and 8.14 give the results of chi-square tests. Figures 8.4a-8.5b show the frequency distributions of the lengths of leaf shoots, current year's leaf shoots and feeding positions in the sample.

Almost all larvae were located on *Calluna* (Table 8.9). Of the larvae observed on this species, most were located on either the current year's leaves or on the stem (Table 8.10). Only 6.7% of larvae on *Calluna* were found on previous years' leaves. 91.4% of larvae positioned on *Calluna* leaves were actively feeding at the time of observation.

Although more previous years' leaves were available on the stems (Table 8.11), the majority of feeding larvae ate the current year's leaves. The difference between the number of larvae feeding on current and previous years' leaves was very highly significant ($P<0.001$), regardless of whether feeding larvae and leaf scars, or feeding larvae only were examined (Table 8.13). The distribution of larval feeding positions was significantly different to the distribution of total shoot lengths available ($P<0.001$, Table 8.14). Feeding locations were biased towards the top of leaf shoots. No feeding larvae or leaf-scars were found more than 6cm below the shoot tip, although leaf growth could occur as much as 18cm below the shoot tip. Most evidence of feeding occurred on current year's leaves. However, feeding positions were not distributed evenly across the lengths of the available current year's shoots, but were much more frequent within 0.5cm of the shoot tips. The distribution of feeding positions was significant ($P<0.001$, Table 8.14).

8.4 A comparison of diurnal and nocturnal densities of Lepidoptera larvae on *Calluna* heathland

8.4.1 Methods

8.4.1.1 Field procedure

An initial investigation was made at two *Calluna* stands on Waskerley Moor on the day of 8 September 1991 and the night of 9 September 1991. The study was repeated at four stands at Penny Pye, near Blanchland, Northumberland on the day and night of 10 October 1993. Sites were visited in daylight between 1100 and 1400 hours to record daytime densities and approximately three to four hours after dark between 2100 and 0000 hours to record night-time densities. A sweepnet was used to take twenty samples

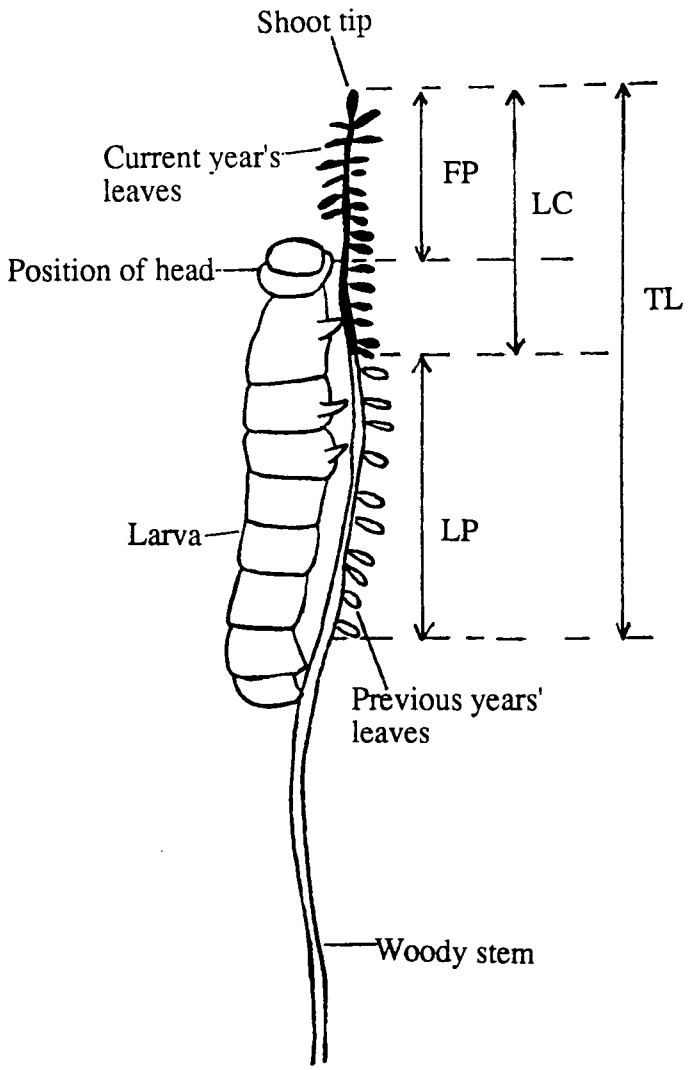


Figure 8.3. The measurements collected in field observations of *Lasiocampa quercus callunae* larvae. Abbreviations are as follows: *FP* the feeding position, the distance between the shoot tip and the larva's head or a feeding scar; *LC* the length of the current year's leaf shoots on the stem, the distance between the shoot tip and the lowest point of current year's leaves on the stem; *LP* the length of the previous years' leaves on the stem, the distance between the lowest point of the current year's growth and the lowest point of continuous leaf growth on the stem; *TL* the total length of stem covered by leaves, the distance between the shoot tip and the lowest point of continuous leaf growth on the stem.

Observations of *L. quercus callunae* larvae on heathland plants	***C. vulgaris***	***E. tetralix***	**Grasses**
Count	60	2	2
Percentage	94%	3%	3%

Table 8.9. The number of *Lasiocampa quercus callunae* larvae found on different heathland plants at Langholm in July 1993.

Observations of *L. quercus callunae* larvae location on *Calluna*	**Current year's leaves**	**Previous years' leaves**	**Stem**
Count	31	4	25
Percentage	52%	7%	42%

Table 8.10. The number of larvae found on different parts of *Calluna vulgaris*. Observations were made at the Langholm site in July 1993.

Observation type	**Total length of current year's leaves on stem (cm)**	**Total length of previous years' leaves on stem (cm)**	**Total length of leaf-shoots examined (cm)**
Feeding larvae + leaf-scars	163 (34%)	320 (66%)	483
Feeding larvae only	86 (34%)	166 (66%)	252

Table 8.11. The total lengths of stem covered in current year's leaves, previous years' leaves and total leaf growth. Data were recorded for plants on which *Lasiocampa quercus callunae* larvae were feeding, at the Langholm site in July 1993.

Behaviour of larvae on *C. vulgaris* shoots.	**Feeding**	**Non-feeding**
Count	32	3
Percentage	91%	7%

Tables 8.12. The behaviour of *Lasiocampa quercus callunae* larvae on *Calluna* leaves. Data were collected at the Langholm site in July 1993.

Observation type	No. of larvae on current year's leaves	No. of larvae on previous years' leaves	χ^2	df	P
No. of feeding larvae + leaf-scars	58	2	106	1	<0.001
No. of feeding larvae only	28	2	45.6	1	<0.001

Table 8.13. The number of feeding larvae and leaf-scars, or feeding larvae only, that were observed on current and previous years' *Calluna* leaves. Only stems that offered both current and previous years' leaves were included. Chi-square tests using Yates' correction for continuity were used to compare the number of observations on both leaf types. Expected values were calculated from the total length of leaf-shoot examined in each leaf-age class.

Comparison	χ^2	df	P
Observed distribution of larvae feeding and leaf-scar positions on leaf shoots, against an expected distribution.	389	6	<0.001
Observed distribution of larvae feeding positions on leaf shoots, against an expected distribution.	110	3	<0.001
Observed distribution of larvae feeding and leaf-scar positions on the current year's leaf-shoots, against an expected distribution.	334	8	<0.001
Observed distribution of larvae feeding positions on the current year's leaf-shoots against an expected distribution	39.7	3	<0.001

Table 8.14 A comparison of the distributions of larvae feeding positions on *Calluna* shoots. The observed distributions are compared, firstly against the frequency distribution of the total lengths of (current + previous years') leaf tissue on stems, and secondly against the frequency distribution of the lengths of current year's leaf tissue on stems. Chi-square tests were used to compare the distributions. Data were divided into observations of feeding larvae and leaf-scars, and feeding-larvae only.

Figure 8.4a

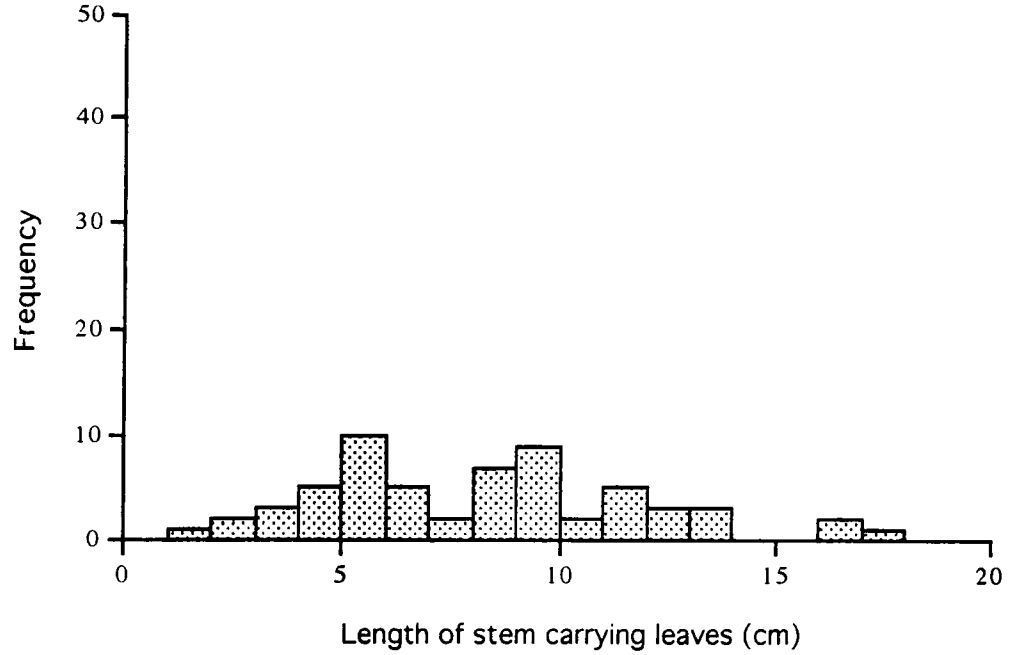
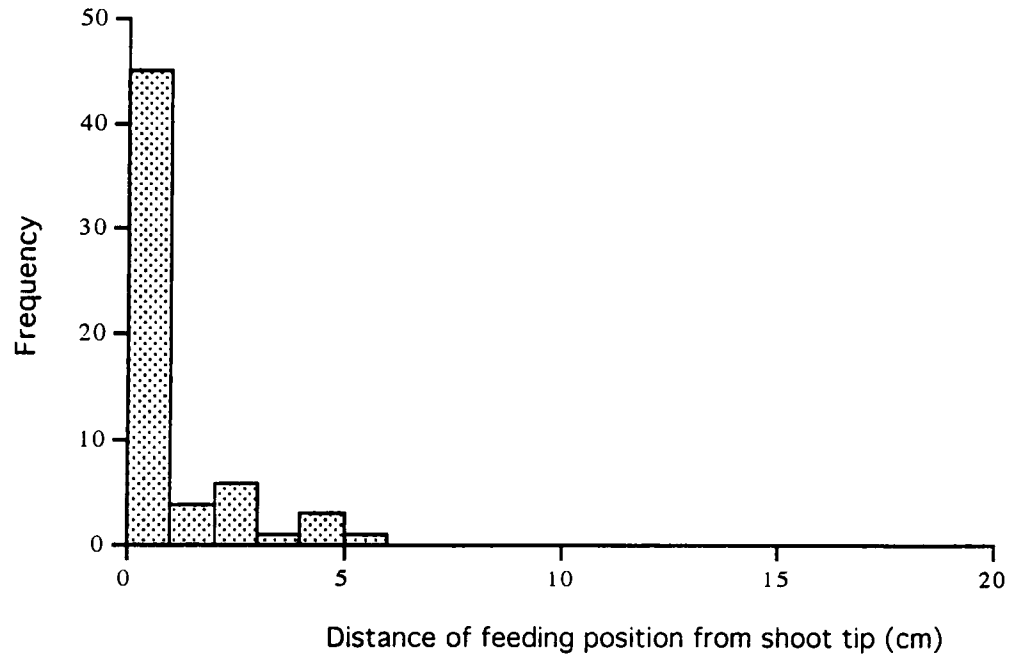


Figure 8.4.b



Figures 8.4a and 8.4b. The frequency distributions of a) the total lengths of leaf shoots and b) the positions of feeding larvae and scars on these shoots. The length of the leaf shoot was the distance between the stem tip and the lowest point of continuous leaf cover on the stem. This included both current and previous years' leaves. Feeding position was the distance between the shoot tip and the head of a feeding larva, or damage scar. All measurements were made to the nearest millimetre and are grouped in 1cm classes. All data refer to second season *Lasiocampa quercus callunae* larvae, observed at Langholm in July 1993. Histograms were compiled from 60 observations.

Figure 8.5a

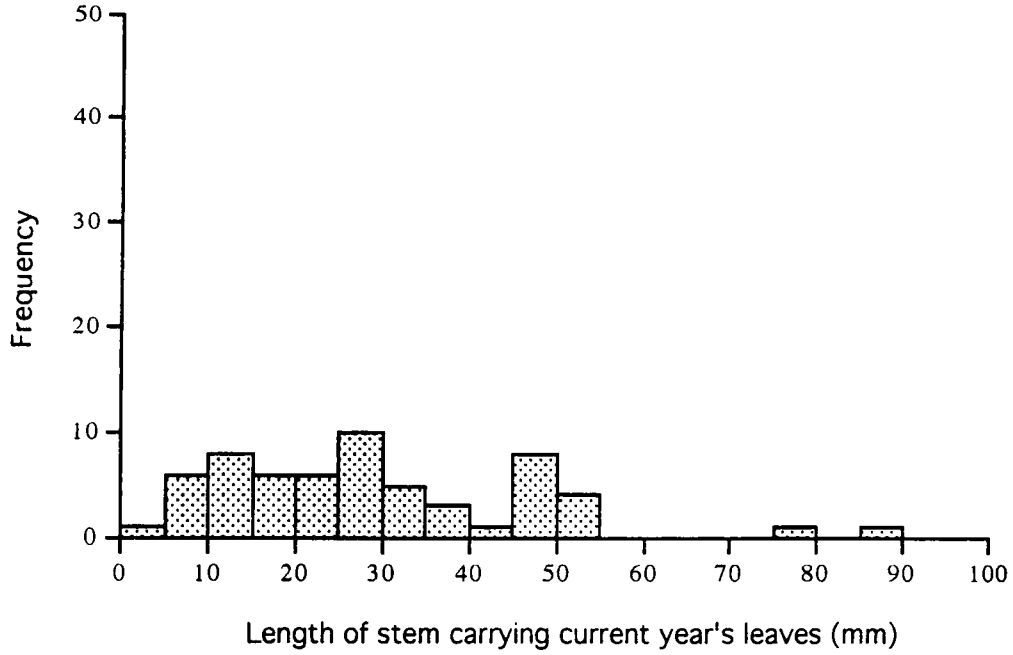
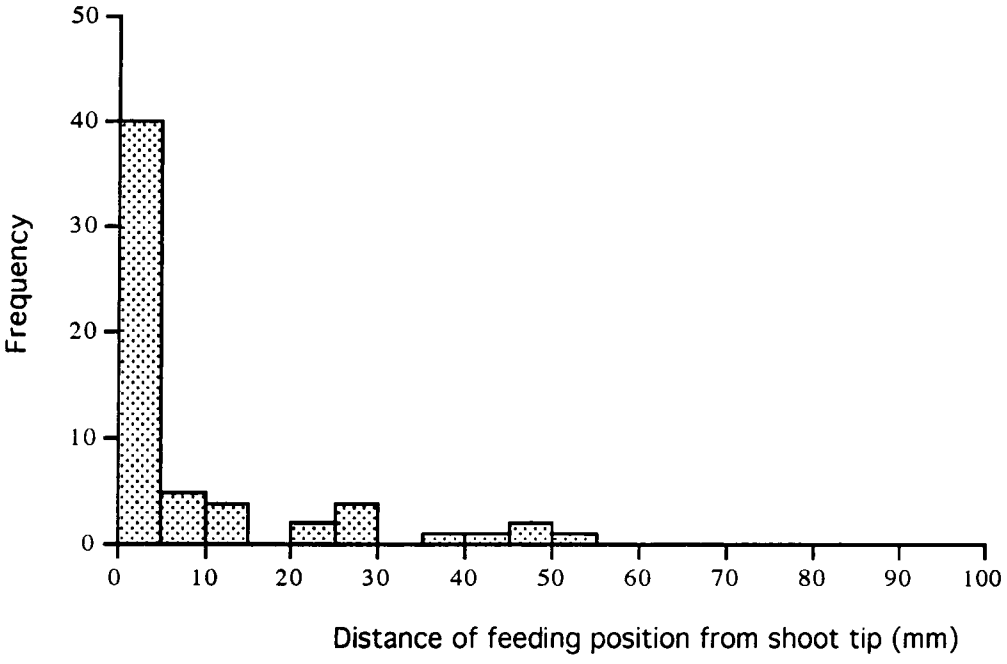


Figure 8.5b



Figures 8.5a and 8.5b. The frequency distributions of a) the lengths of current year's leaf shoots and b) the positions of feeding larvae and scars on these shoots. The length of the leaf shoot was the distance between the stem tip and the lowest point of current year's leaf cover on the stem. Feeding position was the distance between the shoot tip and the head of a feeding larva, or damage scar. All measurements were made to the nearest millimetre and are grouped in 5mm classes. All data refer to second season *Lasiocampa quercus callunae* larvae, observed at Langholm in July 1993. Histograms were compiled from 60 observations.

of ten strokes at each stand, on each visit. Larvae were identified in the field and released after each sample had been recorded.

8.4.1.2 Data analyses

The number of larvae found in day and night samples was compared using chi-square tests. Three abundant species, the geometrids narrow-winged pug *Eupithecia nanata* and ling pug *E. goossensiata* and the noctuid true lover's knot *Lycophotia porphyrea* were examined individually. All other species were examined as one group. Data from the two Waskerley stands, and from the four Penny Pye stands were pooled together.

8.4.2 Results

Table 8.15 summarises the results of daytime and night-time sampling at the two study sites. The density of *L. porphyrea* was significantly different in day and night samples at both sites. At Waskerley, in September 1991 this species was more abundant at night (χ^2=18.8, df=1, P<0.001) but at Penny Pye, in October 1993, more *Lycophotia porphyrea* larvae were found in the daytime samples (χ^2=73.9, df=1, P<0.001).

At Penny Pye, significantly more *E. goossensiata* were found at night (χ^2=4.14, df=1, P<0.05). Few larvae of other species were found, but at Penny Pye significantly higher densities of other species were found at night (χ^2=4.31, df=1, P<0.05).

8.5 Discussion

8.5.1 Selection of plant species

Larvae in the chambers did not feed randomly on the plants, but chose certain species consistently. When offered *Calluna* and *V. myrtillus*, *H. furcata* larvae ate significantly more *Calluna* (P<0.001), *L. quercus callunae* consumed significantly more *V. myrtillus* than *Calluna* (P<0.001) and *A. myrtilli larvae* ate *Calluna* almost exclusively (P<0.001, Table 8.7). Only *L. quercus callunae* larvae presented with *Calluna* and *E. tetralix* showed no preference for either plant. In this last test, the amount of *Calluna* consumed was significantly correlated with the amount of *Erica* eaten (r=0.37, df=28, P<0.05, Table 8.8), as individuals that ate large amounts of *Calluna* also ate quantities of *Erica*.

Without further research, generalisations cannot be made about the behaviour of the three Lepidoptera species, or reasons for their choice of plant. A very limited range of choices were offered, and to anticipate the behaviour of Lepidoptera families on heathlands, other species would have to be exposed to a wider variety of potential host

Site	Date	Species	No. of larvae in day samples	No. of larvae in night samples	χ^2	df	P
Waskerley	Sept. 91	*Eupithecia nanata*	45	48	0.11	1	NS
Penny Pye	Oct. 93		38	33	0.36	1	NS
Waskerley	Sept. 91	*Lycophotia porphyrea*	18	55	18.8	1	<0.001
Penny Pye	Oct. 93		149	33	73.9	1	<0.001
Penny Pye	Oct. 93	*Eupithecia goossensiata*	23	39	4.14	1	<0.05
Waskerley	Sept. 91	All others	8	8	0.06	1	NS
Penny Pye	Oct. 93		5	14	4.31	1	<0.05

Table 8.15. The number of larvae found by sweepnet sampling in day and night samples at Waskerley and Penny Pye. Data from two stands are combined for Waskerley. Data from four stands are combined for Penny Pye. Twenty samples of ten sweepnet strokes were taken at each stand. Data are compared using a chi-square test, employing Yates' correction for continuity.

plants. Laboratory preference data may not match a species' behaviour in the field, where, for example, preference may be offset against the difficulty of locating patchy resources.

Relationships between herbivores and plants are influenced by a number of factors including the predictability of plant resources in space and time, the nutritional levels of plants and plant parts, the diversity of plant mechanical and chemical defences against herbivores, and the diversity of plant species. Cates (1980) suggested that plant chemical defence systems and resource apparentness and predictability were among the most important selection pressures which modify the feeding behaviour of phytophagous insects. The theories of resource apparentness and predictability were described in Chapter Seven. Briefly, theories maintain that "apparent" or "predictable" plants are more likely to utilise dosage dependant, digestibility reducing agents to limit the extent of herbivore feeding. "Unapparent" or "unpredictable" plants have qualitative defences *e.g.* toxins, which exert a general defence that may be circumvented only by specialist herbivores that have coevolved with the plant (Feeny, 1976; Rhoades & Cates 1976).

Faster growth rates or reduced mortality are sometimes experienced by insect herbivores that feed on plants that have higher nitrogen concentrations (Scriber & Slansky 1981), higher water concentrations (Scriber 1977, 1979; Scriber & Slansky 1981; Myer & Montgomery 1987) or lower concentrations of allelochemics (Myer & Montgomery 1987). Very often more than one of these factors occur together and the root causes of herbivore success or failure cannot be separated. Concentrations of nitrogen, phosphorous and calcium are usually higher in *V. myrtillus* than *C. vulgaris* (Pearsall 1950; Moss 1968) but concentrations of tannins are also higher in *Vaccinium myrtillus* (Akhtardzhiev 1966). Since plant suitability will depend on the balance of nutrient, water and allelochemic concentrations the consequence of prolonged larval feeding on the test plants cannot be predicted without further experiment.

The apparentness and predictability of heathland plants as food resources is determined by a combination of spatial and temporal characteristics. *Calluna* is the dominant upland heathland species (Pearsall 1950; Gimingham 1972). In the late building and mature phases the density of its canopy may cause it to outcompete other species, creating a monoculture. Its height and abundance will make it apparent to both the adults and larvae of many Lepidoptera species. For much of the year, species that prefer the less dense, and sometimes smaller *E. tetralix* or *V. myrtillus* will be at a disadvantage unless they have local access to ample resources of these species, since the patchy distribution of these plants will make them more difficult for adults and larvae to locate. The ability of some Lepidoptera larvae to locate food plants is

influenced by the distribution pattern of plants, the age and size of larvae, and whether larvae have recently fed (Cain *et al.* 1985). However, in the early spring, larvae that hatch from eggs or emerge from diapause on or near *E. tetralix* or *V. myrtillus* may be able to survive better than larvae that hatch on *Calluna* monocultures. This is because *V. myrtillus* and *E. tetralix* initiate growth earlier than *Calluna* (Woolhouse & Kwolek 1981) and may be the only available source of food, for larvae that find *Calluna* leaves formed in previous years unpalatable. In the winter moth *Operophtera brumata*, high mortality of first instar larvae occurs if the majority of oak trees open leaf buds later than the peak egg hatch (Varley & Gradwell 1960). Fielding (unpublished Ph.D. thesis 1992) found a time-lapse of approximately 20 days between the development of field populations of *H. furcata* larvae on *Calluna* and *V. myrtillus*. Larvae reached their maximum size earlier on *V. myrtillus*, although growth rates on the two species were similar. It was suggested that this difference occurred because caterpillar growth was initiated earlier on *V. myrtillus*. Species which can feed on *V. myrtillus* and *E. tetralix* may also be able to colonise new ground more quickly than those restricted to *Calluna*, if either of these plants becomes dominant following burning.

Even though a species is often phytophagous over its geographical range, larvae from local populations may be very specialised in their diet (Cates 1980). The plants offered all belonged to one family, the Ericaceae. It is interesting that, with the exception of *Anarta myrtilli*, individuals were able to eat some of each species offered. Since plants were offered in excess, there was no reason to believe that feeding on two species within a short timespan was forced. If animals in the wild are also able to eat more than one species within a short time period, larvae may be able to disperse to other species, in the event of host plant deterioration.

Some species of larvae fed on different host plants or on an artificial diet, then tested individually, may show a preference for the foodplant previously eaten (Jermy *et al.*, 1968). The powers of inducing species may sometimes be so strong that a preference is induced for a less suitable host (Getzova & Lozina-Lozinskii 1955 in Jermy *et al.* 1968). An induced preference may mask a hereditary preference in feeding trials using animals collected from nature, but plants outside the normal host range may not induce preference (Jermy *et al.* 1968). Since all larvae in these experiments were collected from nature, where they were more likely to have encountered *Calluna* than other species, these tests determine preferences which may have been influenced by previous exposure to plants in the field. It is impossible to judge whether induction effects had occurred, without further experiments using larvae hatched from eggs. However, the marked preference of *L. quercus callunae* larvae for *V. myrtillus* instead of *Calluna*,

occurred in a population that would have had little previous exposure to *V. myrtillus*, since this plant was not abundant at the Langholm site where larvae were collected.

The three methods used to assess larvae food preference (observations of larvae positions, number of plant positions damaged and measurements of mass changes) did so with different levels of reliability. Results from observations of feeding damage and measurements of mass change were very similar. This check is useful, since mass change data alone may overestimate the amount consumed, if water losses are much greater from damaged leaves. Position data was considered the least reliable method of assessing food preference, since it reflected use at only a brief moment in a 48 hour period, not use throughout that time. Also larvae were able to climb shoots, without necessarily feeding on the leaves. Position data only agreed with data observed by the other methods when, as in the case of *A. myrtilli*, preference for one species was extremely marked. Observations of larvae would reflect feeding preference more accurately if only actively feeding larvae were recorded.

A. myrtilli was offered *V. myrtillus*, a plant that is not listed among its foodplants (South 1961; Carter & Hargreaves 1986; Emmet & Heath 1991). This test formed a useful control to the other experiments, and validated the findings of these workers. *Lasiocampa quercus callunae* accepted *E. tetralix*, a plant not listed in any of these texts as a host and was also occasionally found on this species in the field.

8.5.2 Selection of *Calluna* leaf age

Both *H. furcata* larvae in the laboratory experiments, and *L. quercus callunae* larvae in the field fed significantly more on current year's leaves than on previous years' leaves ($P<0.001$, Tables 8.5 and 8.13). The preference of *L. quercus callunae* for the current year's leaves occurred despite the much greater availability of previous years' leaves (Table 8.11). *L. quercus callunae* larvae feeding positions were concentrated within 0.5cm of the shoot tip (Figure 8.5b) although current year's leaves extended down the stem as much as 8.5cm below the shoot tip, and previous years' leaves occurred as much as 17.5cm below the apex.

The theories of resource apparentness and predictability that classified herbivore interactions, and chemical defence on different plant species, may also be invoked to describe variation in herbivore utilisation and chemical defence of individual plants (Rhoades & Cates 1976). *Calluna* is evergreen. Leaves from up to four previous growing seasons are retained throughout the year (Gimingham 1960; Chapman *et al.* 1975; Gimingham *et al.* 1979), but on the Pennine moors new growth only occurs between late May and October. The current year's leaves are spatially predictable as

they occur on the very tips of the stems, while the previous years' leaves further down the stem are both spatially and temporally predictable. Caterpillars that prefer, or are restricted to young growth, may find this an unpredictable resource in the early spring, since the current year's long-shoots do not undergo rapid elongation until July. It would be interesting to observe the field preferences of *L. quercus callunae* larvae in May, when the current year's leaves are more scarce.

Many plants have different concentrations of nutrients and allelochemics in "young" and "old" leaves. These include both fixed (determinate) growth plants, where ageing of leaves occurs through the season, and free (indeterminate) growth plants, where several ages of leaves may be present simultaneously. The concentration of nitrogen is often higher in "young" leaves (Feeny 1970; Scriber 1977; McNeill & Southwood 1978; Scriber & Feeny 1979; Mattson 1980; Scriber & Slansky 1981; Damman 1987; Meyer & Montgomery 1987; Stamp & Bowers 1990). Water content is also often greater in young leaves (Woodwell 1974; Scriber 1977; Schweitzer 1979; Scriber & Slansky 1981; Stamp & Bowers 1990). Phenolic concentrations may be higher in "young" leaves (Rhoades & Cates 1976; Macauley & Fox 1980 in Mattson 1980; Coley 1983; Meyer & Montgomery 1987) or "old" leaves (Feeny 1970, 1976; Rhoades & Cates 1976; McKey 1979) depending on plant species. Some plants may even show different concentrations of defensive chemicals in different regions of same-age leaves (Gall 1987).The feeding preference of some insects for certain leaf age classes has sometimes been linked to such variations in chemical content (Feeny 1970; Myers 1981; Damman 1987; Meyer & Montgomery 1987) or to differences in leaf toughness or schlerophyllisation (Feeny 1970; Rausher 1981).

In this study, concentrations of total nitrogen, water and total phenolics were significantly higher in current year's leaves in May, June and October, in all but one test (Chapter Seven). If a similar distribution of nutrients and allelochemics between leaf ages occurred in *Calluna* at Langholm in July, larvae feeding on current year's leaves would have experienced greater concentrations of nitrogen, water and phenolics than those feeding on previous years' leaves. The concentration of nutrients in the top 0.5cm, the region in which most larvae fed, was not analysed separately. Nitrogen concentrations are often highest near sites of rapid cell division *e.g.* meristems (Mattson 1980), so nutrients may have been most concentrated in this region. *H. furcata* and *Lasiocampa quercus callunae* larvae exhibited a stronger preference for current year's *Calluna* leaves, than for any plant species. When offered two plant species, many larvae sampled both plants, but few were observed eating both ages of leaves.

In the laboratory experiments, only *H. furcata* larvae were offered shoots that carried both current and previous years' leaves. When this experiment was executed in June,

little current growth was available and 7cm shoots comprised both leaf types. To standardise variation between plants and chambers, shoots which carried equal quantities of leaf shoots were used. Subsequent experiments with other larvae offered only current year's leaves. If previous years' leaves were in fact unavailable to *Hydriomena furcata* larvae, then unequal masses of edible parts of *V. myrtillus* and *Calluna* were offered in this feeding trial. This would have led to underestimation of the species' preference for *C. vulgaris*.

L. quercus callunae was the only species to be observed in the field. Due to their large size, these larvae are easily observed at all levels of the plant between the canopy and the ground. The smaller *H. furcata* and *A. myrtilli* could not have been located easily by direct searching. Observations would have been more biased toward the location of individuals in canopy positions. *L. quercus callunae* larvae left clear signs of feeding damage in the form of visible leaf-scars. It was hoped that the inclusion of leaf-scar data, for individuals that were found on lower parts of the plant but had previously been feeding would reduce bias of this kind. However, separate analysis of data collected from larvae only, and from larvae and leaf-scars combined gave similar results.

8.5.3 The density of larvae collected in daytime and night-time samples

There was a significant difference between the densities of *L. porphyrea* in daytime and night-time samples at both sites. At Waskerley in September 1991, the density of *Lycophotia porphyrea* was significantly greater at night, but at Penny Pye in October 1993, densities were significantly greater during the day. Without further work, it is not possible to say whether this species is moving between the canopy and ground on a night-day basis, or whether results reflect the species' ability to recover from displacement after earlier sweepnet sampling. A simple control, in which a series of stands are surveyed on two consecutive nights, half being surveyed first in the day, half first in the night, would separate cyclical movements from delayed return to the foliage.

At Penny Pye, there were also significant differences in the densities of *Eupithecia goossensiata* and other species in daytime and night-time samples (*E. goossensiata* $\chi^2=4.14$, df=1, $P<0.05$; other species $\chi^2=4.31$, df=1, $P<0.05$, Table 8.15). However, these results are more ambiguous because the result for *E. goossensiata* was caused by the uneven distribution of larvae in only one of the four stands and the result for other species was based on a small number of individuals. More data are required to understand the diurnal and nocturnal distribution patterns of larvae.

Other authors have noted variations in the activity of Lepidoptera larvae on a daily cycle. Hypotheses have linked some activity patterns to diurnal fluctuations in plant nutrient, water or allelochemic concentrations or variation in predation risk at different times of day.

Leaf quality may change diurnally (Raup & Denno 1983). For example concentrations of nitrogen, water and allelochemics may vary cyclically (Durzan 1968; Haukioja *et al.* 1978; Seigher & Price 1976; Robinson 1974 all cited in Raup & Denno 1983). These differences may affect larvae. If fed on leaves collected at different times of day, larvae may show different rates of development and fecundity (Grison 1952; Haukioja *et al.* 1978 both in Raup & Denno 1983).

Night-time feeding may be a strategy to reduce the exposure of larvae to visually oriented predators and parasites *e.g.* birds (Heinrich 1979; Heinrich & Collins 1983). These authors suggested that "palatable" larvae (those without hairs, spines or noxious body chemicals) were most likely to partition time between feeding and behaviour to escape predators than their "nonpalatable" counterparts. Behaviours thought to reduce exposure to predators included foraging only at night, remaining hidden below leaves, moving away from the feeding site at the end of a feeding bout and limiting the signs of feeding damage by clipping leaves.

Chapter Nine

General Discussion

9.1 Variation in the abundance of Lepidoptera larvae in different heights of *Calluna*

One finding of this study was universal to all study areas. The density of Lepidoptera larvae varied in different heights of *Calluna*, increasing linearly with increment in *Calluna* height (Chapter Six). Although the slopes of these regressions could be significantly different for species examined at different sites, when regression data were converted into units of proportional change in larvae density per cm increase in *Calluna* height, all data fitted the same linear trend.

The reasons for such a pattern could be physical, for example, a change in the biomass of *Calluna* with *Calluna* height, that allows more larvae to be accommodated in older stands, or an artefact of the sweepnet sampling technique. Both these possibilities have been discussed in Chapter Six. The possibility that the distribution pattern was an artefact of the sweepnet sampling method was eliminated when a second method, the combined jarring and Berlese-Tullgren extraction technique, also recorded greater densities of larvae in taller stands. It is also possible that biological mechanisms account, at least in part, for some of the variations in abundance observed, since similar distribution patterns in the literature have been attributed to invertebrate movement patterns (Bach 1980, 1981, 1988b, 1990; Root & Kareiva 1984; Lawrence & Bach 1989), colonisation (Cromartie 1975; Andow 1990), survival (Andow 1990) and egg-laying behaviour (Jones 1977; Latheef & Ortiz 1983; Rausher 1983; Horton & Capinera 1987; Capman *et al.* 1990). Frequently distribution patterns result from more than one of these factors acting together (*e.g.* Bach 1980, 1981, 1988b, 1990; Andow 1990).

The literature describing the mechanisms behind the distribution patterns is rather less extensive than the literature describing the distribution patterns themselves. This is partly due to the tendency of researchers to restrict study to one stage of the invertebrate lifecycle (Andow 1990). Some invertebrates have complex life-histories, with different requirements in the various developmental stages (Wiklund 1977; Thomas 1986; Usher & Jefferson 1991). The Lepidoptera, with four stages of development (egg, larva, pupa

and adult) are exposed to various selection pressures and have different requirements in each phase. Even within one phase, the larva, radical changes in life-history strategy may occur during development (Gaston *et al.* 1991). At least in the macrolepidoptera, the adult and larval stages have some degree of mobility and may influence the distribution of the succeeding phases by their movement patterns and some form of choice, as well as survival. The egg and pupa are immobile and influence other phases only by their survival.

Various studies describe how adult Lepidoptera determine the distribution patterns of eggs and larvae by their flight patterns, choice of oviposition site and regulation of the number of eggs deposited at any location (Rausher & Mackay 1981; Mackay & Singer 1982; Rausher 1983; Latheef & Ortiz 1983; Root & Kareiva 1984). The same distributions of eggs and larvae may result from different imago behaviour (*e.g.* Jones 1977). The oviposition sites of some species *e.g. Pieris rapae* (Root & Kareiva 1984) are dictated by female movement patterns, while other species *e.g. Euphydryas editha* (Rausher & Mackay 1981) are able to recognise the host-plant in the air and exhibit great selectivity of oviposition site after landing on a plant. Although one would expect a female capable of discrimination to select an oviposition site that would enhance larval survival, certain "life-history trade-offs" (Gaston *et al.* 1992) may cause an animal in one stage to make a choice for its immediate benefit, that may not favour a succeeding phase. For example, females of *Cactoblastis cactorum* (Phycitidae) (Robertson 1987 in Gaston *et al.* 1992) attempt to select plots suitable for larval development, but require shelter to achieve oviposition and must lay close to the site of emergence to minimise the energy costs associated with dispersal. Implementation of oviposition preferences may be restricted by the urgency to oviposit, or the relative abundance of food-plants (Reavey & Lawton 1991). The ability of females to select does not always confer enhanced larval performance (*e.g.* Valladares & Lawton 1991). It is also important not to infer preference from the distribution patterns of eggs or larvae (Mackay & Singer 1982; Singer *et al.* 1992). Mackay and Singer (1982) found that Euptychine butterflies which tended to oviposit on isolated plants in the field, actually preferred clumped plants in experiments. The increased risk of attack experienced by isolated plants was a result of the random initiation of the search after each oviposition, and the ability of clumped plants to share the risk of oviposition.

Thus the patterns of larvae distribution on different heights of *Calluna* that were described in Chapter Six, could be mediated by adults via several routes. Not all of these involve active choice. Taller or larger *Calluna* bushes may simply represent a target that is easier to locate for females with a limited "radius of detection" (Cain 1985) or they could accumulate more individuals because of their longer exposure to

Lepidoptera in space and time. For mechanisms that involve female choice, females might select a large plant for a suitable microclimate, or as a nutritional resource for larval development, relatively free from toxins and containing sufficient nutrients for growth. Or the large size may support the larva through the whole of the larva phase. Larvae that exhaust the foliage supplies of one plant, frequently experience greater risks of predation, parasitism or starvation if they leave a plant to search for another host (Rausher 1981; Damman 1991). Alternatively females may oviposit in tall *Calluna* stands because they offer a resource to the adult such as nectar or shelter, or they may oviposit at random.

Larval survival rates may be strongly linked to the female's choice of oviposition site because the mobility of the larva is generally more limited than that of the adult. This is especially true for microlepidoptera larvae, because many species are leaf-miners, cased, or live in shelters made from tied leaves and are virtually immobile. Some exceptions, capable of travelling long distances include the first instar larvae of winter moth *Operophtera brumata*, which are wind-borne on silken threads (Hartley 1993). External feeders in this study were unlikely to encounter problems in locating more *Calluna* after defoliation of one bush, because *Calluna* grows in vast, dense swards and a small movement across the *Calluna* canopy would usually be sufficient to reach more leaves.

In Chapter Seven, the concentrations of nitrogen, phenolics and water in the current and previous years' leaves of different-aged *Calluna* stands were considered. The only significant relationships between plant age and chemical composition were negative correlations between age and the water content of the previous years' leaves in June samples at Slaley and the current and previous years' leaves collected at both Waskerley and Slaley in October ($P<0.05$-$P<0.001$). If leaf water content was crucial to the survival of larvae, a reversal of the observed larval distribution pattern might be expected *i.e.* greater densities of larvae in the shorter, younger stands where water concentration was highest, at least in the autumn when the trend was observed at both study areas. Larval growth rates might be more rapid where water content was high (Scriber 1977, 1979; Scriber & Slansky 1981). Although no study has monitored the nutrient concentrations of individual *Calluna* plants, or even individual stands, through the whole of their lifespan, authors who have studied different-aged stands have found nutrient concentrations to be related to *Calluna* age (Thomas 1934; Lauder & Comrie 1936; Moss *et al.* 1972; Miller 1979). For example, Miller (1979) found that the concentrations of nutrients in shoot tips declined annually to the fourth year after burning. It is possible that these trends occurred at the areas in this study, either not at the times monitored, or were too subtle to be detected by the analyses. Certainly the

distribution of larvae was not in the direction of predicted nitrogen gradients, even though the species examined in Chapter Eight were capable of making feeding choices over short distances. The tendency of two species, the July highflyer *Hydriomena furcata* and the northern eggar *Lasiocampa quercus callunae*, to feed on current year's leaves in preference to previous years' leaves were consistent with the selection of higher concentrations of nitrogen and water, but also higher concentrations of phenolics.

The movement patterns and survival of larvae could affect the distribution and survival of pupae, through exposure to different microclimates in different-aged stands. Mallick (1986) recorded that the top 2cm of soil on a burned site experienced periodic drought in the summer and direct insolation that caused higher temperatures and water pressure deficits at the ground surface. Greater fluctuations in temperature and humidity occur in the pioneer and degenerate phases than in the building and mature stages (Barclay-Estrup 1971). By virtue of their inherent instability the pioneer and degenerate phases may be less suitable for the survival of eggs, larvae and pupae than building and mature age stands.

At present, the reason for the observed distribution patterns of larvae on different-aged *Calluna* remains unresolved. The fact that the relationship between the rate of change in larval density and *Calluna* height was not significantly different for many groups and species of larvae (Chapter Six), suggests that a physical factor such as biomass may be responsible. It would be expected that biological mechanisms elicit more individualistic responses from different species, because species are adapted to particular niches and are affected differently by environmental variables. However, so little is known about the behaviour of each of the lifecycle stages of common heathland Lepidoptera, that biological mechanisms cannot be ruled out as contributory factors in any species distribution pattern. This is an area that would benefit from further research. There are only a few heathland Lepidoptera for which the distribution of eggs and larvae is even partially understood *e.g.* the colonisation of moorland by wind-borne first instar larvae of winter moth *Operophtera brumata* along the path of the prevailing wind (Hartley 1993). Studies of the oviposition behaviour of heathland species and the survival of larvae in different-aged stands could be interesting and productive.

Further development of the feeding trials and field observations described in Chapter Eight, to include more Lepidoptera species, more food-plant combinations and information on the longer term growth rates, survival, pupal weights and adult fecundity of species reared on different host-plants, would improve the understanding of survival in the larval stages. It would be interesting to determine the preference of larvae offered choices of same-aged leaves from different-aged *Calluna* stands, since

this bears most relevance to distribution patterns of larvae in the field. In both short-term preference tests and field situations, insects do not always select the most superior nutritional resources, or those that are most suitable for their long-term development (Getzova & Lozina-Lozinskii 1955 in Jermy *et al.* 1968, Raup & Denno 1983; Damman 1987). Other factors, such as predation, parasitism, competition with other herbivores and the suitability of the plant for other developmental stages may override selection of rich nutritional resources (Raup & Denno 1983; Damman 1987). Experiments concerning the ability of *Calluna*, *Vaccinium myrtillus* and *Erica tetralix* to induce preference in naive larvae would also validate whether feeding trials using larvae collected from nature infer hereditary preferences. The inclusion of field observations is useful since nascent preferences may be offset against the difficulty of locating patchy resources.

9.2 Variation in the diversity of Lepidoptera larvae in different heights of *Calluna*

This study showed slight changes in the diversity of Lepidoptera larvae with *Calluna* height (Chapter Six), but the relationships between *Calluna* height and Lepidoptera diversity were not the same at different study areas. Change in diversity was a result of both the presence of uncommon species and an appreciable change in the contribution of several common species to the community. This resulted in the species list and community composition of stands that were similar in height being more alike than those of stands at which the difference in *Calluna* height was larger. None of the common macrolepidoptera species were restricted to one *Calluna* height class. Most of the common species found in the oldest, tallest stands could also be located in *Calluna* that was less than 10cm tall. Since the age of the shortest stands sampled at Slaley, where most sampling of short stands took place, was two to three years-old, this is a measure of the short period of time necessary for individual species to recolonise a burned piece of moorland. The extremely low densities of larvae on *Calluna* stands less than 10cm tall make it difficult to estimate when a *Calluna* stand is likely to carry all the common species after it has been burned, because larvae are encountered only infrequently. As individuals of all the common species were found in different stands it might be possible for a single stand to carry all the common species within the first two to three years.

As no trend in diversity was repeated at all sites, it could be concluded that diversity changes with *Calluna* height are not of major biological importance. Fielding (unpublished Ph.D. thesis 1992) also found no significant differences in the number of species of Lepidoptera larvae in different phases of *Calluna* and that common species were not restricted to certain age classes. Similarly, Merret (1976) found no clear trend in the species richness of spiders with *Calluna* age. Usher and Smart (1988) found little

difference in the species richness of spiders on unburnt, burnt and cut heather but because the abundance of individual species varied in the three areas, management was still regarded as important. While there may not be a general relationship between diversity and *Calluna* height, the significant change in the composition of the Lepidoptera community in different height classes, may play a role in maintaining the overall species diversity of individual sites. The presence of different-aged stands could allow the coexistence of more species, either by providing separate niches for competing animals or by providing resources that are required by different Lepidoptera species.

There were no strong links between this study and other recent studies of invertebrates living in habitats that are frequently exposed to fire. It might be expected that the diversity of invertebrates in regularly burned habitats is low, because reduced floral diversity can result from the loss of fire sensitive species after repeated burnings (Gimingham *et al.* 1979; Heal 1980). Evans (1988b) found that the species richness of grasshoppers was greater on infrequently burned prairie, than on sites that were burned annually or biennially. The proportion of forb and mixed feeders also increased where fires were less frequent. The results of several studies (Evans 1988a, 1988b; McCoy 1987; McCoy & Kaiser 1990) suggest that repeated fires affect the invertebrate community indirectly, by modifying the structure and species composition of the vegetation. It would be of interest to compare the species composition and diversity of several *Calluna* moors where burning is not practised, against moors managed on the traditional burning rotation.

9.3 Inferences for management of *Calluna* moors for the conservation of Lepidoptera

Given the results of this study, what inferences may be drawn regarding the best management strategy for the preservation of Lepidoptera species on northern heath? The most popular and widely researched invertebrate group, the butterflies, are known to have declined during the present century, both in Britain and in several other European countries (Thomas 1984, 1991; Dempster 1991; Pollard & Yates 1993). Of the 57 species of butterfly resident in Britain since 1900, 20 (35%) have experienced major range contractions and there have been two extinctions this century (Heath *et al.* 1984 in Pollard & Yates 1993). *Calluna* heathland in the uplands is also declining. For example 20% of the heather moorland that was present in the Scottish Borders in the 1940's was lost by the 1970's (National Countryside Monitoring Scheme in Hester & Sydes 1992). There is clearly a case for the careful management of the remaining areas of this habitat.

Unfortunately, research into the status and habitat requirements of invertebrate groups has been neglected until recently. It is only possible to discuss one group in detail, the butterflies. Even for this group most of the research has occurred since the 1960's, when concern about the effects of organochlorine insecticides on wildlife prompted the instigation of a national butterfly monitoring scheme (Pollard & Yates 1993). There have also been several studies of the ecology of individual rare and endangered species (*e.g.* Thomas & Harrison 1992).

The most important factor linked to the decline in the abundance of many butterfly species is likely to be the conversion of many biotopes to agriculture and forestry during this century (Thomas 1984; Dempster 1991; Pollard & Yates 1993). This trend has been especially pronounced since the 1950's (Pollard & Yates 1993). Changed management practices have also resulted in a lower diversity of habitats within the remaining biotopes (Thomas 1984, 1991). However declines have occurred even on land set aside for conservation, as there have been many extinctions on nature reserves (Thomas 1984; Pollard & Yates 1993). The breeding requirements of many British butterflies are much more specific than was previously thought, so that many rare species are limited by the shortage of suitable habitat in the larval stage (Thomas 1984, 1991; Pollard & Yates 1993). It seems that many species have suffered from the assumption that the creation of nature reserves for the more popular plants and vertebrates would automatically benefit invertebrates (Thomas 1984; Fry & Lonsdale 1991) or that provision of the larval food-plant would be sufficient for the maintenance of a butterfly population. Many of the rare butterfly species require a transient successional stage in one part of their lifecycle, which means that active management of habitat is essential for their survival (Thomas 1984, 1991).

An additional problem is the dichotomy in the distribution of British butterflies, species being either common and widespread, or rare and localised (Pollard & Yates 1993). Many rare species are restricted to the remaining fragments of habitat such as nature reserves and have very limited powers of dispersal (Thomas 1984, 1991; Dempster 1991) and 85% live within closed populations (Thomas 1984). While this allows the preservation of viable populations in areas of land less than 50 hectares (Thomas 1984), it also prevents the natural recolonisation of habitat fragments where a species has become extinct (Thomas 1984, 1991; Dempster 1991). Some species *e.g.* *Lysandra bellargus* are unable to travel distances of 100m across an area of unsuitable habitat (Thomas 1983 in Thomas 1991). Stamps *et al.* (1987) propose a model in which the emigration rate depends on both "edge permeability", the tendency of a species to cross a boundary and leave when it reaches the edge of a habitat fragment and the "edge to size ratio" of the habitat. This considers the number of home ranges bordering the

habitat margin. The model claims that in species with a tendency to cross boundaries easily, patch size and shape may affect the rate of emigration. It is likely that dispersal has a genetic component and that in an increasingly fragmented landscape, evolution would select against individuals that emigrated from suitable habitat, if they failed to find new breeding ground. Dempster (1991) used this argument to support his hypothesis that species with low dispersion capabilities today, were not so limited in the past. Dempster cites morphometric evidence that suggests increased habitat isolation can cause reduction in butterfly mobility.

Few butterfly species occur in the uplands (Pearsall 1950). Of the five species listed in Ratcliffe (1977), all feed on grasses and forbs in the larval stages and none on dwarf shrubs, which accounts for the absence of records of butterfly larvae on *Calluna* in this study. Studies of the ecology of individual species of moth being even fewer than similar studies of butterflies, except of course for pest species, one cannot be certain how far butterfly ecology and conservation apply to heathland moths. However, several lessons are likely to be important. These are that the habitat requirements of a species may be different at different stages of the lifecycle (*e.g.* Wiklund 1977; Usher & Jefferson 1991). That the requirements of the larval stage may be precise and larvae may depend on the vegetation structure of a particular, transient, successional stage. That the minimum viable area of habitat to support a population is one capable of supporting at least 200 adults to avoid chance extinctions (studies cited in Thomas 1984) and that the ability of adults to cross even small areas of unsuitable habitat cannot be assumed.

One interesting contrast between the heathland Lepidoptera of Durham and Scotland and several of the butterfly studies in the literature is the stage of succession used by larvae. None of the species in this study, or in the study of Fielding (unpublished Ph.D. thesis 1992) were restricted to a single life-history stage of *Calluna*, but most common species were more abundant in older, taller stands. It is a feature of many temperate butterflies, particularly of the rarer species, that larvae are restricted to the earliest stages of successional habitats (Thomas 1984). One reason for this larval distribution appears to be the requirement of many butterflies for warmth. Many of the rarest species of butterflies in Great Britain occur at the northern limit of their European range (Thomas 1984, 1991) and temperature is one of the factors affecting the position of the northern frontier. The difference between the microclimate of a short, warm early successional phase and a sheltered, cool, later one can be enough to prevent the development of larvae. Thomas (1991) lists studies of a lowland heath butterfly, the silver-studded blue *Plebejus argus*, that show that larvae are restricted to the first five years of *Calluna* growth after a fire in Suffolk, but can breed throughout the pioneer

and building phases in warmer Devon. On upland heaths, where Ratcliffe (1977) considers that reduced sunshine and lower temperatures account for the absence of all but a few butterflies, the evolution of some diurnal forms of nocturnal moth and some species with two-year lifecycles, the opposite situation may apply. The extreme fluctuation of the microclimate in the pioneer stage (Barclay-Estrup 1971; Mallick 1986) and the absence of a litter layer may prove inhospitable to moths that find shelter from the wind and rain and a more stable microclimate in the building and mature phases.

The issue of conservation raises questions about how we judge the value of our existing habitats and what features we wish to maintain and develop in a landscape. Ratcliffe (1977) compiled a list of the most valuable examples of habitat types in Britain, judging sites on ten criteria: size, diversity, naturalness, rarity, fragility, typicalness, recorded history, position in the ecological or geographical unit, potential value and intrinsic appeal. Not all of these criteria adequately reflect the value of heathlands because these are semi-natural, anthropogenic environments characterised by low floral diversity and a relatively high faunal diversity (Ratcliffe & Thompson 1988). For example, studies of the spider and carabid fauna of fragmented lowland heath (Webb & Hopkins 1984; Webb *et al.* 1984) found that species richness was actually higher in degraded heathland because of the invasion of woodland species. Clearly, while wishing to maintain the diversity of species on heathland, we should aim to ensure that these are species typical of the habitat *e.g.* naturalness (Usher & Gardner 1988). Of the species found in this study (Chapter Five), ten were listed in Ratcliffe (1977) as widespread (*i.e.* also occurring in non-upland habitats), but only two, the grey mountain carpet *Entephria caesiata* and the small autumnal moth *Epirrita filigrammaria* as submontane. However, this is not unusual on upland moorlands where there are few species specific to high altitudes (Fielding unpublished Ph.D. thesis 1992). It is of course possible that the system of management adopted in recent centuries has already removed some characteristic or rarer species.

Usher and Jefferson (1991) stated that the management of northern heath by rotational burning appeared to maximise the biodiversity of spiders and beetles (Usher & Gardner 1988; Usher & Smart 1988, both in Usher & Jefferson 1991). Given ambiguous changes of Lepidoptera diversity in *Calluna* of different heights, but close relationships between the abundance of individual species and *Calluna* height and also significant changes in the species composition in different height classes, I suggest this may also be true for caterpillars. As proposed in section 9.2, the presence of different ages of *Calluna* at one site may retain species diversity, because of the different species compositions in certain height classes. This contradicts Gimingham (1985) who

believed that rotational burning could reduce the diversity of the invertebrates, because of the dominance of the low diversity building and mature phases.

A regular burning cycle creates a diversity of vegetation structures of the type advocated by Thomas (1984, 1991). Although slow-moving invertebrates such as caterpillars are likely to be killed by the immediate action of the fire, or by later starvation, some stages *e.g.* eggs or pupae may like some other invertebrates (Gimingham *et al.* 1979) survive in the litter layer. Provided that building or mature age stands are always retained near the site of a burned area, there is a close source population for recolonisation which, this study suggests, may happen even in the first two years of *Calluna* growth. Neither Coulson (1988) nor Gardner and Usher (1989) believed that controlled burning was detrimental to various populations of invertebrates, at least in the short-term if *Calluna* plots were small.

Although there is no evidence to suggest that degenerate stands are of greater conservation value than other phases, a potential flaw of current burning practice is the efficiency with which degenerate phase *Calluna* is removed on many estates. This study found degenerate stands were often difficult to locate because of their scarcity and according to Gimingham (1972) many other authors have also experienced this problem. It is suggested that some areas of degenerate *Calluna* be retained on moorland and the diversity, abundance and species composition of Lepidoptera larvae in this phase be studied, because in this study too few degenerate stands were found to be sure of the patterns of density and diversity in very old *Calluna.*

In Chapter Eight, it was found that larvae of some species that were used in preference tests ate other ericaceous plants readily and even preferred them. It was suggested that Ericaceae that grow new leaves before *Calluna* in the spring *e.g. Vaccinium myrtillus* (Woolhouse & Kwolek 1981) could act as a food reserve, sustaining populations of spring-feeding larvae in years when they failed to synchronise with *Calluna*, so another active conservation measure for Lepidoptera could be the encouragement of some other heathland Ericaceae, especially in degraded *Calluneta.*

As one study inevitably sires further questions, additional directions for research arise from this thesis. Very little is known about the dispersal of the Lepidoptera associated with northern heath. This is potentially worrying, given the example of the butterflies. For example, although the study areas at Waskerley, Slaley and Stuartfield Lodge are probably large enough to sustain their own Lepidoptera populations, it is not known whether there is any exchange between sites. Less than 5km separates some of these study areas, but the intervening land is covered by pasture and forestry. One species, the *Erica* and *Calluna* feeding ling pug *Eupithecia goossensiata*, is highly abundant at both

Slaley and Stuartfield Lodge, but rarely found as a larva at Waskerley. Could low dispersal be responsible? Another explanation for such a difference could be temporal variation in larval densities. Population sizes of Lepidoptera may fluctuate rapidly, sometimes resulting in outbreaks of certain species (Niemelä 1980; Spitzer & Leps 1988; Hunter 1991; Ginzburg & Taneyhill 1994), and may be affected by factors such as weather, predation and parasitism (Varley 1947; Niemelä 1980; Ginzburg & Taneyhill 1994). Further research regarding the dispersal of Lepidoptera and the requirements of the four life-stages must be the way to perpetuate the species associated with northern heath.

Summary

1. Aspects of the ecology of the Lepidoptera associated with *Calluna vulgaris* on northern heath were investigated between 1991 and 1993 at five study areas in County Durham, Northumberland and southern Scotland.

2. All study areas were northern heaths that were managed by rotational burning and were located below 500m above sea-level.

3. A series of different-aged *Calluna* stands that had been created by burning and which comprised plants of the same chronological age and phase of development were selected as sample sites.

4. Vegetation at Waskerley, Slaley, Greenlaw Moor S.S.S.I. and Langholm-Newcastleton Hills S.S.S.I. was characterised. Variables measured were the age, height, green shoot density and flower density of *Calluna* plants, *Calluna* cover and the floristic composition of each stand.

5. At Slaley and Waskerley there were significant positive linear relationships between *Calluna* height and the logarithm of *Calluna* age.

6. When data for stands older than 20 years were excluded from analyses, there were significant positive relationships between green shoot density and stand age. More data are required to estimate the nature of these relationships in older *Calluna.*

7. There were significant positive linear relationships between stand height and green shoot density and between stand height and flower density. These data were combined from Slaley, Waskerley and Greenlaw where trends were similar.

8. The relationships between *Calluna* height and green shoot density, and between height and flower density were different at Langholm. This site was further west than the other three and may have experienced a warmer, wetter climate that promoted denser, more vigorous growth.

9. The densities of *Calluna* green shoots and *Calluna* flowers were closely correlated. When green shoot density doubled, flower density increased by a factor of approximately 2.4.

10. *Calluna* cover was significantly correlated with the logarithm of *Calluna* height, but there were no significant relationships between the cover values of other plant species and *Calluna* height or green shoot density.

11. The suitability of sampling techniques for Lepidoptera larvae were assessed.

12. Relative estimates of macrolepidoptera density obtained by sweepnet sampling were significantly correlated with absolute densities obtained from a combined jarring and Berlese-Tullgren extraction technique, when one species, the noctuid *Lycophotia porphyrea*, was excluded from analyses.

13. There was no significant relationship between the density of *Lycophotia porphyrea* obtained from sweepnet sampling and its density measured by combined jarring and Berlese-Tullgren extraction.

14. In a test of Berlese-Tullgren funnel extraction efficiency, utilising the geometrids *Eupithecia nanata* and *Hydriomena furcata*, the noctuid *Lycophotia porphyrea* and two masses of *Calluna*, the extraction rate in 600g *Calluna* samples was 6%, 87% and 60% for *Eupithecia nanata*, *Hydriomena furcata* and *Lycophotia porphyrea* respectively. In 1200g *Calluna* samples, 4% of *Eupithecia nanata*, 87% of *Hydriomena furcata* and 57% of *Lycophotia porphyrea* were extracted.

15. There was a significant positive relationship between the proportion of each species in the total sweepnet catch and the proportion of each species in the total combined jarring and Berlese-Tullgren extraction catch at sites that were sampled by both techniques on the same day, but only if data for *Eupithecia nanata* and *Lycophotia porphyrea* were excluded.

16. Lack of correlation between the proportions of *Eupithecia nanata* and *Lycophotia porphyrea* in the total sweepnet catch and their proportions in the combined jarring and Berlese-Tullgren catch was attributed to the individual response of these species to different sampling techniques. There was a low extraction rate of *Eupithecia nanata* in Berlese-Tullgren funnels, believed to be caused by the death of individuals in the funnels. Many *Lycophotia porphyrea* were found in the litter when *Calluna* was harvested for Berlese-Tullgren extraction and would have been unavailable to the sweepnet technique.

17. Sweepnetting was used as the main sampling technique in a Lepidoptera larvae monitoring programme at the Durham and Northumberland study areas in 1992 and 1993 and was also used at the Scottish field sites on two visits in the early summer and autumn of 1992.

18. A total of 29 species of macrolepidoptera (11 Geometridae, 11 Noctuidae and 7 "others" were recorded as larvae during the study.

19. Nine macrolepidoptera species (31% of the total number of macrolepidoptera species found) were recorded at all five study areas.

20. When results from this study were combined with those of Fielding (unpublished Ph.D. thesis 1992), the total number of macrolepidoptera species taken as larvae on *Calluna* at sites in County Durham was 34, (14 Geometridae, 11 Noctuidae, 9 "others").

21. The percentage of species found in this study that were known to be associated with *Calluna* and to have a distribution that included County Durham according to a literature review (Fielding unpublished Ph.D. thesis 1992) was 48%, 50%, 35% and 71% for the total macrolepidoptera, Geometridae, Noctuidae and "others" respectively.

22. The degree of similarity between the macrolepidoptera faunas of different study areas was not related to geographical distance.

23. The macrolepidoptera fauna of the study areas was significantly more similar in the autumn than in the summer.

24. For pairs of study areas, values of Sorensen's similarity coefficient were higher than the percentage similarity index, indicating that species lists were similar, but the relative abundance of each species was different.

25. The proportions of individuals from the Geometridae, Noctuidae and "others" were significantly different between study areas in the spring, autumn and 29 April-2 August 1993 time periods.

26. At Waskerley, Slaley and Stuartfield Lodge the proportions of macrolepidoptera and microlepidoptera larvae changed significantly throughout the year. There was an abrupt change in late June from a larval community dominated by macrolepidoptera to one dominated briefly by microlepidoptera.

27. Large spring and autumn peaks in the number of macrolepidoptera larvae were mainly due to changing numbers of geometrids.

28. A stepwise multiple regression program most frequently selected *Calluna* height to explain variation in the density of different groups of Lepidoptera larvae.

29. Other variables, such as *Calluna* green shoot density and flower density, could also have been responsible for variations in larval density, because vegetation characteristics were significantly intercorrelated.

30. The rate of change of larval density was similar for all groups and species of larvae at different study areas. The number of larvae per sweepnet sample increased by 2-9% for every 1cm increase in *Calluna* height.

31. Comparison of the abundance of larvae in short and tall *Calluna* using the combined jarring and Berlese-Tullgren extraction method, also revealed greater densities of larvae in tall *Calluna*.

32. The diversity of macrolepidoptera larvae was related to *Calluna* height at some sites but no consistent trend occurred between different study areas.

33. There were significant negative relationships between the similarity of the macrolepidoptera fauna in pairs of stands and the difference in *Calluna* height.

34. Generally, macrolepidoptera and microlepidoptera larvae occurred in the proportions 87-91% to 9-13% respectively, but there were significant differences between the study areas.

35. The contribution of larvae of several common species to the macrolepidoptera community changed significantly in three height classes of *Calluna* (*Calluna* less than 15cm tall, *Calluna* 16-30cm tall and *Calluna* greater than 30cm tall).

36. Change in the contribution of common Lepidoptera species to the community was more often associated with a shift in the dominance of another common species in certain height classes, than change in the number of rare individuals.

37. Changes in the contribution of individual Lepidoptera species to the community in different height classes of *Calluna* were not consistent between study areas.

38. The larvae of four geometrid species (*Eulithis* sp., *Ematurga atomaria*, *Eupithecia nanata* and *Eupithecia goossensiata*) and three noctuid species (*Anarta myrtilli*, *Lycophotia porphyrea* and *Ceramica pisi*) and several unidentified microlepidoptera were found in *Calluna* stands less than 10cm tall.

39. None of the common Lepidoptera species were restricted to a single height class of *Calluna* but there were changes in the density and dominance of species in different *Calluna* heights.

40. There were no significant relationships between the total foliar concentrations of nitrogen and phenolics and the seral age of *Calluna.*

41. Concentration of water in the previous years' leaves of June samples (Slaley) and current and previous year leaves at Waskerley and Slaley in October showed a significant linear decline with increasing stand age.

42. In October, foliar concentrations of water in the oldest 24-year-old stands were approximately 75% of the youngest 2-year-old stands at Slaley. At Waskerley, 24-year-old stands had water concentrations approximately 91% of 4-5-year-old stands.

43. The concentrations of total nitrogen, total phenolics and water were significantly higher in the current year's *Calluna* leaves than in leaves grown in previous years.

44. The average concentration of nitrogen was 1.3-1.5 times higher, concentration of phenolics was 1.1-2.0 times higher and water content was 1.0-1.1 times higher in current year's *Calluna* leaves than in previous years' leaves.

45. The larvae of *Hydriomena furcata, Lasiocampa quercus callunae* and *Anarta myrtilli* exhibited significant feeding preferences when offered choices of *Calluna, Vaccinium myrtillus* and *Erica tetralix.*

46. In laboratory experiments, *Hydriomena furcata* larvae damaged significantly more current year's leaves than previous years' *Calluna* leaves.

47. Field observations of *Lasiocampa quercus callunae* larvae revealed that feeding locations were biased towards the tops of leaf shoots, usually within 0.5cm of the shoot tip on current year's growth, although more previous years' leaves were available.

48. The density of *Lycophotia porphyrea* was significantly different in daytime and night-time sweepnet samples, but the direction of the difference was different at two sites on different sampling dates.

49. There was no significant difference in the densities of *Eupithecia nanata* in daytime and night-time samples.

50. Recommendations for the management of heathlands for the conservation of Lepidoptera included the maintenance of a range of different-aged *Calluna* stands at a site, the encouragement of some other Ericaceae and further study of Lepidoptera dispersal and the requirements of different Lepidoptera lifecycle stages.

References

Akhtardzhief, K. (1966). Presence of arbutin and tannins in native representatives of the family Ericaceae. *Pharmazie* **21**, 59-60.

Allaby, M. (1992) (Ed.). *The Concise Oxford Dictionary of Botany*. Oxford University Press, Oxford.

Allen, S.E. (1974). *Chemical Analysis of Ecological Materials*. Blackwell, Oxford.

Anderson, P. & Yalden, D.W. (1981). Increased sheep numbers and the loss of heather moorland in the Peak District, England. *Biol. Conserv.* **20**, 195-213.

Andow, D.A. (1990). Population dynamics of an insect herbivore in simple and diverse habitats. *Ecology* **71**, 1006-1017.

Andow, D.A. (1991). Vegetational diversity and arthropod population response. *Ann. Rev. Entomol.* **36**, 561-586.

Anon. (1985). Langholm-Newcastleton Hills unpublished S.S.S.I. schedule. Nature Conservancy Council, Peterborough.

Anon. (1987). Greenlaw Moor unpublished S.S.S.I. schedule. Nature Conservancy Council, Peterborough.

Armstrong, H. (1991). Britain's declining heather moorlands. *Outl. Agric.* **20**, 103-107.

Bach, C.E. (1980). Effects of plant density and diversity on the population dynamics of a specialist herbivore, the striped cucumber beetle, *Acalymma vittata* (Fab.). *Ecology* **61**, 1515-1530.

Bach, C.E. (1981). Host plant growth form and diversity: Effects on abundance and feeding preference of a specialist herbivore *Acalymma vittata* (Coleoptera, Chrysomelidae). *Oecologia* **50**, 370-375.

Bach, C.E. (1988a). Effects of host plant patch size on herbivore density: Patterns. *Ecology* **69**, 1090-1102.

Bach, C.E. (1988b). Effects of host plant patch size on herbivore density: Underlying mechanisms. *Ecology* **69**, 1103-1117.

Bach, C.E. (1990). Plant successional stage and insect herbivory: Flea beetles on sand-dune willow. *Ecology* **71**, 598-609.

Banerjee, B. (1981). An analysis of the affect of latitude, age and area on the number of arthropod pest species of tea. *J. Appl. Ecol.* **18**, 339-342.

Barclay-Estrup, P. (1970). Description and interpretation of cyclical processes in a heath community. II. Changes in biomass and shoot production during the *Calluna* cycle. *J. Ecol.* **63**, 233-258.

Barclay-Estrup, P. (1971). The description and interpretation of cyclical changes in a heath community. III. Microclimate in relation to the *Calluna* cycle. *J. Ecol.* **58**, 243-249.

Barclay-Estrup, P. (1974). Arthropod populations in a heathland as related to cyclical changes in the vegetation. *Ent. Mon. Mag.* **109** 79-84.

Barclay-Estrup, P. & Gimingham, C.H. (1969). The description and interpretation of cyclical processes in a heath community. I. Vegetational changes in relation to the *Calluna* cycle. *J. Ecol.* **57**, 737-758.

Bate-Smith, E.C. (1973). Tannins in herbaceous legumes. *Phytochem.* **12,** 1809-1812.

Beijerinck, W. (1940). *Calluna*: A monograph on the Scotch heather. *Verh. K. Ned Akad. Wet. Tweede Sectie*. **38**, 1-80.

Bernays, E.A. (1978). Tannins: An alternative viewpoint. *Entomolomogia. Exp. Appl.* **24**, 244-253.

Bernays, E.A. (1981) Plant tannins and insect herbivores: An appraisal. *Ecol. Entomol.* **6**, 353-360.

Birks, H.J.B. (1988) Long term ecological change in the British Uplands. In: *Ecological Change in the Uplands*. (Ed. D.B.A. Thompson & M.B. Usher) pp. 37-56. Special Publication Series of the British Ecological Society, Number 7. Blackwell, Oxford.

Bradley, J.D. & Fletcher, D.S. (1979). *A Recorder's Log Book or Label List of British Butterflies and Moths*. Curwen Books, London.

Brian, M.V., Mountford, M.D., Abbott, A. & Vincent, S. (1976). The changes in ant species distribution during ten years post-fire regeneration of a heath. *J. Anim. Ecol.* **45**, 115-133.

Brooks, M. (1991). *A Complete Guide to British Moths (Macrolepidoptera)*. Jonathon Cape, London.

Bryant, J.P. & Kuropat, P.J. (1980). Selection of winter forage by subarctic browsing vertebrates: The role of plant chemistry. *Ann. Rev. Ecol.* **11**, 261-285.

Byerley, K.F., Gutierrez, A.P., Jones, R.E., Jones, R.F., & Luck, R.F. (1978). A comparison of sampling methods of some arthropod populations in cotton. *Hilgardia* **46**, 257-282.

Cain, M.L. (1985). Random search by herbivorous insects: A simulation model. *Ecology* **66**, 876-888.

Cain, M.L., Eccleston J., Kareiva, P.M. (1985). The influence of food plant dispersion on caterpillar searching success. *Ecol. Entomol.* **10**, 1-7.

Capman, W.C., Batzli, G.O. & Simms, L.E. (1990). Responses of the common sooty wing skipper to patches of host plants. *Ecology* **71**, 1430-1440.

Carpenter, J.R. & Ford, J. (1936). The use of sweepnet samples in an ecological survey. *J. Soc. Br. Ent.* **1**, 155-161.

Carter, D.J. & Hargreaves, B. (1986). *A Field Guide to the Caterpillars of Butterflies and Moths in Britain and Europe*. Collins, London.

Cates, R.G. (1980). Feeding patterns of monophagous, oligophagous and polyphagous insect herbivores: The effect of resource abundance and plant chemistry. *Oecologia* **46**, 22-31.

Cates, R.G.& Orions, G.H. (1975). Successional status and the palatability of plants to generalised herbivores. *Ecology* **56**, 410-418.

Cates, R. & Rhoades, D. (1977). Prosopsis leaves as a resource for insects. In: *Mesquite: Its biology in two desert scrub ecosystems*. (Ed. B. Simpson) pp. 61-83. US / IBP Synthesis Series 4. Dowden, Hutchinson & Ross Inc., Stroudsbury, Pennsylvania.

Chapman, R. (1974). The chemical inhibition of feeding by phytophagous insects: A review. *Bull. Entomol. Res.* **64**, 339-363.

Chapman, S.B., Hibble, J. & Rafarel, C.R. (1975). Net aerial production by *Calluna vulgaris* on lowland heath in Britain. *J. Ecol.* **63**, 233-258.

Coley, P.D. (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Mongr.* **53**, 209-233.

Conway, V.M. (1954). Stratigraphy and pollen analyses of southern Pennines blanket peats. *J. Ecol.* **42**, 117-147.

Cornell, H.V. (1986). Oak species attributes and host size influence cynipine wasp species richness. *Ecology* **67**, 1582-1592.

Coulson, J.C. (1988). The structure and importance of invertebrate communities on peatlands and moorlands, and effects of environmental and management changes. In: *Ecological Change in the Uplands*. (Eds. D.B.A. Thompson & Usher M.B) pp. 365-380. Special Publication Series of the British Ecological Society, Number 7. Blackwell, Oxford.

Cromartie, W.J. (1975). The effect of stand size and vegetational background on the colonisation of cruciferous plants by herbivorous insects. *J. Appl. Ecol.* **12**, 517-533.

Daly, H.V., Doyen, J.T. & Erlich, P.R. (1981). *Introduction to Insect Biology and Diversity*. McGraw-Hill International, London.

Damman, A.J. (1987). Leaf quality and enemy avoidance by the larvae of a pyralid moth. *Ecology* **68**, 88-97.

Damman, A.J. (1991). Oviposition behaviour and clutch size in a group-feeding pyralid moth, *Omphalocerca munroei*. *J. Anim. Ecol.* **60**, 193-204.

Davidson, V.G. & Shackleford, M.W. (1929). Diurnal variations in the vernal invertebrate population of a central Oklahoma prairie. *Proc. Okla. Acad. Sci.* **9**, 54-59.

Davies, R.I., Coulson, C.B. & Lewis, D.A. (1964). Polyphenols in plant, humus and soil. IV. Factors leading to increase in biosynthesis of polyphenols in leaves and their relationship to mull and mor formation. *J. Soil Sci.* **15**, 310-318.

Dempster, J.P. (1991). Fragmentation, isolation and mobility of insect populations. In: *The Conservation of Insects and their Habitats*. (Eds. N.M.Collins & J.A. Thomas) pp. 143-154. Academic Press, London.

Den Otter, C.J. (1992). Responses of the african armyworm and three species of borers to carbohydrates and phenolic substances: An electro and behavioural physiological study. *Entomologia. Exp. Appl.* **63**, 27-37.

Dickson, R. (1976). A Lepidopterist's Handbook. (Ed. P.W. Cribb). The Amateur Entomologist's Society, Hanworth, Middlesex.

Diemont, W.H. & Heil, G. (1984). Some long-term observations on cyclical and seral processes in Dutch heathlands. *Biol. Conserv.* **30**, 283-290.

Dietrick, E.J. (1961). An improved backpack motor fan for suction sampling of insect populations. *J. Econ. Entomol.* **54**, 394-395.

Dunn, T.C. & Parrack, J.D. (1986). *The Moths & Butterflies of Northumberland & Durham*. Part 1. Macrolepidoptera. The Vasculum Supplement Number 2. Northern Naturalist's Union.

Ellington, J. Kiser, K. Ferguson, A., Cardenas, M. (1984). A comparison of sweepnet, absolute, and insectavac sampling methods in cotton ecosystems. *J. Econ. Entomol.* **77**, 599-605.

Emmet, A.M. & Heath, J. (1991). *The Moths and Butterflies of Great Britain and Ireland*. Volume 7(ii) Lasiocampidae to Thyatiridae. Harley Books, Colchester, Essex.

Evans, E.W. (1988a). Community dynamics of prairie grasshoppers subjected to perodic fire: Predictable trajectories or random walks in time? *Oikos* **52**, 283-292.

Evans, E.W. (1988b). Grasshopper (Insecta, Orthoptera, Acrididae) assemblages of tallgrass prairie: Influences of fire frequency, topography and vegetation. *Canad. J. Zool.* **66**, 1495-1501.

Feeny, P. (1969). Inhibitory effect of oak leaf tannins on the hydrolysis of proteins by trypsin. *Phytochem.* **8**, 2119-2126.

Feeny, P. (1970). Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* **51**, 566-578.

Feeny, P. (1976). Plant apparency and chemical defence. In: *Biochemical Interaction Between Plants and Insects*. Recent Advances in Phytochemistry Volume 10. (Eds. J.W. Wallace & R.L. Marseli). pp. 1-40. Plenum Press, New York.

Fewkes, D.W. (1961). Diel movements in some grassland Nabidae (Heteroptera). *Ent. Mon. Mag.* **97**, 128-130.

Fielding, C.A. (1992). Aspects of the Ecology of the Lepidoptera Associated with Heather *Calluna vulgaris*. Unpublished Ph.D. Thesis, University of Durham.

Fisher, R.A., Corbet, A.S. and Williams, C.B. (1943). The relation between the number of species and the number of individuals in a random sample from an animal population. *J. Anim. Ecol.* **12**, 42-58.

Forrest, G.I. (1971). Structure and production of north Pennine blanket bog vegetation. *J. Ecol.* **59**, 453-479.

Fowler, S. & Lawton, J.H. (1982). The effects of host-plant distribution and local abundance on the species richness of agromyzid flies attacking British umbellifers. *Ecol. Entomol.* **7**, 257-265.

Fry, R. & Lonsdale, D. (1991) (Eds.). *Habitat Conservation for Insects: A Neglected Green Issue*. The Amateur Entomologists' Society, Middlesex.

Gall, L.F. (1987). Leaflet position influences caterpillar feeding and development. *Oikos* **49**, 172-176.

Gardner, S.M. & Usher, M.B. (1989). Insect abundance on burned and cut upland *Calluna* heath. *The Entomologist* **108**, 147-157.

Gaston, K.J. & Reavey, D. (1989). Patterns in the life histories and feeding strategies of British macrolepidoptera. *Biol. J. Linn. Soc.* **37**, 367-381.

Gaston, K.J. Reavey, D & Valladares, G.R. (1991). Changes in feeding habit as caterpillars grow. *Ecol. Entomol.* **16**, 339-344.

Gaston, K.G., Reavey, D.& Valadares G.R. (1992). Intimacy and fidelity: Internal and external feeding by the British microlepidoptera. *Ecol. Entomol.* **17**, 86-88.

Giavelli, G., Rossi, O.& Sartore, F. (1986). Comparitive evaluation of four species diversity indices related to two specific ecological situations. *Field Stud.* **6**, 429-438.

Gibb, J.A. & Betts, M.M., (1963). Food and food supply of nestling tits (Paridae) in Breckland pine. *J Anim. Ecol.* **32**, 489-533.

Gill, A.M. & Groves, R.H. (1981) Fire regimes in heathlands and their plant-ecological effects. In: *Ecosystems of the World. Volume 9B: Heathlands and Related Shrublands. Analytical Studies*. (Ed. R.L. Specht) pp. 61-84. Elsevier Scientific, Amsterdam.

Gimingham, C.H. (1960). Biological flora of the British Isles. *Calluna vulgaris* (L.) Hull *J. Ecol.*, **48**, 455-483.

Gimingham, C.H. (1972). *The Ecology of Heathlands*. Chapman & Hall, London.

Gimingham, C.H. (1981). Conservation: European Heathlands. In: *Ecosystems of the World. Volume 9B: Heathlands and Related Shrublands. Analytical Studies*. (Ed. R.L. Specht) pp. 249-259. Elsevier Scientific, Amsterdam.

Gimingham, C.H. (1985). Age-related interactions between *Calluna vulgaris* and phytophagous insects. *Oikos* .**44**, 12-16.

Gimingham, C.H. (1988). A reappraisal of cyclical processes in *Calluna* heath. *Vegetatio* **77**, 61-64.

Gimingham, C.H. (1989). Heather and heathlands. *Bot. J. Linn. Soc.* **101**, 263-268.

Gimingham, C.H., Chapman, S.B. & Webb, N.R. (1979). European Heathlands. In: *Ecosystems of the World. Volume 9A: Heathlands and Related Shrublands. Descriptive Studies*. (Ed. R.L.Specht) pp. 365-413. Elsevier Scientific, Amsterdam.

Ginzburg, L.R. & Taneyhill, D.E. (1994). Population cycles of forest Lepidoptera: A maternal effect hypothesis. *J. Anim. Ecol.* **63**, 79-82.

Grant, S.A. (1971). Interactions of grazing and burning on heather moors. 2. Effects on primary production and level of utilization. *J. Br. Grassld. Soc.* **26**, 173-181.

Grant, S.A. & Hunter, R.F. (1962). Ecotypic differentiation of *Calluna vulgaris* (L.) in relation to altitude. *New Phytol.* **61**, 44-55.

Grant, S.A. & Hunter, R.F. (1968). Interactions of grazing and burning on heather moors and their implications in heather management. *J. Br. Grassld Soc.* **23**, 285-293.

Gray J.S. (1987). Species-abundance patterns. In: *Organisation of Communities Past and Present*. (Ed J.H.R. Gee & P.S. Giller) pp. 53-67. Blackwell, Oxford.

Gross, S.W. & Fritz, R.S. (1982). Differential stratification, movement and parasitism of sexes of the bagworm, *Thyridopteryx ephemeraeformis* (Haworth) on redcedar. *J. Econ Entomol* . **7**, 149-154.

Harrison, S. & Thomas, C.D. (1991). Patchiness and spatial pattern in the insect community on ragwort *Senecio jacobea*. *Oikos* **62**, 5-12.

Hartley, S.E. (1993). Insect pests on heather moorland. In: *The Joseph Nickerson Reconciliation Project. Ninth Annual Report.* pp. 46-47.

Heal, O.W. (1980). Fauna of heathlands in the United Kingdom. *Bull. Ecol.* **11**, 413-420.

Heinrich, B. (1979). Foraging strategies of caterpillars: Leaf damage and possible predator avoidance strategies. *Oecologia*, **42**, 325-337.

Heinrich, B. & Collins, S.L. (1983). Caterpillar leaf damage and the games of hide and seek with birds. *Ecology* **64**, 592-602.

Hester, A.J. & Sydes, C. (1992). Changes in the burning of Scottish heather moorland since the 1940's from aerial photographs. *Biol. Conserv.* **60**, 25-30.

Hewson, R. (1962). Food and feeding habits of the mountain hare, *Lepus timidus scotius*, Hilzheimer. *Proc. Zool. Soc. Lond.* **139**, 515-526.

Hill, R.L. (1982). Seasonal patterns of plytophage activity on gorse (*Ulex europaeus*), and host plant quality. In: *Proceedings of the Fifth International Symposium on Insect-Plant Relationships.* (Eds. J.H. Visser & A.K. Minks) pp. 232-247. Pudoc, Wageningen, The Netherlands.

Hobbs, R.J. (1984). Length of burning rotation and community composition in high-level *Calluna-Eriophorum* bog in N England. *Vegetatio* **57**, 129-136.

Hobbs, R.J. & Gimingham, C.H. (1980). Some effects of fire and grazing on heath vegetation. *Bull. Ecol.* **3**, 709-715.

Hobbs, R.J. & Gimingham, C.H. (1987). Vegetation, fire and herbivore interactions in heathlands. *Adv. Ecol. Res.* **16**, 87-173.

Hodkinson, I.D. (1973). The population dynamics and host-plant interactions of *Strophingia ericae* (Curt.) (Homoptera, Psylloidea). *J. Anim. Ecol.* **42**, 565-583.

Horton, D.R. & Capinera, J.L. (1987). Effects of plant diversity, host density, and host size on population ecology of the colorado potato beetle (Coleoptera, Chysomelidae). *Environ. Entomol.* **16**, 1019-1026.

Hughes, R.D. (1955). The influence of the prevailing weather on the numbers of *Meromyza variegata* Meigen (Diptera, Chloropidae) caught with a sweepnet. *J. Anim. Ecol.* **24**, 324-335.

Hunter, A.F. (1991). Traits that distinguish outbreaking and nonoutbreaking macrolepidoptera feeding on northern hardwood trees. *Oikos* **60**, 275-282.

Jalal, M.A.F., Read, D.J. & Haslam, E. (1982). Phenolic composition and its seasonal variation in *Calluna vulgaris*. *Phytochem.* **21**, 1397-1401.

Jermy, T., Hanson, F.E. & Dethier, V.G. (1968). Induction of specific food preferences in Lepidopterous larvae. *Entomologia Exp.Appl.* **11**, 211-230.

Johnson, C.G., Southwood, T.R.E. & Entwhistle, H.M. (1957). A new method of extracting arthropods and molluscs from grassland with a suction apparatus. *Bull. Ent. Res.* **48**, 211-218.

Jones, R.E. (1977). Movement patterns and egg distribution in cabbage butterflies. *J. Anim. Ecol.* **46**, 195-211.

Kempton, R.A. & Taylor, L.R. (1974). Log-series and log-normal parameters as diversity determinants for the Lepidoptera. *J Anim. Ecol.* **43**, 381-399.

Krebs, C.J. (1985). *Ecology. The Experimental Analysis of Distribution and Abundance*. Third Edition. Harper & Row, New York.

Krebs, C.J. (1989). *Ecological Methodology*. Harper Collins, New York.

Latheef, M.A. & Ortiz, J.H. (1983). The influence of companion herbs on egg distribution of the imported cabbageworm, *Pieris rapae* (Lepidoptera, Pieridae) on collard plants. *Can. Ent.* **115**, 1031-1038.

Lauder, A. & Comrie, A. (1936). The composition of heather (*Calluna vulgaris*) *Scot J. Agric.* **19**, 148-152.

Lawrence, W.S. & Bach, C.E. (1989). Chrysomelid beetle movements in relation to host-plant size and surrounding non-host vegetation. *Ecology* **70**, 1679-1690.

Lawton, J.H. (1978). Hostplant influences on insect diversity: The effects of space and time. In: *Diversity of Insect Faunas*. (Eds. L.A. Mound & N. Waloff) pp. 105-125. Blackwell, Oxford.

Lawton, J.H. (1983). Plant architecture and the diversity of phytophagous insects. *Ann. Rev. Ent.* **28**, 23-39.

Lawton, J.H. & McNeill, S. (1979). Between the devil and the deep blue sea: On the problems of being a herbivore. In: *Population dynamics*. (Eds. R.M. Anderson, B.D. Turner & L.R. Taylor) pp. 223-244. Blackwell, Oxford.

Lawton, J.H. & Price, P.W. (1979). Species richness of parasites on hosts: Agromyzid flies on the British Umbelliferae. *J. Anim. Ecol.* **48**, 619-637.

Lawton, J.H. and Schröder D. (1977). Effects of plant type, size of geograhical range and taxonomic isolation on the number of insect species associated with British plants. *Nature* **265**, 137-140.

Lawton, J.H. & Schröder, D. (1978). Some observations on the structure of phytophagous inect communities: The implications for biological control. In: *Proceedings of the Fourth International Symposium. Biological Control of Weeds*. (Ed. T.H. Freeman) pp. 57-73. Centre for Environmental Programs, University of Florida, Gainesville.

Lewis, T. & Taylor, L.R. (1974). *Introduction to Experimental Ecology*. Academic Press, London.

MacArthur, R.H. (1957). On the relative abundance of bird species. *Proc. Nat. Acad. Sci. USA*. **43**, 293-295.

MacArthur, R.H. (1972). *Geographical Ecology*. Harper & Row, New York.

MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.

MacGarvin, M. (1982). Species-area relationships of insects on host plants: Herbivores on rosebay willowherb. *J. Anim. Ecol.* **51**, 207-223.

MacKay, D.A. & Singer, M.C. (1982). The basis for an apparent preference for isolated host plants by ovipositing *Euptychia libye* butterflies. *Ecol. Ent.omol.* **7**, 299-303.

Magurran, A.E. (1988). *Ecological Diversity and its Measurement*. Croom Helm, London.

Mallik, A.U. (1986). Near-ground microclimate of burned and unburned *Calluna* heathland. *J. Environ. Manage.* **23**, 157-171.

Marrs, R.H. (1986). The role of catastrophic death of *Calluna* in heathland dynamics. *Vegetatio* **66**, 109-115.

Marrs, R.H. (1993). An assessment of change in *Calluna* heathlands in Breckland, eastern England, between 1983 and 1991. *Biol. Conserv.* **65**, 133-139.

Martin, J.S. & Martin, M.M. (1982). Tannin assays in ecological studies: Lack of correlation between phenolics, proanthocyanidins and protein-precipitating constituents in mature foliage of six oak species. *Oecologia* **54**, 205-211.

Martin, M.M. & Martin, J.S. (1984) Surfactants: Their role in preventing the precipitation of proteins by tannins in insect guts. *Oecologia* **61**, 342-345.

Mattson, W.J. (1980). Herbivory in relation to plant nitrogen content. *Ann. Rev. Ecol.* **11**, 119-161.

McCoy, E.D. (1987). The ground-dwelling beetles of periodically-burned plots of sandhill. *Fla. Ent.* **70**, 31-39.

McCoy, E.D. & Kaiser, B.W. (1990). Changes in foraging activity of the southern harvester ant *Pogonomyrmex badius* (Latreille) in response to fire. *Amer. Midl. Nat.* **123**, 112-123.

McKey, D. (1979). The distribution of secondary compounds within plants. In: *Herbivores: Their Interactions with Secondary Plant Metabolites.* (Eds. G.A. Rosenthal & D.H. Janzen) pp. 56-133. Academic Press, New York.

McNeill, S. & Southwood, T.R.E. (1978). The role of nitrogen in the development of insect / plant relationships. In: *Biochemical Aspects of Plant and Chemical Coevolution.* (Ed. J. Harborne) pp. 77-98. Academic Press, London.

Merret, P. (1976). Changes in the ground-living spider fauna after heathland fires in Dorset. *Bull. Br. Arachnol. Soc.* **3**, 214-221.

Meyer, G.A. & Montgomery, M.E. (1987). Relationships between leaf age and the food quality of cottonwood foliage for the gypsy moth, *Lymantria dispar*. *Oecologia* **72**, 527-532.

Miller, G.R. (1979). Quantity and quality of the annual production of shoots and flowers by *Calluna vulgaris* in northeast Scotland. *J. Ecol.* **67**, 109-129.

Miller, G.R. (1980). The burning of heather moorland for red grouse. *Bull. Ecol.* **11**, 725-733.

Miller, G.R. & Miles, A.M. (1969). Productivity and management of heather. In: *Grouse Research in Scotland*. Nature Conservancy Council Report 13, pp. 31-45. Nature Conservancy Council, Banchory.

Miller, G.R. & Miles, J. (1970). Regeneration of heather (*Calluna vulgaris* (L.) Hull) at different ages and seasons in northwest Scotland. *J. Appl. Ecol.* **7**, 51-60.

Miller, G.R. & Watson, A. (1978). Territories and the food plant of individual red grouse. I. Territory size, number of mates and brood size compared with the abundance, production and density of heather. *J. Anim. Ecol.* **47**, 293-305.

Milne, J. (1974). The effects of season and age of stand on the nutritive value of heather (*Calluna vulgaris,* L. Hull) to sheep. *J. Agric. Sci.* **83**, 281-288.

Mitchell, H.L. & Chandler, R.F. (1939). *The Nitrogen Nutrition and Growth of Certain Deciduous Trees of Northeastern United States*. Black Rock For. Bull. No.11, Cornwall-on-the-Hudson, New York.

Mole, S. & Waterman, P.G. (1987). A critical analysis of techniques for measuring tannins in ecological sites. *Oecologia* **72**, 137-147.

Moore, N.W. (1962). The heaths of Dorset and their conservation. *J. Ecol.* **50**, 369-391.

Morris, R.F. (1955). The development of sampling techniques for forest insect defoliators, with partiular reference to the spruce budworm. *Can. J. Zool.* **33**, 225-294.

Moss, R. (1968). Food selection and nutrition in ptarmigan (*Lagopus mutus*) In: *Comparative Nutrition of Wild Animals*. (Ed. M.A. Crawford). Symposium of the Zoological Society of London Number 21. pp. 207-216. Academic Press, London.

Moss, R. (1969). A comparison of red grouse (*Lagopus l. scoticus*) stocks with the production and nutritive value of heather (*Calluna vulgaris*). *J. Anim. Ecol.* **38**, 103-122.

Moss, R. (1989). Management of heather for grouse and livestock. *Bot. J. Linn. Soc.* **101**, 301-306.

Moss, R. & Hewson, R. (1985). Effects on heather of heavy grazing by mountain hares. *Holarctic Ecol.* **8**, 280-284.

Moss, R. & Miller, G.R. (1976). Production, dieback and grazing of heather (*Calluna vulgaris*) in relation to numbers of red grouse (*Lagopus l. scoticus*) and mountain hare (*Lepus timidus)* in northeast Scotland. *J. Appl. Ecol.* **13**, 369-377.

Moss, R., Miller, G.R. & Allen, S.E. (1972). Selection of heather by captive red grouse in relation to the age of the plant. *J. Appl. Ecol.* **9**, 771-781.

Mowforth, M.A. & Sydes, C. (1989). *Moorland Management: A Literature Review.* Research and Survey in Nature Conservation Number 25. Nature Conservancy Council, Peterborough.

Myers, J.H. (1981). Interactions between western tent caterpillars and wild rose: A test of some general plant herbivore hypotheses. *J. Anim. Ecol.* **50**, 11-25.

Neuvonen, S., & Niemelä, P. (1981). Species richness of macrolepidoptera on Finnish decidicus trees and shrubs. *Oecologia* **51**, 364-370.

Nicholson, I.A., Paterson, I.S. & Currie, A. (1970). A study of vegetational dynamics: Selection by sheep and cattle in Nardus pasture. In: *Animal Populations in Relation to Their Food Resources*. (Ed. A. Watson) pp. 129-143. Blackwell, Oxford.

Niemelä, P. (1980). Dependence of *Oporinia autumnata* (Lepidoptera, Geometridae) outbreaks on summer temperature. Rep. Kevo Subarctic Res. Stat. **16**, 27-30.

Niemelä, P. Haukioja, E. (1982) Seasonal patterns in species richness of herbivores: Macrolepidoptera larvae on Finnish decidious trees. *Ecol. Entomol.* **7**, 169-175.

Niemelä, P., Iso-Iivari, L., Laine, C. & Laine, U.J. (1980a). Food plant preference and larval growth of larval colour forms of *Entephra caesiata* (Schiff). (Lepidoptera, Geometridae). *Rep Kevo Subarctic. Res. Stat.* **16**, 45-48.

Niemelä, P., Tuomi, J. & Haukioja, E. (1980b). Age specific resistance in trees: Defoliators of tamaracks (*Larix laricina*) by larch bud moth (*Zeiraphera improbana*) (Lepidoptera, Tortricidae). *Ann. Univ. Turk. Ser. A. II. BIOL-GEOGR-GEOL* **63**, 49-58.

Oates, J.F., Waterman, P.G. & Choo, G.M. (1980). Food selection by the south Indian leaf-monkey, *Presbytes johnii* in relation to leaf chemistry. *Oecologia* **45**, 45-56.

Pearsall, W.H. (1950). *Mountains and Moorlands*. New Naturalist Series. Collins, London.

Petraitis, P.S., Latham R.E. & Niesenbaum, R.A. (1989). The maintenance of species diversity by disturbance. *Quart. Rev. Biol.* **64**, 393-418.

Pianka, E.R. (1970). On r- and k-selection. *Amer. Nat.* **104**, 592-597.

Pimentel, D. (1961). The influence of plant spatial patterns on insect populations. *Ann. Entomol. Soc. Am.* **54**, 61-69.

Poinar, G.O. & Gyrisco, G.G. (1960). Effects of light, temperature and relature humidity on the diel behaviour of the alfalfa weevil, *Hypera postica*, *J. Econ. Ent.* **53**, 675-677.

Pollard, E. (1977). A method for assessing changes in abundance of butterflies. *Biol. Conserv.* **12**, 115-134.

Pollard, E., Elias, D.O., Skelton, M.J. & Thomas, J.A. (1975). A method of assessing the abundance of butterflies in Monks Wood National Nature Reserve in 1973. *Entomologist's Gaz.* **26**, 79-88.

Pollard, E. & Yates, T.J. (1993). *Monitoring Butterflies for Ecology and Conservation.* Chapman & Hall, London.

Price, M.P. & Butler, L.G. (1977). Rapid visual estimation and spectrophotometric determination of tannin content of *Sorghum* grain. *J. Agric. Food. Chem.* **25**, 1268-1273.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. & Weis, A.E. (1980). Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. *Ann. Rev. Ecol.* **11**, 41-65.

Ratcliffe, D.A. (1977). *A Nature Conservation Review.* Volume 1. Cambridge University Press, Cambridge.

Ratcliffe, D.A. & Thompson, D.B.A. (1988) The British Uplands: Their ecological character and international significance. In: *Ecological Change in the Uplands.* (Ed M.B. Usher & D.B.A. Thompson) pp. 9-36. Special Publication Series of the British Ecological Society, Number 7. Blackwell, Oxford.

Raup, M.J. & Denno R.F. (1983). Leaf age as a predictor of herbivore distribution and abundance. In: *Variable Plants and Herbivores in Natural and Managed Systems.* (Eds. R.F. Denno & M.S. McClure) pp. 91-124. Academic Press, New York.

Rausher, M.D. (1981). Host plant selection by *Battus philenor* butterflies: The roles of predation, nutrition and plant chemistry. *Ecol. Monogr.* **51,** 1-20.

Rausher, M.D. (1983). Alteration of oviposition behaviour by *Battus philenor* butterflies in response to variation in host-plant density. *Ecology* **64**, 1028-1034.

Rausher, M.D., MacKay, D.A. and Singer, M.C. (1981). Pre-alighting and post-alighting host discrimination by *Euphydryas editha* butterflies: The behavioural mechanisms causing clumped distributions of egg clusters. *Anim. Behav.* **29**, 1220-1228.

Reavey, D. & Lawton, J.H (1991). Larval contribution to fitness in leaf-eating insects. In: *Reproductive Behaviour of Insects: Individuals and Populations*. (Eds. W.J. Bailey & J. Ridsdill-Smith) pp. 292-329. Chapman & Hall, London.

Renkonen, O. (1938). Statisch-okologische Untersuchungen uber die terrestiche kaferwelt der finnishchen bruchmoore. *Ann. Zool. Soc. Bot. Fenn. Vanamo.* **6**, 1-231.

Rhoades, D. & Cates, R. (1976). Toward a general theory of plant antiherbivore chemistry. In: *Biochemical Interaction Between Plants and Insects*. Recent Advances in Phytochemistry Volume 10. (Eds. J. Wallace & R. Mansell) pp. 168-213. Plenum Press, New York.

Robins, C.T., Hanley, T.A., Hagerman, A.E., Hjeljord, O., Baker, D.L., Schwarz, C.C. & Mautz, W.W. (1987). Role of tannins in defending plants against ruminants: Reduction in protein availability. *Ecology* **68**, 98-107.

Rodin, L.E. & Bazilevich, N.I. (1967). *Production and Mineral Cycling in Terrestial Vegetation*. Oliver & Boyd, London.

Rodwell, J.S. (1991). *British Plant Communities*. Volume 2. Cambridge University Press, Cambridge.

Romney, V.E. (1945). The effect of physical factors upon catch of the beet leafhopper (*Eutettix tenellus*) by a cylinder and two sweepnet methods. *Ecology* **26**, 135-148.

Root, R.B. (1973). Organisation of a plant-arthropod association in simple and diverse habitats: The fauna of collards *Brassica oleracea*. *Ecol. Monogr.* **43**, 95-124.

Root, K.B. & Kareiva, P.M. (1984). The search for resources by cabbage butterflies *Pieris rapae:* Ecological consequences and adaptive significance of Markovian movements in a patchy environment. *Ecology* **65**, 147-165.

Rose, F. (1981). *The Wild Flower Key*. Warne & Co. Ltd., London.

Rudd, W.G. & Jensen, R.L. (1977). Sweepnet and ground cloth sampling for insects in soybeans. *J. Econ. Entomol.* **70**, 301-304.

Russell, E.P. (1989) Enemies hypothesis: A review of the effect of vegetational diversity on predatory insects and parasitoids. *Environ. Entmol.* **18**, 590-599.

Saugstad, E.S., Bram, R.A. & Nyquist, W.E. (1967) Factors influencing sweepnet sampling of alfalfa. *J. Econ. Entomol.* **60**, 421-426.

Savory, C.J. (1983). Selection of heather age and chemical composition by red grouse in relation to physiological state, season and time of day. *Ornis Scandinavica* **14**, 135-143.

Schoener, T.W. (1988). Leaf damage in island buttonwood, *Conocarpus erectus*: Correlations with pubesence, island area, isolation and the distribution of major carnivores. *Oikos* **53**, 253-266.

Schotzko, D.J. & O'Keeffe, L.E. (1986a). Comparison of sweepnet, D-vac and absolute sampling for *Lygus hesperus* (Heteroptera, Miradae) in lentils. *J. Econ. Entomol.* **79**, 224-228.

Schotzko, D.J. & O'Keefe, L.E. (1986b). Evaluation of diel variation of sweepnet effectiveness in lentils for sampling *Lygus hesperus* (Heteroptera, Miridae). *J. Econ. Entomol.* **79**, 447-451.

Schweitzer D.F. (1979). Effects of foliage age on body weight and survival in larvae of the tribe Lithophanini (Lepidoptera, Noctiudae). *Oikos* **32**, 403-408.

Scriber, J.M. (1977). Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of *Hyalophora cecropia*. *Oecologia* **28**, 269-287.

Scriber, J.M. (1979). Effects of leaf-water supplementation upon post-ingestive nutritional indices of forb-, shrub-, vine-, and tree-feeding Lepidoptera. *Entomologia. Exp. Appl.* **25**, 240-252.

Scriber, J.M. & Feeny, P. (1979). Growth of herbiverous caterpillars in relation to feeding specialisation and to growth form of their food plants. *Ecology* **60**, 829-850.

Scriber, J.M & Slansky, F. Jnr. (1981). The nutritional ecology of immature insects. *Ann Rev. Entomol.* **26**, 183-211.

Segarra-Carmona, A. & Barbosa, P. (1990). Influence of patch plant-density on herbivory levels by *Etiella zinckenella* (Lepidoptera, Pyralidae) on *Glycine max* and *Crotalaria pallida*. *Environ. Entomol.* **19**, 640-647.

Sheail, J. (1979). Documentary evidence of changes in the use, management and appreciation of the grass-heaths of Breckland. *J. Biogeogr.* **6**, 277-292.

Simpson, E.H. (1949). Measurement of diversity. *Nature* **163**, 688.

Skinner, B. (1984). *Colour Identification Guide to Moths of the British Isles, Macrolepidoptera*. Viking, London.

Sorensen, T. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Kong. Dan. Vidensk. Selsk. Biol. Skr* **5**, 1-34.

South, R. (1961). *The Moths of the British Isles*. Series I and II. Warne & Co. Ltd., London.

Southwood, T.R.E. (1961). The number of insects associated with various trees. *J. Anim. Ecol.* **30**, 1-8.

Southwood, T.R.E. (1978). *Ecological Methods with Particular Reference to the Study of Insect Populations*. Second Edition. Chapman & Hall, London.

Spitzer, K. & Leps, J. (1988). Determinants of temporal variation in moth abundance. *Oikos* **53**, 31-36.

SPSS, (1990). Release 4. Spss Inc., 444 North Michigan Avenue, Chicago, Illinois 60611

Stamp, N.E. & Bowers, D.M. (1990). Phenology of nutritional differences between new and mature leaves and its effect on caterpillar growth. *Ecol. Entomol.* **15**, 447-454.

Stamps, J.A., Buechner, M. & Krishnan, V.V. (1987). The effects of edge permeability and habitat geometry on emigration from patches of habitat. *Amer. Nat.* **129**, 533-552.

Stokoe, W.J. (1948). *The Caterpillars of British Moths*. Series I and II. Warne & Co. Ltd., London.

Strong, D.R., Lawton, J.H. & Southwood, T.R.E. (1984). *Insects on Plants: Community Patterns and Mechanisms*. Blackwell, Oxford.

Summers, C.F. (1978). Production in montane dwarf shrub communities. In: *Production Ecology of British Moors and Montane Grasslands*. (Eds. O.W. Heal & D.F. Perkins) pp. 263-276. Ecological Studies 27. Springer-Verlag, Berlin.

Tahvanainen, J.O. & Root, R.B. (1972). The influence of vegetational diversity on the population ecology of a specialised herbivore, *Phyllotreta cruciferae* (Coleoptera, Chrysomelidae). *Oecologia* **10**, 321-346.

Tenow, O. & Larsson, S. (1987). Consumption by needle-eating insects on scots pine in relation to season and stand age. *Holarctic Ecol.* **10**, 249-260.

Thomas, B. (1934). On the composition of common heather (*Calluna vulgaris*). *J. Agric. Sci.* **24**, 151.

Thomas, B. (1937). On the composition and feeding value of heather at different times of the year. *J. Min. Agric* **43**, 1050.

Thomas, B. (1956). Heather (*Calluna vulgaris)* as a food for livestock. *Herb Abstr* **26**, 1-7.

Thomas, C.D. (1986). Butterfly larvae reduce host-plant survival in vicinity of alternative host species. *Oecologia* **70**, 113-117.

Thomas, C.D. & Harrison, S. (1992). Spatial dynamics of a patchily distributed butterfly species. *J. Anim Ecol.* **61**, 437-446.

Thomas, J.A. (1984) The conservation of butterflies in temperate countries: Past efforts and lessons for the future. In: *Biology of Butterflies*. (Eds. R.Vane-Wright & P. Ackery) pp. 333-353. Academic Press, London.

Thomas, J.A. (1991). Rare species conservation: Case studies of European butterflies. In: *The Scentific Management of Temperate Communities for Conservation*. (Eds. I. Spellerberg, B. Goldsmith & M.G.Morris) pp. 149-197. Blackwell, Oxford.

Thompson, J.N. (1983a). Selection pressures on phytophagous insects feeding on small host plants. *Oikos* **40**, 438-444.

Thompson, J.N. (1983b). The use of ephemeral plant parts on small host plants: How *Depressaria leptotaeniae* (Lepidoptera, Oecophoridae) feeds on *Lomatium dissectum* (Umbelliferae). *J. Anim. Ecol.* **52**, 281-292.

Tokeshi, M. (1993). Species abundance patterns and community structure. *Adv. Ecol. Res.* **24**, 111-186.

Turner, J. (1965). A contribution to the history of forest clearance. *Proc. Roy. Soc. B.* **161**, 343-354.

Turner, J., Hewetson, V.P., Hibbert, F.A., Lowry, K.H. & Chambers, C. (1973). The history of the vegetation and flora of Widdybank Fell and the Cow Green reservoir basin, Upper Teesdale. *Phil. Trans. R. Soc. B* . **265**, 327-408.

Usher, M.B. (1983). Species diversity: A comment on a paper by W.B. Yapp. *Field Stud.* **5**, 825-832.

Usher, M.B. & Gardner, S.M. (1988) Animal communities in the uplands: How is naturalness influenced by management? In: *Ecological Change in the Uplands* (Ed. M.B. Usher & D.B.A. Thompson) pp. 75-92. Special Publication Series of the British Ecological Society, Number 7. Blackwell, Oxford.

Usher, M.B. & Jefferson, R.G. (1991). Creating new and successional habitats for arthropods. In: *The Conservation of Insects and their Habitats.* (Eds. N.M. Collins & J.A.Thomas) pp. 253-291. Academic Press, London.

Usher, M.B. & Smart, L.M. (1988). Recolonisation of burnt and cut upland heathland by arachnids. *The Naturalist*, **113**, 103-111.

Usher, M.B. and Thompson, D.B.A. (1993). Variation in the upland heathlands of Great Britain: Conservation Importance. *Biol. Conserv.* **66**, 69-81.

Valladares, G. & Lawton, J.H. (1991). Host-plant selection in the holly leaf miner: Does mother know best? *J. Anim. Ecol.* **60**, 227-240.

Varley, G.C. (1947). The natural control of population balance in theknapweed gallfly (*Urophora jaceana*). *J. Anim Ecol.* **16**, 139-187.

Varley, G.C. & Gradwell, A.R. (1960). Key factors in population studies. *J. Anim. Ecol.* **29**, 399-401.

Vicari, M. & Bazely, D.R. (1993). Do grasses fight back? The case for antiherbivore defenses. *Trends in Ecology and Evolution* **8**, 137-141.

Wallace, R. & Kind, E. (1884). The natural and artificial food of Scotch hill sheep. *Trans. Highl. Agric. Soc. Scotl.* **16**, 250.

Ward, L.K. & Lakhani, K.H. (1977). The conservation of juniper: The fauna of food-plant island sites in southern England. *J. Appl. Ecol.* **14**, 121-135.

Watson, A. (1964). The food of ptarmigan (*Lagopus mutus*) in Scotland. *Scott. Nat.* **71**, 60-66.

Watt, A.S. (1947) Pattern and process in the plant community. *J. Ecol.* **35**, 1-22.

Watt, A.S. (1955). Bracken versus heather, a study in plant sociology. *J. Ecol.* **43**, 490-506.

Webb, N.R. (1972). Cryptostigmatid mites recorded from heathland in Dorset. *Ent. Mon. Mag.*, **107**, 228-229.

Webb, N.R. (1986). *Heathlands*. Collins, London.

Webb, N.R. (1989). The invertebrates of heather and heathland. *Bot. J. Linn. Soc.* **101**, 307-312.

Webb, N.R., Clarke, R.T. & Nicholas, R.T. (1984). Invertebrate diversity on fragmented *Calluna* heathland: Effects of surrounding vegetation. *J. Biogeogr*, **11**, 41-46.

Webb, N.R. & Haskins, L.E. (1980). An ecological survey of heathlands in the Poole Basin, Dorset, England, in 1978. *Biol. Conserv.* **17**, 281-296.

Webb, N.R. & Hopkins, P.J. (1984). Invertebrate diversity on fragmented *Calluna* heathland. *J. Appl. Ecol.* **21**, 921-933.

Welch, D. (1984). Studies in the grazing of heather moorland in north-east Scotland. III Floristics. *J. Appl. Ecol.* **21**, 209-225.

White, T.C.R. (1975). A quantitative method of beating for sampling larvae of *Selidosema suavis* (Lepidoptera, Geometridae) in plantations in New Zealand. *Can. Ent.* **107**, 403-412.

Whittaker, E. (1961). Temperatures in heath fires. *J. Ecol.* **49**, 709-715.

Wiklund, C. (1977). Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of *Leptidea sinapsis* (Lepidoptera). *Oikos* **28**, 56-68.

Williams, C.B. (1944). Some applications of the logarithmic series and the index of diversity to ecological problems. *J. Ecol.* **32**, 1-44.

Williams, C.B. (1964). *Patterns in the Balance of Nature*. Academic Press, London.

Woodwell, G.M. (1974). Variation in the nutrient content of leaves of *Quercus alba, Q. coccinea* and *Pinus rigida* in the Brookhaven Forest from bud break to abscisscion. *Amer. J. Bot.* **61**, 749-753.

Woolhouse, H.W. & Kwolek, A.V.A. (1981). Seasonal growth and flowering rhythms in European heathlands. In: *Ecosystems of the World. Volume 9B: Heathlands and Related Shrublands. Analytical Studies.* (Ed. R.L. Specht) pp. 29-38. Elsevier Scientific, Amsterdam.

Wright, A.F. & Stewart, A.J.A. (1992). A study of the efficacy of a new inexpensive type of suction apparatus in quantitative sampling of grassland invertebrate populations. *Bulletin of the British Ecological Society* **23**, 116-120.

Zar, J.H. (1984). *Biostatistical Analysis*. Prentice International Editions.

Stand	Mean age (years)	SD	Maximum age (years)	n	Life history phase	Mean height (cm)	SD	n
SL-1	2.7	0.5	3	10	Pioneer	8.0	2.5	40
SL-2	10.0	1.6	12	10	Building	33.4	7.5	40
SL-3	23.3	3.1	26	10	Degenerate	54.7	10.1	40
SL-4	9.1	0.7	10	10	Building	38.5	7.0	40
SL-5	4.7	0.9	6	10	Late pioneer	11.2	3.1	40
SL-6	11.5	1.3	13	10	Late building	45.3	8.3	40
SL-7	7.9	0.7	9	10	Building	27.4	3.3	40
SL-8	4.0	0.5	5	10	Pioneer / building	20.7	4.7	40
SL-9	18.0	1.2	20	10	Mature	47.4	6.3	40
SL-10	8.5	1.0	11	10	Building	35.2	3.7	40
SL-K	2.2	0.8	3	10	Pioneer	7.6	3.2	20
SL-L	2.3	0.5	3	10	Pioneer	5.5	1.8	20
SL-M	2.2	0.4	3	10	Pioneer	7.7	2.6	20
SL-N	2.8	0.4	3	10	Pioneer	7.4	3.3	20
SL-O	2.0	0.7	3	10	Pioneer	8.8	2.7	20

Appendix A.1. The mean age, life history phase and mean height of *Calluna* plants in the 15 stands studied at Slaley (SL). The heights and ages of stands SL-1 to SL-10 were measured in autumn 1992. Stands SL-K to SL-O were incorporated into the study in 1993 and their heights and ages were measured in early October 1993. The mean age is the average annual ring count from the stems of ten plants, when thin sections were examined under light microscope. The life history phases follow Watt (1947, 1955). The mean height was the distance between the ground and the nearest shoot tip (measured to the nearest 0.5cm) when *Calluna* height was measured at 40 positions within each stand.

Stand	Mean age (years)	SD	Maximum age (years)	n	Life history phase	Mean height (cm)	SD	n
WK-1	18.3	1.8	21	10	Mature	34.8	6.6	40
WK-2	6.0	0.7	7	10	Pioneer	13.3	3.0	40
WK-7	21.8	1.1	24	10	Mature / degenerate	34.8	7.6	40
WK-8	11.3	1.2	13	10	Building	27.5	5.1	40
WK-10	5.4	1.0	7	10	Pioneer	12.7	3.2	40
WK-23	18.3	2.3	22	10	Building / mature	31.8	6.5	40
WK-24	5.3	1.3	7	10	Pioneer	11.1	2.6	40
WK-25	18.9	3.6	22	10	Late mature	30.2	5.8	40
WK-26	11.9	0.7	13	10	Building	28.8	3.3	40
WK-35	22.6	3.5	26	10	Degenerate	26.4	6.1	40
WK-A	4.0	0.6	5	10	Pioneer	8.6	2.3	20
WK-B	3.7	0.7	5	10	Pioneer	7.4	3.1	20
WK-C	6.4	0.8	8	10	Pioneer	8.2	3.2	20
WK-D	4.6	0.8	6	10	Pioneer	8.3	2.9	20
WK-E	3.6	0.3	5	10	Pioneer	7.4	2.4	20

Appendix A.2. The mean age, life history phase and mean height of *Calluna* plants in the 15 stands studied at Waskerley (WK). The heights and ages of stands WK-1 to WK-35 were measured in autumn 1992. Stands WK-A to WK-E were incorporated into the study in 1993 and their heights and ages were measured in early October 1993. The mean age is the average annual ring count from the stems of ten plants, when thin sections were examined under light microscope. The life history phases follow Watt (1947, 1955). The mean height was the distance between the ground and the nearest shoot tip (measured to the nearest 0.5cm) when *Calluna* height was measured at 40 positions within each stand.

Stand	Life history phase	Mean height (cm)	SD	n
GL-1	Building	20.4	3.5	40
GL-2	Mature	31.9	8.1	40
GL-3	Pioneer	8.6	2.2	40
GL-4	Building	28.8	5.0	40
GL-7	Building	23.1	4.0	40
GL-8	Late mature	33.9	8.9	40
GL-16	Pioneer	8.6	2.3	40
GL-17	Building	28.3	6.5	40
GL-18	Pioneer	9.8	2.7	40
GL-19	Late mature	29.8	5.2	40
GL-20	Early building	17.6	3.2	40
GL-21	Mature	31.6	5.9	40
GL-22	Pioneer	11.6	2.7	40
GL-23	Mature	35.9	5.4	40
GL-24	Late mature	36.8	6.6	40
GL-25	Late mature	27.3	4.6	40
GL-26	Pioneer	9.3	2.1	40
GL-27	Mature	27.3	5.2	40
GL-28	Pioneer	7.8	2.0	40
GL-29	Building	19.4	7.3	40

Appendix A.3. The mean age, life history phase and mean height of *Calluna* plants in the 20 stands studied at Greenlaw Moor (GL). The heights of the stands were measured in autumn 1992. The life history phases follow Watt (1947, 1955). The mean height was the distance between the ground and the nearest shoot tip (measured to the nearest 0.5cm) when *Calluna* height was measured at 40 positions within each stand.

Stand	Life history phase	Mean height (cm)	SD	n
LG-1	Late mature	40.5	7.0	40
LG-2	Pioneer	9.9	3.3	40
LG-3	Pioneer / building	12.0	3.2	40
LG-4	Building / mature	40.1	2.9	40
LG-5	Degenerate	34.9	12.3	40
LG-6	Early building	27.3	4.4	40
LG-7	Pioneer	13.7	3.4	40
LG-8	Mature	51.3	4.6	40
LG-9	Pioneer	11.8	2.6	40
LG-10	Mature	41.0	5.2	40
LG-11	Building	28.5	4.3	40
LG-12	Pioneer	14.1	3.1	40
LG-13	Building	21.6	2.9	40
LG-14	Building	34.7	4.3	40
LG-15	Pioneer	13.3	2.6	40
LG-16	Building	32.8	4.2	40
LG-17	Pioneer / building	14.6	2.6	40
LG-18	Building	17.6	2.9	40
LG-19	Building	26.6	4.1	40
LG-20	Pioneer	12.2	4.2	40

Appendix A.4. The mean age, life history phase and mean height of *Calluna* plants in the 20 stands studied at Langholm (LG). The heights of the stands were measured in autumn 1992. The life history phases follow Watt (1947, 1955). The mean height was the distance between the ground and the nearest shoot tip (measured to the nearest 0.5cm) when *Calluna* height was measured at 40 positions within each stand.

Stand	*Calluna vulgaris*	*Vaccinium myrtillus*	*Erica tetralix*	*Erica cinerea*	*Empetrum nigrum*	*Juncus squarrosus*	Bryophytes	Lichens	Grasses	Other
SL-1	73	-	-	-	-	-	10	5	-	-
SL-2	100	-	13	-	-	-	23	-	-	-
SL-3	100	-	-	-	-	-	23	5	5	-
SL-4	100	-	20	-	-	-	35	-	8	-
SL-5	80	-	-	-	-	3	18	-	-	-
SL-6	100	-	-	-	-	-	35	3	3	-
SL-7	98	-	-	-	-	-	-	5	-	-
SL-8	88	-	23	-	-	-	25	-	3	-
SL-9	98	-	3	-	-	-	20	-	-	-
SL-10	98	-	33	-	-	-	25	3	-	-
SL-K	68	-	-	-	-	-	50	-	20	-
SL-L	93	-	-	-	-	-	-	13	-	-
SL-M	98	-	-	-	-	-	-	3	-	-
SL-N	90	-	-	3	-	-	13	5	5	-
SL-0	83	-	-	10	-	-	25	-	-	-

Appendix A.5. The percentage ground cover occupied by different plant species at the 15 stands studied at Slaley (SL). Cover was estimated using a point quadrat technique. Species were recorded as present if they touched a vertical pin at any point between ground level and the canopy. A total of 40 samples were taken at each stand. The proportion of pins that touched each species was calculated as a percentage and taken as the species' cover.

Stand	*Calluna vulgaris*	*Vaccinium myrtillus*	*Erica tetralix*	*Erica cinerea*	*Empetrum nigrum*	*Juncus squarrosus*	Bryophytes	Lichens	Grasses	Other
WK-1	100	-	-	-	-	-	8	3	-	-
WK-2	45	-	-	-	-	-	20	3	-	-
WK-7	100	-	-	-	-	-	10	-	-	-
WK-8	93	-	-	-	-	-	8	-	-	-
WK-10	63	-	8	-	-	-	68	3	18	-
WK-23	98	-	-	-	-	-	45	5	-	-
WK-24	88	-	-	-	3	-	45	5	-	-
WK-25	93	8	3	-	3	-	73	3	-	-
WK-26	100	-	-	-	8	-	55	-	-	-
WK-35	83	-	-	-	10	-	65	-	18	-
WK-A	65	-	-	-	-	-	80	5	-	-
WK-B	65	-	-	-	-	-	50	-	-	-
WK-C	100	-	-	-	5	-	15	-	-	-
WK-D	75	-	-	-	-	-	60	-	28	5
WK-E	85	-	-	-	-	-	80	-	-	-

Appendix A.6. The percentage ground cover occupied by different plant species at the 15 stands studied at Waskerley (WK). Cover was estimated using a point quadrat technique. Species were recorded as present if they touched a vertical pin at any point between ground level and the canopy. A total of 40 samples were taken at each stand. The proportion of pins that touched each species was calculated as a percentage and taken as the species' cover.

Stand	*Calluna vulgaris*	*Vaccinium myrtillus*	*Erica tetralix*	*Erica cinerea*	*Empetrum nigrum*	*Juncus squarrosus*	Bryophytes	Lichens	Grasses	Other
GL-1	100	-	-	-	-	-	18	3	-	-
GL-2	100	-	-	-	-	-	95	-	-	-
GL-3	90	-	5	-	-	-	25	15	-	-
GL-4	100	-	8	-	-	-	68	-	10	-
GL-7	98	-	-	-	-	-	65	3	5	-
GL-8	100	-	-	-	-	-	95	-	-	-
GL-16	90	-	-	-	-	-	18	3	5	-
GL-17	100	-	3	-	-	-	48	3	-	-
GL-18	80	-	-	-	-	-	38	-	-	-
GL-19	98	-	-	-	-	-	55	-	-	-
GL-20	95	-	-	-	-	-	58	-	-	-
GL-21	95	-	-	-	-	-	35	15	-	-
GL-22	43	-	-	-	-	-	-	73	-	-
GL-23	98	-	-	-	-	-	63	-	-	-
GL-24	93	-	-	-	-	-	78	-	-	-
GL-25	93	-	-	-	-	-	90	-	-	-
GL-26	38	-	-	-	-	-	85	-	-	-
GL-27	100	-	3	-	-	-	38	3	5	-
GL-28	85	-	13	-	-	-	23	-	-	-
GL-29	90	-	-	-	-	-	13	25	-	-

Appendix A.7. The percentage ground cover occupied by different plant species at the 20 stands studied at Greenlaw (GL). Cover was estimated using a point quadrat technique. Species were recorded as present if they touched a vertical pin at any point between ground level and the canopy. A total of 40 samples were taken at each stand. The proportion of pins that touched each species was calculated as a percentage and taken as the species' cover.

Stand	*Calluna vulgaris*	*Vaccinium myrtillus*	*Erica tetralix*	*Erica cinerea*	*Empetrum nigrum*	*Juncus squarrosus*	Bryophytes	Lichens	Grasses	Other
LG-1	100	-	3	-	-	8	55	-	-	-
LG-2	88	-	3	-	-	3	83	-	5	-
LG-3	80	-	28	-	-	50	60	-	-	-
LG-6	100	-	25	-	-	20	83	-	-	-
LG-7	55	-	25	-	-	15	75	-	8	-
LG-9	85	-	13	-	-	8	68	-	8	-
LG-10	98	-	5	-	-	-	43	-	10	-
LG-11	100	-	-	-	-	-	73	-	8	-
LG-12	95	-	18	-	-	15	73	-	-	-
LG-13	98	-	8	-	-	8	35	-	-	3
LG-14	100	-	20	-	-	15	58	-	-	-
LG-15	90	-	3	-	-	-	85	-	10	-
LG-16	98	-	10	-	-	3	58	-	5	-
LG-17	100	-	-	-	-	-	60	-	3	-
LG-18	100	-	-	-	-	3	75	3	-	-
LG-19	95	-	8	-	-	-	-	-	-	-
LG-20	68	-	5	-	-	3	80	-	-	-

Appendix A.8. The percentage ground cover occupied by different plant species at 17 stands studied at Langholm (LG). Cover was estimated using a point quadrat technique. Species were recorded as present if they touched a vertical pin at any point between ground level and the canopy. A total of 40 samples were taken at each stand. The proportion of pins that touched each species was calculated as a percentage and taken as the species' cover. Stands LG-4, LG-5 and LG-8 were burned in the autumn of 1992 before their floral composition could be assessed.

		Waskerley										Slaley										Stuartfield		
Visit No.	**Date**	**1**	**2**	**7**	**8**	**10**	**23**	**24**	**25**	**26**	**35**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**30**	**31**	**34**
1	5.5.92							X	X	X														
	14.5.92																					X	X	
2	19.5.92	X	X				X	X																
	22.5.92																					X	X	
3	26.5.92	X	X	X	X		X	X																
	28.5.92																					X	X	X
	29.5.92										X													
4	4.6.92			X	X		X	X	X	X	X													
	6.6.92										X											X	X	
	8.6.92	X	X																					
5	10.6.92			X	X																			
	12.6.92	X	X				X	X	X	X	X											X	X	X
6	24.6.92	X	X	X	X		X	X	X	X	X													
	26.6.92											X	X	X	X	X	X	X						
	28.6.92																					X	X	X

Appendix B.1. The dates on which *Calluna* stands at Waskerley, Slaley and Stuartfield Lodge were sampled by sweepnetting in 1992. X indicates that the stand was sampled on that date. Twenty samples of ten sweepnet strokes were taken at a stand on each sampling occasion. **(Continued overleaf).**

		Waskerley										Slaley										Stuartfield		
Visit No.	**Date**	**1**	**2**	**7**	**8**	**10**	**23**	**24**	**25**	**26**	**35**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**30**	**31**	**34**
7	6.7.92																					X	X	X
	7.7.92	X	X	X	X		X	X	X	X	X													
	10.7.92											X	X	X	X	X	X	X	X	X	X			
8	14.7.92																					X	X	X
	16.7.92	X	X	X	X																			
	17.7.92					X	X	X	X	X	X	X	X	X	X									
	18.7.92															X	X	X	X	X	X			
9	23.7.92																					X	X	X
	24.7.92	X	X	X	X	X	X	X	X	X	X													
	28.7.92											X	X	X	X	X	X	X	X	X	X			
10	3.8.92	X	X	X	X	X	X	X	X	X	X													
	4.8.92											X	X	X	X	X	X	X	X	X	X			
	6.8.92																					X	X	X
11	24.8.92	X	X	X	X	X	X	X			X													
	25.8.92								X	X		X	X	X	X									
	27.8.92															X	X	X	X	X	X			
	28.8.92																					X	X	X

Appendix B.1 (Continued from previous page. Continues overleaf)

		Waskerley										Slaley										Stuartfield		
Visit No.	**Date**	**1**	**2**	**7**	**8**	**10**	**23**	**24**	**25**	**26**	**35**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**30**	**31**	**34**
12	7.9.92	X	X	X	X	X	X	X	X	X	X													
	8.9.92											X	X	X	X	X	X	X	X	X	X			
	9.9.92																					X	X	X
13	15.9.95																					X	X	X
	17.9.92	X	X	X	X	X	X	X	X	X	X													
	18.9.92											X	X	X	X	X	X	X	X	X	X			
14	5.10.92											X	X	X	X	X	X	X	X	X	X			
	6.10.92																					X	X	X
	8.10.92	X	X	X	X	X	X	X	X	X	X													
15	30.10.92																					X	X	X
	3.11.92	X	X	X	X	X	X	X	X	X	X													
	5.11.92											X	X	X	X	X	X	X	X	X	X			

Appendix B.1 (continued from previous page).

		Waskerley										Slaley									
Visit No.	Date	1	2	7	8	10	23	24	25	26	35	1	2	3	4	5	6	7	8	9	10
1	29.4.93	X	X	X	X	X	X	X	X	X	X										
	30.4.93											X	X	X	X	X	X	X	X	X	X
2	21.5.93											X	X	X	X	X	X	X	X	X	X
	24.5.93	X	X	X	X	X	X	X	X	X	X										
3	6.6.93											X	X	X	X	X	X	X	X	X	X
	8.6.93	X	X	X	X	X	X	X	X	X	X										
4	21.6.93											X	X	X	X	X	X	X	X	X	X
	24.6.93	X	X	X	X	X	X	X	X	X	X										
5	30.7.93	X	X	X	X	X	X	X	X	X	X										
	2.8.93											X	X	X	X	X	X	X	X	X	X

Appendix B.2a The dates on which *Calluna* stands at Waskerley and Slaley were sampled by sweepnetting in 1992. X indicates that the stand was sampled on that date. Twenty samples of ten sweepnet strokes were taken at a stand on each sampling occasion.

		Waskerley					Slaley				
Visit No.	**Date**	**A**	**B**	**C**	**D**	**E**	**K**	**L**	**M**	**N**	**O**
1	2.6.93	X	X	X	X	X	X	X	X	X	X
2	13.7.93						X	X	X	X	X
3	2.8.93						X	X	X	X	X

Appendix B.2b. The dates on which *Calluna* stands A-E at Waskerley and K-O at Slaley were sampled by sweepnetting. X indicates that a stand was sampled by sweepnetting on that date. Twenty samples of ten sweepnet strokes were taken at a stand on each sampling occasion.