PLANT HERBIVORE INTERACTIONS WITHIN A COMPLEX MOSAIC OF GRASSLAND, MIRE AND MONTANE COMMUNITIES

By

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SUMMARY

Commercial sheep farming in the Highlands of Scotland has had a considerable influence on the landscape, ecology and economy of the region. The hill sheep industry developed in the Highlands in the mid 18^{th} Century and remains the dominant form of agriculture in the hills and uplands. The hill grazings used by these sheep are dominated by unimproved semi-natural grassland, heather moorland and blanket bog. There is considerable concern from conservationists over the impact that sheep grazing is having on these semi-natural habitats, in particular the loss of heather moorland and the expansion of *Nardus stricta*-dominated grasslands. The government response to this has revolved around encouraging hill farmers to reduce sheep numbers (i.e. extensify). The semi-natural hill grasslands are of considerable economic importance to the sheep industry. *Nardus stricta* and *Juncus squarrosus* dominate a large proportion of these grasslands. The production and grazing utilisation of these semi-natural hill grasslands, and their response to extensification are therefore of considerable interest.

This study investigated the effect that changes in grazing management had on species composition, vegetation structure, above-ground biomass, production and utilisation of a range of hill grassland and mire communities. The data collected from the study was then used to test and evaluate the vegetation component of the Hill Grazing Management Model (HGMM). The HGMM is a computer model designed to assist grazing management decision-making on British hill farms. The HGMM has a number of weaknesses, the main one being the limited range of vegetation types. The model does not include communities dominated by *Juncus squarrosus*, and although it does include *Nardus stricta* grassland it is only considered in terms of the *Festuca - Agrostis* growing

between the *Nardus stricta* tussocks. One of the main aims of this study was to modify the HGMM to improve its predictive ability for sites with high proportions of *Nardus stricta* and *Juncus squarrosus* dominated grassland, using data collected from the study site.

The study was carried out at a system scale level, using three large enclosures of approximately 40 hectares each. Two enclosures were grazed by sheep at mean annual stocking rates of 0.074 LU ha^{-1} and 0.051 LU ha^{-1}, and the third enclosure was grazed by sheep and summer grazing cattle at a mean annual stocking rate of 0.096 LU ha^{-1}.

A quadrat survey and a vegetation mapping exercise were carried out to provide detailed information on the floristic composition of the vegetation community types, their areas, and spatial and altitudinal distributions. A detailed vegetation map was produced using a total survey station and a geographic information system. The study site consisted of a complex mosaic of twenty-two NVC vegetation types. Communities dominated by *Nardus stricta* covered over half the study area.

Permanent nested quadrats and monthly sward surface height measurements were used to monitor changes in the composition and structure of the vegetation under the different grazing treatments. Few changes in species composition or the abundance of dominant species were observed, and none of the monitored vegetation types changed their NVC type. A number of ruderal and grazing tolerant species increased in frequency within the sheep and cattle grazed enclosure, as did the area of bare ground. The sward was also significantly shorter in the sheep and cattle grazed enclosure.

Monthly above-ground biomass values of four vegetation types were estimated by harvesting strips of vegetation, sub-sampling, sorting, drying and weighing. Biomass varied significantly through the year. Mean summer biomass values varied from year to year. The biomass of both the *Nardus stricta* grassland and *Juncus acutiflorus* mire were significantly lower in the enclosure with the sheep and summer grazing cattle.

The work presented in this thesis indicates that in the short term, extensification has very little impact on the species composition of hill grasslands and only minor effects on the structure and biomass of these grasslands. Entering into short-term management agreements to reduce sheep numbers is unlikely to result in any major environmental benefits if *Nardus stricta* and *Juncus squarrosus* dominate the hill vegetation.

The production and utilisation of four vegetation types were estimated using an exclosure cage technique. Production values ranged from 1.88 tonnes ha^{-1} for a *Festuca - Agrostis* grassland, to approximately 4.09 tonnes ha^{-1} for a *Nardus stricta* grassland. Production of vascular plant biomass was highest in June and July, with little or no production during the winter.

Offtake of green material from the *Nardus stricta* grassland was higher than from the *Nardus stricta - Juncus squarrosus* grassland. The highest estimated offtakes were recorded from the enclosure containing the summer grazing cattle. Under the two higher stocking rates the offtakes of live *Nardus stricta* and inter-tussock vegetation from the *Nardus stricta* grassland were similar.

The HGMM was tested and evaluated using data from the study site. The HGMM under-estimated the production, green biomass, sward height and offtake of inter-tussock material from the *Nardus stricta* grasslands. The HGMM was therefore modified to allow the input of data from the *Nardus stricta* and *Nardus stricta - Juncus squarrosus* grasslands. Data from the study site and an independent data set were used to validate the modified model. Modification improved the accuracy of the model's predictions. The modified HGMM predicted higher offtake from the *Nardus stricta* grasslands and higher total offtake than the original HGMM. The full inclusion of the *Nardus stricta* and *Nardus stricta - Juncus squarrosus* grasslands into the model improved the model's applicability for use in sites where these communities are widespread and abundant. However, the improvements were relatively minor and further development of model is required.

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PLANT HERBIVORE INTERACTIONS WITHIN A COMPLEX MOSAIC OF GRASSLAND, MIRE AND MONTANE COMMUNITIES

CHAPTER 1 – INTRODUCTION

1.1 Summary

Commercial sheep farms have been present in the Highlands of Scotland for over 200 years, and this has had a considerable effect on the landscape, ecology and economy of the region. Hill sheep farming remains the dominant form of agriculture in the Scottish hills and uplands. Of the 3.9 million breeding ewes in Scotland over half are hardy hill breeds kept on hill farms within the Scottish Less Favoured Areas (SERAD, 2000a; MAFF, 1999). The hill grazings used by these sheep are dominated by unimproved semi-natural grassland, heathland and blanket bog. The regions where these hill sheep systems are found, often have landscapes of outstanding natural beauty, are important for tourism and outdoor recreation, and contain a significant proportion of land designated for its nature conservation value. There is considerable concern from conservationists over the impact that sheep grazing is having on these semi-natural habitats. The loss of biodiversity through overgrazing, and the displacement of heather moorland by *Nardus stricta*-dominated grassland, have been of particular concern. The government response to this has revolved around encouraging farmers (through agri-environment schemes and to some extent through cross compliance within the main livestock subsidy schemes) to reduce their sheep numbers (i.e. to extensify).

Semi-natural grasslands or habitat mosaics containing semi-natural grasslands cover 26 % of upland Scotland (Milne *et al.*, 1998), and form an important grazing resource. They are therefore of considerable economic importance to the sheep industry. Over 50 % of these grasslands are characterised by the dominance of *Nardus stricta*, *Molinia caerulea* or *Juncus* species (Milne *et al.*, 1998). The production and grazing utilisation of these semi-natural hill grasslands, and their response to extensification are therefore of considerable interest.

1.2 The development of the sheep industry in the Highlands of Scotland

Prior to the period of rapid social change commonly known as the Highland clearances, farming in the Highlands was carried out at a subsistence level, with very little being bought or sold (Smout, 1969; Prebble, 1963). The most important livestock were small, 'old type', Highland cattle (Watson, 1932). Poultry and goats were often numerous, but sheep were less abundant and kept only in sufficient numbers to clothe the population (Watson, 1932). Throughout the West Highlands native ponies were kept as the main work animal (Watson, 1932). Even in the most mountainous regions, the fertile glens were cultivated. The main crops were bere, a type of four-rowed barley (*Hordeum vulgare*), bristle oat (*Avena strigosa*), and on the better land, the common oat (*Avena sativa*) (Watson, 1932; Stace, 1991). Flax, which was retted and spun on the farms, was also grown (Watson, 1932). The potato became a major and very important component of the diet of the highland population after its introduction into the Highlands in the mid 18th Century (Watson, 1932). The old types of sheep kept by the highland farmers were small, with average adult carcass weights of less than 11 kg

(Watson, 1932). They produced lean mutton and fine soft wool. The sheep varied considerably in colour and stature, but could be broadly classified into three main types: a short-tailed type, with black, grey or piebald colouration (similar to the current Shetland breed), which was found mainly in the Orkney Isles, the Northern Hebrides and the north-west coast of the mainland; a tan-faced type (similar to the current Welsh Mountain breed), which occurred mainly in the west; and a short, narrow framed, blackfaced type, known as the Kerry, which was found in Caithness and Sutherland (Watson, 1932). Each summer the cattle, sheep and goats were taken up to the hill pastures to graze for 6 to 8 weeks (Watson, 1932). The people remained with their stock during the summer, living in primitive stone dwellings known as shielings. None of the animals could survive the winter on the open hill and had to be moved to lower ground, often over-wintering with the people inside longhouses (Watson, 1932).

Large-scale sheep farming in the south of Scotland was in existence in the 12th Century, with documentary evidence showing that the monks of Kelso Abbey had considerable flocks on the Cheviot Hills, exporting their wool from Berwick (Watson, 1932). Commercial sheep farming in the Highlands developed much later, arriving in Argyll in about 1760, and gradually spreading north over the whole of the region, reaching Caithness and Sutherland by the beginning of the 19th Century (Watson, 1932). The traditional, transhumance farming system, which had focused on the seasonal grazing of hill pastures by cattle, plus some arable cultivation in the glens, was replaced by an industry dominated by commercial sheep production. Enticed by the low price/rent of land in the highlands, a comparatively small number of pioneer lowland farmers moved north with their flocks, producing twice the output from mutton compared with that from beef, plus highly valued wool (Watson, 1932; Prebble, 1963).

The Blackface sheep, which could survive on the poorest pastures and in the most extreme environments, dominated the early sheep industry in the West Highlands, Perthshire and Inverness-shire. However, during the early 19th Century, the high price of fine wool led to an increase in the numbers of Cheviot sheep, which displaced the Blackface flocks (Watson, 1932). After 1860 the replacement of Blackface sheep with Cheviots was reversed, due to a combination of factors (Watson, 1932). The factor that initiated this change was the harsh winter of 1860, which highlighted the superior hardiness of the Blackface (Watson, 1932). Also at this time, increasing amounts of fine, high-quality Merino wool, were reaching Europe from Australia, reducing the demand for Cheviot wool (Watson, 1932). There was also a rise in the price of mutton and store sheep, which favoured the Blackface, as hill grazings could carry greater numbers of Blackface sheep compared with Cheviots (Watson, 1932). Later, at the end of the 19th Century, the number of wether sheep (castrated males) began to decline rapidly, due to a decline in the value of wethers relative to that of lambs, causing farmers to dispense with their wether flocks in favour of ewes (Watson, 1932). Since much of the hill land that had been grazed by Cheviot wethers was not suitable for Cheviot ewes, graziers changed to Blackface ewe flocks (Watson, 1932). Sheep numbers in the Highlands and north of Scotland increased by approximately 20 % between 1855 and 1880, and then stabilised (Watson, 1932). From 1895 until the start of the First World War there was a gradual decline in sheep numbers in the more mountainous areas of the Highlands, however in the northern lowlands numbers continued to increase (Watson, 1932). In the first decade of the 20th Century there were approximately 7.1 million sheep in Scotland (Ritchie, 1919). Since the development of the sheep industry in Scotland, hill sheep numbers have fluctuated in response to economic factors, disease epidemics and severe weather events (Sydes and Miller, 1988). However, since the Second World War, government policies and their associated subsidy payments, have increasingly influenced sheep numbers (Sydes and Miller, 1988; Topp, 1998). In the Loch Lomond area in the Southern Highlands of Scotland, breeding ewe numbers increased by 39 % between 1945 and 1965 (Topp, in press). There was then a 15 % decline in ewe numbers between 1965 and 1985, followed by a 10 % increase in numbers up to 1991 (Topp, 1998).

It is difficult to assess how many sheep there are in the hills and uplands of Scotland today, however in 1999, 3.5 million breeding ewes were on major holdings within the Less Favoured Areas (LFAs) (MAFF, 1999). Of these ewes, 62 % received the higher rate of Hill Livestock Compensatory Allowance (HLCA) payments, which can only be claimed for the hardy hill breeds within the Severely Disadvantaged Areas (MAFF, 1999). Over the period 1976 to 1999 the number of breeding ewes on major holdings within the Scottish Severely Disadvantaged Areas increased by 17 % (MAFF, 1999). Over the same period the number of beef cows within the Scottish Severely Disadvantaged Areas (in receipt of HLCA payments) declined by 3 % (from 457,000 to 442,000 animals) (MAFF, 1999).

Hill livestock production has changed markedly over the last 250 years. The system of farming, the breed of sheep, the principal product, and the number of sheep and cattle have all changed in response to economic and environmental factors. Despite these many changes, the system of all year round grazing of hill pastures by hardy hill sheep has been in place in much of Highland Scotland since the beginning of the 19th Century.

1.3 The present day Scottish sheep industry

Scotland's present day sheep industry is based on a stratified production system, in which there are three main components: hill flocks, upland flocks and lowland flocks. The hill flocks are composed mainly of Scottish Blackface sheep and some North and South Country Cheviots, which are hardy hill breeds that can survive the poor grazings and harsh climate of the Scottish mountains (Dewar-Durie, 2000). The hill flocks are almost exclusively breeding flocks, with a high proportion of ewe lambs retained as flock replacements to cover ewe mortality and the sale of older draft ewes. The draft ewes are typically sold on to upland farms on slightly lower and more fertile ground, usually after four lamb crops (Dewar-Durie, 2000). Most of the male lambs are sold at the autumn sales as stores to be finished on lowland farms, or as fat lambs for slaughter, many going for export to meet the demand for light weight lambs on the continent. The upland flocks are composed largely of draft hill ewes that are mated with rams of more prolific breeds (e.g. Bluefaced Leicester, Border Leicester) to produce crossbred lambs (e.g. Scotch Mule, Scottish Halfbred, Greyface) (Dewar-Durie, 2000). The crossbred male lambs are sold fat for slaughter, while the crossbred ewe lambs, which benefit from high fertility and hybrid vigour, are sold to lowland farms or other upland farms, where they are crossed with meat breed terminal sires (e.g. Suffolk, Texel, Charolais), to produce high-quality, prime lamb (Dewar-Durie, 2000). In 1999 there were 18,320 sheep producers in Scotland, and a total of 9,705,320 sheep (SERAD, 2000a). The ewe breeding flock was 3,877,890 (SERAD, 2000a). In 1999, direct EU subsidy support, in the form of Sheep Annual Premium (SAP) and HLCA payments, totalled £103 million, which represents approximately £30 for each ewe in the hills and uplands (Dewar-

Durie, 2000). Without public subsidy most Scottish hill farms would not be economically viable (SERAD, 2000a; 2000c).

In Britain, hill sheep are generally reared as free-ranging animals without the presence of a shepherd, and are kept on the hill ground throughout the year (Waterhouse, 1999). The animals are retained within specific areas through a combination of shepherding, long-term selection for home-range behaviour, culling of habitually straying sheep, and some fencing (Waterhouse, 1999). The hill sheep breeds tend to forage in a dispersed manner with individual animals retaining a home-range within the larger home-range of the management flock, a behaviour known as hefting (Hunter and Milner, 1963).

1.4 The semi-natural vegetation of the Scottish hills

There are approximately 4.0 million hectares of rough grazing land in Scotland (66% of the agricultural area) (SERAD, 2000a), most of which occurs in the hills and uplands. These rough grazings are composed of grassland, heath, mire, bracken, and montane communities. The vegetation of the Scottish hills is largely semi-natural, having been affected by human activities for many centuries (Fenton, 1937a; 1937b). The anthropogenic activity that has had the greatest impact on the vegetation of the Scottish hills, over the last 250 years, has been the grazing of domestic herbivores, in particular sheep grazing (Fenton, 1937a).

The semi-natural grasslands of the Scottish hills cover in excess of 1 million hectares (Milne *et al.*, 1998), and are widely used for large-scale sheep production. In many places this is their sole economic use. They are therefore of considerable economic significance to both the agricultural sector and the overall economy of upland Scotland (Maxwell, 1994; Frame *et al.*, 1985; Cunningham and Groves, 1985).

These grasslands are dominated by the grasses, *Agrostis capillaris, Agrostis vinealis, Festuca ovina, Festuca vivipara, Nardus stricta, Deschampsia flexuosa* and *Molinia caerulea*; and the rush, *Juncus squarrosus* (Rodwell, 1992). The majority of upland grasslands can be separated into two main categories: "good rough grassland", which is found on relatively dry, nutrient-rich soils, and is dominated by *Agrostis capillaris* and *Festuca ovina*; and "poor rough grassland", which is found on wetter, more acidic soils, and is characterised by the abundance of *Nardus stricta, Molinia caerulea* and/or *Juncus squarrosus* (Milne *et al.*, 1998).

Many authors have drawn attention to the decline in the cover of heather moorland in Britain, and its replacement with semi-natural grassland, in particular 'poor rough grassland' dominated by *Nardus stricta* (Fenton, 1936; 1937a; 1937b; Thomas and Fairbairn, 1956; Anderson and Yalden, 1981; Marsden, 1990; Tudor and Mackey, 1995).

Between the 1940's and the 1970's the cover of heather moorland in Scotland declined by almost 18 %, from 15,377 km^2 to 12,636 km^2 (Tudor and Mackey, 1995). During this period there was a high degree of interchange between heather moorland and unimproved grassland, with a net reduction in the cover of heather moorland of 848 km^2 (Tudor and Mackey, 1995). The overall area of unimproved grassland also declined over this period, from 12,608 km^2 to 11,414 km^2 (Tudor and Mackey, 1995). Afforestation and conversion to semi-improved or improved grassland accounted for much of this net loss (Tudor and Mackey, 1995). Within Central Region (which is the local government region containing the study site) the area of heather moorland declined by 19 % between 1947 and 1988, mainly as a result of net conversion to unimproved grassland and coniferous plantation (Tudor and Mackey, 1995). The total area of unimproved grassland within Central Region remained little changed between 1947 and 1973, but declined by 12 % between 1973 and 1988, with much of this loss due to grassland improvement (Tudor and Mackey, 1995).

There is common agreement that the major factors contributing to the increase in *Nardus stricta* within the hills and uplands of Britain have been the reduction in cattle numbers, the disappearance of wether sheep, and the increase in breeding ewes (producing store lambs) (Fenton, 1937a; Roberts, 1959; Grant *et al.*, 1985). Whether this increase in *Nardus stricta* has occurred at the expense of more productive grass species or of heather, it is generally perceived as a retrograde step. Most, though not all, *Nardus*-dominated grasslands are relatively species-poor (Rodwell, 1992) and are of limited nature conservation value, which contrasts with the internationally important heather communities, which they have replaced (Ratcliffe and Thompson, 1988; Sydes and Miller, 1988; Thompson *et al.*, 1995). *Nardus stricta*-dominated pastures have long been held to have limited grazing value (Smith, 1918; Fenton, 1936). *Nardus stricta* has a lower growth rate than most of the broad-leaved hill grasses (Grant and Hunter, 1968; Rawes and Welch, 1969; Grime *et al.*, 1988), and a lower digestibility than that of *Agrostis-Festuca* grasslands (Armstrong *et al.*, 1986). During diet selection studies using sheep and cattle, Grant *et al.* (1985), also observed that *Nardus stricta* had a very low preference ranking compared with other hill grasses. However, Thomas and Fairbairn (1956) showed that in early summer, *Nardus stricta* may contain as much as 16 % crude protein and have a digestibility of nearly 60 %, clearly indicating that it does have nutritive value, particularly in the early stages of growth. According to

Thomas and Fairbairn (1956), the view that *Nardus stricta* is worthless is untenable, and it must be accepted that it is of some value to grazing livestock in spring and early summer. A species that covers such a large proportion of the uplands, even though it only has a moderate nutritive value, must represent a useful seasonal resource, and deserves consideration.

Much effort has been invested in practical techniques to improve the agricultural value of *Nardus stricta* pastures. Such techniques have included, burning; the application of lime, mineral fertilisers and farmyard manure; surface cultivation; the introduction of sown grasses and white clover; and controlled grazing, using a variety of herbivores including sheep, goats and cattle (Chadwick, 1960; Agladze and Lechborashvily, 1968; Nicholson *et al.*, 1970; Floate *et al.*, 1972; Frame *et al.*, 1985; Grant *et al.*, 1985; Common *et al.*, 1991; Grant *et al.*, 1996b). However, without sustained effort the improvements tend to be of limited success. Many of these techniques are also impractical on high ground or rough terrain where there is no vehicular access.

1.5 The impact of sheep-rearing on the native flora and fauna of Scotland

The long history of sheep farming in the Scottish Highlands has had considerable direct and indirect impacts on the native flora and fauna (Ritchie, 1919; Fenton, 1935; 1937a; 1937b; Welch, 1974; Ratcliffe, 1991).

The introduction of large-scale sheep farming to the Highlands increased the rate of forest clearance. Grazing sheep also prevented natural tree regeneration, reducing the available habitat for many woodland species. The geographical range of many woodland birds (e.g. great-spotted woodpecker, capercaillie), mammals (e.g. roe deer and red squirrel) and invertebrates would have contracted into the ever-shrinking pockets of woodland that remained (Ritchie, 1919; Sharrock, 1976). Heathland, moorland and marsh would have been transformed into pasture (by drainage, ploughing and liming etc.), displacing many animal species (Ritchie, 1919; Fenton, 1935). The vast numbers of sheep must also have competed directly with the native herbivores, whose numbers, prior to the sheep invasion, would have been in balance with the available food resources and limited by the native carnivores (Ritchie, 1919). Predatory mammals and birds such as the fox, golden eagle and white-tailed eagle were persecuted in order to protect the sheep flocks (Ritchie, 1919). Both native species of eagle were regarded as potential threats to lambs, and suffered a prolonged campaign of persecution at the hands of the sheep farmers, particularly the larger white-tailed eagle, which as a carrion feeder was particularly susceptible to poisoning (Love, 1993). During the 19th Century there still remained at least 100 white-tailed eagle eyries in Britain, and in many coastal parts of the north and west it was more common than the golden eagle (Love, 1983). However, by 1916 the white-tailed eagle had been driven to extinction (Love, 1993). The white-tailed eagle has since been reintroduced into Britain (Sandeman, 1965; Love, 1989).

The grazing of vertebrate herbivores, in particular sheep, continues to have an impact on the natural heritage of upland habitats by modifying vegetation structure and species composition, which in turn has impacts on the whole ecosystem (McFerran *et al.*, 1994a; 1994b; Milne *et al.*, 1998; Fuller and Gough, 1999). The landscape of upland Scotland is considered to be of outstanding natural beauty, and a number of mountain ranges have been designated as National Scenic Areas, because of their scenic significance (Scottish Office, 1996). The Scottish mountains are important for tourism and outdoor recreation, and contain a significant proportion of land statutorily designated for its nature conservation value (Scottish Office, 1996). There is concern amongst ecologists and conservationists that European Union livestock subsidies (i.e. SAP and HLCA payments) have led to increased sheep stocking rates in the hills and uplands of Britain (The Wildlife Trusts, 1996). This has resulted in large-scale overgrazing, which has led to a decline in biodiversity and has caused major habitat changes (The Wildlife Trusts, 1996). There has however, been no pressure from conservationists to reduce the grazing intensity of cattle in the hills, indeed recent policy moves to encourage extensive cattle (Bignal, 1999; SERAD, 2000e) have been widely advocated by conservation bodies, such as the Royal Society for the Protection of Birds (Badger, 1999). Cattle and sheep have different diet selection and foraging strategies, and therefore cattle grazing has a different impact upon the vegetation (Buttenschøn and Buttenschøn, 1982a; 1982b; Hodgson and Grant, 1981; Grant *et al.*, 1985; Hodgson *et al.*, 1991). The change in the cattle to sheep ratio in the Scottish hills and uplands and the move to a more intensive management system has resulted in major changes in the structure and composition of the hill vegetation (Bignal and McCracken, 1996). An increase in hill cattle and a return to low-intensity mixed sheep and cattle grazing, may increase the structural diversity of the vegetation and lead to increased biodiversity and the enhanced nature conservation value of hill pastures (Bignal and McCracken, 1996).

In order to prevent over-grazing and increase biodiversity, the European Union and UK Government are now encouraging hill sheep farmers to reduce sheep numbers (i.e. extensify), through payments under agri-environment schemes, such as the Environmentally Sensitive Areas scheme and the Countryside Premium Scheme

(SERAD, 2000d). Under Agenda 2000 CAP reforms LFA support payments are to be paid on an area rather than a headage basis from 2001 (SERAD, 2000d; 2000e). The new LFA scheme will also provide additional payments per hectare for extensive mixed cattle and sheep farms (SERAD, 2000e). This is likely to encourage a reduction in sheep numbers and a stabilisation or increase in the number of hill cattle. It is the hope of policy makers and conservationists that extensification will lead to an increase in biodiversity, and in particular to an increase in the area of heather moorland. However, as preferred species are likely to be grazed proportionately more than non-preferred species under an extensive system (Hunter, 1962; Grant *et al.*, 1996b), it is possible that some detrimental changes may occur. For example, light grazing results in an increased accumulation of litter, and forage with a low protein content and low digestibility, which animals then avoid (Bakker *et al.*, 1983).

Most research to date has concentrated on the effects of excluding sheep from hill vegetation altogether (e.g. Welch and Rawes, 1964; Rawes, 1981; Hill *et al.*, 1992), and little is known of the effect that reduced sheep numbers may have on hill pastures. The studies reported by Grant *et al.* (1985; 1996b) and Gordon and Dennis (1996) suggest that grazing by cattle alone, or in combination with sheep, will have a different impact on *Nardus*-dominated grasslands than grazing by sheep alone.

Since the semi-natural hill grasslands of Scotland generate such controversy, it is important that the dynamics of these communities are clearly understood. There is only limited information on the productivity, grazing utilisation and vegetation dynamics of these plant communities. This thesis was therefore undertaken to supply information on the production and grazing offtake of a range of communities, including *Nardus stricta* and *Juncus squarrosus*-dominated grasslands. Changes in the species composition, structure and biomass of these vegetation types, in response to a variety of different grazing regimes, were also studied.

1.6 Grazing models

The plant species within the hill grassland and mire communities exhibit a wide range of life forms, with large differences in seasonality of growth, potential herbage production (in terms of both quantity and quality), digestibility, nutritive value, and grazing tolerance (Hodgson and Grant, 1981; Newbould, 1981). Different communities will therefore have different grazing thresholds, beyond which significant changes in structure, composition and productivity will occur. These different communities often occur side-by-side within complex mosaics. It is therefore often difficult to produce precise management guidelines that can be used at different sites. Computer based models and decision support systems built on sound biological principles can aid in the management process. With this view in mind the Macaulay Land Use Research Institute (MLURI) has developed a series of computer based hill grazing management models (Sibbald *et al.*, 1979; 1987; Armstrong, 1991; Grant and Armstrong, 1993; Armstrong and Milne, 1995; Armstrong *et al.*, 1997a; 1997b). The key to these management aids is a sound knowledge base, which requires access to accurate information on the vegetation structure, composition and productivity of all the main upland vegetation types, an understanding of the factors that determine when different plant communities and species will be grazed, and finally how the plant species respond to different patterns and levels of grazing. The current Hill Grazing Management Model (HGMM) (Armstrong *et al.*, 1997a; 1997b) has been developed using a fairly extensive set of data on the production and utilisation of *Calluna*-dominated heathlands. However, for the semi-natural hill grasslands the model relies on a much more limited data set (Armstrong *et al.*, 1997a). There are also a number of hill vegetation types that are not included in the model, because of insufficient data (Armstrong *et al.*, 1997a). Gaps in the HGMM and in the scientific literature relate particularly to the acid grasslands dominated by *Nardus stricta* and *Juncus squarrosus*, and to the sedge and rush-dominated mires, that are widespread in upland Britain, particularly in the wetter regions of the North West. Currently the HGMM cannot be used effectively on sites that have a large proportion of *Nardus stricta* or *Juncus squarrosus*-dominated grasslands, as it predicts no intake of *Nardus stricta* or *Juncus squarrosus* regardless of the areas involved. As part of this thesis, data on the biomass, production, senescence and sward structure of *Nardus stricta* and *Juncus squarrosus*-dominated grasslands have been collected, and incorporated into a modified version of the HGMM. This will improve the model's applicability and accuracy for sites with high proportions of these grassland types.

1.7 Rationale behind the system scale study

There have been many grazing experiments using small enclosures (e.g. Clarke *et al.*, 1995a; Grant *et al.*, 1996b; Hulme *et al.*, 1999), but these fail to replicate the scale of grazing choices available to hill sheep in rangeland situations (Hunter, 1962). Furthermore, some of the studies in the past have used wethers (e.g. Hulme *et al.*, 1999) or oesophagcally fistulated sheep (e.g. Hodgson *et al.*, 1991). These animals may behave quite differently from breeding ewes. For this study to be relevant to rangeland management and to simulate reality, it needed to be carried out on a semi-commercial scale, thus providing system level information. The study required enclosures that were large enough to allow breeding ewes to make grazing decisions based on a lifetime's experience. This unfortunately imposed some logistical constraints, making replication impractical and consequently leading to limitations in the statistical analyses of the results. This study is therefore more accurately described as a system scale case study rather than a plot experiment.

1.8 Hypotheses and main aims of the study

This thesis tested three main hypotheses:

(1) Extensification (i.e. a reduction in the annual stocking rate) results in an increase in plant species diversity and greater structural heterogeneity within hill grassland swards.

(2) Grazing systems using both sheep and cattle, lead to increased plant species diversity, a reduction in the cover of *Nardus stricta*, and greater structural diversity, compared with grazing systems using sheep only.

(3) Modification of the Hill Grazing Management Model (Armstrong *et al.*, 1997a; 1997b) through the inclusion of data for the production, sward height and digestibility of *Nardus stricta* grasslands, will improve the accuracy of the offtake values predicted by the model, when used on sites with a high proportion of *Nardus stricta* grasslands.

The main aims of the study covered in this thesis were:

(1) To characterise the vegetation of the study site and produce a detailed vegetation map, which could be used to determine accurate areas of the different vegetation types.

(2) To measure what impact changes in grazing management (i.e. extensification, and grazing by sheep and cattle) had on species composition, vegetation structure and above-ground biomass, within a range of hill grassland and mire communities.

(3) To measure the above-ground net primary production of a range of hill vegetation types within the study site.

(4) To estimate the offtake from these vegetation types by the grazing animals under the different grazing regimes.

(5) To test and evaluate the published MLURI Hill Grazing Management Model (HGMM) using information from the study site.

(6) To modify the HGMM using data collected from the study site, in order to improve its applicability for use on sites containing a high proportion of *Nardus stricta* and *Juncus squarrosus*-dominated grasslands.

(7) To test the modified model using data from the study site and an independent data set.

(8) To critically review the use of grazing models as decision support tools.

This thesis covers only part of a much larger study, which includes linked work on vegetation dynamics, grazing behaviour and modelling. The grazing behaviour work is not covered in this thesis and is being reported separately (e.g. Hulbert *et al.* 1998).

CHAPTER 2 – STUDY SITE, AND CASE STUDY DESIGN, PROTOCOL AND MANAGEMENT

2.1 Summary

1) A semi-commercial, systems scale grazing trial was established at the Scottish Agricultural College's Hill and Mountain Research Centre in West Perthshire, Scotland.
2) Three large fenced enclosures (approximately 40 ha) were erected in the autumn of 1993 on a northwest-facing slope between 300 and 690 metres above sea level.
3) The enclosures were maintained at a similar pre-trial stocking rate until mid-August 1994 when the trial grazing regimes were established.
4) Enclosures 1 and 2 were grazed by sheep only at mean annual stocking rates of 0.074 LU ha^{-1} and 0.051 LU ha^{-1} respectively. Sheep and summer grazing cattle were kept in Enclosure 3 at a mean annual stocking rate of 0.096 LU ha^{-1}.

2.2 Study site

2.2.1 LOCATION OF THE STUDY SITE

The study site was at the Scottish Agricultural College's Hill and Mountain Research Centre at Kirkton and Auchtertyre Farm, West Perthshire, Scotland (Ordnance Survey grid reference NN 360 283) (Figure 2.1). The Research Centre is at the western end of the Breadalbane Mountain range, which stretches some 45 km from Ben Lui in the west (NN 2626) to Ben Lawers in the east (NN 6341).

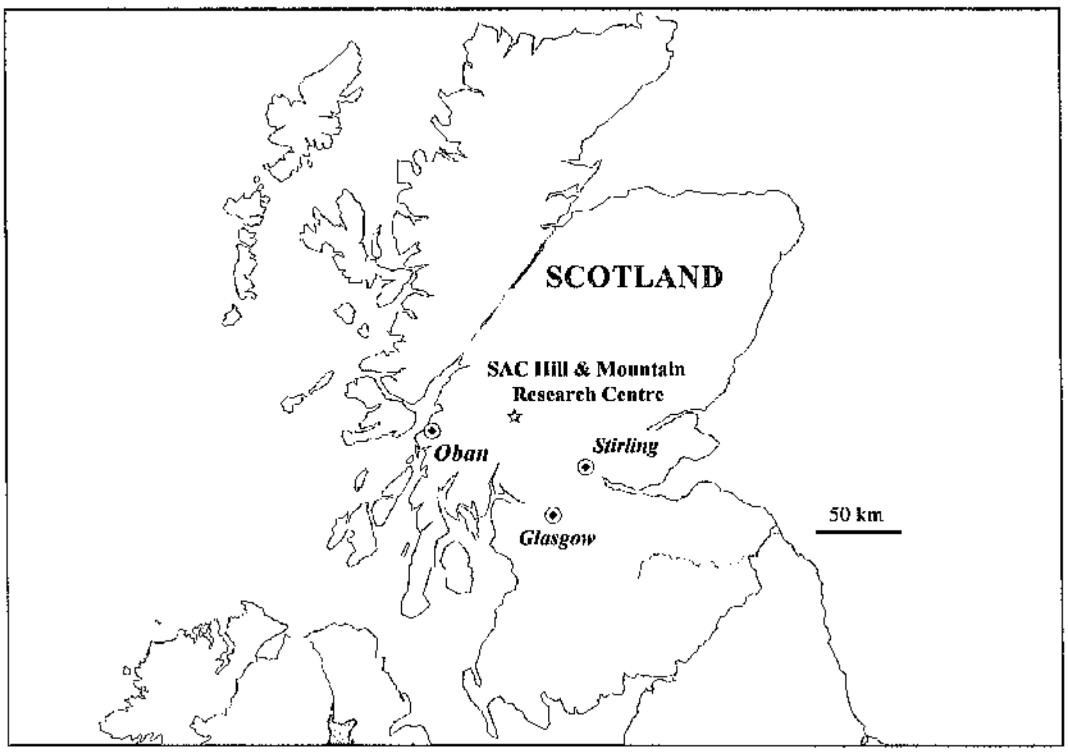


Figure 2.1 - Location of the SAC Hill and Mountain Research Centre

2.2.2 GEOLOGY AND TOPOGRAPHY

The study site was on the northwest-facing slope of the broad southwest ridge of Ben Challum, known locally as the Kirkton Face, between 300 and 690 metres above mean sea-level (OS grid reference NN 368 303) (Plate 2.1). The underlying geology of the site is Cambrian metamorphic quartzose mica-schist from the Dalradian series (British Geological Survey, 1979). A number of streams drain off the Kirkton Face, and there is evidence of past drainage management in the form of vertical drainage ditches on the lower slopes.

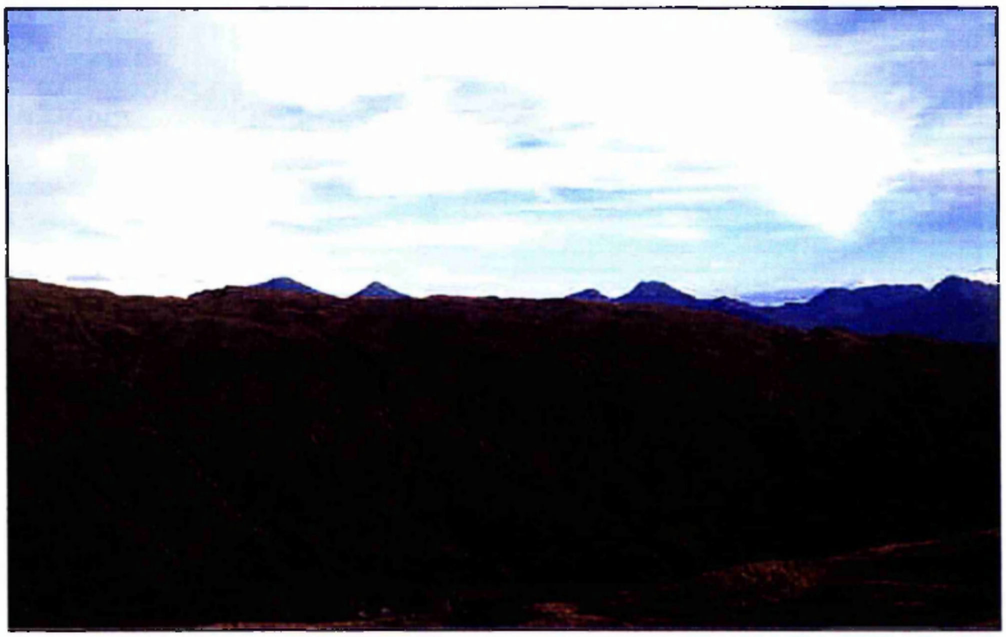


Plate 2.1 - The Kirkton Face

2.2.3 CLIMATE

The climate of the study site reflected its relatively high altitude, mountainous topography and northwesterly location within the United Kingdom. Meteorological data was not collected from the study site itself, since there was data available from the Meteorological Office Recording Station at Kirkton Farm (NN 3595 2838; altitude 169 m), which was 2 km south of the study site. During the study period 1994 to 1998 the mean annual rainfall recorded at the Meteorological Station was 2440 mm, with 70% of the rainfall occurring between October and March (Figure 2.2). Summers were cool with a mean maximum August temperature of 18.5°C. Winters were relatively mild, wet and windy, with a mean maximum January temperature of 5.7°C (Figure 2.2). The mean minimum temperature fell below 0°C only during January. There was partial or complete cover of winter snow on the study site (i.e. above 300 m) from December through to April. At the Meteorological Station, soil temperatures of below 6°C persisted from the beginning of December to mid-April giving a delayed and relatively short growing season (Appendices 2.1 and 2.2). Ground frosts occurred in all months apart from July and August.

Within the study period (1994 to 1998) the summer of 1995 and the winter of 1995/96 were climatic anomalies (Appendix 2.1). 1995 had a significantly higher mean summer maximum temperature, which was 1.5°C higher than in any other year of the study ($F_{4,\,455}$ = 14.91, P < 0.001). It also had the highest maximum June, July and August temperatures (all above 26°C, a temperature not achieved in any other year), and a significantly higher mean summer soil temperature, which was between 0.72°C and 2.0°C higher than in any other year ($F_{4,\,455}$ = 17.90, P < 0.001). June and August rainfall totals were also lower than in any other year (37.1 mm and 27.2 mm respectively). The rainfall between the beginning of December 1995 and the end of March 1996 (473.6 mm) was less than half the amount recorded in any other year. During this period there were only 3 days when rainfall exceeded 25 mm, compared with between 15 and 24 days in the other years. The lowest minimum temperature was also recorded during this period at -19.1°C on the 28th December 1995.

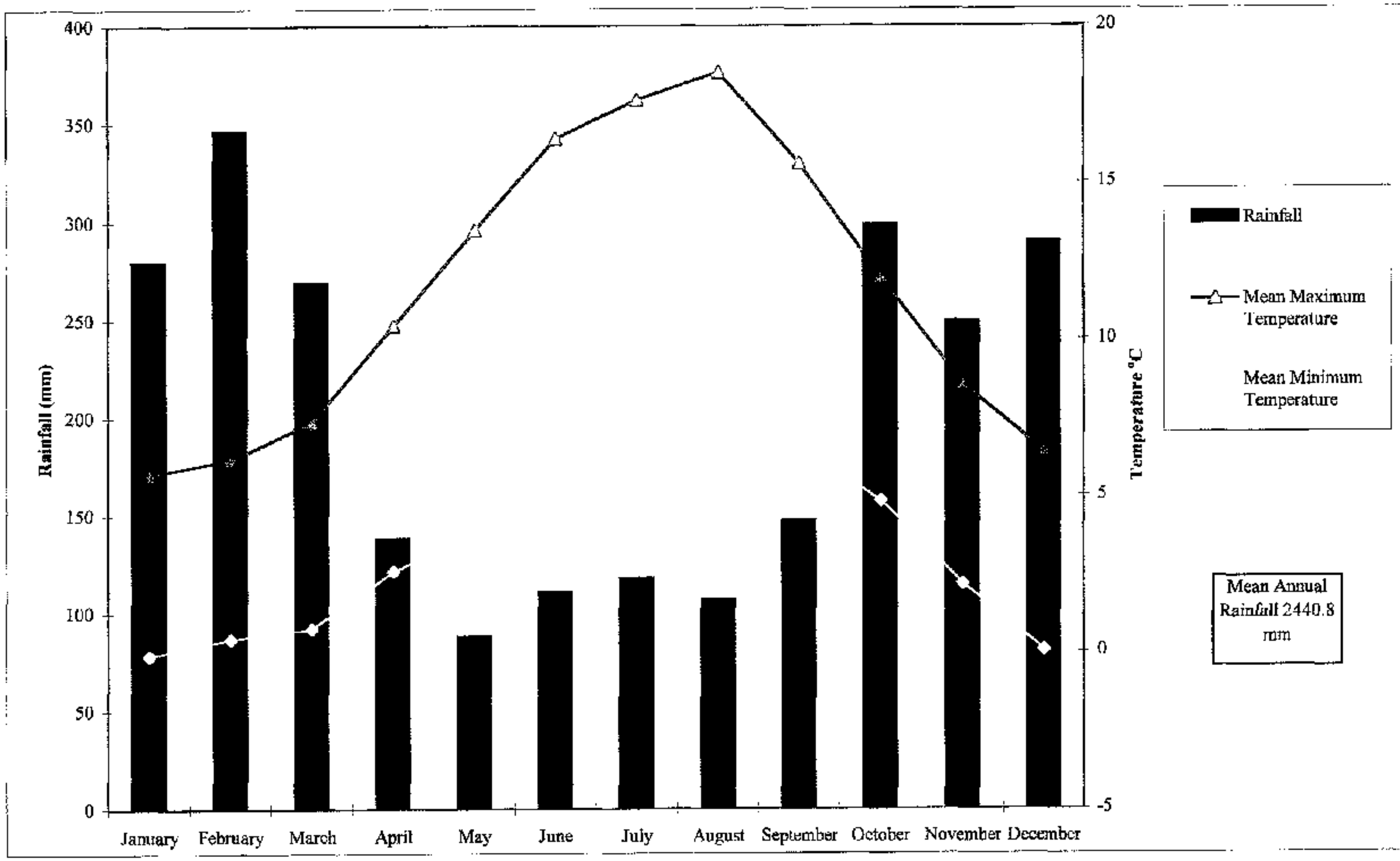


Figure 2.2 - Mean rainfall and temperature data for the Kirkton Farm meteorological station (grid reference NN 3595 2838; altitude 169 m) over the period 1994 to 1998.

2.2.4 Stocking levels prior to the commencement of the study

Large-scale sheep farming was introduced into Perthshire in the mid-eighteenth century (Watson, 1932). Kirkton Farm has therefore probably been used for extensive sheep production for over 200 years. Documentary evidence of large-scale sheep farming at Kirkton Farm exists in the form of logbooks written between 1869 and 1923 by the then tenant farmer, John Paterson. The overall stocking rate in 1869 for the Kirkton Farm holding was 1.37 sheep ha^{-1}, which is very similar to the 1.38 sheep ha^{-1} present in 1998, although the proportion of male and female sheep has changed. In 1869, 35% of the animals on the farm were wethers (castrated male sheep) older than a year, whereas today only ewes and a few breeding rams are kept on the farm past the age of 6 months (Appendix 2.3).

It was important to know in more detail what grazing had occurred on the main study site in the years prior to the setting up of the trial, as the species composition and biomass of the vegetation types at the start of the trial would have been influenced by this previous management. The trial stocking rates would only influence the future composition and biomass of the vegetation.

In the period 1990 to 1993 the actual area used for the study was unfenced and formed part of a 282.5 ha block of land, comprising 60 ha of improved rough grazing (between 220 and 300 metres above mean sea level) and 222.5 ha of enclosed unimproved hill pasture (which included the study site). The whole area was divided into six fenced blocks which could be opened or closed as required, and carried a stock of 600 Scottish Blackface ewes, and 22 suckler cows with calves that were present during September only. The sheep had access to the better quality improved rough pasture for eight months of the year, and during the winter months received supplementary feed in the form of hay and pelleted concentrates. All the stock were removed from the area during December. The annual overall stocking rate was approximately 0.14 Livestock Units ha^{-1} (Appendix 2.4).

2.3 Case study design and management

The main study area consisted of three large fenced enclosures of a similar size (44.40, 40.78 and 47.46 hectares), which were erected in the autumn of 1993 (Figure 2.3). The enclosures contained a range of upland grassland and mire communities, and were subject to controlled grazing at a range of different stocking levels.

From November 1993 until mid-August 1994 the three enclosures were maintained at a similar pre-trial mean annual stocking rate in order to standardise the grazing across all three enclosures (Table 2.1). On the 19th August 1994 the trial stocking rates were established (Table 2.1).

Purebred Scottish Blackface ewes with a mean body weight of 48.6 kg (Plate 2.2) (Appendix 2.6) and crossbred bullocks with a mean body weight of 309.7 kg (Appendix 2.7) were used in the study.

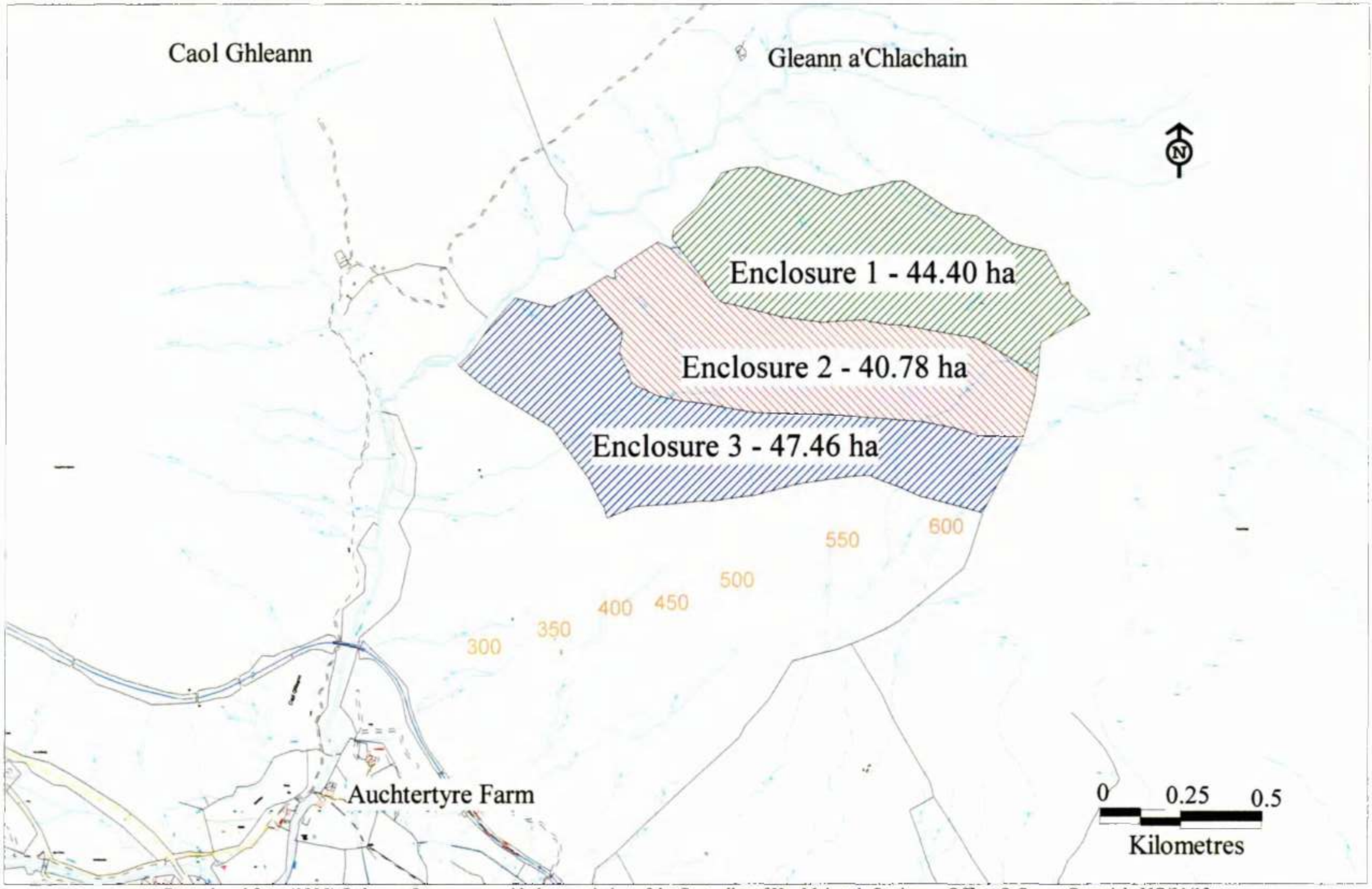


Figure 2.3 - Location and size of the enclosures that form the study site

Table 2.1 - The number of adult ewes, hoggs (yearling, unmated ewes) and cattle present within the enclosures, and the mean annual stocking rates

	Grazing Animals	**Pre-trial** November 1993 - mid-August 1994	**Trial** mid-August 1994 - December 1998
Enclosure 1	Ewes	**37**	**37**
	Hoggs*	13	13
	Mean Annual Stocking Rate (Livestock Units ha^{-1})	*0.074*	*0.074*
Enclosure 2	Ewes	**44**	**22**
	Hoggs*	15	8
	Mean Annual Stocking Rate (Livestock Units ha^{-1})	*0.081*	*0.051*
Enclosure 3	Ewes	**48**	**24**
	Hoggs*	16	9
	Bullocks**	0	14-16 (June-September)
	Mean Annual Stocking Rate (Livestock Units ha^{-1})	*0.076*	*0.096*

* Yearling un-mated ewes, which were present within the enclosures for a period of 130 days, between the end of March and the middle of August each year.

** Crossbred bullocks (with an annual mean total weight of 4646kg), which were present within Enclosure 3 for a mean period of 89 days, between June and September (the equivalent by weight of 0.50 ewes ha^{-1} $year^{-1}$)

Note - Livestock Units: ewe = 0.08, hogg = 0.08, ram = 0.08, lamb = 0.04, bullock (12-24 months) = 0.65 (Chadwick, 1997).

(See Appendix 2.5 for the age structure of the ewes)

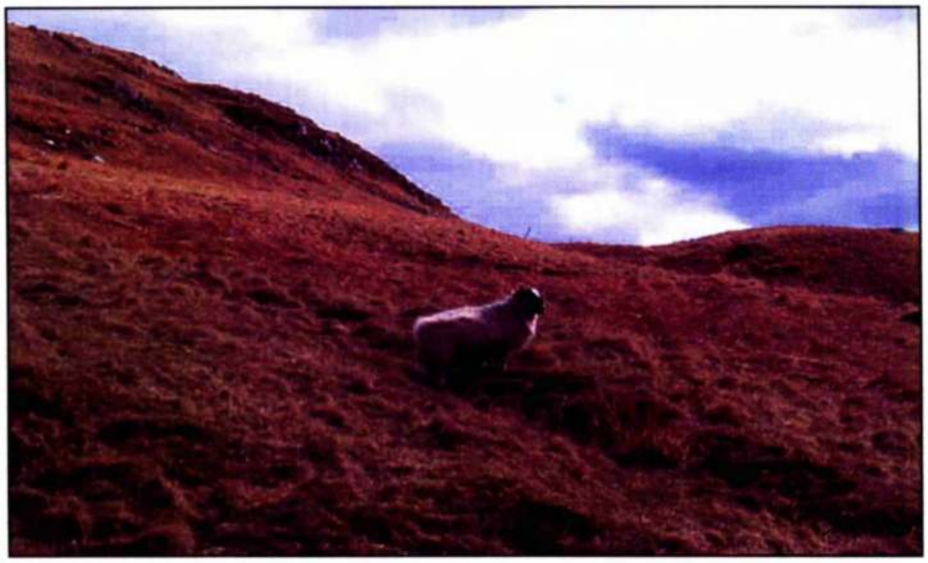


Plate 2.2 - A Scottish Blackface ewe on a U5b *Nardus stricta* - *Galium saxatile* (*Agrostis canina* - *Polytrichum commune*) grassland

As this was a systems scale study the flock management and stocking rates varied according to the time of year (Table 2.2, Figure 2.4). The actual number of animals present within the enclosures varied slightly from year to year due to annual differences in the number of lambs, the death of individuals, the movement of animals between and outwith the enclosures through gaps in the fence, over snow drifts (Plate 2.3), or over stretches of snow damaged fence, and the managed removal of the animals from the enclosures during severe winter weather. The actual numbers of animals within each enclosure on a monthly basis from January 1994 to December 1998 are given in Appendix 2.9.

The ewes remained in their allocated enclosures throughout their productive adult lives (to a maximum of 5 years old), except when removed for management purposes. All replacement ewes were homebred from within each flock. This approach replicated commercial practice with ewes being retained and drawing replacements from particular sections of hill grazings (often referred to as hefts). This allowed ewes the opportunity to gain a lifetimes experience of the enclosures.

Plate 2.3 - A snowdrift covering the fence between Enclosure 2 and 3 (20/03/96)

Crossbred bullocks with a combined weight of approximately 4500 kg (equivalent in weight to 94 ewes) were introduced into Enclosure 3 at the start of each summer grazing period in each of the four years. Since the initial mean body weight of the individual bullocks varied, the number of animals introduced each year into the enclosure ranged from 14 to 16 (Appendix 2.7). The bullocks were not reared on the farm and therefore their behaviour varied from year to year, possibly depending on their previous experience of grazing extensive hill grasslands or their tolerance of humans.

Table 2.2 - The annual stock management within all three enclosures

Time of Year	Period	Management	Additional Notes
mid-November to December	Mating	The ewes were mated in the enclosures on a rotational system. All 83 ewes in: Enclosure 1 for 17 days, Enclosure 2 for 10 days, Enclosure 3 for 11 days.	Three rams were put to the ewes.
January to the end of February	Pregnancy (pre-ultrasonographic pregnancy scanning)	All the ewes present within the enclosures: Enclosure 1 - 37 ewes Enclosure 2 - 22 ewes Enclosure 3 - 24 ewes	Each ewe allocated 180g day^{-1} of a proprietary feedblock, fed at two fixed sites within each enclosure, throughout their pregnancy.
end of February	Ultrasonographic pregnancy scanning	The ewes were scanned and twin-bearing ewes removed and put onto improved pasture. Non-pregnant ewes replaced the twin-bearing ewes. The single-bearing and non-pregnant ewes were returned to the enclosures.	All the ewes were weighed.
end of February to mid-June	Pregnancy (post-ultrasonographic pregnancy scanning) to Marking	Single-bearing and non-pregnant ewes present within the enclosures: Enclosure 1 - 37 ewes Enclosure 2 - 22 ewes Enclosure 3 - 24 ewes At the end of March, yearling, un-mated ewes (hoggs) returned to the enclosures in which they were born: Enclosure 1 - 13 hoggs Enclosure 2 - 8 hoggs Enclosure 3 - 9 hoggs	Single-bearing ewes lambed within the enclosures, from mid-April to mid-May. The twin-bearing ewes lambed on low-lying improved pasture.
mid-June	Marking	All the lambs were ear tagged and the male lambs were castrated. All the sheep including the twin-bearing ewes (which re-substituted the replacement barren ewes) were returned to the enclosures.	All the ewes and lambs were weighed.
mid-June to mid-August	Marking to Weaning	All ewes, lambs and hoggs present within the enclosures: Enclosure 1 - 37 ewes, 13 hoggs Enclosure 2 - 22 ewes, 8 hoggs Enclosure 3 - 24 ewes, 9 hoggs, 14-16 bullocks	14-16 bullocks (initial total body weight of approx. 4500 kg) were put in to Enclosure 3 in the middle of June.
mid-August	Weaning	The lambs were weaned and removed from the enclosures, along with the draft ewes (breeding ewes of 5.5 years of age which are sold to lowland farmers), which were replaced by the hoggs.	All the ewes and lambs were weighed.
mid-August to mid November	Post Weaning	The correct ewe numbers were re-established: Enclosure 1 - 37 ewes Enclosure 2 - 22 ewes Enclosure 3 - 24 ewes, 14-16 bullocks	The bullocks were removed from Enclosure 3 at the end of September, after a period of 89 days, and were weighed.

(See Appendix 2.8 for the actual dates of pregnancy scanning, marking and weaning)

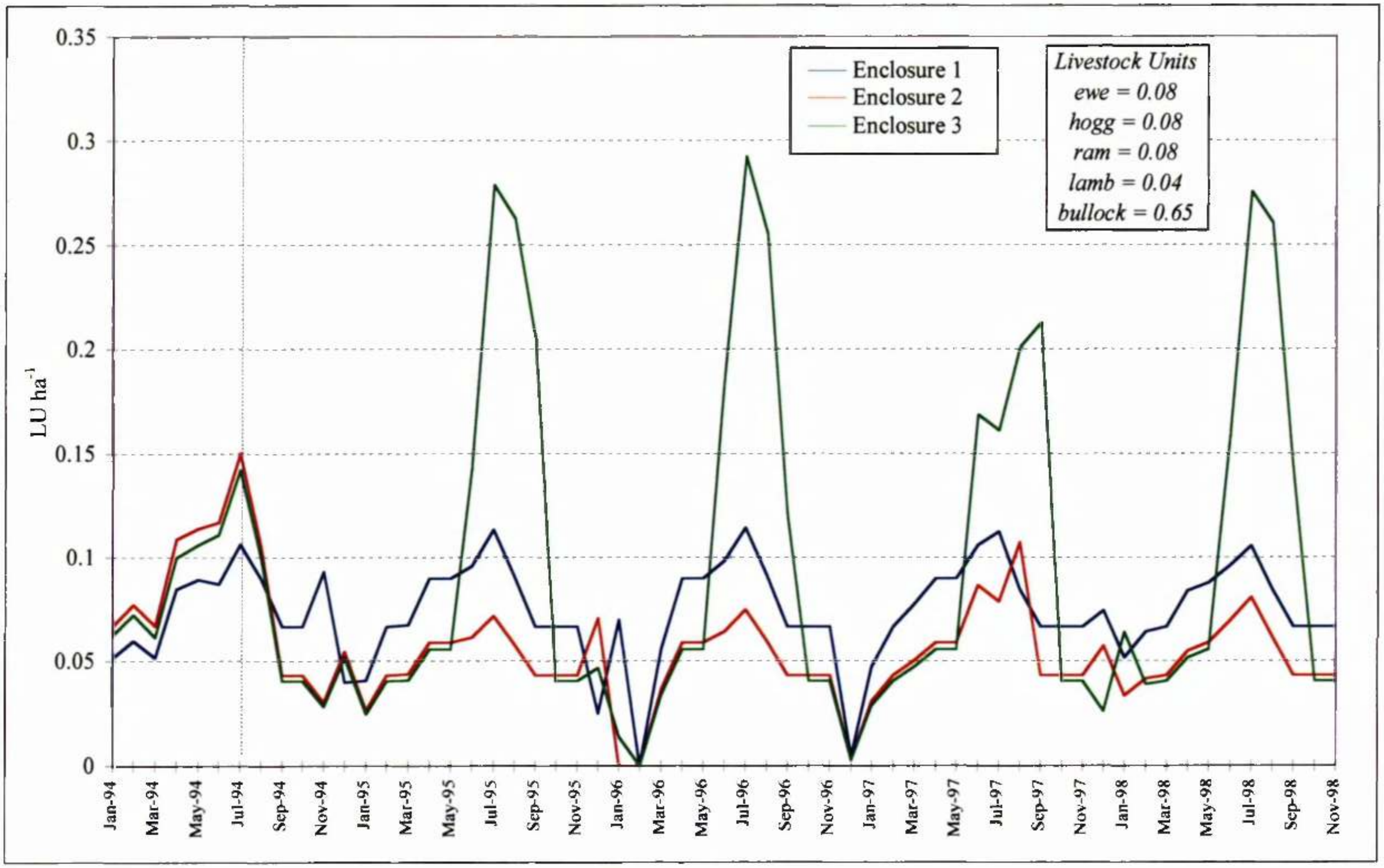


Figure 2.4 - Monthly stocking rates (LU ha^{-1}) in the three study enclosures (1994 - 1998)

2.4 Discussion

2.4.1 CHOICE OF STUDY SITE

The study site was chosen for a number of reasons:

a) Three enclosures large enough to be used for a systems scale study, which were of a similar size and had comparable aspects, slope angles, altitudinal ranges and vegetation types, could be created on the site.

b) The site had a long documented history of extensive, but managed sheep grazing.

c) The hill vegetation was dominated by *Nardus stricta* and *Juncus squarrosus*, two of the principal species within the grazed hill grasslands of the Western and Central Highlands. Data on the production and utilisation of communities dominated by these two species were required, since the current Hill Grazing Management Model (HGMM) assumes that these species are not utilised by the grazing animal (Armstrong *et al.*, 1997a; 1997b).

d) A key requirement of the site was the presence of vegetation types that were already included within the HGMM (i.e. blanket bog, suppressed heather and *Festuca - Agrostis* grassland) (Armstrong *et al.*, 1997a). The site also contained a mosaic of other plant communities, including mire, calcicolous grassland and montane heath, giving a range of available food resources for the grazing animals.

e) The site had an oceanic climate typical of the Western Highlands, which was significantly different from the climate of the Eastern Highlands and mid-Wales from where most of the production and utilisation data for the HGMM was obtained (Moss, 1969; Barclay-Estrup, 1970; Grant, 1971; Forrest and Smith, 1975; Moss and Miller, 1976; Job and Taylor, 1978; Miller, 1979; Moss *et al.*, 1981).

f) There were practical management and monitoring advantages in locating the study site at the Hill and Mountain Research Centre.

2.4.2 Replication

Replication was impractical because of the cost; the lack of available or suitable land at any of SAC's research farms; and the time constraints and infeasibility of carrying out fieldwork if replicate plots of a similar size had been used.

2.4.3 Choice of treatments

Prior to the establishment of the three grazing treatments in August 1994, all three flocks were managed in a similar manner, with an approximate stocking rate of 0.08 LU ha^{-1} (1.0 ewe ha^{-1}). This is a standard commercial stocking rate and is typical of the more intensive, specialist hill-sheep farms in the Western and Central Highlands of Scotland. Enclosure 1 was kept at this stocking rate throughout the trial period.

Changes in European Union agricultural policy (following the reform of the Common Agricultural Policy in 1992 and the Agenda 2000 reforms) have encouraged farmers in the hills and mountains of Western Europe to extensify. A desire to control the EU farm budget, reduce production and pollution, and improve the environment, has helped drive this policy change (Waterhouse and Ashworth, 1996; Whitby *et al.*, 1996; Bignal, 1999). In the UK specific measures to reduce stocking rates on hill farms have been developed through agri-environment and extensification schemes, such as the Beef and Sheep Extensification Scheme, the Environmentally Sensitive Areas Scheme, the Countryside Premium Scheme, and the Moorland Scheme (SERAD, 2000d). In addition to these schemes, the control of 'over-grazing' is included within the Sheep Annual Premium and Hill Livestock Compensatory Allowance regulations as a cross-compliance measure (SERAD, 2000d). Many semi-natural hill pastures have also been notified as Sites of Special Scientific Interest (SSSIs) under the 1981 Wildlife and Countryside Act, or as candidate Special Areas of Conservation (cSACs) under the 1992 EC Directive on the Conservation of Natural Habitats of Wild Fauna and Flora (92/43/EEC) - the Habitats and Species Directive (Hopkins, 1995; Scottish Office, 1996). The Government's statutory nature conservation agencies are required to protect and enhance the nature conservation interests within these sites (Scottish Office, 1996), and one of the key management tools to achieve these requirements has been the control of grazing. Whatever the driving force behind extensification, it is important to measure its impact on the vegetation, to determine the success of the policy on one of its primary objectives of improving the environment. In order to achieve an extensive system within the Kirkton Face study, the number of ewes within Enclosure 2 was reduced by 50 %. A farm scale experiment that complements this study has also been carried out at SAC's Hill and Mountain Research Centre, looking at the impact of extensification policies on animal performance and welfare (Waterhouse, 1994; 1996), and its effects on farm economics, profitability and labour requirements (Ashworth and Waterhouse, 1994; Waterhouse and Ashworth, 1996).

Cattle were traditionally grazed on hill pastures during the summer months, however this practice declined after the development of large-scale sheep farming in the mid 18th Century (Watson, 1932; Fenton, 1937a; Sydes and Miller, 1988). Studies have shown that cattle graze more *Nardus stricta* than do sheep (Grant *et al.*, 1985; Hodgson *et al.*, 1991; Grant *et al.*, 1996b), and that controlled cattle grazing can lead to a reduction in the cover of *Nardus stricta* and an increase in *Festuca* and *Agrostis* (Grant *et al.*, 1996b). Species diversity has also been shown to increase following the introduction of free-ranging cattle onto a grass-heath mosaic in the Netherlands (Bokdam and Gleichman, 2000). The role of cattle on British hill farms today is often that of a grassland improver, maintaining and improving the forage quality for the sheep that form the main livestock enterprise (Broadbent, 1981). Suckler herds are most commonly used in this role, producing weaned calves or store cattle (Broadbent, 1981). The cattle are kept on the hill pastures during the summer months (June to September), but are wintered on lower ground where they receive winter-feed (hay, silage etc.). Enclosure 3 was set up in order to test whether the traditional management of summer grazing store cattle combined with all year round sheep grazing would result in a reduction in the cover of *Nardus stricta* and a change in the floristic composition, structure and biomass of the vegetation.

CHAPTER 3 – CHARACTERISATION OF THE VEGETATION

3.1 Summary

1) In order to objectively test and develop the vegetation component of the MLURI Hill Grazing Management Model (Armstrong *et al.*, 1997a), detailed information on the floristic composition of the vegetation community types present within the Kirkton Face study enclosures, their areas, and spatial and altitudinal distributions were required.
2) A quadrat survey and a vegetation mapping exercise were carried out to provide the detailed floristic information.
3) Thirty-one, one metre square quadrats were used to characterise the main vegetation types within one of the enclosures. Seventy-seven species of vascular plant were recorded within the quadrats, and a further fifty-nine species were identified within the three enclosures.
4) A detailed vegetation map of all three enclosures was produced using a novel technique, involving the use of a total survey station and a geographic information system (GIS). The study site consisted of a complex mosaic of vegetation types, their spatial distribution being related to changes in altitude, slope, pedology and hydrology. Twenty-two National Vegetation Classification (NVC) types were identified and mapped within the 132.6 ha study area. These vegetation types included calcareous and acidic grasslands, montane moss-heaths, acidic mires, heaths and calcareous flushes.
5) Communities dominated by *Nardus stricta* covered over 52% of the study area.

6) The cover and distribution of NVC community types was similar across all three enclosures.
7) The NVC was found to be an appropriate and exceedingly useful system for classifying vegetation types within the study site, allowing an accurate map and inventory of vegetation types to be produced.
8) The vegetation of the Kirkton Face was relatively species rich and typical of the base-rich Dalradian mica-schists of the Breadalbane Mountains, which contrasts with the depauperate calcifuge flora of the acidic, siliceous rocks of much of upland Scotland.

3.2 Introduction

The Breadalbane Mountains form a distinctive landscape dominated by grassland and mire in which the grasses *Nardus stricta*, *Festuca vivipara* and *Agrostis capillaris*, together with *Juncus squarrosus*, *Trichophorum cespitosum* and *Calluna vulgaris* are the dominant species. The vegetation is semi-natural, reflecting a long history of human intervention and management, particularly since 1770 when large-scale sheep farming arrived in Central Perthshire (Watson, 1932). The landscape is composed of a complex mosaic of vegetation patches. This mosaic of vegetation types has developed through the interaction of a range of environmental and anthropogenic factors including bioclimate, geology, pedology, hydrology, topography and grazing (Dickinson, 1998b). The Breadalbane Mountains are of national and international importance for their species-rich *Nardus* grasslands, alpine calcareous grasslands, flushes, montane willow scrub and cliff ledge communities, which support a diverse and rare arctic-alpine flora (Ratcliffe, 1977; Perring and Farrell, 1983; Stewart *et al.*, 1994). A number of these important vegetation types occur within the Kirkton and Auchtertyre farm boundary, and over three hundred species of vascular plant, including fifteen nationally scarce species (Stewart *et al.*, 1994) and three nationally rare red data book species (Perring and Farrell, 1983) have been recorded by the author. The study site itself does not include the most species-rich areas within the farm, which occur at higher altitudes on the neighbouring Cam Chreag (Holland and Gooding, 1998). However, the vegetation communities that are present within the study site contain an element of this diverse arctic-alpine flora.

A key requirement of any systems scale grazing study is the provision of information on the vegetation types available to the grazing animals. Only through the detailed characterisation and mapping of the vegetation can an accurate picture of the range of plant community types present and the heterogeneity and complexity of the vegetation mosaic be obtained. Any changes that occur in species composition, biomass, structure or grazing utilisation within a particular vegetation type, as a result of a change in grazing management, will be influenced by the initial composition, area and distribution of that vegetation type, its spatial relationship with regard to other vegetation types, its spatial distribution in relation to environmental factors, and the composition, area and distribution of the other vegetation types. This information can only be obtained by the accurate classification and mapping of the vegetation. Detailed information on the floristic composition of the vegetation community types present within the enclosures, together with accurate data on their areas, and spatial and altitudinal distributions, were also required in order to objectively test and develop the vegetation component of the MLURI Hill Grazing Management Model (Armstrong *et al.*, 1997a). Without this detailed information neither the published version nor any modified version of the model could be tested with any degree of confidence, nor could the sensitivity to more rapid and less accurate data collection be evaluated. Two methods were used in the characterisation of the vegetation. Firstly, a quadrat survey was carried out in order to classify the main vegetation communities into appropriate National Vegetation Classification types (Rodwell, 1991; 1992), and also to determine the floristic diversity of the site. This information was then used to aid in the second stage of the characterisation, which involved accurately mapping the vegetation types using a total survey station and a geographic information system (Gooding *et al.*, 1997).

3.3 Materials and methods

3.3.1 QUADRAT SURVEY

3.3.1.1 *Sampling strategy, vegetation description and collection of environmental data*

An initial survey of the study site indicated that the plant communities were not randomly distributed, and therefore in order to record as much floristic variability as possible, sampling was deliberately stratified. The survey indicated that the vegetation could be split into five main habitat types: montane grass-heath; calcifuge grassland; calcicolous grassland; mire and heath; and flush. The areas and spatial distributions of these habitat types were not the same, although all five habitat types were found in the three enclosures. Enclosure 2 was randomly selected for the quadrat survey. Quadrats were surveyed in all of the habitat types. Within each habitat type, patches of vegetation were randomly selected. The number of patches selected in each habitat type was related to the estimated area of that habitat within the enclosure. A single 1 m^2 quadrat, sub-divided into one hundred 10 cm x 10 cm squares, was randomly placed within each of these selected patches. Each vascular plant species within the quadrat was identified and the number of sub-squares in which any above-ground part of the species occurred was recorded, to give a percentage frequency score (Smith *et al.*, 1985; Kent and Coker, 1992). This technique is time-consuming but provides more accurate data than simply recording the presence or absence of a species within the whole quadrat or than estimating the percentage cover of each species (Kent and Coker, 1992). The cover of each species was also visually estimated and given a DOMIN cover scale value (Kershaw and Looney, 1985). No attempt was made to identify bryophytes to species level, although the presence of *Sphagnum* species and *Racomitrium lanuginosum* were noted.

Members of the *Taraxacum*, *Hieracium* and *Euphrasia* aggregates were recorded under their group headings. A total of thirty-one quadrats were surveyed. Plant nomenclature followed Stace (1991).

Data were collected on slope angle (using a hand held clinometer) and aspect (using a compass) for each quadrat. The position of the quadrat was determined using a sighting compass, and the Ordnance Survey grid reference and altitude were recorded. Twenty soil sample cores (20 mm in diameter and 100 mm in length) were taken from each of the quadrats. The soil samples from each quadrat were combined and analysed for pH, extractable phosphorus (mg l^{-1}), extractable potassium (mg l^{-1}), extractable magnesium (mg l^{-1}) and organic matter (loss on ignition (%)) using standard methods of analysis as recommended by the Agricultural Development and Advisory Service (MAFF, 1986).

The National Vegetation Classification (NVC) (Rodwell, 1991; 1992) was used to classify the quadrat vegetation types. The plant community data, soil analysis results and other habitat characteristics were compared with the National Vegetation Classification keys, floristic tables and descriptions (Rodwell, 1991; 1992) to determine the most appropriate NVC community or sub-community for each quadrat. The computer program Tablefit (Hill, 1996) and the ordination method of detrended correspondence analysis (DECORANA) (Hill, 1979; Hill and Gauch, 1980) were used to crosscheck the assigned community types.

3.3.1.2 *Statistical analysis of the quadrat data*

The product moment correlation coefficient (Fowler and Cohen, 1990) was used to determine whether there was any correlation between plant species richness and soil pH, and plant species richness and soil extractable phosphorus content. The soil phosphorus values were first normalised using a square root transformation.

3.3.2 INVENTORY OF VASCULAR PLANT SPECIES

In addition to the quadrat data a comprehensive inventory of the vascular plant species present within the whole 132.6 ha study area was compiled. All vascular plant species identified within the study area between 1994 and 1998 were included in this inventory.

3.3.3 VEGETATION MAPPING

In order to create a detailed and accurate vegetation map of the study site, the area was mapped using a total survey station (Topcon - model GTS-4B) (Topcon Instrument Corporation, Tokyo) and a geographic information system (GIS) (MapInfo® Professional Version 4 (MapInfo Corporation, Troy, New York) with the add-on package Vertical Mapper® Version 1.5 (Northwood Geoscience Ltd., Nepean, Ontario)) (Gooding *et al.*, 1997).

The total survey station combines in one instrument a theodolite for measuring vertical and horizontal angles with an electronic distance measurement (EDM) system (Bannister *et al.*, 1992). The EDM system uses a modulated beam of infrared light to measure the slope distance from the instrument to a corner reflector prism mounted on a 2.0 m telescopic surveying pole held at the point of interest. The microprocessor in the instrument combines the measured slope distance with the vertical angle measurement to display both horizontal and vertical distance from the instrument to the prism. The EDM system is potentially highly accurate, with a specified error of 4.5 mm on a measurement of 1000 metres, and a maximum range of up to 1400 metres in good visibility (Topcon Instrument Corporation, 1990).

The total survey station (TSS) was set up on a vantage point from which the largest proportion of the survey area could be seen. The first location of the TSS was determined by taking readings from three points which were readily identified on the Ordnance Survey 1:25,000 map of the area. Two field surveyors (including the author) then surveyed the boundary fences of the three enclosures. The surveyors were in radio contact with the TSS operator throughout the survey. The surveyors, walking in parallel, then traversed the area within the enclosures, taking position readings at regular intervals. Where the mosaic of community types was complicated, readings were taken from the centre of homogeneous patches and the size of these determined the proximity and number of readings. In larger more homogeneous areas, readings were made at approximately ten metre intervals with the surveyors traversing on parallel paths approximately ten metres apart. At each point the vegetation was visually assessed and allocated a National Vegetation Classification (NVC) type (Rodwell, 1991; 1992). The information derived from the quadrat survey, together with the surveyors own knowledge and experience of using the NVC, were used in the assessment and classification of the vegetation. The vegetation was not mapped to sub-community level, apart from the U5 and M6 communities, which were split into U5b and U5c, and M6b and M6d sub-community types respectively. Details of the NVC plant community type along with any supporting information, such as the dominant plant species, were relayed by radio from each position and recorded by the TSS operator. Once the area visible from the first survey position had been fully surveyed, a reading was made to the next appropriate vantage point. The TSS was then set up on this position and a back bearing taken to the previous position or other known points. This procedure was repeated until the survey was completed.

The data from each point were recorded on to a data-logger. The data were downloaded onto a personal computer (PC), where Land Survey System software (McCarthy Taylor Systems, Birdlip, Gloucester) was used to convert the positional readings to National Grid co-ordinates. The co-ordinate data were then transferred onto a Microsoft Excel spreadsheet (Microsoft Corporation, Seattle) and merged with the vegetation data. The merged spreadsheet was then imported into the PC based MapInfo® Professional Version 4 geographic information system (MapInfo Corporation, Troy, New York). The GIS was used to map points from the Ordnance Survey co-ordinates and select from these individual plant communities to produce a thematic point map (Figure 3.1).

The MapInfo® add-on package Vertical Mapper® Version 1.5 (Northwood Geoscience Ltd., Nepean, Ontario), which is a contour modelling and display software package, was then used to create regions ('natural neighbourhoods') around each point. This was achieved using a nearest neighbour technique known as Delauney triangulation (Watson, 1992). This technique results in a mosaic of thiessen polygons creating a voronoi diagram, where any location that lies within any single polygon lies closer to the enclosed point than to any other neighbouring point (Northwood Geoscience Ltd., 1996) (Figure 3.1).

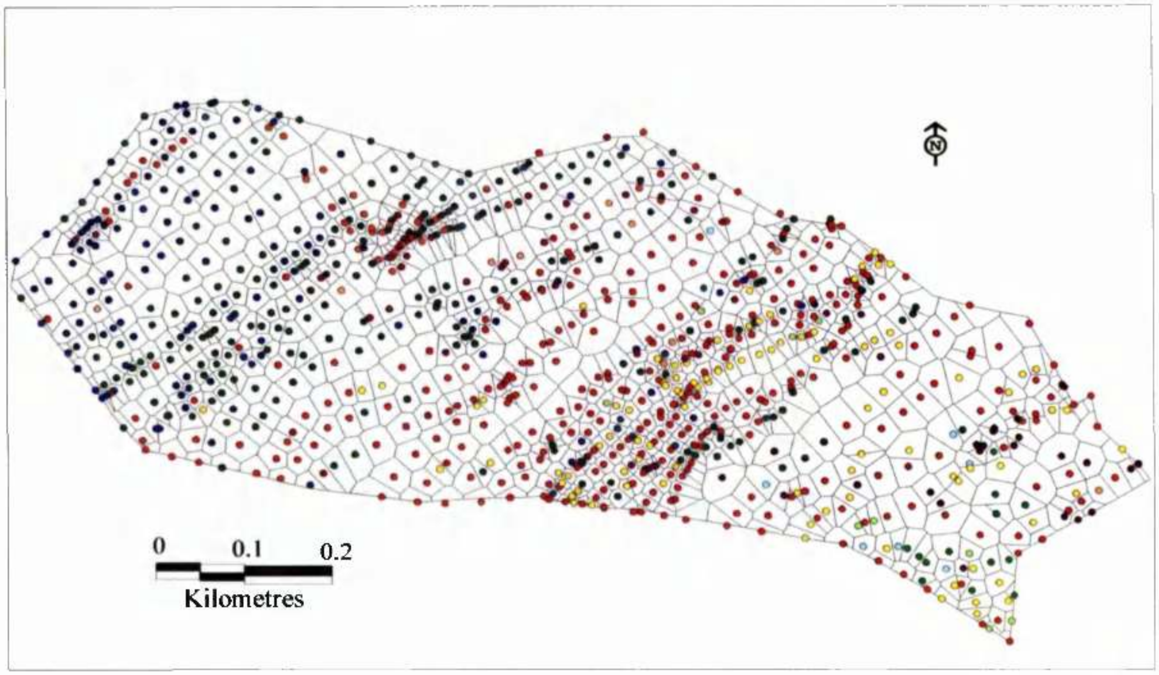


Figure 3.1 - Voronoi diagram of Enclosure 1 showing the network of thiessen polygons created around each data point using Delauney triangulation

A thematic map coloured according to NVC type was then created using MapInfo® and was overlain onto the appropriate Ordnance Survey 'Landline®' digital map (Figure 3.4). At present there is no agreed standard for the colour coding or shading of NVC maps (Rodwell, 1997), and therefore the colours used were chosen for their ease of viewing. Vertical Mapper® was also used to produce a contour map and a topographical map using the altitude data from the TSS survey.

The area, mean altitude and mean slope angle of each plant community were calculated using the GIS. Neighbouring polygons of the same NVC type were combined allowing area data for the discrete vegetation patches to be calculated.

The mapping methodology used is described in more detail in Gooding *et al.* (1997).

3.4 Results

3.4.1 QUADRAT SURVEY

3.4.1.1 *Vegetation and soils*

The distribution of the thirty-one quadrats surveyed in Enclosure 2 was not random (Figure 3.2) as some of the vegetation types had restricted distributions and not all of the vegetation types were sampled. This resulted in a concentration of quadrats in the upper and lower sections of the enclosure where there was greater plant community variation. The thirty-one quadrats were classified into seventeen NVC sub-community types (Tables 3.1 and 3.2). Seventy-seven species of vascular plant were identified within the quadrats (Table 3.1), with a further fifty-nine species (including ferns and horsetails) identified within the whole 132.6 ha study site. Most of the additional species were found as scattered individuals within base rich flushes, flushed calcicolous grassland, on ungrazed cliff ledges, or within acidic bog pools (Table 3.3). The number of vascular plant species found within the quadrats (i.e. species richness) ranged from 8 to 28 (Table 3.2). The U6c and M17b communities had the lowest species richness, while the M6d, CG10b and M11a communities had the highest.

None of the vascular plant species occurred in all thirty-one of the quadrats, however *Nardus stricta, Festuca ovina* and *Galium saxatile* were found in over 75% of the quadrats (Table 3.1). Thirty eight percent of the recorded vascular plant species occurred in only one quadrat (Table 3.1).

The interaction of six soil forming factors: parent material; time; climate; topography; biotic factors; and human modification, has led to the development of a range of leached, gleyed and organic soils (Pulford, 1998). The main soil types within the site were peaty podzols and peaty mineral soils, with some peaty gleys, peats and poorly developed mineral soils (Table 3.4). Soil pH ranged from 3.6 - 7.3, and extractable phosphorus ranged from 0.4 mg l^{-1} to 34.0 mg l^{-1} (Table 3.2). There was a significant positive correlation between plant species richness and soil pH ($r = 0.83$, $p < 0.001$), and a significant negative correlation between plant species richness and soil extractable phosphorus content (square root transformed) ($r = -0.59$, $p < 0.001$).

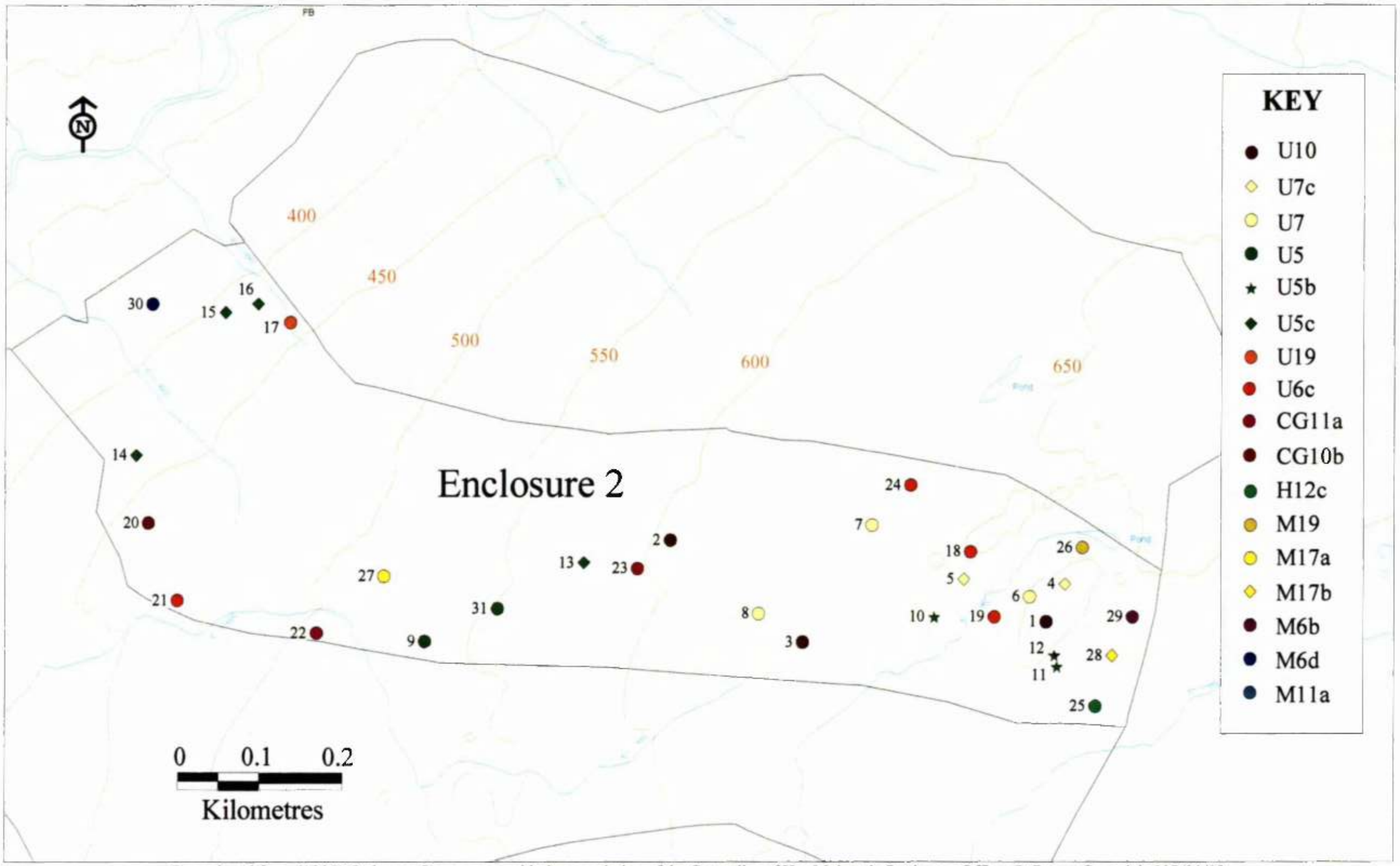


Figure 3.2 - Location of the 31 quadrats within Enclosure 2

Table 3.1 - Percentage frequency of each species within the 31 quadrats

Quadrat	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Species																															
Holcus lanatus																														15	
Achillea millefolium															47																
Achillea ptarmica																														4	
Agrostis capillaris		44	2	4		15	77	4	65	71	98	77	75	70	99	97	60					2	87	2	2		2			1	9
Agrostis vinealis	33	5	21	85	74	25	20	61		27	3	21		8		12		12				82	15	3					2		
Alchemilla alpina	7	33		18	15												10					95	86	5							
Alchemilla filicaulis																								1							
Alchemilla glabra																								1						3	
Anemone nemorosa									31				38	58		51	19														
Anthoxanthum odoratum		4				1		8	32	61	50	45	25	12	19	5	30			21		9	8	18						13	2
Bellis perennis																								3							
Blechnum spicant																6	14														
Calluna vulgaris				2		7																			99	71	59	100	59		
Campanula rotundifolia													10		2								14	3							
Carex bigelowii	97	81				75	88	19															3								
Carex binervis									20		70		12			35															
Carex capillaris																								13							
Carex dioica																															14
Carex echinata																											2		65	1	
Carex hostiana																														4	
Carex nigra																													92	15	
Carex panicea													2	3		5						57	1	67						4	28
Carex pilulifera	1	10	27	32	50	18	8		3	4			2	28	20	25	11					46	28		1						
Carex pulicaris																								21							
Carex viridula ssp. *oedocarpa*																															32
Cerastium fontanum															1								2								
Cirsium palustre																														12	
Crepis paludosa																														6	
Danthonia decumbens															1		7														
Deschampsia cespitosa													17																		
Deschampsia flexuosa			4		1		2	10	8	4		8						85	70	83	36				75	27					
Diphasiastrum alpinum			98	30	59																				2						
Drosera rotundifolia																											3				
Empetrum nigrum	70		14	78	21	41	4												27						91	59			3		
Epilobium palustre																														3	
Erica tetralix																											16	35			
Eriophorum angustifolium													11														68	12	38	4	4
Eriophorum vaginatum																										58	17	87	15		
Euphrasia officinalis agg.																						11								3	
Festuca ovina/vivipara/tenuifolia	80	81	79	60	87	18	16	71	36	74	58	83	43	69	99	62	61	70	66	30	6	98	99	60	6				11	83	52
Festuca rubra															1															2	
Galium saxatile	63	82	17	35	10	58	23	15	41	100	99	100	94	19	100	99	58	62	19	100		17	100			1				6	

Table 3.1 (continued) - Percentage frequency of each species within the 31 quadrats

Quadrat	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Species																															
Huperzia selago				2																											
Juncus acutiflorus																														99	
Juncus conglomeratus																													4		
Juncus squarrosus				3	32	34	14	80	17	39	37	74	18					87	92	99	90				1	58					3
Juncus triglumis																															3
Leontodon autumnalis													5																		
Linum catharticum																								2							
Luzula multiflora		40						4	3				3	4	21	10	2				7	31	35							6	
Lysimachia nemorum																														31	
Molinia caerulea																											96	1			2
Nardus stricta				40	67	83	87	32	81	59	68	17	88	53	26	67	36	2	4	7	57	2		2	9	1	1		15	1	4
Narthecium ossifragum														8													33	85			7
Oreopteris limbosperma																	44														
Persicaria vivipara														7	13									67						4	
Pinguicula vulgaris																													2		6
Plantago lanceolata														4	6									27						3	
Polygala serpyllifolia																	1					6					9				
Potentilla erecta		13				37	16	1	35	11	28	13	5	60	10	85	57				31	87	17		4	2	31	1	37	53	
Prunella vulgaris																								1							9
Ranunculus acris														2	75									6						38	3
Ranunculus flammula																														2	53
Salix herbacea	28	5		48																											
Saxifraga aizoides																								67							61
Saxifraga oppositifolia																								8							
Selaginella selaginoides														1										5							3
Taraxacum vulgare agg.																														4	2
Thalictrum alpinum																															13
Thymus polytrichus																								58							
Trichophorum cespitosum				2	4	10	34							40						1	6						81	58	2		1
Vaccinium myrtillus	71	21	81	49	98	66	37	5	92	42		89				7	2	84	90	6	98	57	39		71	87					
Vaccinium oxycoccos																													6		
Vaccinium uliginosum																										28					
Vaccinium vitis-idaea	66	1	81	19	45	12	1	2										2	39			8			24						
Viola palustris													14	1	70							59	20						22	21	
Viola riviniana																								3							
Bryophytes (excluding *Sphagnum*)	100	100	95	100	100	100	100	93	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	55	98	92	26		99	62	100
Sphagnum spp.							5											5	30	10	5					1	69	25	28	51	
Lichens (*Cladonia* spp.)	40		68	19	15	7		2									2		5		15				32	2		1			
Lichen (*Cetraria islandica*)		1																							1						
Rock (lichen encrusted) & bare soil	10	20		2													6						1	35	1						71
NVC Community Type	U10	U10	U10	U7c	U7c	U7	U7	U7	U5	U5b	U5b	U5b	U5c	U5c	U5c	U5c	U19	U6c	U6c	U6c	U6c	GC11a	CG11a	CG10b	H12c	M19	M17a	M17b	M6b	M6c	M11a
Number of Vascular Plant Species	**10**	**13**	**10**	**16**	**13**	**15**	**14**	**13**	**13**	**11**	**9**	**10**	**17**	**18**	**17**	**14**	**15**	**8**	**8**	**8**	**8**	**16**	**15**	**23**	**12**	**10**	**13**	**8**	**15**	**28**	**21**

Table 3.2 - Summary of the quadrat data
(The NVC communities and sub-communities have been blocked together)

Quadrat Number	NVC Vegetation Community Type	Number of vascular plant species	Altitude (metres above sea level)	Aspect (degrees)	Slope (degrees)	Soil pH	Extractable Phosphorus ($mg\ l^{-1}$)	Extractable Potassium ($mg\ l^{-1}$)	Extractable Magnesium ($mg\ l^{-1}$)	Organic Matter (loss on ignition) (%)
1	**U10**	10	654	270	5	4.2	3.7	101	59.9	19.7
2	**U10**	13	606	255	20	4.3	4.8	157	77.8	48.6
3	**U10**	10	631	318	2	4.1	3.0	128	73.1	27.0
4	**U7c**	16	652	305	26	4.4	2.2	61.3	33.6	21.6
5	**U7c**	13	641	230	9	4.5	1.9	70.5	32.7	16.9
6	**U7**	15	645	290	16	4.2	3.3	111	47.0	44.5
7	**U7**	14	638	285	13	4.0	2.7	63.5	66.2	57.2
8	**U7**	13	625	280	15	4.2	11.2	187	97.9	73.9
9	**U5**	13	535	290	23	4.3	5.6	139	94.2	44.9
10	**U5b**	11	638	160	28	3.8	2.3	97	66	34.2
11	**U5b**	9	645	155	19	4.2	5.0	115	34	81.6
12	**U5b**	10	649	175	29	4.0	2.9	109	67	23.9
13	**U5c**	17	573	310	20	4.8	2.8	82.8	56.6	28.5
14	**U5c**	18	429	328	20	4.7	1.8	76.7	77.3	16.4
15	**U5c**	17	405	325	23	4.8	1.4	63	58.8	14.5
16	**U5c**	14	415	315	25	4.3	3.5	136	46.1	25.8
17	**U19**	15	427	305	35	4.4	2.1	123	47.6	20.1
18	**U6c**	8	648	315	18	3.6	10.5	78.5	160	83.9
19	**U6c**	8	637	325	11	3.6	7.9	62.7	116	82.5
20	**U6c**	8	635	280	20	3.7	7.3	55.3	84.5	72.3
21	**U6c**	8	467	300	12	3.7	34.0	110	225	84.9
22	**CG11a**	16	505	295	10	5.0	3.4	497	128	41.4
23	**CG11a**	15	598	280	15	4.8	3.3	161	101	36.3
24	**CG10b**	23	461	315	40	7.3	0.7	60	123	20.9
25	**H12c**	12	632	220	12	3.9	1.6	57.2	49.9	20.0
26	**M19**	10	641	310	10	3.7	11.2	105	169	83.2
27	**M17a**	13	510	300	10	4.2	6.6	76.9	101	82.8
28	**M17b**	8	636	0	0	3.8	3.8	39.2	87.6	84.7
29	**M6b**	15	639	0	0	4.3	5.3	38.3	96.1	81.5
30	**M6d**	28	385	320	8	5.4	1.3	59.2	65.6	42.4
	M11a	21	548	305	18	6.1	0.4	37.4	163	17.9

Notes
red - montane grass-heath (8 quadrats), blue - calcifuge grassland (13 quadrats), green - calcicolous grassland (3 quadrats), black - mire and heath (6 quadrats), - flush (1 quadrat)

Table 3.3 - Additional species recorded outside the quadrats

Species	NVC Community	Species	NVC Community
Agrostis stolonifera	M4	*Luzula sylvatica*	U5
Antennaria dioica	CG10b	*Lycopodium clavatum*	H12
Betula pubescens	scattered seedlings	*Menyanthes trifoliata*	M4, M6a
Botrychium lunaria	CG10b	*Myrica gale*	M6d, M25
Cardamine pratensis	M6d	*Oreopteris limbosperma*	U19
Carex flacca	CG10b	*Oxalis acetosella*	U5, U19
Carex pallescens	U5	*Parnassia palustris*	M6a, M6b, M6d
Carex pauciflora	M17	*Pedicularis palustris*	M6d, M15
Carex rostrata	M4	*Pedicularis sylvatica*	M15, M17, M6d
Cirsium helenoides	U5	*Phegopteris connectilis*	boulder scree
Dactylorhiza maculata	M6d, M15, U5, U6	*Poa annua*	U4
Eleocharis quinqueflora	M11	*Poa pratensis*	U4
Epilobium brunnescens	M10, M11	*Potamogeton polygonifolius*	M4
Equisetum fluviatile	M6d	*Potentilla palustris*	M4
Erica cinerea	U5, H12	*Pteridium aquilinum*	U19
Eriophorum latifolium	M11	*Ranunculus repens*	M6d, U4
Galium boreale	CG11, cliffs	*Rhinanthus minor*	M6d, CG10
Gentianella campestris	M11	*Rubus chamaemorus*	M19
Geranium sylvaticum	CG11.	*Rumex acetosa*	U19, U4
Gnaphalium supinum	CG11, U10	*Salix aurita*	scattered seedlings
Helictotrichon pratense	U5	*Saxifraga stellaris*	M10, M11
Hieracium agg.	CG10	*Silene acaulis*	CG10
Holcus mollis	M6d	*Sorbus aucuparia*	cliff ledge, scattered seedlings
Hypericum pulchrum	M11	*Stellaria alsine*	M6d
Juncus articulatus	M10, M11, M6d	*Tofieldia pusilla*	M11
Juncus bulbosus	M4, M6, M11, M32	*Trientalis europaea*	U6
Juncus effusus	M6a, M6b, M6d, U5	*Trifolium repens*	U4, U5, CG10, CG11, M6d, U19
Juncus triglumis	M11	*Veronica officinalis*	U19, U4
Lathyrus montanus	U5	*Veronica serpyllifolia*	U4
Leontodon autumnalis	U5		

Note - The codes and names of all the NVC types found within the study site enclosures are given in Appendix 3.1

Table 3.4 - Principal soil types

Vegetation Type	Soil Type
U10	Shallow (<10 cm), stony, poorly developed, mineral soil
U7, U7c	Shallow (<20 cm), peaty podzols
U5, U5b	Base-poor, podzolic, peaty-mineral soil (>30 cm)
U5c	Peaty-mineral soils (>20 cm deep), irrigated by moderately base-rich water.
U6c	Moist, acidic, peaty podzols and shallow peats (>30 cm)
U19	Shallow (10-20 cm), rocky, peaty-mineral soil.
CG11a, CG10b	Shallow (<20 cm), rocky, free-draining (though moist), brown earths of moderate base status
H12c	Base-poor, podzolic, peaty-mineral soil (>30 cm)
M6b, M17a, M17b, M19	Peat (>50 cm)

3.4.1.2 *Ordination plots*

Various groupings of quadrats are visible on the DECORANA ordination plot of quadrat sample scores (Figure 3.3). The NVC type that was assigned to each quadrat using the keys, floristic tables and descriptions within the NVC, has been superimposed onto the ordination plot. The ordination quadrat groupings tend to support the classifications that were made. The permanently waterlogged peatland communities are found to the right of the ordination plot, while the drier communities on shallower soils are found to the left. The ordination plot of the species scores clearly shows some groupings of species (Figure 3.4). Axis one appears to be related to increasing soil moisture content and increasing soil depth.

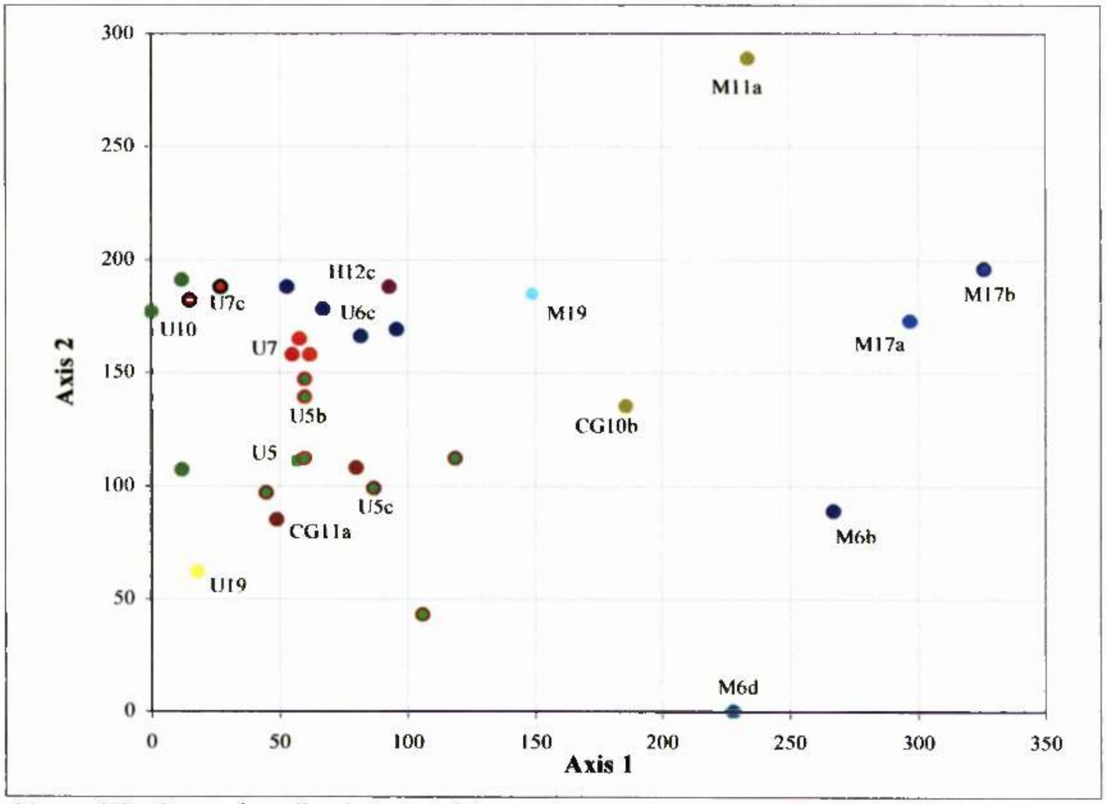


Figure 3.3 - Two-axis ordination plot of the quadrat sample scores produced by DECORANA

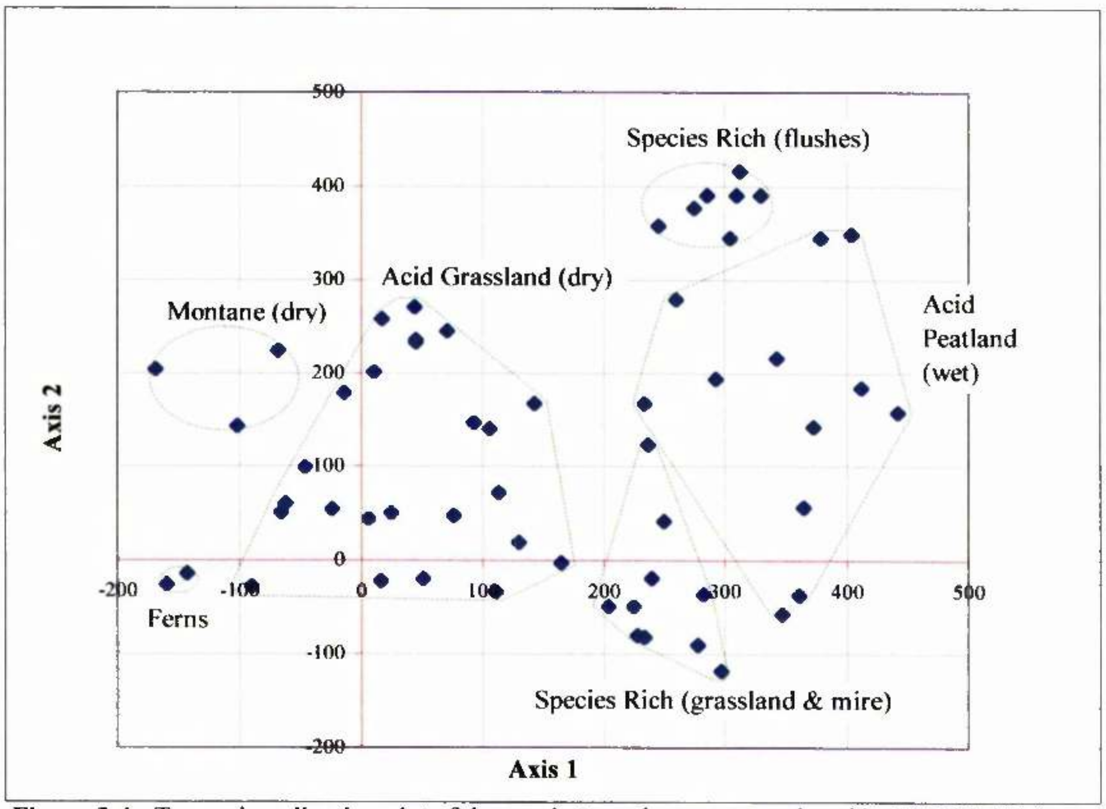


Figure 3.4 - Two-axis ordination plot of the quadrat species scores produced by DECORANA

3.4.2 MAPPING

3.4.2.1 *Topographical map*

The study site, which covers an area of 132.6 ha, ranges in altitude from 284 m at the base of Enclosure 3, to 685 m at the top of Enclosure 1 (Figure 3.5).

The topography of the site is complex, but can be split into five major topographical Zones (Figure 3.6):

Zone 1 - Steep slope in excess of 20°, below 360 m, within Enclosure 3 only.

Zone 2 - Shallow slope (less than 15°), in a band across all three enclosures, from 370 m to 410 m.

Zone 3 - Uniform, steep slope (15 - 20°), most extensive in Enclosure 1 where it reaches 550 m.

Zone 4 - Moderately steep slope (10 - 20°) bisected by rock outcrops that run NE-SW across the angle of slope as steep sided broken ridges, often with peat filled hollows on their upper sides. The most extensive zone within Enclosures 2 and 3.

Zone 5 - Complex upper zone above 600 m, composed of steep sided ridges and knolls separated by large peat filled hollows and shallow sloped blanket mire.

The topography of Enclosure 1 is less complex than the other enclosures. It contains a more extensive Zone 3, has fewer knolls and more linear ridges within Zone 4, and has larger peatland hollows within Zone 5.

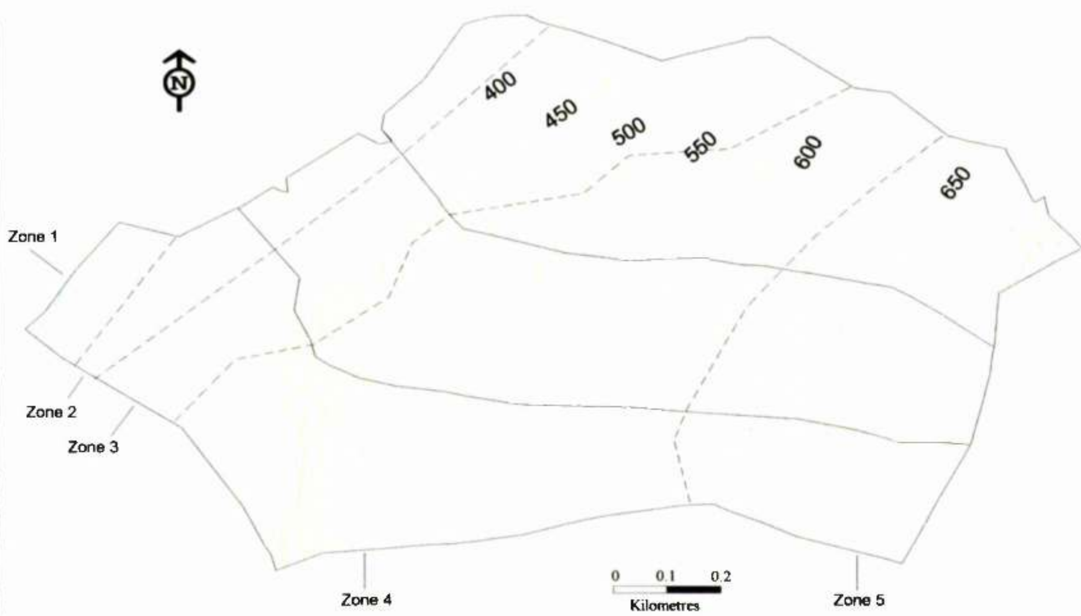


Figure 3.5 - Contour map (10m intervals) of the Kirkton Face study site

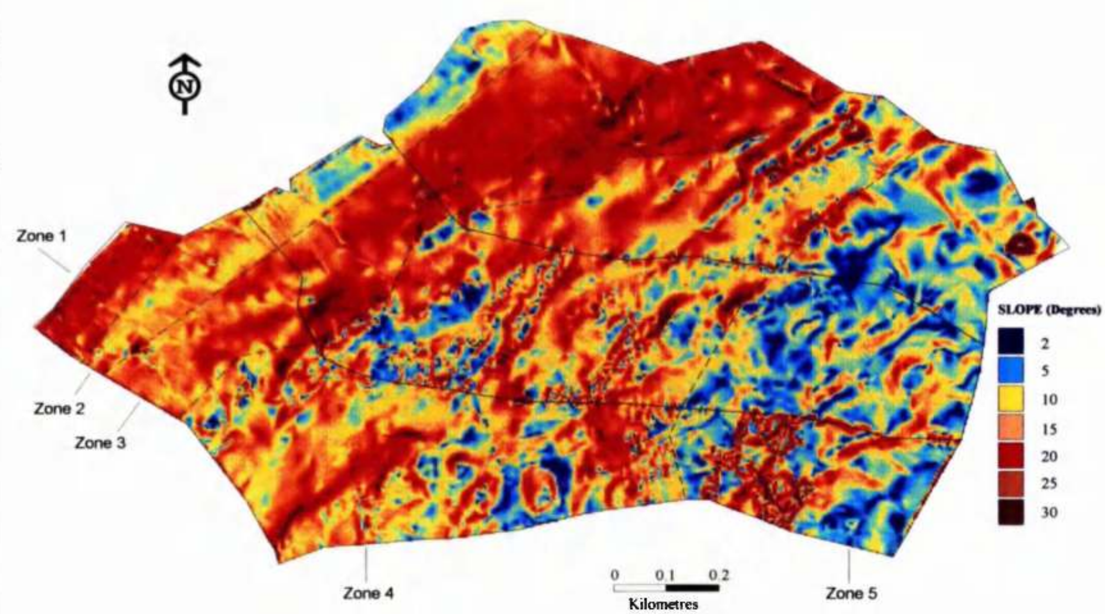


Figure 3.6 - Topographical map of the Kirkton Face study site

3.4.2.2 *Vegetation map*

6102 data points were used to create the voronoi diagram and thematic map (Figure 3.7a), and 2047 discrete vegetation patches were produced by combining neighbouring polygons of the same vegetation type (Appendix 3.2). Enclosure 1 had fewer data points than the other two enclosures (922 compared with 2257 and 2923), due to its more uniform topography, and consequently it had a larger mean polygon area (481.6 m^2 compared with 180.7 m^2 and 162.4 m^2).

A total of twenty-two plant community types were mapped (Figure 3.7a). The inherent variation that exists within vegetation communities inevitably meant that in some cases the NVC description alone could not clearly define the vegetation type, however, all the patches of vegetation were classified into the most appropriate NVC community type.

The most abundant community types were the *Nardus stricta* dominated U5b/U6 and U5c communities, which covered 52 % of the total study area. The M17, M6d and U4 communities occupied a further 26.7 %, with the remaining seventeen communities covering only 21.3 % (Table 3.5).

Patch size ranged from 13.38 ha to less than 1 m^2, with an overall mean patch size of 648 m^2. The mean patch size of the individual communities ranged from 177.2 m^2 for the U7 community to 1526.7 m^2 for the U5b/U6 community (Appendix 3.2). The calcicolous grasslands and flushes, and the *Carex* dominated mires tended to have smaller mean patch sizes (<408 m^2), and smaller ranges and standard errors, than the acidic grasslands, and *Trichophorum cespitosum* and *Juncus acutiflorus* dominated mires (Appendix 3.2). The U5b/U6 community, which was the most abundant vegetation type, had both the largest mean patch size and largest standard error (Appendix 3.2).

The three enclosures were similar in their cover and distribution of NVC community types (Figure 3.7a and Table 3.5), although Enclosure 2 had a lower proportion of U5c (14.8 % compared with over 23 % in Enclosures 1 and 3), and a higher proportion of M17 (16.5 % compared with less than 8.3 % in Enclosures 1 and 3), and Enclosure 3 had a higher proportion of U4 (10.6 % compared with less than 4.4 % in Enclosures 1 and 2).

Two key factors that influenced the distribution of plant communities within the enclosures were slope angle and altitude. The different plant communities had different slope angle means and ranges (Appendices 3.3 and 3.4). The blanket mire and heath communities had mean slope angles of less than 12°, the acidic grasslands and flush communities had mean slope angles of 12 - 18°, while the calcicolous grasslands and fern dominated communities had mean slope angles of greater than 18°. Of the two *Nardus stricta* dominated communities the U5c community tended to occur on steeper slopes than the U5b/U6 community (Appendix 3.4). Some of the vegetation types such as the U5c community had altitudinal ranges which covered the whole of the study site (i.e. from below 300 m to over 650 m), and their distribution within the site was determined by other factors, whereas other vegetation types had more restricted altitudinal ranges, such as the U10 community which was not found below 600 m, and the M6d community which was not found above 600 m and had 77 % of its total area below 440 m (Appendix 3.5).

A detailed description of the vegetation types and their distribution within the study site is given in Appendix 3.6.

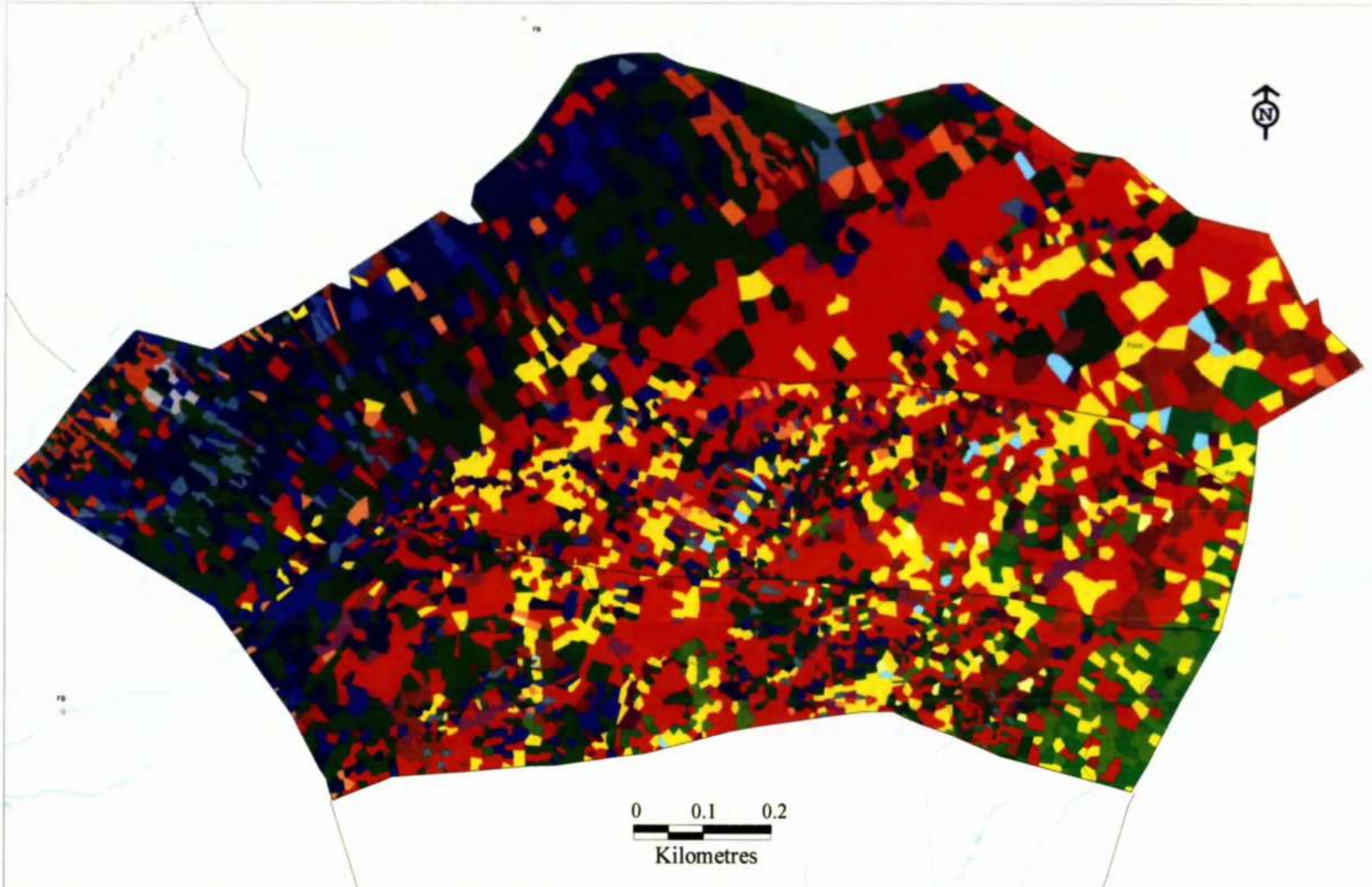


Figure 3.7(a) – Vegetation map of the Kirkton Face study site

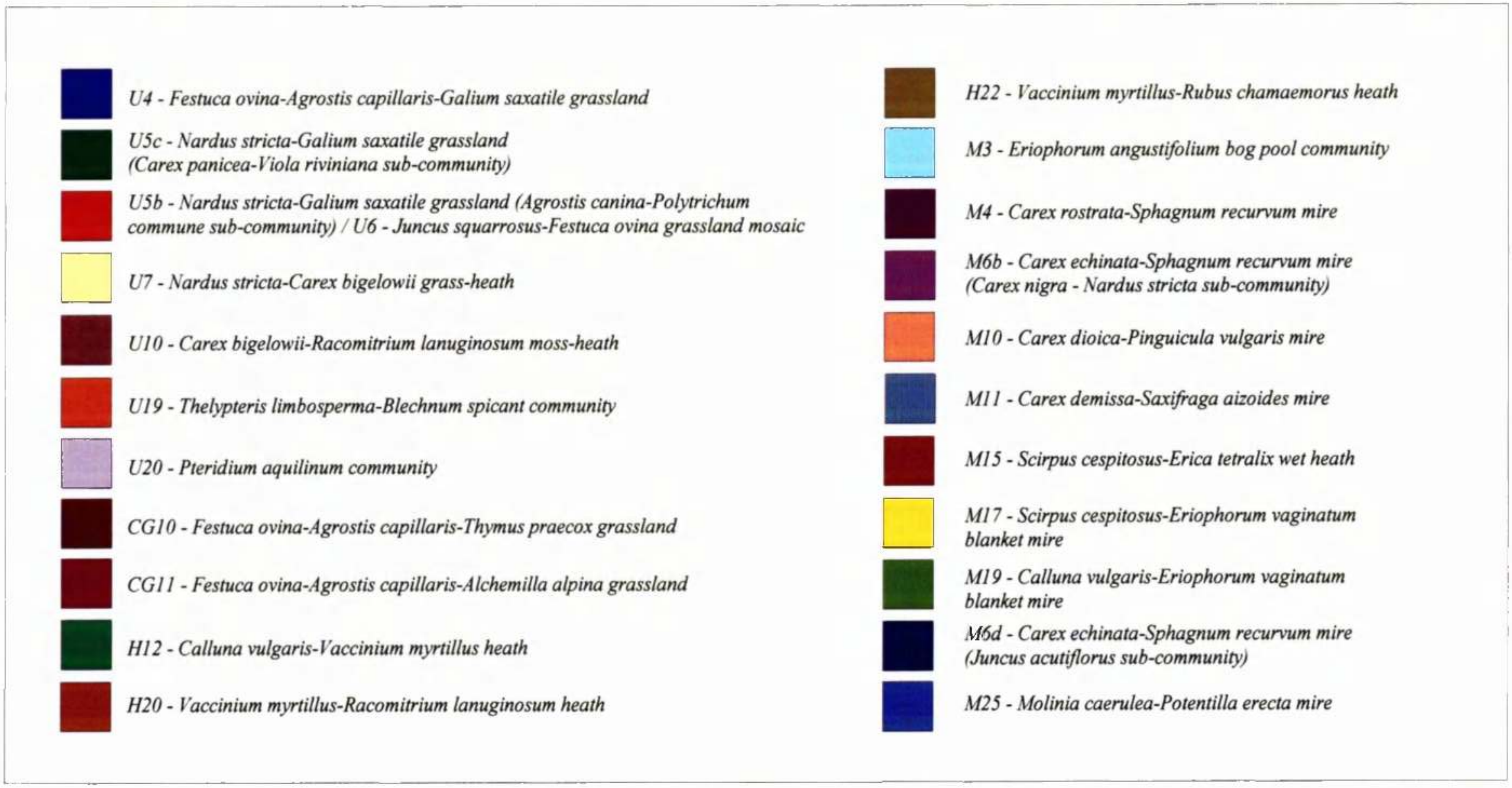


Figure 3.7(b) - Key to the NVC community types

Table 3.5 - Area of each NVC community type within each enclosure.

Communities are arranged in order of total area, from highest to lowest

NVC Community Type	Area (hectares and percentage)			
	Enclosure 1	Enclosure 2	Enclosure 3	All Enclosures
U5b/U6	16.40 (36.9%)	13.10 (32.1%)	11.88 (25.0%)	41.37 (31.2%)
U5c	10.52 (23.7%)	6.04 (14.8%)	11.10 (23.4%)	27.66 (20.9%)
M17	3.66 (8.3%)	6.74 (16.5%)	3.82 (8.0%)	14.22 (10.7%)
M6d	4.33 (9.8%)	3.24 (7.9%)	5.13 (10.8%)	12.71 (9.6%)
U4	1.64 (3.7%)	1.77 (4.4%)	5.01 (10.6%)	8.43 (6.4%)
H12	0.80 (1.8%)	0.89 (2.2%)	1.99 (4.2%)	3.68 (2.8%)
U10	1.21 (2.7%)	1.64 (4.0%)	0.37 (0.8%)	3.22 (2.4%)
M19	0.31 (0.7%)	1.02 (2.5%)	1.88 (4.0%)	3.21 (2.4%)
M6b	0.23 (0.5%)	1.67 (4.1%)	0.85 (1.8%)	2.75 (2.1%)
M11	0.62 (1.4%)	0.57 (1.4%)	1.41 (3.0%)	2.60 (2.0%)
M15	0.23 (0.5%)	0.98 (2.4%)	1.27 (2.7%)	2.48 (1.9%)
CG11	1.25 (2.8%)	0.79 (1.9%)	0.26 (0.5%)	2.30 (1.7%)
U19	1.06 (2.4%)	0.14 (0.3%)	0.82 (1.7%)	2.01 (1.5%)
M10	0.71 (1.6%)	0.52 (1.3%)	0.47 (1.0%)	1.70 (1.3%)
M4	0.24 (0.5%)	0.56 (1.4%)	0.31 (0.7%)	1.11 (0.8%)
M25	0.09 (0.2%)	0.60 (1.5%)	0.21 (0.4%)	0.90 (0.7%)
H20	0.60 (1.3%)	0.02 (0.04%)	0.18 (0.4%)	0.79 (0.6%)
M3	0.45 (1.0%)	0.23 (0.6%)	0.07 (0.1%)	0.75 (0.6%)
U7		0.19 (0.5%)	0.19 (0.4%)	0.37 (0.3%)
U20			0.18 (0.4%)	0.18 (0.1%)
CG10	0.07 (0.16%)	0.07 (0.2%)	0.06 (0.1%)	0.2 (0.15%)
H22		0.02 (0.05%)		0.02 (0.02%)
Total Area	**44.404**	**40.776**	**47.459**	**132.639**

3.5 Discussion

3.5.1 Use of the National Vegetation Classification

The National Vegetation Classification scheme was designed to help identify and understand vegetation types found in the field (Rodwell, 1997), and is now widely used by the UK statutory conservation agencies and other governmental and non-governmental environmental bodies to produce maps and inventories of plant communities on designated or locally important sites (e.g. Gray *et al.*, 1996). The NVC has also been used extensively in scientific research investigating the relationship between plant communities and the environmental factors which influence them (e.g. Wallace *et al.*, 1992; Brown *et al.*, 1993a; Brown *et al.*, 1993b; Furley, 1998; Holland and Gooding, 1998). Other vegetation classification systems describing the mountain vegetation of Scotland, which are also based on a phytosociological approach, do exist (Poore and McVean, 1957; McVean and Ratcliffe, 1962; Burnett, 1964). However, due to the comprehensive nature, reliability and widespread use of the NVC throughout the whole of Britain, for both scientific and conservation purposes, it was thought that this would be the most appropriate system to use.

Within the NVC system each vegetation type has to be defined, and must therefore have descriptive boundaries. Inevitably when dealing with the vegetation of the whole of Britain there are some vegetation types that fall in between named types, or are so distinctly different from any defined type that they warrant their own description. Even if a vegetation type identified in the field fits within a defined type it may have a species composition or structure that requires further description.

The quadrat surveys and vegetation mapping carried out on the Kirkton Face study site identified some vegetation types that could not be described fully using the NVC.

The community dominated by *Juncus acutiflorus*, which was found mainly at the base of the enclosures, was classified as an M6d *Carex echinata - Sphagnum recurvum* (*Juncus acutiflorus*) mire, however it contained a number of key species with high frequencies which were not present within the M6d floristic table (Rodwell, 1991), namely *Lysimachia nemorum*, *Parnassia palustris*, *Pedicularis sylvatica*, *Pedicularis palustris*, *Euphrasia officinalis* agg. and *Persicaria vivipara*. This community also had affinities to the M23a *Juncus acutiflorus - Galium palustre* rush pasture, however it did not contain two of the M23a 'constant species', *Galium palustre* and *Lotus uliginosus* (Rodwell, 1991). Although similar mires containing these two species are present at lower altitudes on the farm (below 200 m), it was decided that classification of this community within the study site as an M6d mire was the most appropriate option.

The community dominated by *Nardus stricta* and *Juncus squarrosus* was classified as a U5b *Nardus stricta - Galium saxatile* (*Agrostis canina - Polytrichum commune*) grassland, however this classification fails to indicate the importance of *Juncus squarrosus* and *Trichophorum cespitosum*, or the limited cover of *Deschampsia flexuosa* within the community. This classification did however separate this community from the more freely drained, species rich U5c community in which *Juncus squarrosus* was only a minor component.

The remaining plant communities identified during the mapping exercises and quadrat surveys fitted reasonably clearly into existing NVC types and apart from the few problems outlined above, the NVC was found to be an appropriate and exceedingly useful system for classifying vegetation types in the uplands of Western Scotland. It allows accurate maps and inventories of vegetation types to be produced that can be compared with any other site in Britain.

3.5.2 ACCURACY OF THE MAPPING

The lack of identifiable landscape features, the constantly changing mosaic of vegetation types and the undulating terrain made the site impossible to map with any degree of accuracy using simple field based mapping techniques, which rely on surveyors sketching boundaries between community types on to large-scale field maps. Modification of these field maps by comparison with aerial photographs can improve their accuracy, however it is of limited value in complex grassland mosaics where different vegetation types are visually similar in terms of colour and structure, but are compositionally quite distinct. Any attempt to determine the area occupied by specific vegetation types would have been speculative and probably misleading if a simple field based sketch map had been used.

The mapping technique used in this study was based on the classification of vegetation types at known points rather than the mapping of boundaries between the vegetation types. The GIS was used to artificially create these boundaries. By using the total survey station the location of individual survey points was highly accurate (Topcon Instrument Corporation, 1990), however in order to minimise any boundary errors it was essential that the vegetation type be recorded as frequently as possible and this was achieved by taking readings at approximately 10 metre intervals.

Hand held Global Positioning System (GPS) units, which are widely available, could have been used instead of the total survey station to determine point locations.

However, during the survey period, GPS accuracy was deliberately downgraded by the US Department of Defense by a process known as selective availability, which results in locational errors of between 10 - 100 m, 95 % of the time (Dodson and Haines-Young, 1993). Errors of this magnitude were not acceptable.

All vegetation mapping involves some degree of subjective decision-making, where a surveyor has to classify each patch of vegetation into a particular community type, and it is therefore prone to within and between-observer variation. Cherrill and McClean (1999), studying between-observer variation in Phase 1 habitat mapping (England Field Unit, 1990), found that in pair-wise comparisons between maps independently surveyed by six ecologists, spatial agreement in terms of land-cover type occurred over only 17.3 - 38.8 % of the study site area. Furthermore, the numbers of land-cover types that were identified ranged from 13 to 21. Phase 1 mapping (England Field Unit, 1990) uses much broader habitat types than the NVC, and it is therefore likely that between-observer variation in the subjective classification of particular vegetation patches into NVC types would also be high. In the present study between-observer variation was reduced by:

a) Using only three trained vegetation surveyors.
b) Ensuring that the surveyors were in radio and visual contact throughout the surveying process, which enabled immediate crosschecking of classifications.
c) The use of a field summary sheet that contained details of the most likely NVC communities to be found within the site.
d) The cross-checking of preliminary classifications against field notes.
e) The point based survey technique, which removed the problem of mapping boundaries that are often unclear.

These measures ensured that the vegetation map was as accurate as possible.

3.6 Conclusions

Although the Kirkton Face study site only reaches 685 m in altitude and is only 132.6 ha in area, its past and present management, together with its varied topography, hydrology and soil types, have allowed the development of a complex mosaic of vegetation types containing a diverse range of plant species. This mosaic of vegetation types is typical of the Breadalbane district, where the calcareous Dalradian mica-schists give rise to moderately base-rich soils supporting a diverse flora of national and international importance (Ratcliffe, 1977; Smith *et al.*, 1992). The high biodiversity of this area is in contrast to the depauperate flora and predominance of calcifuge species that are characteristic of the hard siliceous rocks that form a large proportion of upland Scotland (Ratcliffe and Thompson, 1988).

There has been a long history of vegetation description and mapping in Scotland (reviewed in Gimingham, 1997; Dickinson, 1998a; Mather, 2000) and this study continues this tradition using modern technology and a widely used, contemporary classification system. The detailed vegetation map produced using the total survey station and GIS provided accurate information on the areas of each vegetation type, which was required for the testing and development of the Hill Grazing Management Model (Chapter 7). The mapped distribution of vegetation patches also provides a valuable resource for determining the foraging behaviour of free ranging sheep. A foraging behaviour study using Global Positioning System collars is being carried out by other researchers in parallel with the study described in this thesis (Hulbert *et al.*, 1998).

CHAPTER 4 – VEGETATION CHANGE

4.1 Summary

1) Permanent nested quadrats and monthly sward surface height measurements were used to monitor changes in the composition and structure of the vegetation within a range of community types subject to the three different grazing treatments.
2) Few changes in species composition or the abundance of dominant species within the monitored communities were observed, and no vegetation types changed their NVC type. The higher stocking rates in Enclosures 1 and 3 resulted in an increase in the frequency of low growing forbs within the more species rich calcareous grasslands.
3) Trampling and ground disturbance by the cattle resulted in an overall increase in the amount of bare ground, potentially providing more gaps for seedling recruitment. However, very few additional species appeared within any of the quadrats. Cattle grazing did not reduce the cover of *Nardus stricta* within the U5c community.
4) All treatments resulted in an increase in the cover of *Juncus acutiflorus* within the M6d community and *Juncus squarrosus* within the U5b community.
5) The highest stocking rate resulted in significantly shorter swards in all three communities.
6) There was a change in the structure of the *Nardus stricta* grasslands within all three enclosures to a shorter, more homogeneous, less tussocky sward. The results indicated that the study grazing regimes were quite different from the former grazing regime.

4.2 Introduction

There has been intensive study of Britain's hill grasslands and allied communities for many years. Their botanical composition (McVean and Ratcliffe, 1962; Burnett, 1964; Rodwell, 1992), productivity (Rawes, 1963; Rawes and Welch, 1969; Job and Taylor, 1978; Perkins *et al.*, 1978; Harrison *et al.*, 1994), utilisation (Grant *et al.*, 1996a; 1996b) and response to grazing (Welch and Rawes, 1964; Ball, 1974; Marrs *et al.*, 1988; Hill *et al.*, 1992) have been described in detail by many authors. In spite of all this information, the dynamics of these upland communities and the rates and directions in which they change, are poorly understood. The vegetation of hill grasslands tends to be slow growing, and many of the dominant species such as *Juncus squarrosus* (Welch, 1966), *Festuca ovina* and *Nardus stricta* (Chadwick, 1960) are long-lived perennial species, which spread predominantly by clonal growth, and therefore tend to regenerate episodically (Hill *et al.*, 1992). It is likely that due to their slow dynamics, these upland grasslands take many years to reach equilibrium with their new environment following a change in the environmental or management conditions (Hill *et al.*, 1992).

Much of the research into changes in upland grasslands has concentrated on *Nardus stricta* (Nicholson *et al.*, 1970; Floate *et al.*, 1972; Common *et al.*, 1994; 1998; Grant *et al.*, 1996b; 1996c), as an increase in this species at the expense of other more palatable species, such as *Agrostis capillaris* and *Festuca ovina*, is thought to be a retrograde step, leading to pasture degradation (Milton, 1934; Fenton, 1936; 1937a; Chadwick, 1960; Perkins, 1968). *Nardus stricta* has a low calcium content and compared with many other upland plants it has an exceptionally high silica content (de Coulon, 1923; Thomas and Fairbairn, 1956; Chadwick, 1960). It has a slightly lower digestibility than *Agrostis capillaris* with which it often occurs (Thomas and Fairbairn, 1956; Hodgson *et al.*, 1991) and has a much higher proportion of fibrous tissue in its wiry foliage (Burr and Turner, 1933). It therefore tends to be avoided by selective grazers like sheep (Grant *et al.*, 1985; 1996b). It is thought that the increase in *Nardus stricta* and *Juncus squarrosus*, which has an even lower dry matter digestibility (Grant and Campbell, 1978), over the last century, has been caused by a number of factors: an overall increase in sheep numbers; the loss of wether sheep (castrated males over a year old); a reduction in the number of hill cattle; and a change in some parts of Britain from all-year-round sheep grazing to summer only grazing (Fenton, 1936; Roberts, 1959; Perkins, 1968; Hughes, 1973). In heavily grazed situations *Nardus stricta* is a better competitor than *Calluna vulgaris* (King, 1960; Hartley, 1997; Alonso and Hartley, 1998; Hartley and Amos, 1999) and in many parts of Britain *Calluna vulgaris* moorland is being replaced by grassland that is often dominated by *Nardus stricta* (Anderson and Yalden, 1981; Welch, 1986; Sydes, 1988; Welch and Scott, 1995; Whitelaw and Kirkpatrick, 1997). This loss of heather moorland is causing concern because of its high conservation and landscape value (Thompson *et al.*, 1995; Tudor and Mackey, 1995). It has been shown that the spread of *Nardus stricta* can be prevented under a controlled intermittent grazing regime together with the application of fertiliser (Common *et al.*, 1991), however in many upland situations this management is not practical. The use of controlled grazing alone, with summer grazing cattle, has also been demonstrated to reduce the cover of *Nardus stricta* (Grant *et al.*, 1996b; Common *et al.*, 1998) and may be an effective method of modifying *Nardus stricta*-dominated pastures. In some situations management to replace *Nardus stricta*-dominated grasslands with more productive *Festuca - Agrostis* grassland or with *Calluna vulgaris* heath, is not appropriate. For example, in the Breadalbane Mountains in west-central Perthshire, extensive areas of species rich *Nardus stricta* grassland occur on moderately base-rich soils derived from calcareous Dalradian mica-schists (Smith *et al.*, 1992; Gray *et al.*, 1996). This vegetation is of national and international importance for its rich arctic-alpine flora and is protected under the EU Habitats Directive (92/43/EEC) (Hopkins, 1995). Changes in the management of this semi-natural grassland, such as the complete removal of grazing livestock, may result in a decline in plant species diversity and a reduction in its conservation value. A change from a heterogeneous, tussocky, *Nardus stricta*-dominated grassland, to a shorter, more homogeneous *Festuca* - *Agrostis* sward, may also have a negative impact on the population and biodiversity of invertebrates (Gordon and Dennis, 1996; Dennis *et al.*, 1997; 1998). This may in turn affect the populations of some bird species.

The probable response of a particular vegetation type to a change in grazing management can best be inferred from studies carried out in the field (Hill *et al.*, 1992). There have been many medium to long term studies looking at changes in plant species composition and structure following alterations in grazing management within upland grassland communities in Britain (Welch and Rawes, 1964; Rawes, 1981; Davies, 1987; Marrs *et al.*, 1988; Hill *et al.*, 1992; Grant *et al.*, 1996a; 1996b; Common *et al.*, 1998). Most of the studies have looked at the impact of complete exclusion of domestic herbivores (Rawes, 1981; Hill *et al.*, 1992), with only a few looking at the response of vegetation to different sheep stocking rates (Davies, 1987) or to cattle grazing (Grant *et al.*, 1996a; Common *et al.*, 1998). The majority of studies have used small fenced enclosures, with few having been carried out on large enclosures or on open hillsides (Ball, 1974; Anderson and Radford, 1994; Hope *et al.*, 1996). Similar trends in the response of particular species to changing management have been observed (e.g. Marrs *et al.* (1988) and Hill *et al.* (1992) both observed declines in the cover of *Juncus squarrosus* within a range of communities following the removal of grazing animals), however some species have reacted in a rather unpredictable manner (e.g. the cover of *Nardus stricta* has shown both an increase and a decrease following the exclusion of grazing stock (Rawes, 1981; Hill *et al.*, 1992)). This unpredictability in vegetation response may be a consequence of the fact that no two vegetation patches have identical species compositions, structures, environments or management histories. Hence the starting point will differ, even between patches of similar vegetation type on the same hillside, and therefore the response of the vegetation to the same grazing regime will not always be the same (Hulme *et al.*, 1999). This varying response at the species level, and its associated unpredictability, is likely to be magnified on open hillsides containing a range of vegetation types.

How a particular patch of vegetation responds to grazing is dependent upon a complex set of direct and indirect interactions between the grazing animal and the individual plants within the grazed vegetation. The way in which an individual plant responds to grazing damage depends upon the functional attributes of the species, together with the time of year in which the damage occurred, the environmental conditions (e.g. climate, soil, altitude and topography), and the competitive interactions with other plants within the vegetation that are themselves responding to the effects of the grazing (Noble and Slatyer, 1980; Grime *et al.*, 1988; Milne *et al.*, 1998). Functional attributes include physical attributes (such as life form, longevity and maximum height), attributes related to growth and reproduction (such as regeneration mechanism, position of the meristem, and the optimum and range of soil and climate conditions under which the species can compete effectively), and attributes related to grazing (such as digestibility and the presence of anti-herbivore mechanisms) (Grime *et al.*, 1988; Armstrong and Milne, 1995). To obtain a detailed understanding of vegetation response requires taking into account both the species dynamics, determined by their functional attributes, and the spatial relationship between individual plants and between different vegetation patches.

The purpose of this chapter is to report on changes in species composition, sward height and cover that have occurred within a range of upland grassland and mire communities subjected to the three different grazing regimes established within the Kirkton Face enclosures (Chapter 2). The monitoring was carried out at two scales; a quadrat scale for monitoring changes in species composition, and a community patch scale for monitoring changes in sward structure and species cover abundance.

The main aims were:

1) To measure any changes in species composition in response to the three grazing treatments.
2) To determine whether there was any change in the community type in response to the treatments.
3) To measure any changes in sward structure and species cover in response to the treatments.
4) To assess whether summer grazing cattle caused a reduction in the cover of *Nardus stricta* and an increase in species diversity.

4.3 Choice of monitoring methodology

The fundamental requirement of any monitoring methodology is the ability to detect change over time. Survey differs from monitoring since its objective is either to provide a description of a site at a single point in time, or to compare different sites (Critchley and Poulton, 1998). Monitoring methods, which have originated from survey methods (e.g. Smith *et al.*, 1985), may not be sensitive enough to detect minor changes (Critchley and Poulton, 1998). The method used in this project was developed specifically for monitoring grasslands and related communities (Critchley and Poulton, 1994; Critchley, 1997; Critchley and Poulton, 1998; Glaves, 1998). This 'nested quadrat' system takes into account the range of scales at which different species are found, it is sensitive to changes in species frequency, and uses an objective presence or absence criteria, which reduces the error involved in subjective cover estimates (Critchley and Poulton, 1998).

The main disadvantage of traditional methods of monitoring using qualitative estimates of cover (such as the percentage cover (Cameron *et al.*, 1997) or Domin cover scale (Kershaw and Looney, 1985)) within permanent or non-permanent quadrats, is the subjective nature of the assessment (Ball, 1974; Hope *et al.*, 1996; Cameron *et al.*, 1997; Cummins *et al.*, 1997). This can lead to within and between observer variation, leading to difficulties in determining whether changes are real or simply observer error. The use of a qualitative method in which the presence or absence of a species is recorded within a 10 x 10 gridded quadrat (i.e. 100 sub-squares) reduces subjectivity (Grant, 1993). However, this method is extremely time consuming, which limits the number of quadrats and the area that can be monitored, and is insensitive to changes where cover is high (Grant, 1993). Although the scale of the fixed-unit in a gridded quadrat is small (i.e. 10

cm x 10 cm within a 1 m^2 quadrat), it still only produces an estimate of species abundance at a single scale.

One of the most widely used methods for monitoring sward responses to changing management is the point quadrat (Grant, 1993). It is less subjective than many other non-destructive methods, as the observer has only to decide whether a pin has made contact with a plant and then to identify the species (Grant, 1993). Both vertical point quadrats (Wells, 1971; Rawes, 1981; 1983; Welch, 1984; 1986; Marrs *et al.*, 1988; Hill *et al.*, 1992; McFerran *et al.*, 1994a; 1995; Welch and Scott, 1995) and inclined point quadrats (Grant *et al.*, 1985; 1996a; 1996b), of which the latter have been shown to reduce errors due to foliage angle (Warren Wilson, 1959), have been widely used in the monitoring of grassland and heath communities. Graduated point quadrats can be used to determine the percentage cover of a species and its relative frequency within the sward, as well as provide information on the sward structure (Grant, 1993). There are however drawbacks with the technique, which include the loss of accuracy for describing and quantifying the sparse upper layer of the sward, and the problem of obtaining accurate data from the dense, litter-rich, lower layer of the sward (Grant, 1993). When using point quadrats some species will inevitably be missed, which introduces sampling error, and biases may occur due to differences in the spatial distribution of plant parts, especially if vertical point quadrats are used (Critchley and Poulton, 1998). There are a number of other problems associated with the use of point quadrats that meant they were unsuitable for this project:

1) The monitoring sites had slope angles of 10 - 25° and uneven ground surfaces, which made the use of a point quadrat frame difficult.

2) The high altitude (over 420 m) and exposed positions of the monitoring sites were subject to some degree of air movement even on the calmest day, resulting in movement of the foliage and instrument vibration.

These factors, which lead to a subjective element in deciding what constitutes a point contact, outweighed any benefits of using the point quadrat technique.

Large-scale changes in vegetation can be monitored using aerial photographs and ground checked vegetation maps (Anderson and Yalden, 1981), or by remote sensing (e.g. multi-temporal analysis of LANDSAT data (Jano *et al.*, 1998)). At present the limited sensitivity of these methods means that only major changes in vegetation boundaries can be detected with any degree of accuracy. In this project the vegetation types were visually very similar, boundaries were unclear and vegetation changes were likely to be subtle, and hence none of these techniques were suitable. Though a detailed vegetation map was produced at the start of the experiment (Chapter 3), the scale of mapping, the classification system used, and the degree of accuracy, particularly in regards to boundaries, meant that a re-survey using the same technique would not have been suitable for detecting change.

An assessment of the advantages and disadvantages of the various techniques indicated that the nested quadrat system, which optimises precision and scale, was the most appropriate monitoring method to use within this study.

4.4 Materials and methods

4.4.1 Study site

Descriptions of the stocking levels, past and present grazing management, and the vegetation and physical environment of the study site are given in Chapters 2 and 3.

4.4.2 Overview of the permanent quadrat methodology

The method, which is described in more detail later in the chapter, uses a rectangular block of thirty-two quadrats (in an 8 x 4 grid) known as a 'sample stand'. Each 1 m^2 quadrat, called a 'nest', is itself formed from a series of cells of increasing size, nested within each other (Critchley and Poulton, 1998). Plant species are recorded cumulatively within the series of cells (Critchley and Poulton, 1998).

4.4.3 Location of sample stands

Sample stands composed of thirty-two nested quadrats (Figure 4.1) were established within each enclosure on three community types: a *Nardus stricta*-dominated grassland (U5c *Nardus stricta* - *Galium saxatile* (*Carex panicea* - *Viola riviniana* sub-community)); a species-rich calcicolous grassland (CG10b *Festuca ovina* - *Agrostis capillaris* - *Thymus praecox* (*Carex pulicaris* - *Carex panicea* sub-community)); and a montane moss-heath (U10a *Carex bigelowii* - *Racomitrium lanuginosum* (*Galium saxatile* sub-community)). For each community type, a single sample stand was set up in each of the enclosures, giving a total of nine sample stands. The U5c community was chosen as it was one of the most abundant community types, occupying over 20 % of the study area, and was dominated by the three most abundant vascular plant species i.e.

Nardus stricta, *Festuca vivipara* and *Agrostis capillaris* (Chapter 3). The U5c sample stands were located within topographical Zone 3 (Chapter 3) between 400 and 450 m, and were established within extensive patches of the community type, away from patch edges. There were only five small patches of the CG10b community within the whole site, covering only 0.15 % of the study area (Chapter 3), and therefore the sample stands were located within the largest of these patches within each enclosure. The CG10b community was chosen because of its high species diversity (including a large number of herbaceous species), and dominance of the palatable grasses *Festuca vivipara* and *Agrostis capillaris*. The U10a community covers 2.4 % of the study area, mainly within topographical Zone 5 (Chapter 3). This community was sampled because of its spatial location on exposed sites, and the presence of montane sedges, dwarf shrubs and clubmosses, which were rare or absent from the other communities. The U10a sample stands were established above 600 m close to the summits of three exposed knolls. For all the communities a subjective visual assessment of the vegetation and the physical location (i.e. altitude, slope, aspect and exposure) was made to ensure that all three sample stands were comparable, however some variation in species composition and abundance was inevitable.

The sample stands were marked using lengths of copper piping hammered into the corners, and a wooden marker post was positioned 1 m to the north of the northeast corner. The quadrats within the sample stand were numbered 1 - 32 (Figure 4.1). The corner of the quadrat from which all the cells originate was always the northeast corner.

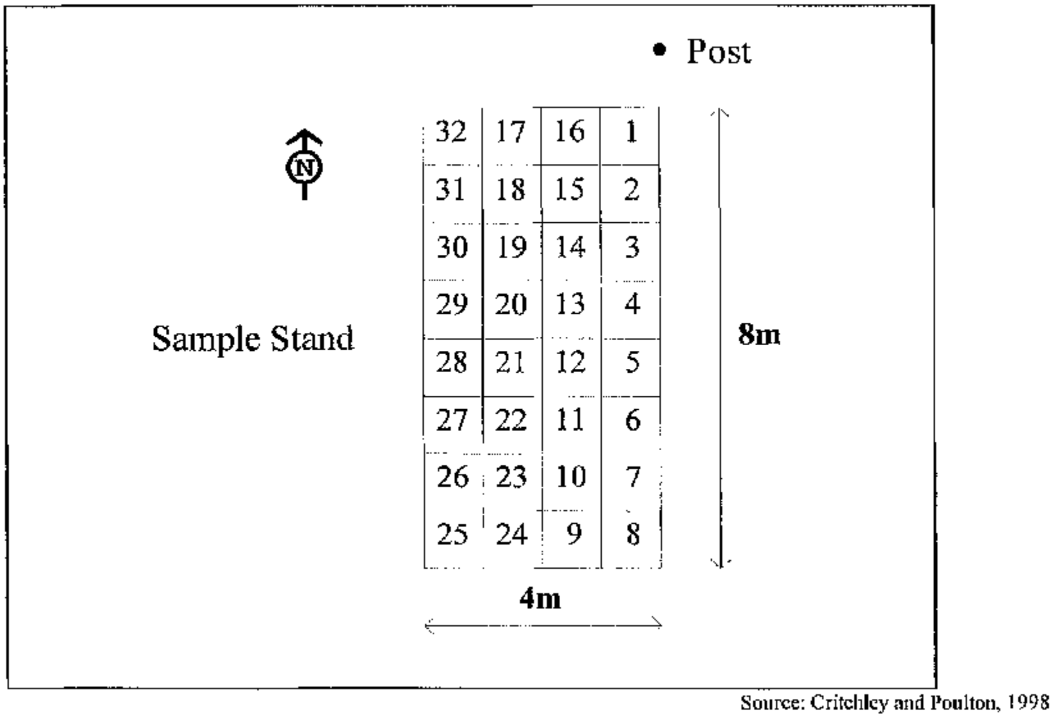


Figure 4.1 - Diagram of a sample stand

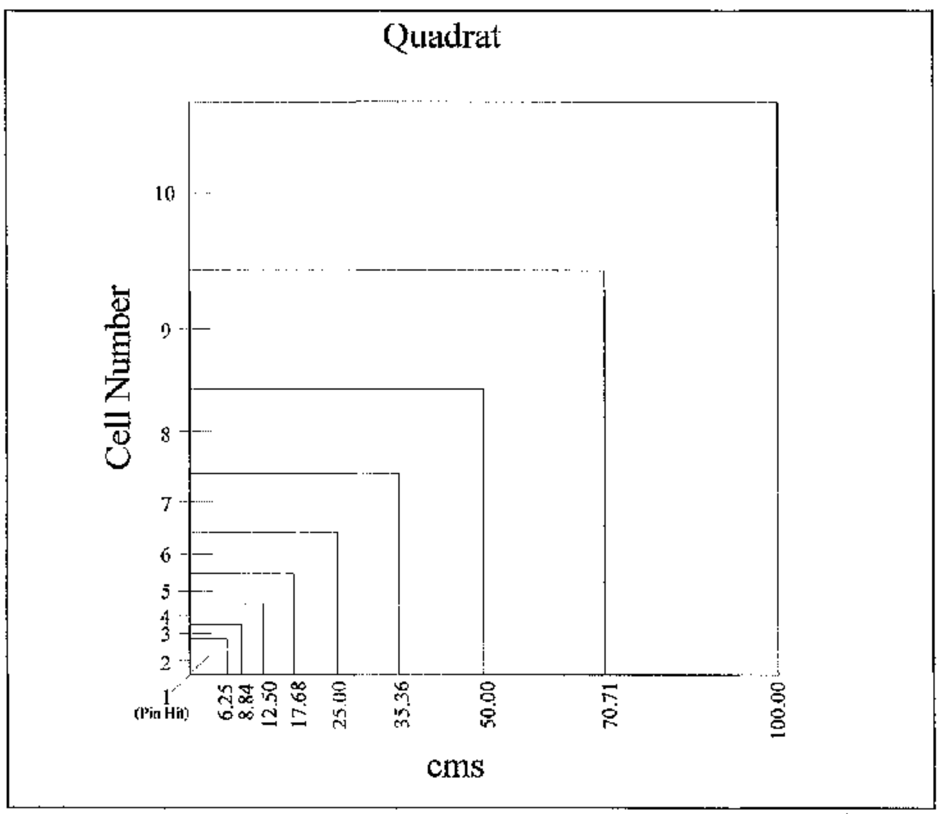
4.4.4 Soil analysis

Twenty soil sample cores (20 mm in diameter and 100 mm in length) were randomly taken from within each sample stand. The combined soil samples were analysed for pH, extractable phosphorus (mg l^{-1}), extractable potassium (mg l^{-1}), extractable magnesium (mg l^{-1}) and organic matter (loss on ignition (%)) using standard methods of analysis as recommended by the Agricultural Development and Advisory Service (MAFF, 1986).

4.4.5 Nested quadrat technique

Each 1 m^2 nested quadrat within a sample stand, is composed of a single pin hit and a series of 9 cells, each cell being twice the area of the preceding cell (Figure 4.2). The plant species hit by a single pin angled at 32.5° from the corner of the quadrat was recorded and allocated a value of 1. All rooted species found in the smallest cell (6.25

cm x 6.25 cm) were then recorded and allocated a value of 2. The presence of any additional species in each of the subsequent cells was recorded and given the appropriate cell value (3 - 10) (Figure 4.2). This provides a measure of the scale at which each species occurs within each quadrat. The methodology allows the whole nest to be searched systematically in a consistent and efficient manner (Critchley and Poulton, 1998). Since the whole of the sample stand is searched and therefore a complete census is carried out, there are no sampling errors and any changes detected over time are therefore real (within the constraints of observer error and accuracy of plot relocation) (Critchley and Poulton, 1998). All the monitoring was carried out by the author, who had extensive experience of using this technique, which minimised observer error.



Source: Critchley and Poulton, 1998

Figure 4.2 - Diagram of a nested quadrat

The lightweight quadrat, which could easily be dismantled, was made from two 1.0 m lengths of plastic tubing, a plastic connector piece, two fibreglass rods and two plastic rings (to which the fibreglass rods were attached and which could slide along the tubing) (Plate 4.1).

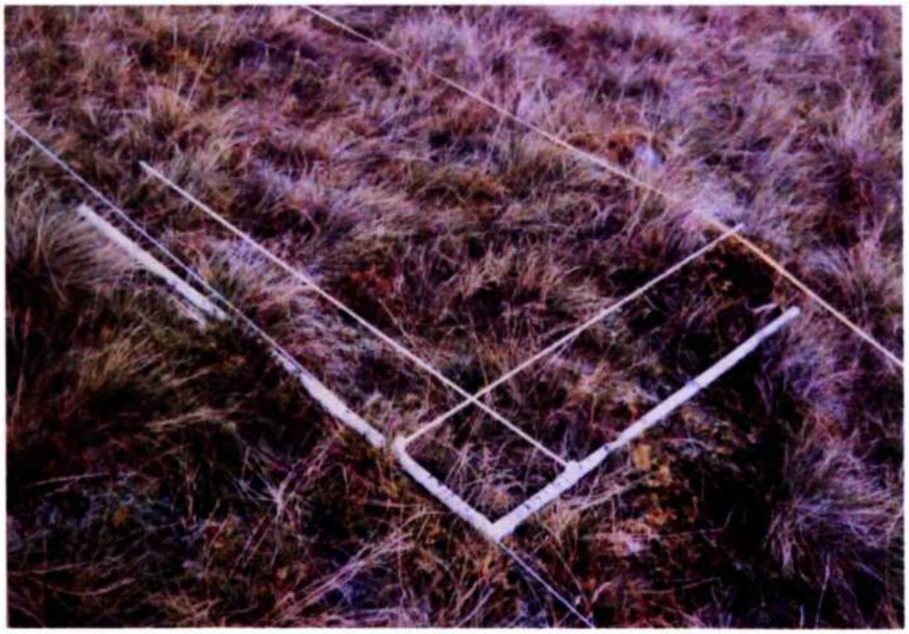


Plate 4.1 - Expanding, nested quadrat (1 m^2) set up at scale 6 (25 cm x 25 cm) being used on a **U5c** *Nardus stricta* - *Galium saxatile* (*Carex panicea* - *Viola riviniana*) grassland.

Because of time constraints it was only possible to carry out baseline monitoring of one of the communities in 1994 (i.e. the U5c community). Baseline monitoring of the other two communities was carried out in the summer of 1995 (Table 4.1). All three communities were resurveyed in the summer of 1998. The monitoring was carried out between the beginning of June and the middle of September (Table 4.1).

Plant nomenclature followed Stace (1991).

Table 4.1 - Nested quadrat monitoring dates

Enclosure	NVC Type	Date of Baseline Monitoring	Date of Second Survey
1	U5c	01/09/94	16/06/98
2	U5c	13/09/94	17/06/98
3	U5c	30/08/94	09/07/98
1	CG10b	31/07/95	10/09/98
2	CG10b	04/08/95	25/08/98
3	CG10b	15/09/95	02/09/98
1	U10a	28/06/95	03/06/98
2	U10a	30/06/95	04/06/98
3	U10a	07/07/95	08/06/98

4.4.6 SWARD SURFACE HEIGHT MEASUREMENTS

Random sward surface height measurements were taken from three of the most abundant plant communities: a U5c *Nardus stricta - Galium saxatile* (*Carex panicea - Viola riviniana*) grassland; a U5b *Nardus stricta - Galium saxatile* (*Agrostis canina - Polytrichum commune*) grassland; and an M6d *Carex echinata - Sphagnum recurvum* (*Juncus acutiflorus*) mire. These three communities cover 65 % of the study site area (Chapter 3). The sward heights of the CG10b and U10a communities were not measured because of their limited cover and distribution. The sampling areas were subjectively chosen to be both extensive and homogeneous, with similar species compositions and altitudinal ranges across the three enclosures. For each community three sampling areas were chosen within each enclosure. The U5c sampling areas were within topographical Zone 3 between 400 - 450 m (Chapter 3). The U5b sampling areas were within topographical Zone 4 between 450 - 520 m, and the M6d sampling areas were within topographical Zone 2 between 360 - 400 m (Chapter 3). Within each sampling area random sward height measurements were taken at monthly intervals, using a Hill Farming Research Organisation (HFRO) sward stick (Bircham, 1981). The HFRO sward stick is a rapid, easy to use, objective means of measuring sward surface height (Barthram, 1986). It is composed of a small, transparent plastic tongue, which is attached to an outer metal sleeve that slides up and down over an inner graduated metal rod (Barthram, 1986). Readings are taken by placing the base of the rod on the ground and lowering the sleeve until the base of the plastic tongue makes contact with any part of a leaf lamina or flower stalk, and the height is then read off on the scale (Barthram, 1986). Records were made of the plant species with which the sward stick connected, its height and whether the tissue was live or dead.

The sward heights of the two *Nardus stricta* dominated communities (U5c and U5b) were measured in all three enclosures at monthly intervals from May 1994 to December 1998 (Table 4.2). Because of time constraints the sward height of the M6d community was not measured in 1994, however measurements were taken in all enclosures from May 1995 to October 1998. Due to the height of the M6d community a modified sward stick made from plastic tubing, with a sliding platform, was used to allow measurements up to 1.0m in height. Snow cover and hard frosts prevented measurements being taken in some winter months, notably January (Table 4.2).

The number of measurements required to give a stable estimate of sward surface height was determined by plotting cumulative mean sward height against the number of measurements for each community from a total of 120 measurements taken in June 1994 for the U5c and U5b communities and June 1995 for the M6d community (Mueller-Dombois and Ellenberg, 1974) (Figure 4.3). This indicated that a total of 90 measurements per enclosure (i.e. 30 measurements per sampling area) were required for each of the three communities.

Table 4.2 - Sward height sampling dates

NVC	Year	Date of Sward Height Measurement											
		Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sep	Oct	Nov	Dec
U5c	1994					18	15	15	10	8	5	3	1
	1995		8		18	18	16	12	1	7	11	14	12
	1996			5	3	3	6	8	7	4	4		
	1997				8	14	16	17	12	30	23		
	1998		3	31	29		1	6	17		2, 30		9
U5b	1994					18	15	13	10	7	5	2	1
	1995		9		18	19	15	12	9	5	9	10	11
	1996			4	2	2	5	8	5	2	1		
	1997				11	14	16	17	14	30	23		
	1998		3	31	29		1	6	17		2, 30		9
M6d	1995					18	19	26	22	21		9	7
	1996			12	11	15	25	30	28	27	29		
	1997				11	14	16		14	30	23		
	1998						1	6	18		2		
H12	1998				6								
M19	1998				6								

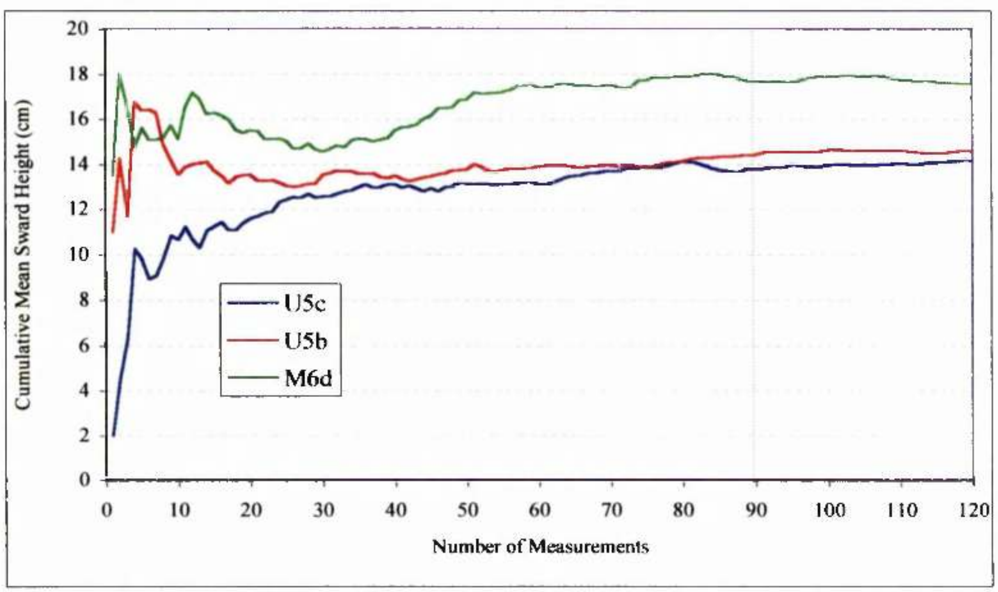


Figure 4.3 - Cumulative mean sward height of the U5c and U5b communities in June 1994 and the M6d community in June 1995, which indicates that 90 sward surface height measurements were required in order to achieve a steady mean

4.4.7 *CALLUNA VULGARIS* HEIGHT MEASUREMENTS

Random *Calluna vulgaris* height measurements were taken in April 1998, from two communities, an M19 *Calluna vulgaris* - *Eriophorum vaginatum* blanket mire and a H12 *Calluna vulgaris* - *Vaccinium myrtillus* heath, using a HFRO sward stick (Barthram, 1986). The distribution of the two communities was determined from the vegetation map (Chapter 3, Figure 3.15), and the sampling areas were randomly chosen from within topographical Zone 5 above 600 m (Chapter 3). One hundred *Calluna vulgaris* height measurements were taken from each community within each enclosure.

4.4.8 SUMMER SPECIES COVER

The species data collected when measuring the sward surface heights was used to estimate the percentage cover of the main species or species groups during the summers of 1994 to 1998 for the U5c and U5b communities, and during the summers of 1995 to 1998 for the M6d community. The percentage of sward stick contacts was used as an estimate of the percentage cover. Cover percentage values for the main species or species groups for each sampling area and for each of the summer months (July, August and September) were calculated, giving a total of 9 values per community per enclosure per year.

4.4.9 Statistical analysis

4.4.9.1 *Permanent nested quadrats*

In the field, the species and scale data were recorded for each consecutive quadrat within the sample stand of 32 nested quadrats (Appendix 4.1). For the purposes of analysis the quadrat data was transferred into a two-dimensional matrix of species x scale, in which the matrix components were the number of nests in which each species was recorded at each scale (Appendix 4.2) (Critchley and Poulton, 1998). In order to detect changes in the abundance of a species it is necessary to choose the most appropriate scale, which is called the 'optimum scale' (Critchley and Poulton, 1998). Critchley and Poulton (1998) define this as "the scale, which is most sensitive for detecting change *a priori*, in either direction". The optimum scale is the one for which the frequency count is closest to its mid-point value (i.e. 16 which is the mid-point between 1 and 32), and in situations in which there is a tie, it is the one nearest the mid-scale within the cell range (i.e. 5 which is the mid-scale within the range 1 to 10) (Critchley and Poulton, 1998). The optimum scale for each species within each sample stand was set in the baseline year.

Changes in the frequency of each species at each scale were calculated for each sample stand by subtracting the baseline data (1994/1995) from the 1998 data (Appendix 4.3). Two summary statistics were calculated which allow an overall comparison to be made between the performance of the optimum scale and any single scale. The first, which is a measure of the overall sensitivity to change, is the sum of the absolute changes in frequency (Critchley and Poulton, 1998). The higher the value the greater the sensitivity. The second statistic, known as the 'blindness', is the number of species at each scale that showed no change in frequency, excluding any species that showed no change at any scale (Critchley and Poulton, 1998).

Major changes were considered to be those in which there was an increase or decrease in the frequency of a species of three or more at the optimum scale.

4.4.9.2 *Sward heights*

Since the data on sward surface height was unbalanced within and between treatments and had missing values, a variance-component model was fitted by Residual Maximum Likelihood (REML) to calculate means and standard errors of difference (SED) (Genstat 5 Committee, 1993). The Wald test, which has a Chi squared distribution, was used to test the fixed effects and interactions of treatment, year and season on sward surface height of each of the communities (Buist and Engel, 1993). Tests for statistically significant differences between values were made by subtracting one value from another and dividing the result by the standard error of difference produced by REML. This is comparable to the least significant difference test (Snedecor and Cochran, 1980).

4.4.9.3 *Species cover*

The percentage cover values did not have a normal distribution and therefore they were arcsine transformed (Fowler and Cohen, 1990). Means and standard errors of difference were calculated using REML (Genstat 5 Committee, 1993). The Wald test was used to test main effects of treatment and year on cover percentage of individual species or species groups within each of the communities (Buist and Engel, 1993).

4.5 Results

4.5.1 PERMANENT NESTED QUADRATS

4.5.1.1 *Species change within the U5c sample stands*

A total of thirty-nine vascular plant species were recorded within the sample stand in Enclosure 1 compared with thirty-seven species in Enclosure 2 and only twenty-two species in Enclosure 3. This difference in species number was coupled with a higher soil pH, and lower soil phosphorus, potassium, magnesium and organic matter content (Table 4.3).

Table 4.3 - Altitude and soil properties of the U5c quadrat sample stands

Enclosure Number	NVC Type	Altitude (metres)	Soil pH	Extractable Phosphorus mg l^{-1}	Extractable Potassium mg l^{-1}	Extractable Magnesium mg l^{-1}	Organic Matter (loss on ignition) %	Number of Vascular Plant Species
1	U5c	515	4.7	1.4	101	50	19.6	39
2	U5c	470	4.2	2.3	105	71	26.3	37
3	U5c	425	4.0	2.8	128	78	31.6	22

Over the monitoring period none of the sample stands changed in species composition to such an extent that they changed their vegetation type. They all remained dominated by the perennial grasses *Nardus stricta*, *Agrostis capillaris* and *Festuca ovina/vivipara*, which occurred in all ninety-six quadrats in both monitoring years (see Appendix 4.1). These three species together with *Galium saxatile*, had optimum scales of three or less in all three sample stands, while between 41 % (Enclosure 3) and 70 % (Enclosure 2) of species had an optimum scale of ten. This indicates that the community was composed of a small number of very abundant key species, and a large number of scarce species. In all three sample stands, the optimum scale showed more sensitivity and less blindness than any individual scale (Table 4.4 and Appendix 4.3).

Table 4.4 - A comparison of the total absolute change (sensitivity) at each individual scale with the total absolute change at the optimum scale (U5c).

U5c Sample Stands		Scale										
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Optimum**
Enclosure 1	Total absolute change (sensitivity)	11	52	76	78	88	80	79	85	79	77	**95**
	No. of species showing no change (blindness)	31	20	18	16	11	14	12	15	11	13	**9**
Enclosure 2	Total absolute change (sensitivity)	17	36	47	54	53	40	49	50	48	48	**63**
	No. of species showing no change (blindness)	26	16	17	14	12	17	12	11	10	13	**6**
Enclosure 3	Total absolute change (sensitivity)	18	31	29	30	29	24	26	24	29	20	**46**
	No. of species showing no change (blindness)	10	8	7	7	8	8	8	10	7	10	**3**

The sample stand within Enclosure 1 showed the greatest overall species change, with the highest total absolute change in frequency at optimum scale and the highest number of species showing a frequency increase or decrease of 3 or more at the optimum scale (Table 4.5).

There was some variation in the response of individual species to the three treatments (Table 4.5). Some species showed little or no change in response to any of the three treatments (e.g. *Nardus stricta*, *Carex binervis* and *Juncus squarrosus*), others showed similar changes across two or more of the treatments (e.g. *Carex nigra* and *Luzula multiflora*), whilst some responded differently to all three treatments (e.g. *Carex panicea*) (Tables 4.5 and 4.6).

Table 4.5 - A comparison of the change in frequency values at the optimum scale between the three enclosures
U5c *Nardus stricta - Galium saxatile* grassland (*Carex panicea - Viola riviniana* sub-community)

Species	Enclosure 1 (0.074 LU / ha)				Enclosure 2 (0.051 LU / ha)				Enclosure 3 (0.096 LU / ha)			
	Optimum Scale (set in 1994)	Frequency at Optimum Scale 1994	Frequency at Optimum Scale 1998	Change in Frequency	Optimum Scale (set in 1994)	Frequency at Optimum Scale 1994	Frequency at Optimum Scale 1998	Change in Frequency	Optimum Scale (set in 1994)	Frequency at Optimum Scale 1994	Frequency at Optimum Scale 1998	Change in Frequency
Agrostis capillaris	1	12	12	**0**	2	18	22	4	2	26	27	**1**
Anthoxanthum odoratum	2	16	18	**2**	4	16	12	-4	6	15	12	-3
Danthonia decumbens									9	15	13	**-2**
Deschampsia cespitosa	9	18	24	6								
Deschampsia flexuosa	10	1	0	-1	10	0	1	1	9	16	18	2
Festuca ovina/vivipara	2	19	17	-2	2	18	19	1	2	23	29	6
Festuca rubra	9	15	15	**0**								
Molinia caerulea					10	9	10	1	10	1	0	-1
Nardus stricta	2	12	12	**0**	2	20	18	-2	2	14	16	2
Carex binervis	5	16	18	**2**	6	18	20	2	10	9	11	2
Carex viridula ssp. *oedocarpa*	10	6	6	**0**	10	2	2	**0**				
Carex echinata					10	11	6	-5				
Carex hostiana					10	1	0	-1				
Carex nigra	10	14	19	5	9	20	24	4	6	16	13	-3
Carex pallescens	10	5	4	-1								
Carex panicea	4	16	12	-4	10	25	23	-2	5	16	19	3
Carex pilulifera	7	17	19	**2**	8	16	16	**0**	2	17	11	-6
Carex pulicaris	9	15	14	-1	10	3	6	3				
Eriophorum angustifolium					10	10	11	1				
Trichophorum cespitosum	10	6	4	-2	8	15	16	1	7	14	14	**0**
Juncus bulbosus					10	2	0	-2				
Juncus effusus					10	4	3	-1				
Juncus squarrosus	10	5	4	-1	10	15	15	**0**	10	9	9	**0**
Luzula multiflora	9	13	22	9	10	9	18	9	6	17	21	4
Sorbus aucuparia					10	0	1	1	10	1	2	**1**
Vaccinium myrtillus	10	2	2	**0**	10	14	14	**0**	10	17	20	3

Species	Enclosure 1 (0.074 LU / ha)				Enclosure 2 (0.051 LU / ha)				Enclosure 3 (0.096 LU / ha)			
	Optimum Scale (set in 1994)	Frequency at Optimum Scale 1994	Frequency at Optimum Scale 1998	**Change in Frequency**	Optimum Scale (set in 1994)	Frequency at Optimum Scale 1994	Frequency at Optimum Scale 1998	**Change in Frequency**	Optimum Scale (set in 1994)	Frequency at Optimum Scale 1994	Frequency at Optimum Scale 1998	**Change in Frequency**
Euphrasia officinalis agg.	10	4	2	**-2**	10	1	0	**-1**				
Alchemilla alpina	10	0	1	**1**								
Alchemilla glabra	10	5	5	**0**								
Anemone nemorosa	10	8	32	24					10	2	4	**2**
Campanula rotundifolia	10	6	7	**1**								
Cerastium fontanum	10	5	5	**0**								
Crepis paludosa					10	0	2	**2**				
Galium saxatile	3	17	21	**4**	2	16	15	**-1**	2	29	27	**-2**
Leontodon autumnalis	10	3	4	**1**	10	9	12	**3**				
Narthecium ossifragum	10	0	2	**2**	10	15	16	**1**	10	13	13	**0**
Oxalis acetosella	7	4	2	**-2**								
Pinguicula vulgaris	10	3	0	**-3**	10	0	2	**2**				
Plantago lanceolata	10	8	5	**-3**	10	1	1	**0**				
Persicaria vivipara	10	15	15	**0**								
Potentilla erecta	6	17	14	**-3**	3	14	13	**-1**	3	15	17	**2**
Prunella vulgaris	10	1	0	**-1**	10	1	0	**-1**				
Ranunculus acris	7	17	17	**0**	10	6	8	**2**				
Rumex acetosa	10	2	3	**1**								
Thymus polytrichus	10	0	1	**1**								
Veronica officinalis	10	0	1	**1**								
Viola spp.	3	15	16	**1**	6	16	17	**1**	10	1	1	**0**
Blechnum spicant					10	1	1	**0**	10	1	2	**1**
Oreopteris limbosperma					10	1	1	**0**				
Selaginella selaginoides	10	3	3	**0**	10	5	2	**-3**				
Sphagnum spp.					10	15	15	**0**				
Bare Soil	10	0	6	**6**								
Total absolute change				95				63				46
No. of species showing no change				9				6				3
No. of species showing a change in frequency of 3 or more				10				8				7

Note - Species have been blocked together into six groupings; grasses, sedges, rushes, dwarf shrubs, forbs, and ferns, clubmosses and *Sphagnum*
Increases in frequency at the optimum scale of 3 or more are marked in blue, decreases in frequency at the optimum scale of 3 or more are marked in red

Only two species increased at their optimum scale under all three treatments, *Luzula multiflora* and *Carex binervis*, of which only *Luzula multiflora* increased in frequency by three or more within all three sample stands. *Anemone nemorosa* showed the largest change in abundance of any species, appearing in an additional twenty-four quadrats within Enclosure 1. No species declined in all three sample stands.

Table 4.6 - Key changes in species frequency within the U5c community

	Species Frequency	
	Increase in frequency of 3 or more	**Decrease** in frequency of 3 or more
Enclosure 1 only (high sheep)	Bare soil *Deschampsia cespitosa** *Anemone nemorosa* *Galium saxatile*	*Potentilla erecta* *Plantago lanceolata* *Carex panicea* *Pinguicula vulgaris*
Enclosure 2 only (low sheep)	*Agrostis capillaris* *Carex pulicaris* *Leontodon autumnalis*	*Carex echinata** *Selaginella selaginoides*
Enclosures 1 and **2** (high and low sheep)	*Carex nigra*	
Enclosure 3 only (low sheep plus summer cattle)	*Carex panicea* *Festuca ovina* *Vaccinium myrtillus*	*Carex nigra* *Carex pilulifera*
Enclosures 1 and 3 (high sheep and low sheep plus summer cattle)		
Enclosures 2 and 3 (low sheep and low sheep plus summer cattle)		*Anthoxanthum odoratum*
Enclosures 1, 2 and 3 All Treatments	*Luzula multiflora*	

* species only recorded in one sample stand

Though some species were lost from the sample stands and others appeared, none of the species in either of theses categories were recorded in more than three of the thirty-two quadrats within each sample stand, and most of these gains or losses involved individual plants (Table 4.7).

Table 4.7 - New species gained and species lost from the U5c sample stands

Sample Stand	Additional species recorded in the sample stands in 1998	Species lost from the sample stands between 1994 and 1998
Enclosure 1	*Alchemilla alpina* *Narthecium ossifragum* *Thymus polytrichus* *Veronica officinalis*	*Deschampsia flexuosa* *Pinguicula vulgaris* *Prunella vulgaris*
Enclosure 2	*Deschampsia flexuosa* *Sorbus aucuparia* *Crepis paludosa* *Pinguicula vulgaris*	*Carex hostiana* *Juncus bulbosus* *Euphrasia officinalis* *Prunella vulgaris*
Enclosure 3		*Molinia caerulea*

4.5.1.2 *Species change within the CG10b sample stands*

The sample stand in Enclosure 1, which had the highest soil pH, contained the highest number of species (Table 4.8).

Table 4.8 - Altitude and soil properties of the CG10b quadrat sample stands

Enclosure Number	NVC Type	Altitude (metres)	Soil pH	Extractable Phosphorus mg l^{-1}	Extractable Potassium mg l^{-1}	Extractable Magnesium mg l^{-1}	Organic Matter (loss on ignition) %	Number of Vascular Plant Species
1	CG10b	495	5.2	1.8	82	91	12.8	49
2	CG10b	465	4.7	2.7	130	87	24.7	39
3	CG10b	432	4.7	1.6	96	46	12.2	44

In all three sample stands, the optimum scale showed more sensitivity and less blindness than any individual scale (Tables 4.9 and Appendix 4.3).

Table 4.9 - A comparison of the total absolute change (sensitivity) at each individual scale with the total absolute change at the optimum scale (CG10b).

CG10b Sample Stands		**Scale**										
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Optimum**
Enclosure 1	Total absolute change (sensitivity)	18	54	50	65	59	64	74	72	81	91	**99**
	No. of species showing no change (blindness)	34	18	18	18	16	21	14	16	12	12	**9**
Enclosure 2	Total absolute change (sensitivity)	14	48	41	38	52	54	53	68	69	74	**100**
	No. of species showing no change (blindness)	29	21	17	17	16	11	12	11	10	11	**4**
Enclosure 3	Total absolute change (sensitivity)	23	58	61	79	76	82	98	111	127	150	**181**
	No. of species showing no change (blindness)	32	18	17	17	20	19	16	14	9	11	**5**

Table 4.10 - A comparison of the change in frequency values at the optimum scale between the three enclosures

CG10b *Festuca ovina -Agrostis capillaris -Thymus praecox* grassland (*Carex pulicaris -Carex panicea* sub-community)

Species	Enclosure 1 (0.074 LU / ha)				Enclosure 2 (0.051 LU / ha)				Enclosure 3 (0.096 LU / ha)			
	Optimum Scale (set in 1995)	Frequency at Optimum Scale 1995	Frequency at Optimum Scale 1998	Change in Frequency	Optimum Scale (set in 1995)	Frequency at Optimum Scale 1995	Frequency at Optimum Scale 1998	Change in Frequency	Optimum Scale (set in 1995)	Frequency at Optimum Scale 1995	Frequency at Optimum Scale 1998	Change in Frequency
Agrostis capillaris	2	27	25	-2	2	22	28	6	1	13	4	-9
Anthoxanthum odoratum	2	13	14	1	3	15	13	-2	3	16	22	6
Danthonia decumbens	10	5	12	7	10	9	7	-2	10	10	22	12
Deschampsia cespitosa					10	1	2	1	10	2	5	3
Deschampsia flexuosa					10	7	10	3				
Festuca ovina/vivipara	1	8	12	4	1	12	7	-5	2	28	27	-1
Festuca rubra	10	16	25	9	10	2	14	12	10	6	26	20
Helictotrichon pratense									10	1	1	0
Holcus lanatus									10	1	8	7
Nardus stricta	5	15	14	-1	5	14	14	0	3	13	12	-1
Carex bigelowii	10	1	2	1								
Carex binervis	10	2	2	0	10	3	3	0	10	8	11	3
Carex capillaris	10	2	3	1								
Carex viridula ssp. *oedocarpa*	10	6	8	2	10	3	4	1	10	9	11	2
Carex flacca									10	1	0	-1
Carex nigra									10	0	1	1
Carex pallescens					10	1	3	2	10	0	5	5
Carex panicea	8	16	14	-2	8	16	17	1	6	16	16	0
Carex pilulifera	5	15	9	6	6	16	17	1	4	13	12	-1
Carex pulicaris	10	17	16	-1	10	11	10	-1	10	18	22	4
Trichophorum cespitosum	10	1	1	0								
Juncus bulbosus	10	1	0	-1								
Luzula multiflora	5	14	15	1	7	15	12	-3	8	17	26	9
Betula pubescens	10	0	1	1								
Sorbus aucuparia					10	0	2	2				
Vaccinium myrtillus	10	1	1	0	4	16	14	-2	10	0	1	1
Blechnum spicant					10	8	8	0				
Diphasiastrum alpinum	10	2	3	1								
Huperzia selago					10	0	2	2				
Oreopteris limbosperma	10	1	1	0	10	9	7	-2				
Phegopteris connectilis					10	3	4	1				
Selaginella selaginoides	10	11	13	2	10	15	21	6	10	1	1	0

Species	Enclosure 1 (0.074 LU / ha)				Enclosure 2 (0.051 LU / ha)				Enclosure 3 (0.096 LU / ha)			
	Optimum Scale	Frequency at Optimum Scale		Change in	Optimum Scale	Frequency at Optimum Scale		Change in	Optimum Scale	Frequency at Optimum Scale		Change in
	(set in 1995)	1995	1998	Frequency	(set in 1995)	1995	1998	Frequency	(set in 1995)	1995	1998	Frequency
Achillea ptarmica	7	15	8	-7					10	10	15	5
Alchemilla alpina	10	13	13	0	2	19	15	-4	10	3	3	0
Alchemilla glabra	10	14	15	1	10	2	2	0	10	13	15	2
Anemone nemorosa					9	16	6	-10	10	1	2	1
Bellis perennis	10	10	13	3					9	16	20	4
Campanula rotundifolia	9	16	16	0	5	16	11	-5	5	15	10	-5
Cerastium fontanum	10	6	8	2	10	0	1	1	10	7	14	7
Euphrasia officinalis agg.	10	15	20	5	9	14	12	-2	10	18	27	9
Galium saxatile	2	25	26	1	2	21	23	2	2	23	22	-1
Hieracium sp.									10	1	0	-1
Linum catharticum	10	7	11	4								
Lysimachia nemorum									10	1	1	0
Narthecium ossifragum					10	7	8	1				
Oxalis acetosella					10	5	6	1	10	5	5	0
Parnassia palustris	10	0	2	2								
Pinguicula vulgaris	10	2	0	-2					10	0	1	1
Plantago lanceolata	8	15	15	0	7	15	17	2	4	15	16	1
Polygala serpyllifolia					10	6	4	-2	10	2	0	-2
Persicaria vivipara	4	14	13	-1	10	17	19	2	5	17	16	-1
Potentilla erecta	5	17	19	2	4	17	12	-5	10	16	23	7
Prunella vulgaris	10	12	19	7	10	2	5	3	8	18	15	-3
Ranunculus acris	5	17	17	0	8	16	19	3	2	20	23	3
Ranunculus repens	10	13	13	0								
Rumex acetosa	10	2	1	-1								
Saxifraga aizoides	10	3	4	1								
Saxifraga oppositifolia	10	2	4	2								
Silene acaulis	10	4	4	0								
Taraxacum agg.	10	2	6	4					10	0	1	1
Thalictrum alpinum	10	7	9	2								
Thymus polytrichus	5	16	18	2	5	16	17	1	2	15	16	1
Trifolium repens	6	16	15	-1					4	14	20	6
Veronica officinalis	10	14	18	4					10	6	7	1
Viola spp.	4	17	19	2	7	17	16	-1	5	17	13	-4
Bare Soil									10	0	29	29
Total absolute change				99				100				181
No. of species showing no change				9				4				5
No. of species showing a change in frequency of 3 or more				11				12				20

Note - Species have been blocked together into six groupings; grasses, sedges, rushes, dwarf shrubs, ferns and clubmosses, and forbs

Increases in frequency at the optimum scale of 3 or more are marked in blue, decreases in frequency at the optimum scale of 3 or more are marked in red

The sample stand within Enclosure 3 showed the largest change in species abundance of the three enclosures, with the highest total absolute change in frequency at optimum scale and the highest number of species showing a frequency change of three or more at the optimum scale (Table 4.10). In all three sample stands, more species showed an increase in frequency (of one or more) at optimum scale than a decrease (Table 4.10).

The perennial grass *Festuca rubra* was the only species to increase in all three sample stands (Tables 4.10). It also had the largest increases in frequency at optimum scale of any species in all three sample stands (Table 4.10). The greatest change recorded within any sample stand was the increase in the amount of bare ground within Enclosure 3.

A number of low growing perennial and annual forbs, including grazing tolerant ruderal species, increased under the higher grazing regimes of Enclosures 1 and/or 3 (Table 4.10 and 4.11). Of the relatively few species which declined, the most obvious at all scales within both Enclosure 2 and 3 was *Campanula rotundifolia*, a species whose diminutive shade tolerant leaves are easily overlooked.

After three years all three sample stands were still classified as CG10b, although the two enclosures subject to the higher stocking rates (in particular the enclosure grazed by both sheep and cattle) showed clear increases in grazing tolerant ruderal species.

Table 4.11 - Key changes in species frequency within the CG10b community

	Species Frequency	
	Increase of 3 or more at the optimum scale	**Decrease** of 3 or more at the optimum scale
Enclosure 1 only (high sheep)	*Festuca ovina / vivipara* *Linum catharticum** *Taraxacum* spp. *Veronica officinalis*	*Carex pilulifera* *Achillea ptarmica*
Enclosure 2 only (low sheep)	*Agrostis capillaris* *Selaginella selaginoides* *Deschampsia flexuosa**	*Festuca ovina / vivipara* *Luzula multiflora* *Alchemilla alpina* *Anemone nemorosa* *Potentilla erecta*
Enclosure 3 only (low sheep plus summer cattle)	*Anthoxanthum odoratum* *Deschampsia cespitosa* *Holcus lanatus** *Carex palescens* *Carex pulicaris* *Carex binervis* *Luzula multiflora* *Achillea ptarmica* *Cerastium fontanum* *Potentilla erecta* *Trifolium repens* Bare Soil	*Agrostis capillaris* *Prunella vulgaris* *Viola* spp.
Enclosure 1 and **2** (high and low sheep)	*Prunella vulgaris*	
Enclosure 1 and **3** (high sheep and low sheep plus summer cattle)	*Danthonia decumbens* *Bellis perennis* *Euphrasia officinalis*	
Enclosure 2 and **3** (low sheep and low sheep plus summer cattle)	*Ranunculus acris*	*Campanula rotundifolia*
Enclosure 1, 2 and 3 All Treatments	*Festuca rubra*	

* species only recorded in one sample stand

4.5.1.3 *Species change within the U10a sample stands*

The three sample stands had shallow, poorly developed soils with similar pH's, nutrient levels and organic matter contents (Table 4.12). The number of vascular plant species found in the U10a sample stands ranged from nineteen in Enclosure 2, to twenty-three in Enclosure 3 (Table 4.12). Fifteen species were found in all three sample stands.

Table 4.12 - Altitude and soil properties of the U10a quadrat sample stands

Enclosure Number	NVC Type	Altitude (metres)	Soil pH	Extractable Phosphorus mg l^{-1}	Extractable Potassium mg l^{-1}	Extractable Magnesium mg l^{-1}	Organic Matter (loss on ignition) %	Number of Vascular Plant Species
1	U10a	665	4.4	2.4	96	56	24.9	21
2	U10a	655	4.3	2.4	94	57	21.6	19
3	U10a	612	4.3	3.7	129	56	25.0	23

In all three sample stands, the optimum scale showed more sensitivity than any individual scale (Tables 4.13). The optimum scale in Enclosure 3 did not however have the lowest blindness value (Table 4.13). The sample stands within Enclosures 2 and 3 had higher values of total absolute change in frequency at optimum scale than Enclosure 1 (Table 4.13). In Enclosure 1 only one species (*Carex binervis*) showed a decrease in frequency of three or more at optimum scale compared with five species in Enclosure 2 and six species in Enclosure 3 (Table 4.14). Enclosure 1 had the highest number of species to show an increase in frequency of three or more at optimum scale (Table 4.14). The changes in species frequency that occurred during the monitoring period were not large enough to result in a change in the NVC community type of any of the sample stands.

Table 4.13 - A comparison of the total absolute change (sensitivity) at each individual scale with the total absolute change at the optimum scale (U10a).

U10a Sample Stands		Scale										
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Optimum**
Enclosure 1	Total absolute change (sensitivity)	15	34	29	35	29	29	27	18	20	25	**48**
	No. of species showing no change (blindness)	14	6	10	9	10	10	9	12	11	11	**5**
Enclosure 2	Total absolute change (sensitivity)	16	45	39	31	35	23	30	33	23	29	**62**
	No. of species showing no change (blindness)	10	8	4	7	4	9	6	7	12	10	**3**
Enclosure 3	Total absolute change (sensitivity)	17	42	39	37	42	42	44	42	41	47	**60**
	No. of species showing no change (blindness)	15	8	5	6	7	6	4	2	5	7	**4**

All three sample stands showed increases in the perennial grass *Deschampsia flexuosa* and this was greatest in the enclosure with the lowest stocking rate (Enclosure 2) (Table 4.14). *Campanula rotundifolia* showed the largest increase of any species under the lower stocking rate of Enclosure 2. There was some variation in the response of individual species to the three treatments (Tables 4.14 and 4.15). *Potentilla erecta*, *Salix herbacea* and *Vaccinium myrtillus* showed little or no change in frequency in response to any of the three treatments, whereas some species showed similar changes across two or more of the treatments, and others responded differently to all three treatments (Table 4.15).

Table 4.14 - A comparison of the change in frequency values at the optimum scale between the three enclosures
U10a *Carex bigelowii -Racomitrium lanuginosum* moss-heath (*Galium saxatile* sub-community)

	Enclosure 1 (0.074 LU / ha)				Enclosure 2 (0.051 LU / ha)				Enclosure 3 (0.096 LU / ha)			
	Optimum Scale	Frequency at Optimum Scale		Change in	Optimum Scale	Frequency at Optimum Scale		Change in	Optimum Scale	Frequency at Optimum Scale		Change in
Species	(set in 1995)	1995	1998	**Frequency**	(set in 1995)	1995	1998	**Frequency**	(set in 1995)	1995	1998	**Frequency**
Agrostis capillaris & A. vinealis	2	24	27	3	2	26	20	-6	1	15	10	-5
Anthoxanthum odoratum	7	15	20	5	8	17	13	-4	7	14	15	1
Deschampsia flexuosa	7	15	20	5	6	14	22	8	10	11	15	4
Festuca ovina/vivipara	2	23	24	1	2	21	20	-1	2	19	22	3
Nardus stricta	4	14	15	1	8	17	20	3	9	16	16	0
Carex bigelowii	10	11	14	3	4	17	15	-2	4	19	18	-1
Carex binervis	10	9	2	-7								
Carex panicea									10	11	15	4
Carex pilulifera	4	16	17	1	6	15	16	1	4	17	13	-4
Trichophorum cespitosum									10	0	2	2
Juncus squarrosus	10	7	7	0					10	10	11	1
Luzula multiflora	8	16	17	1	10	17	13	-4	10	9	6	-3
Alchemilla alpina	9	16	14	-2	5	19	18	-1	5	16	15	-1
Campanula rotundifolia	10	7	8	1	10	4	13	9				
Cerastium fontanum									10	3	0	-3
Euphrasia officinalis agg.					10	1	0	-1	10	7	1	-6
Galium saxatile	2	18	24	6	2	26	15	-11	2	17	19	2
Potentilla erecta	10	13	12	-1	10	2	2	0	10	14	14	0
Viola palustris	10	0	2	2								
Viola riviniana	10	1	0	-1								
Empetrum nigrum	10	14	14	0	9	16	16	0	10	15	19	4
Salix herbacea	10	3	3	0	10	11	10	-1	9	17	18	1
Sorbus aucuparia									10	1	3	2
Vaccinium myrtillus	2	28	28	0	2	23	24	1	5	17	19	2
Vaccinium vitis-idaea	5	18	25	7	6	17	17	0	10	17	17	0
Blechnum spicant									10	1	1	0
Diphasiastrum alpinum	6	17	17	0	4	15	16	1				
Huperzia selago					10	5	8	3	10	7	7	0
Lichens (*Cladonia* spp.)	2	18	17	-1	4	16	11	-5	3	15	9	-6
Bare Soil									10	3	8	5
Total absolute change				48				62				60
No. of species showing no change				5				3				4
No. of species showing a change in frequency of 3 or more				7				9				11

Note - Species have been blocked together into six groupings; grasses, sedges, rushes, dwarf shrubs, forbs, and ferns, clubmosses and *Sphagnum*
Increases in frequency at the optimum scale of 3 or more are marked in blue, decreases in frequency at the optimum scale of 3 or more are marked in red

Table 4.15 - Key changes in species frequency within the U10a Community

	Species Frequency	
	Increase of 3 or more at the optimum scale	**Decrease** of 3 or more at the optimum scale
Enclosure 1 only (high sheep)	*Agrostis* spp. *Anthoxanthum odoratum* *Carex bigelowii* *Galium saxatile* *Vaccinium vitis-idaea*	*Carex binervis**
Enclosure 2 only (low sheep)	*Nardus stricta* *Campanula rotundifolia* *Huperzia selago*	*Galium saxatile* *Anthoxanthum odoratum*
Enclosure 1 and **2** (high and low sheep)		
Enclosure 3 only (low sheep plus summer cattle)	*Festuca ovina/vivipara* *Carex panicea** *Empetrum nigrum* Bare Soil	*Carex pilulifera* *Cerastium fontanum** *Euphrasia officinalis* agg.
Enclosure 1 and **3** (high sheep and low sheep plus summer cattle)		
Enclosure 2 and **3** (low sheep and low sheep plus summer cattle)		*Agrostis* spp. *Luzula multiflora* *Cladonia* spp.
Enclosure 1, 2 and **3** All Treatments	*Deschampsia flexuosa*	

* species only recorded in one sample stand

4.5.1.4 *Comparisons between the species changes within the three community types*

The total absolute change in frequency at optimum scale within all three enclosures was higher in the CG10b community than in the U5c and U10a communities. Species rarely responded in a consistent manner across the three communities (Table 4.16). No species showed a consistent increase or decrease in frequency of three or more at the optimum scale in all three community sample stands within any one of the three enclosures.

Table 4.16 - A comparison of the absolute change values at the optimum scale between the three communities within each enclosure
Only those species which were found in five or more sample stands are shown in the table

Species found in five or more sample stands	Change in Frequency at the Optimum Scale								
	Enclsoure 1			Enclosure 2			Enclosure 3		
	U5c	CG10b	U10a	U5c	CG10b	U10a	U5c	CG10b	U10a
Agrostis capillaris	0	-2	3	4	6	-6	1	-9	-5
Anthoxanthum odoratum	2	1	5	-4	-2	-4	-3	6	1
Deschampsia flexuosa	-1		5	1	3	8	2		4
Festuca ovina/vivipara	-2	4	1	1	-5	-1	6	-1	3
Nardus stricta	0	-1	1	-2	0	3	2	-1	0
Carex binervis	2	0	-7	2	0		2	3	
Carex viridula ssp. *oedocarpa*	0	2		0	1			2	
Carex panicea	-4	-2		-2	1		3	0	4
Carex pilulifera	2	-6	1	0	1	1	-6	-1	-4
Carex pulicaris	-1	-1		3	-1			4	
Trichophorum cespitosum	-2	0		1			0		2
Juncus squarrosus	-1		0	0			0		1
Luzula multiflora	9	1	1	9	-3	-4	4	9	-3
Alchemilla alpina	1	0	-2		-4	-1		0	-1
Campanula rotundifolia	1	0	1		-5	9		-5	
Cerastium fontanum	0	2			1			7	-3
Euphrasia officinalis agg.	-2	5		-1	-2	-1		9	-6
Galium saxatile	4	1	6	-1	2	-11	-2	-1	2
Plantago lanceolata	-3	0		0	2			1	
Potentilla erecta	-3	2	-1	-1	-5	0	2	7	0
Prunella vulgaris	-1	7		-1	3			-3	
Ranunculus acris	0	0		2	3			3	
Viola spp.	1	2	1	1	-1		0	-4	
Vaccinium myrtillus	0	0	0	0	-2	1	3	1	2
Selaginella selaginoides	0	2		-3	6			0	

Notes - Species have been blocked together into six groupings; grasses, sedges, rushes, forbs, dwarf shrubs and clubmosses
Increases in frequency at the optimum scale of 3 or more are marked in blue, decreases in frequency at the optimum scale of 3 or more are marked in red

4.5.2 SWARD SURFACE HEIGHT

4.5.2.1 *U5c community*

Seasonal changes in the sward surface height of the U5c community

The mean sward surface height of the U5c community varied through the year (fixed effect of month: Wald = 1743.4, df = 9, $P < 0.001$), being shortest prior to the onset of growth in early spring and tallest in mid to late summer (Figure 4.4 shows the data for 1995 as an example).

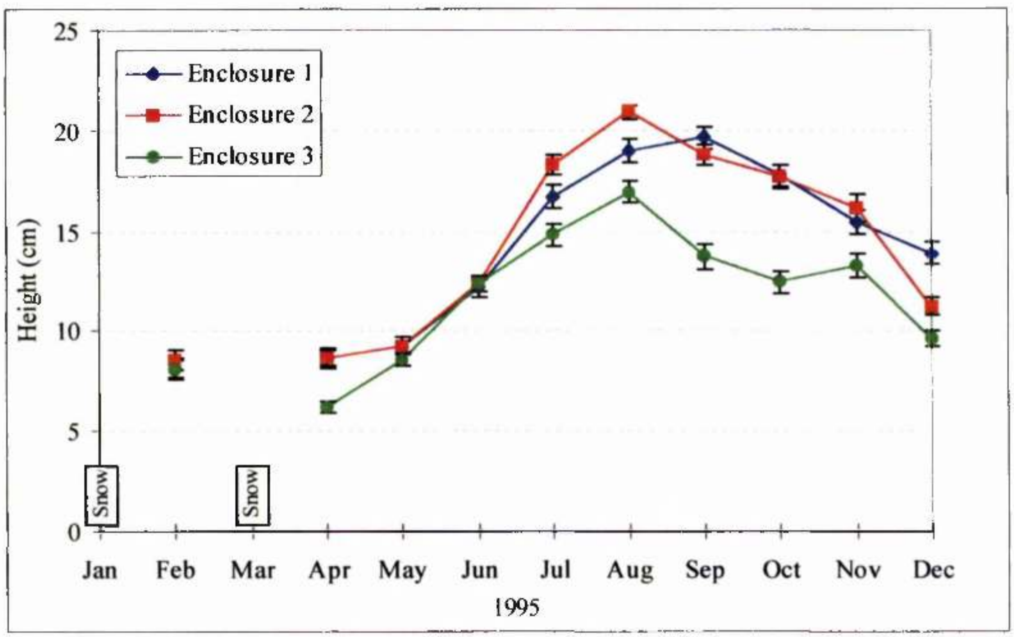


Figure 4.4 – Seasonal variation in mean sward surface height of the U5c grassland during 1995 within all three enclosures.

In order to compare treatments and years the sward surface heights at the two key periods of spring and mid to late summer were analysed. To reduce the effect of annual variations in the on-set and peak of the growing season, April and May heights were combined to produce an annual mean spring sward surface height, and July, August and September heights were combined to produce an annual mean summer sward surface height.

U5c mean summer sward surface heights

Prior to the establishment of the experimental stocking rates, the mean summer sward surface height of the U5c community was significantly higher in Enclosure 1 than in the other two enclosures (Wald = 10.9, df = 2, $P < 0.005$) (Figure 4.5).

The mean summer sward surface height declined in all three enclosures during the years 1995 to 1997, after which it appeared to stabilise (fixed effect of year: Wald = 661.6, df = 3, $P < 0.001$) (Figure 4.5). From 1995 to 1997 the median, range and standard deviation of the summer sward surface heights also declined in all three enclosures (Enclosure 1 is shown as an example in Figure 4.6). During the trial period (1995 to 1998) the summer sward surface height varied significantly between treatments (Wald = 150.9, df = 2, $P < 0.001$) (Figure 4.5). Enclosure 2, which had the lowest stocking rate, consistently had a mean summer sward surface height that was higher-than or equal-to the other two enclosures.

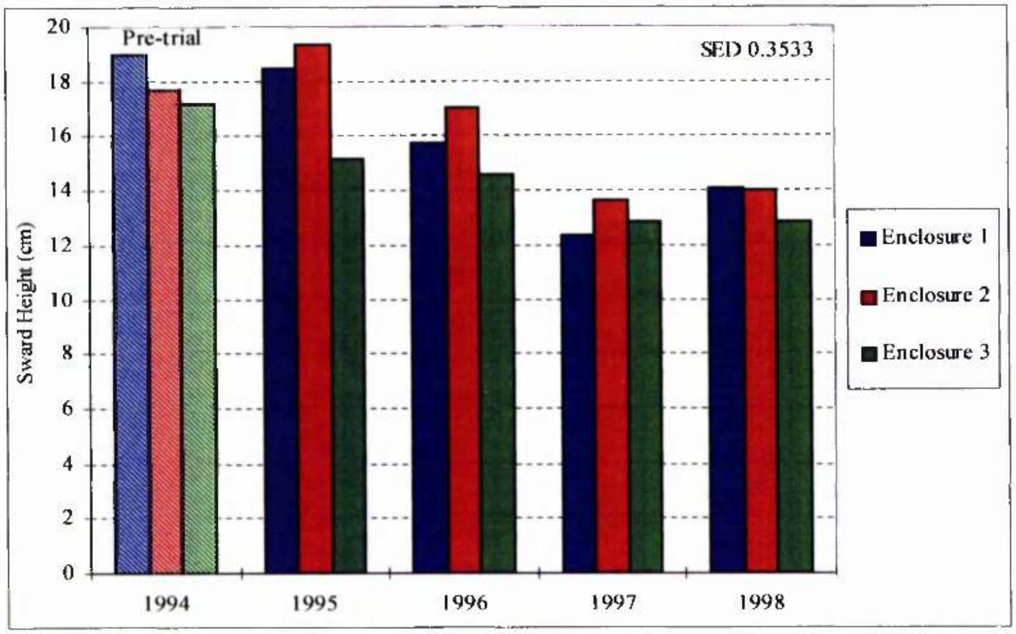


Figure 4.5 – Mean summer sward surface height (cm) of the U5c community within all three enclosures from 1994 to 1998 (n = 270 per enclosure per year). SED shown is for the trial period only (1995 – 1998).

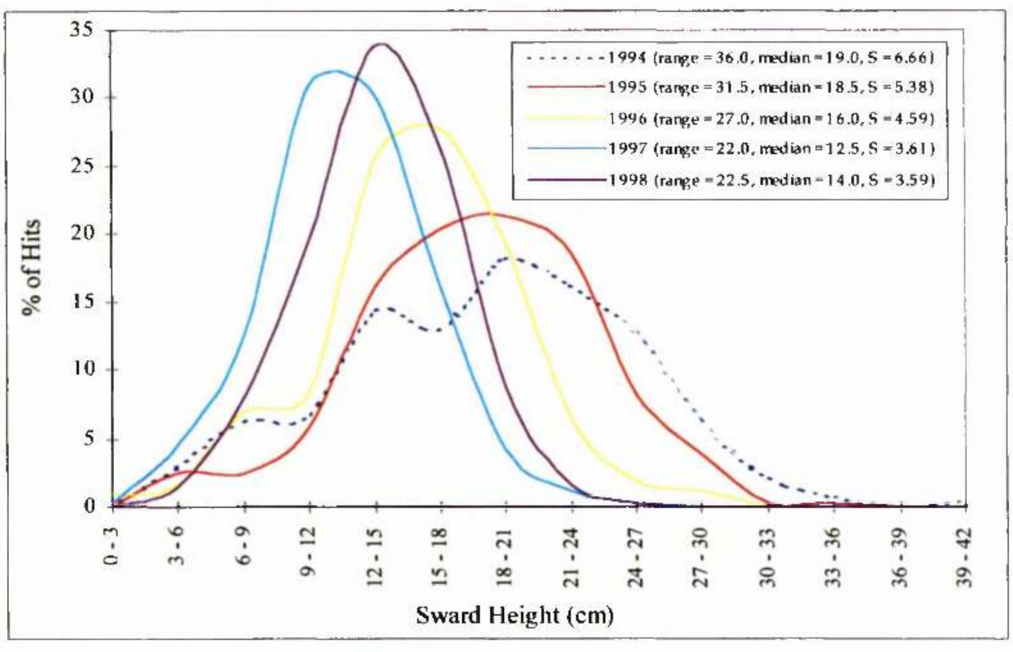


Figure 4.6 – Changes in the summer sward surface height distribution of the U5c community in Enclosure 1 (high sheep 0.074 LU ha^{-1}) from 1994 to 1998.

The sward surface heights of the dominant grass *Nardus stricta* were extracted from the data and analysed separately. In 1994 prior to the establishment of the experimental stocking rates, the mean summer sward surface height of *Nardus stricta* varied significantly between the enclosures (Wald = 7.2, df = 2, $P < 0.05$). It was highest in Enclosure 1 and lowest in Enclosure 2 (Table 4.17).

The change over time in the mean *Nardus stricta* summer sward surface height followed the same trend as that shown by the overall mean summer sward surface height (Table 4.17). It declined in all three enclosures during the years 1995 to 1997 after which it appeared to stabilise (fixed effect of year: Wald = 341.9, df = 3, $P < 0.001$). During the trial period (1995 to 1998) the mean *Nardus stricta* summer sward surface height varied significantly between treatments (Wald = 70.5, df = 2, $P < 0.001$), with the mean in Enclosure 2 being greater than or equal to that observed in the other two enclosures, in each of the years (Table 4.17).

Table 4.17 - Mean *Nardus stricta* summer sward surface heights (cm) from the grazed U5c community within each enclosure.

	Enclosure 1 (high sheep) (0.074 LU ha^{-1})	Enclosure 2 (low sheep) (0.051 LU ha^{-1})	Enclosure 3 (low sheep plus summer cattle) (0.096 LU ha^{-1})
1994 (pre-trial)	19.24	17.51	18.36
1995	19.04	19.27	15.71
1996	16.79	17.59	15.50
1997	13.55	14.86	14.04
1998	15.07	15.07	13.98
		Mean SED 0.4225 (trial period only)	

U5c mean spring sward surface heights

Mean spring sward surface heights varied significantly between years (Wald = 253.7, df = 3, $P < 0.001$) and between treatments (Wald = 72.7, df = 2, $P < 0.001$) (Figure 4.7). The variation in mean spring sward surface heights showed no clear trend over time, although within each enclosure it was significantly higher in 1998 than in any other year (L.S.D. Test, $P < 0.05$). Enclosure 2 consistently had higher mean spring sward surface heights than the other two enclosures (Figure 4.7).

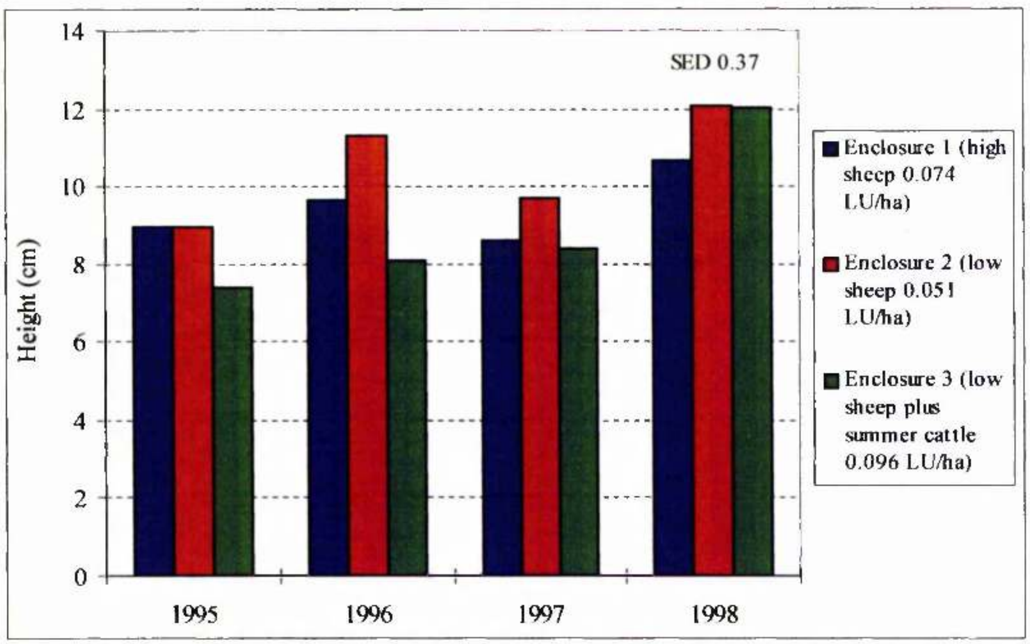


Figure 4.7 – Mean spring sward surface height (cm) of the U5c community within all three enclosures from 1995 to 1998 (n = 180 per enclosure per year).

4.5.2.2 *U5b community*

Seasonal changes in the sward surface height of the U5b community

The mean sward surface height of the U5b community varied through the year (fixed effect of month: Wald = 1205.2, df = 9, $P < 0.001$), being at its shortest in late spring and reaching a peak in mid to late summer (Figure 4.8 shows the data for 1995 as an example).

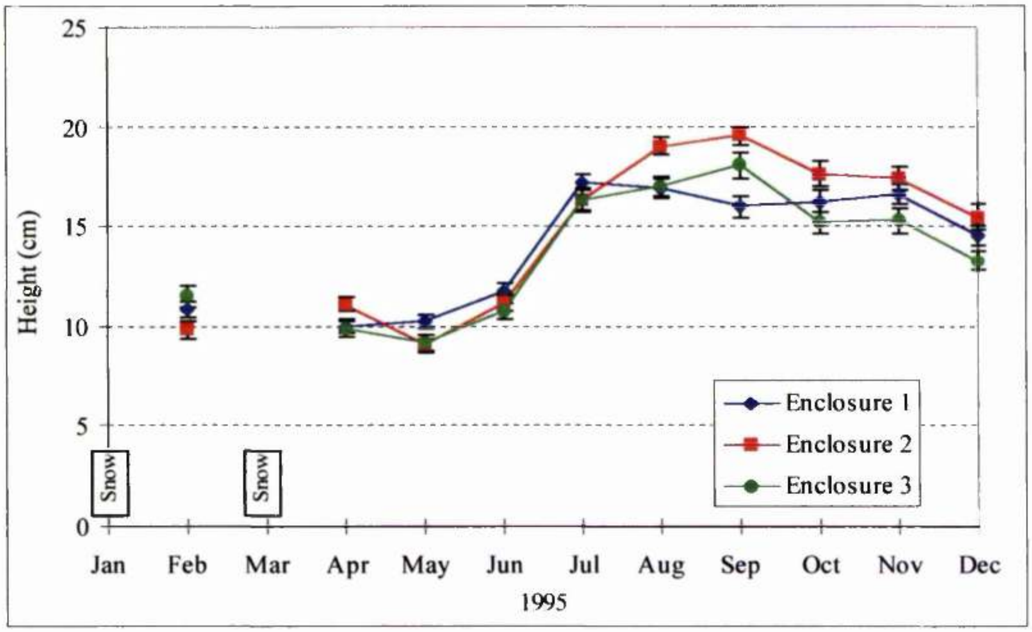


Figure 4.8 – Seasonal variation in the mean sward surface height of the U5b grassland during 1995 within all three enclosures.

In order to compare treatments and years the sward surface heights at the two key periods of spring and mid to late summer were analysed in the same way as the U5c community (see 4.5.2.1).

U5b mean summer sward surface heights

In 1994, prior to the establishment of the trial stocking rates, there was no significant difference between the mean summer sward surface heights of the U5b community within the three enclosures (fixed effect of enclosure: Wald = 5.4, df = 2, $P > 0.05$).

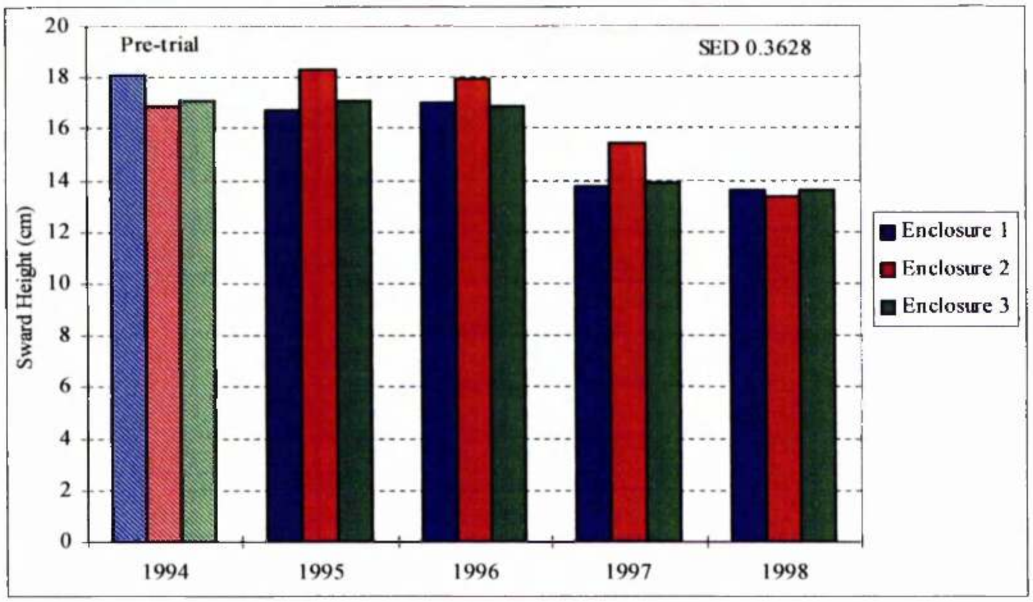


Figure 4.9 – Mean summer sward surface height (cm) of the U5b community within all three enclosures from 1994 to 1998 (n = 270 per enclosure per year). SED shown is for the trial period only (1995 – 1998).

During the trial period (1995 - 1998) the mean summer sward surface height of the U5b community varied significantly between treatments (Wald = 35.6, df = 2, $P < 0.001$) and between years (Wald = 542.9, df = 3, $P < 0.001$) (Figure 4.9). During 1995, 1996 and 1997 the mean summer sward surface height was significantly higher in Enclosure 2 than in the other two enclosures (L.S.D. Tests, $P < 0.05$), however there was no significant difference between the enclosures in 1998. There was no significant difference between the mean summer sward surface heights in Enclosure 1 and Enclosure 3 in any year (Figure 4.9). The mean summer sward surface height of the U5b community declined significantly between 1996 and 1997 in all three enclosures (Figure 4.9).

The sward surface heights of the two dominant species *Juncus squarrosus* and *Nardus stricta* were extracted from the data and analysed separately. Though there was some annual variation in the mean summer sward surface height of *Juncus squarrosus* during the trial period (Wald = 26.2, df = 3, $P < 0.001$), it showed no clear trend towards an overall decline or increase in height in any of the enclosures, however the same pattern over time was observed across all three enclosures (Figure 4.10).

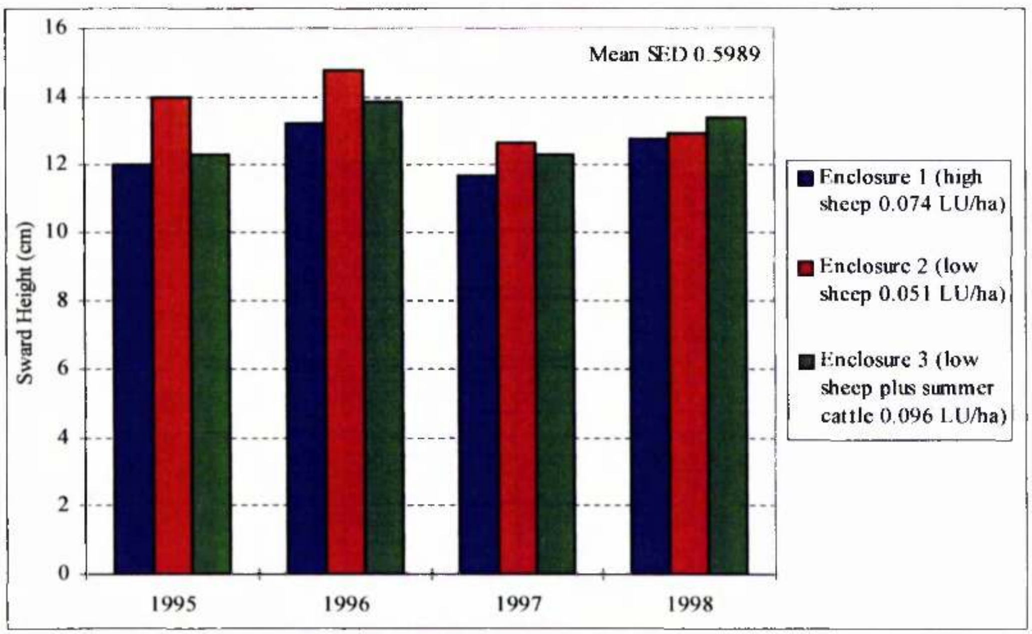


Figure 4.10 – Mean summer sward height (cm) of *Juncus squarrosus* in the U5b community within all three enclosures from 1995 to 1998.

The mean summer sward surface height of *Nardus stricta* did show a clear decline in all enclosures, following the same stepped trend as shown by the overall mean summer sward heights (fixed effect of year: Wald = 188.9, df = 3, $P < 0.001$) (Figure 4.11).

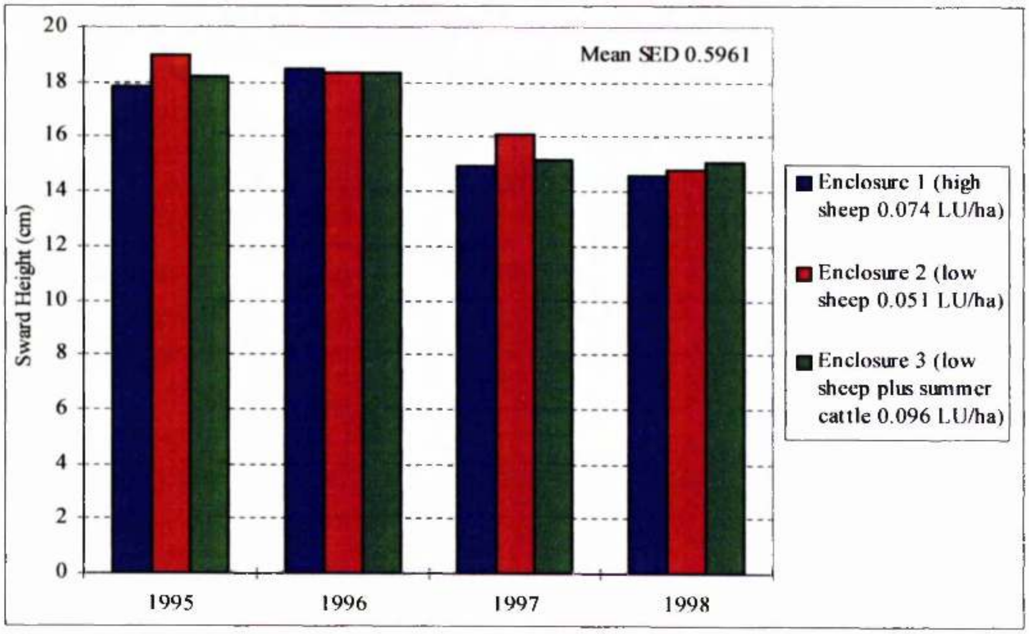


Figure 4.11 – Mean summer sward height (cm) of *Nardus stricta* in the U5b community within all three enclosures from 1995 to 1998.

U5b mean spring sward surface heights

Mean spring sward surface heights varied significantly between years (Wald = 207.3, df = 3, $P < 0.001$) and between treatments (Wald = 26.1, df = 2, $P < 0.005$). All three enclosures showed a similar pattern, with peaks in mean spring sward surface height recorded in 1996 and 1998 (Figure 4.12). From 1996 to 1998 the mean spring sward surface height of the U5b community was consistently higher in Enclosure 2 than in the other two enclosures (Figure 4.12).

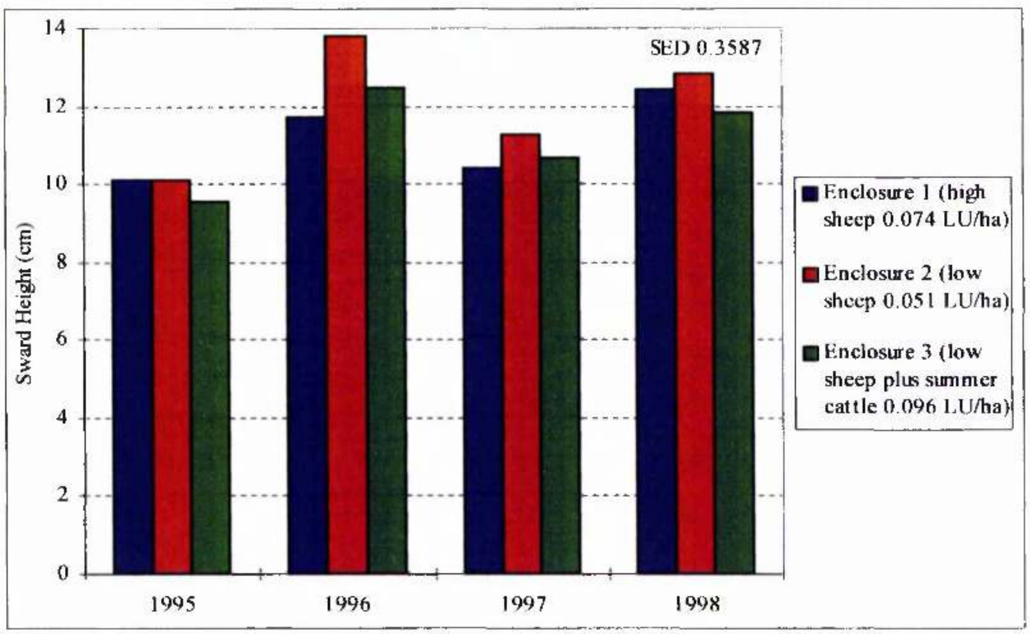


Figure 4.12 – Mean spring sward surface height (cm) of the U5b community within all three enclosures from 1995 to 1998 (n = 180 per enclosure per year).

4.5.2.3 *M6d community*

Changes in the sward surface height of the M6d community

There was a clear seasonal change in the mean sward surface height of the M6d community (fixed effect of month: Wald = 2485.3, df = 7, $P < 0.001$), being shortest in late spring and tallest in autumn or early winter before the first snows crushed the dying *Juncus acutiflorus* stems (Figure 4.13). The month in which the peak height was reached varied between enclosures and between years, occurring anytime between August and December.

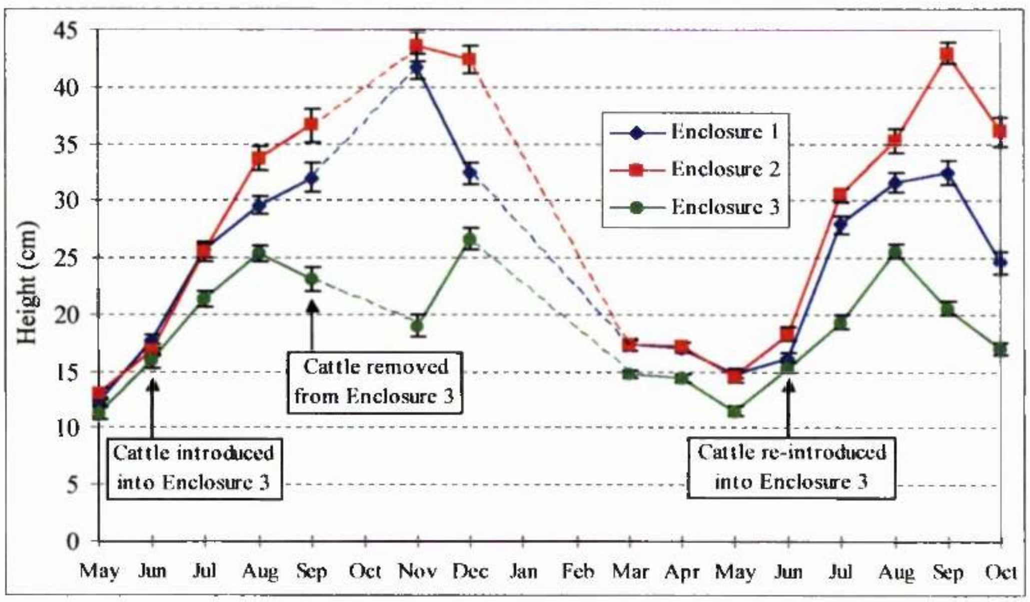


Figure 4.13 – Seasonal variation in the mean sward surface height of the M6d mire community (May 1995 to October 1996) within all three enclosures.

In order to compare treatments and years the sward surface heights in late summer were analysed. To reduce the effect of annual variations in the peak of the growing season, August and September heights were combined to produce an annual mean summer sward surface height for the M6d community. July sward heights were not used because of the later peak in sward height within this community. Mean spring sward surface heights were not analysed for the M6d community, since there was very little live material within this community during April and May.

M6d mean summer sward surface heights

During the trial period the mean summer sward surface height of the M6d community varied significantly between treatments (Wald = 588.1, df = 2, $P < 0.001$). It was significantly shorter in Enclosure 3 than in Enclosures 1 and 2, in all years (L.S.D. Test, $P < 0.05$). There were some minor year-to-year fluctuations in the mean summer sward surface height between 1995 and 1997 in all three enclosures. This was followed by a significant increase in the mean summer sward surface height of over 13 cm in all three enclosures between 1997 and 1998 (Wald = 1530.2, df = 2, $P < 0.001$) (Figure 4.14).

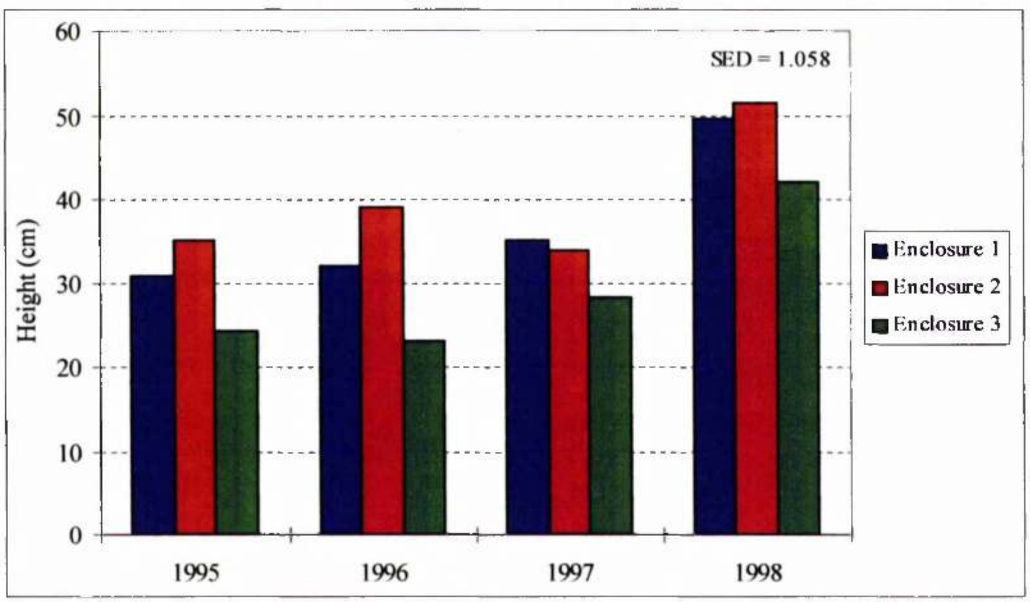


Figure 4.14 – Mean summer sward surface height of the M6d community within all three enclosures (1995 to 1998) (n = 180 per enclosure per year).

4.5.2.4 *Calluna vulgaris sward heights (April 1998)*

The mean height of *Calluna vulgaris* was significantly higher in the M19 community than in the H12 community (fixed effect of community: Wald = 169.0, df = 1, $P < 0.001$). Within the M19 community the mean height of the *Calluna vulgaris* varied between treatments (fixed effect of enclosure: Wald = 85.8, df = 2, $P < 0.001$). The mean height of *Calluna vulgaris* was significantly higher in Enclosure 3 than in the other two enclosures (L.S.D. Test, $P < 0.05$), and was significantly higher in Enclosure 2 than in Enclosure 1 (L.S.D. Test, $P < 0.05$) (Figure 4.15). There was no significant difference in the mean height of *Calluna vulgaris* within the H12 community between the three enclosures (Wald = 3.6, df = 2, $P > 0.05$). The *Calluna vulgaris* within the H12 community had a mean height of 10cm or less, and formed a very low-growing mat. There was clear evidence of grazing of this species within all three enclosures, however it is likely that the exposed position of the *Calluna vulgaris* at the summit of the Kirkton Face, above 600m, may also have contributed to its suppressed growth form.

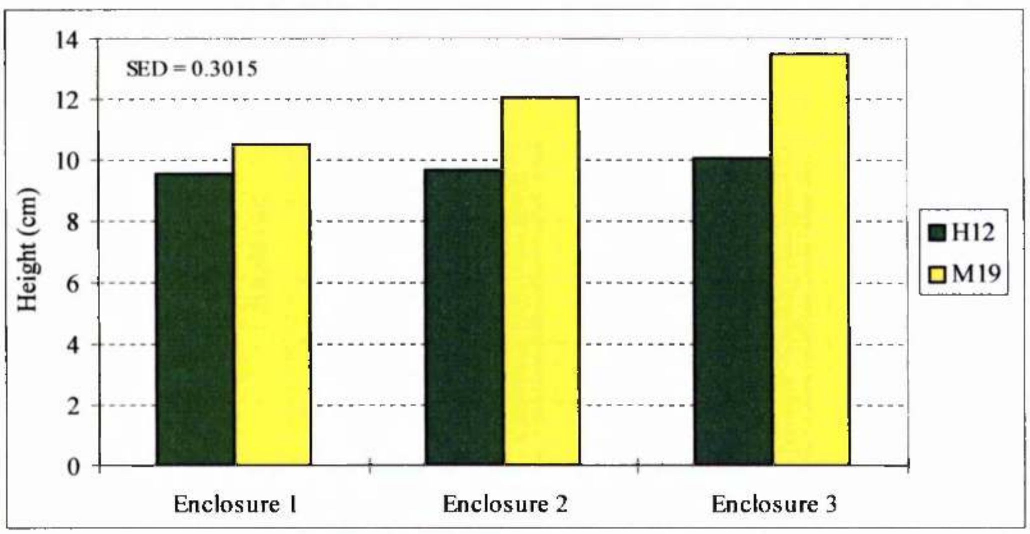


Figure 4.15 – Mean *Calluna vulgaris* height within the H12 and M19 communities in each enclosure (April 1998) (n = 100 per community per enclosure).

4.5.3 CHANGES IN SPECIES COVER (USING THE SWARD STICK DATA)

4.5.3.1 *U5c community*

In 1994, prior to the establishment of the experimental stocking rates, the summer percentage cover of some of the species and species groups within the sampled patches of U5c varied significantly between the enclosures. The percentage covers of both *Nardus stricta* and combined sedges were significantly lower in Enclosure 3 than in the other two enclosures (*Nardus stricta*, Wald = 11.3, df = 2, $P < 0.005$; sedges, Wald = 11.2, df = 2, $P < 0.005$) (Figure 4.16, 4.17 and 4.18). Enclosure 1 had a significantly higher percentage cover of *Anthoxanthum odoratum* (Wald = 9.3, df = 2, $P < 0.01$) and a significantly lower percentage cover of *Trichophorum cespitosum* than the other enclosures (Wald = 9.5, df = 2, $P < 0.01$) (Figure 4.17, 4.18 and 4.19).

There was little change in species cover within the U5c community in any of the enclosures during the period 1994 to 1998 (Figures 4.16, 4.17 and 4.18).

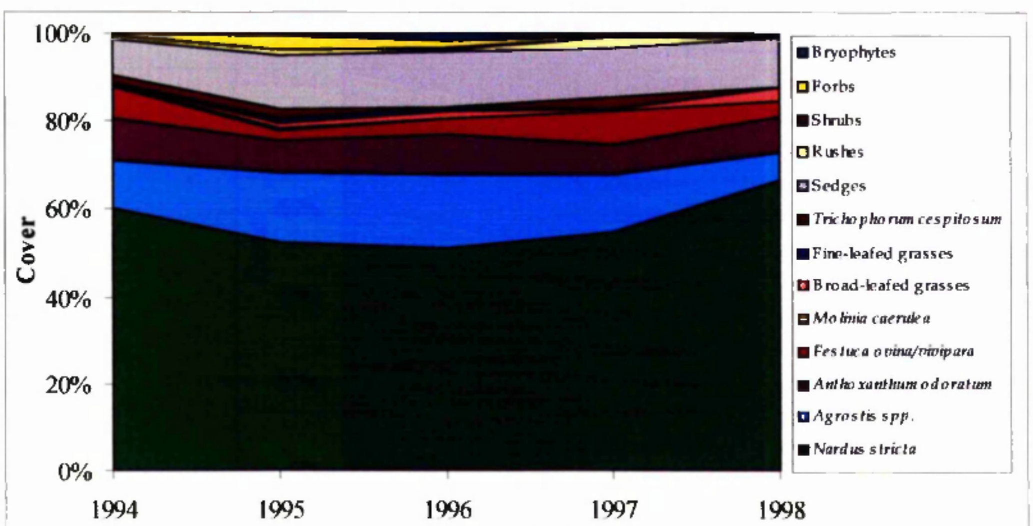


Figure 4.16 – Change in the summer species cover of the U5c community in Enc. 1

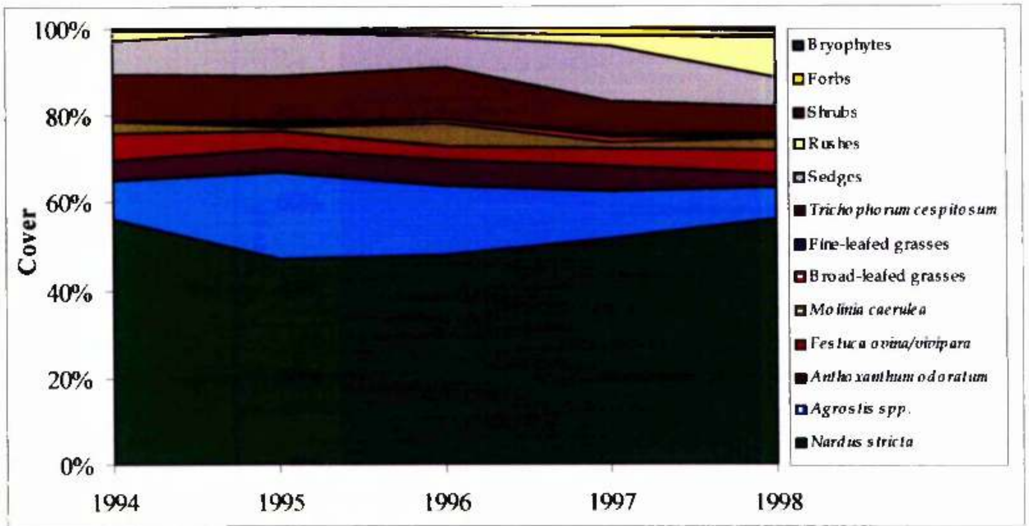


Figure 4.17 – Change in the summer species cover of the U5c community in Enc. 2

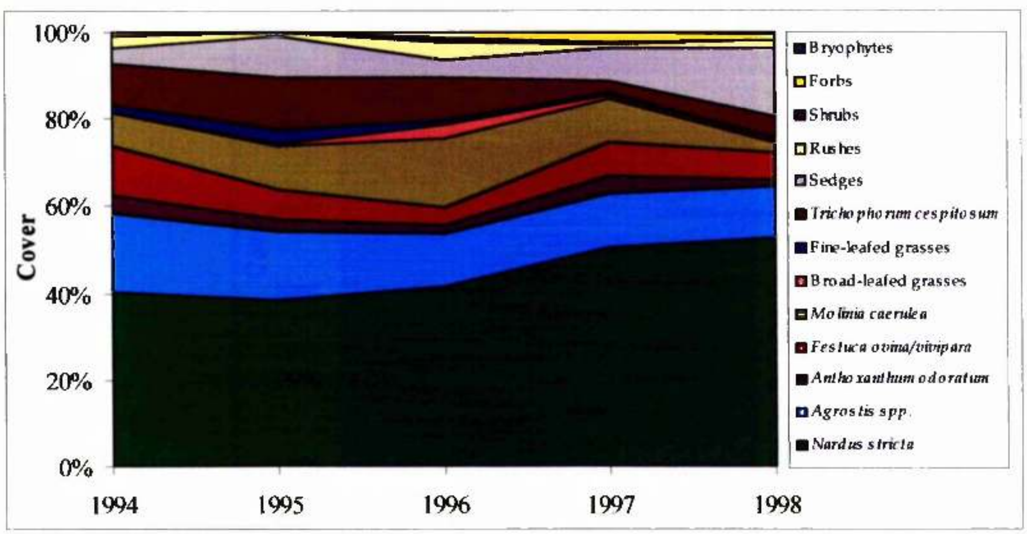


Figure 4.18 – Change in the summer species cover of the U5c community in Enc. 3

All the enclosures showed some annual variation of which some was significant (Table 4.18), however there were few clear trends, apart from the significant increase in *Nardus stricta* within Enclosure 3.

Table 4.18 - Species that showed significant year-to-year variation in percentage cover within the U5c community.

Enclosure	Species	% cover in 1998 significantly **lower** than in 1994 (L.S.D. test $P < 0.05$)	% cover in 1998 significantly **higher** than in 1994 (L.S.D. test $P < 0.05$)
1	*Nardus stricta* (Wald = 17.7, df = 4, $P < 0.005$)		
	Festuca ovina (Wald = 18.0, df = 4, $P < 0.005$)	*	
	Agrostis capillaris (Wald = 9.9, df = 4, $P < 0.005$)		
2	*Agrostis capillaris* (Wald = 15.3, df = 4, $P < 0.005$)		
	Rushes (Wald = 15.4, df = 4, $P < 0.005$)		*
3	*Nardus stricta* (Wald = 14.5, df = 4, $P < 0.01$)		*
	Sedges (Wald = 17.7, df = 4, $P < 0.005$)		*

4.5.3.2 *U5b community*

At the start of the experiment there were significant differences between the enclosures in the percentage cover of some of the species and species groups within the sampled patches of U5b. Enclosure 2 had significantly higher percentage covers of *Nardus stricta* (Wald = 15.7, df = 2, $P < 0.001$), *Agrostis capillaris* (Wald = 21.1, df = 2, $P < 0.001$), *Anthoxanthum odoratum* (Wald = 12.0, df = 2, $P < 0.005$) and *Festuca ovina* (Wald = 8.3, df = 2, $P < 0.05$) than the other two enclosures, and a significantly lower percentage cover of *Trichophorum cespitosum* (Wald = 42.6, df = 2, $P < 0.001$). The percentage cover of *Juncus squarrosus* was not significantly different between the enclosures (Wald = 1.4, df = 2, $P > 0.05$).

All the enclosures showed some year-to-year variation, but unlike the U5c community, changes in the cover of some species or groups of species did show clear and consistent increases or decreases over time (Figures 4.19, 4.20 and 4.21). There was a significant increase in the cover of *Juncus squarrosus* in all three enclosures between 1994 and 1998 (Enclosure 1, Wald = 21.9, df = 4, $P < 0.001$; Enclosure 2, Wald = 51.7, df = 4, $P < 0.001$; Enclosure 3, Wald = 49.0, df = 4, $P < 0.001$). The cover of *Nardus stricta* varied significantly in Enclosure 2 (Wald = 29.8, df = 4, $P < 0.001$) showing a stepped decline between 1995 (43.7%) and 1996 (26.3%), but showed no significant change in Enclosures 1 or 3 ($P > 0.05$). The cover of *Festuca ovina* also declined significantly within Enclosure 2 (Wald = 12.4, df = 4, $P < 0.05$). Between 1994 and 1998 *Trichophorum cespitosum* declined significantly in both Enclosure 1 (Wald = 12.7, df = 4, $P < 0.05$) and Enclosure 3 (Wald = 16.2, df = 4, $P < 0.005$), whereas *Anthoxanthum odoratum* increased significantly within both of these enclosures (Enclosure 1, Wald = 9.8, df = 4, $P < 0.05$; Enclosure 3, Wald = 11.7, df = 4, $P < 0.05$).

Molinia caerulea declined significantly within Enclosure 3 between 1994 and 1998 (Wald = 9.9, df = 4, $P < 0.05$).

By the summer of 1998 the only significant differences between the three enclosures were in the cover of *Trichophorum cespitosum* (Enclosure 1 = 12.96%, Enclosure 2 = 6.30%, Enclosure 3 = 5.19%: Wald = 7.0, df = 2, $P < 0.05$), and dwarf shrubs (Enclosure 1 = 0%, Enclosure 2 = 2.22%, Enclosure 3 = 6.67%: Wald = 9.1, df = 2, $P < 0.05$).

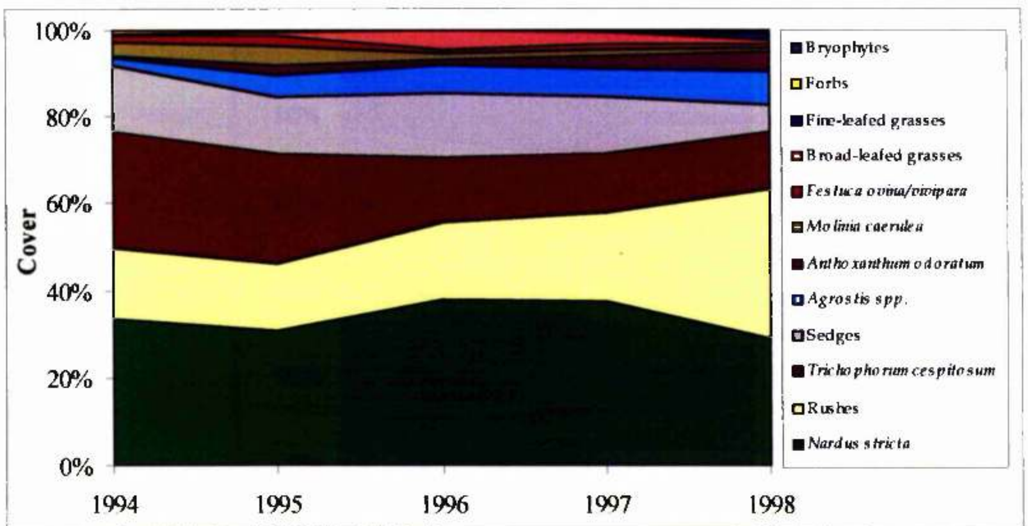


Figure 4.19 – Change in the summer species cover of the U5b community in Enc. 1

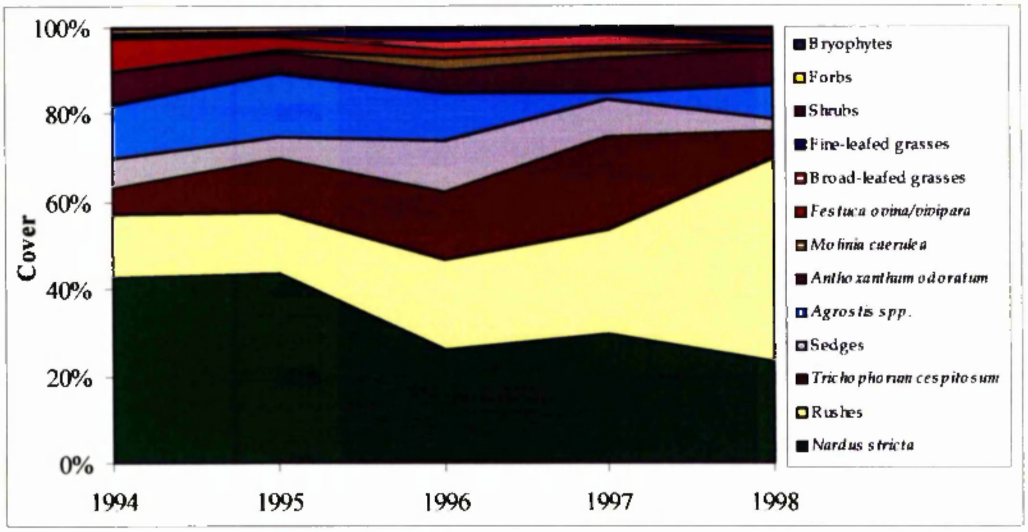


Figure 4.20 – Change in the summer species cover of the U5b community in Enc. 2

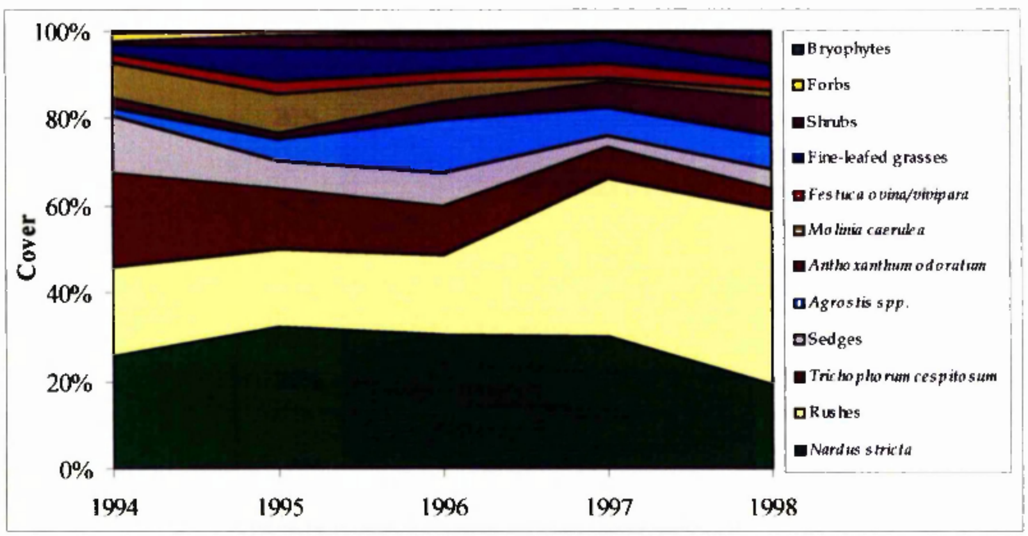


Figure 4.21 – Change in the summer species cover of the U5b community in Enc. 3

4.5.3.3 *M6d community*

In 1995, the three enclosures had very similar percentage covers of the main species and species groups within the sampled patches of M6d, differing significantly only in their percentage cover of *Nardus stricta* (Wald = 22.5, df = 2, $P < 0.001$).

All three enclosures showed significant increases in the cover of *Juncus acutiflorus* over the three year monitoring period (Enclosure 1 Wald = 41.5, df = 3, $P < 0.001$; Enclosure 2 Wald = 9.2, df = 4, $P < 0.05$; Enclosure 3 Wald = 74.9, df = 4, $P < 0.001$), particularly Enclosure 3 where the cover of *Juncus acutiflorus* increased from 44.8% to 83.3% (Figure 4.22, 4.23 and 4.24). There was a significant decline in the cover of *Molinia caerulea* and sedge species in all three enclosures over the period 1995 to 1998 ($P < 0.05$). The change over time in the cover of *Nardus stricta* showed a similar pattern across all three enclosures, with an initial increase between 1995 and 1996, followed by a steady decline. By the summer of 1998 there were no significant differences between the three enclosures in the percentage cover of the main species and species groups.

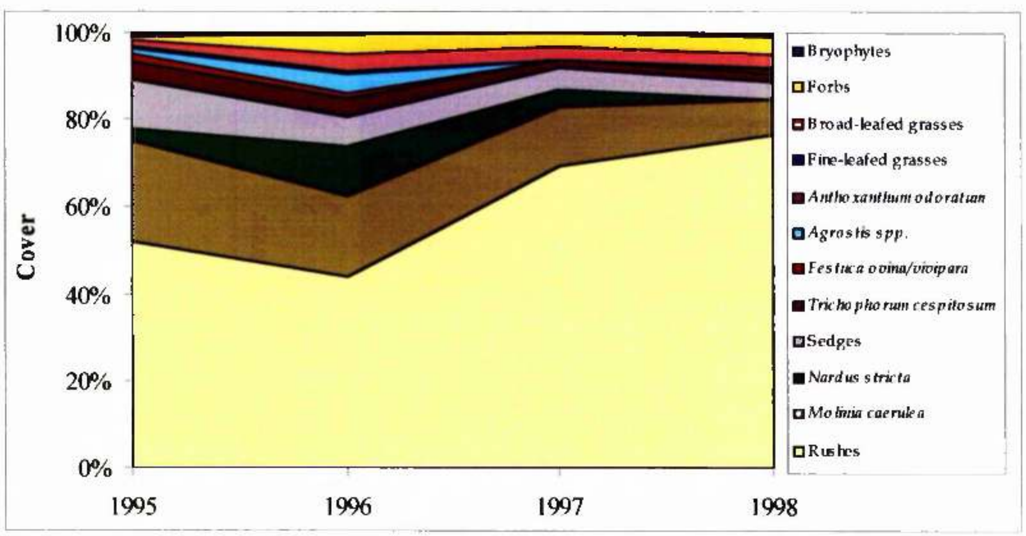


Figure 4.22 – Change in the summer species cover of the M6d community in Enc. 1

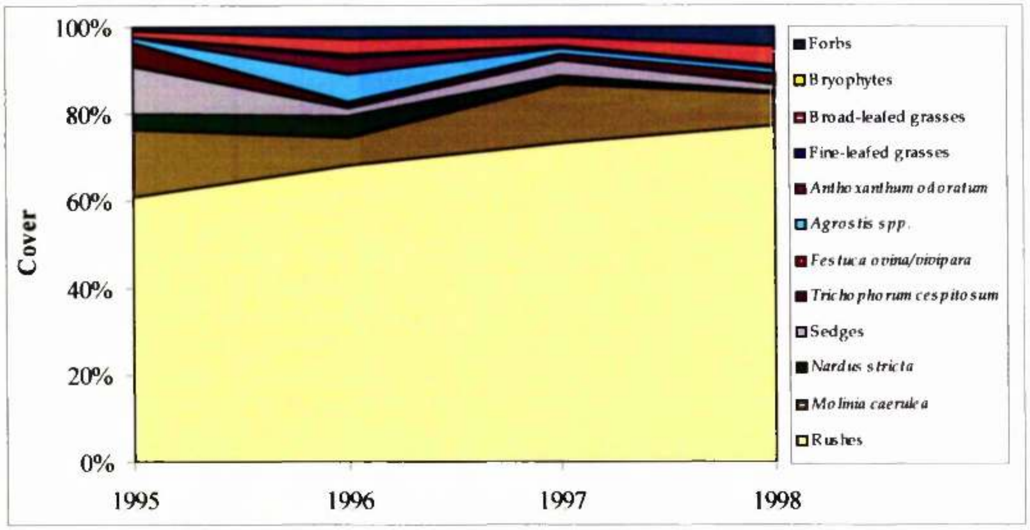


Figure 4.23 – Change in the summer species cover of the M6d community in Enc. 2

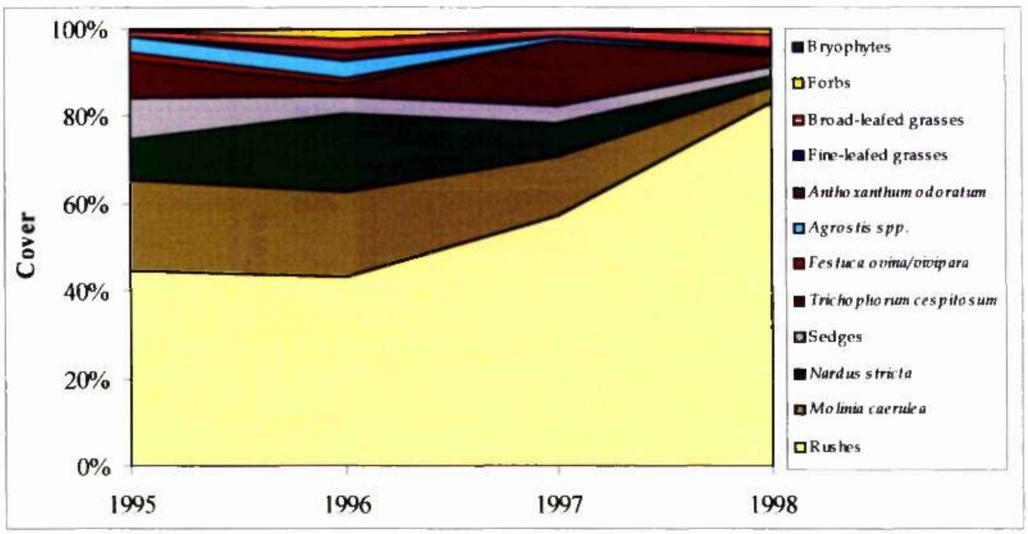


Figure 4.24 – Change in the summer species cover of the M6d community in Enc. 3

4.6 Discussion

4.6.1 ASPECTS OF THE NESTED QUADRAT METHODOLOGY

Different species have different optimum scales depending upon their frequency within the vegetation. For the most abundant species the optimum scale is low, while for progressively less frequent species the optimum scale increases. Not only are different optimum scales required for different species, but they are also required for the same species within different community types, and the same species within the same community type. This adds further emphasis to the need to take not only community type, but also the composition of that community into account before deciding on which scale is best able to identify changes in vegetation composition over time.

4.6.2 CHANGES IN SPECIES COMPOSITION

Most of the changes observed within the U5c sample stands over the study period were minor and all stands remained dominated by the perennial grasses *Nardus stricta*, *Agrostis capillaris* and *Anthoxanthum odoratum*. The long-lived, clonal species *Nardus stricta* showed no response to the treatments. A number of sedge species did show differences between treatments. The low growing, winter-green, rhizomatous sedge, *Carex panicea*, increased in Enclosure 3, perhaps due to the seasonal increase in grazing pressure suppressing the growth of potential dominants, whereas the much taller *Carex nigra* declined in Enclosure 3 perhaps in response to the cattle grazing. *Carex pilulifera*, which is a short, tufted, winter-green sedge, also declined in Enclosure 3. This species is moderately resistant to trampling, however it is more susceptible to close grazing than more productive species such as *Agrostis capillaris* (Grime *et al.*, 1988).

Luzula multiflora was shown by Marrs *et al.* (1988) to have increased within a *Juncus squarrosus* grassland grazed by free ranging sheep at 1.4 ewes ha^{-1} (i.e. 0.112 LU ha^{-1}), however in an area where stock were excluded the species declined. Ball (1974) also observed a decline in the cover of *Luzula multiflora* following both a reduction in grazing and the exclusion of grazing. The general increase in *Luzula multiflora* across all enclosures within this study is an indication that the grazing pressure imposed in all three of the treatments is different from that which existed prior to the erection of the fences. The overall annual stocking rate for the 282.5 ha area, which included the enclosures, prior to the erection of the fences, was approximately 0.14 LU ha^{-1}. This was considerably higher than the treatment stocking rates, however for eight months of the year the sheep had access to better quality improved rough pasture, and during December there were no sheep grazing the area. Month to month variations in the grazing pressure were likely to have been much greater prior to the study than under the fixed treatments, with periods when there was very high grazing pressure and periods when there was no grazing, although it is not possible to accurately determine the seasonal variation in grazing pressure within the area of the enclosures themselves. Therefore in some periods of the year the grazing pressure has increased, while in other periods it has decreased. The relative grazing pressure on the different communities will also have changed. The overall annual stocking rate may be lower in all three enclosures, however the increase in *Luzula multiflora* is probably a result of changes in the grazing pressure at a much smaller spatial and temporal scale.

The observed increase in *Anemone nemorosa* within Enclosure 1 was almost certainly due to the different times of year when the monitoring took place, and was not an actual increase in the number of plants. In 1994 the census was carried out at the beginning of September, compared with a mid-June survey in 1998. *Anemone nemorosa* is a vernal species, and by mid-July most of the above-ground parts of the plant have died back and are no longer visible (Grime *et al.*, 1988). The tissues of *Anemone nemorosa* contain protoanemonin making it unpalatable to stock, however it can survive occasional defoliation (Grime *et al.*, 1988). *Anemone nemorosa* remained a frequent component of the *Nardus stricta* grasslands within the study site. This species is a poor colonist, regenerating mainly through rhizome growth, which leads to the development of slow growing clonal patches (Grime *et al.*, 1988). These patches can become very large, particularly within woodland. However, within the Kirkton Face U5c community the patches tended to be small, consisting of isolated clumps of only a few individuals, or as extensive but diffuse patches. Seed set does occur regularly even though *Anemone nemorosa* is self-incompatible, but this is less frequent in grasslands than in woodland sites (Shirreffs, 1985). Germination requires prolonged moist conditions and the development of the seedling is very slow (Shirreffs, 1985). Seed dispersal is also very limited (Shirreffs, 1985). These factors mean that this species has a low colonising ability, suggesting that the observed change in species abundance was a seasonal change in above-ground tissue and not an actual change in whole plant abundance. None of the other species identified within the U5c sample stands were vernal species, which die back completely in late summer, however there were some species such as the diminutive annual, *Euphrasia officinalis* agg., which show later growth and therefore may have been under-recorded in June compared to September. The flowering shoots of the creeping perennial species, *Potentilla erecta*, die back in winter, with new ones being produced in late spring (Grime *et al.*, 1988). Therefore, this species may also have been under-recorded in June compared to September. *Potentilla erecta* has a creeping habit, which increases the likelihood of over-recording the species in September, due to the difficulty of determining whether the plant was rooted within a particular cell or simply growing through it. Both *Euphrasia officinalis* agg. and *Potentilla erecta* showed a decline in abundance within Enclosures 1 and 2, both of which were monitored in September and then in June.

Nardus stricta is a long-lived perennial grass (Chadwick, 1960), which spreads mainly by rhizomes; it has a higher silica content, and a slightly lower digestibility than *Agrostis capillaris* (Hodgson *et al.*, 1991). The spreading tussocks of *Nardus stricta* are also resistant to some degree of trampling (Grime *et al.*, 1988). Selective grazers such as sheep tend to have a low intake of *Nardus stricta* and therefore it is unlikely that sheep grazing would cause major changes in grasslands dominated by this species, unless the grazing intensities increased to such an extent that the nutritional intake of the animals suffered, and unacceptable pressure was placed on the better quality U4, CG10 and CG11 grasslands (Rodwell, 1992). Even the presence of cattle within Enclosure 3, which are less selective than sheep (Buttenschøn and Buttenschøn, 1982b; Grant *et al.*, 1985; Common *et al.*, 1998; Hoffman, 1989; Hodgson *et al.*, 1991) had little impact upon the species composition of the U5c community, and had no apparent impact on *Nardus stricta*, a species which has been shown to decline when grazed by cattle during the growing season (Grant *et al.*, 1996b; Common *et al.*, 1998).

Changes in species abundance within the CG10b community were greater than in the other two communities. This grassland, which is dominated by *Agrostis capillaris* and *Festuca vivipara*, has a higher digestibility than the other grasslands (Hodgson *et al.*, 1991) and has only a limited cover of the tussock forming *Nardus stricta*, and was therefore probably utilised more than the U5c and U10a communities. The lower altitude of the CG10b sample stands also made them more accessible, particularly to the cattle within Enclosure 3. The CG10b sample stands also contained a higher total number of species than those in the other community types, including more annual and biennial species. Within the two enclosures subject to the higher stocking rates there were clear increases in low growing perennial and annual forbs, in particular ruderal species, which were either unpalatable, and therefore probably avoided (*Euphrasia officinalis* agg., *Prunella vulgaris* and *Linum catharticum*) or were tolerant of both grazing and trampling (*Taraxacum* agg. and *Bellis perennis*) (Grime *et al.*, 1988). Within these two enclosures the dominant grass *Agrostis capillaris* declined, whereas in Enclosure 2 it increased along with another perennial grass *Deschampsia flexuosa*. The greatest change recorded within the CG10b sample stands was in the amount of bare ground within the enclosure grazed by sheep and cattle. Ground disturbance and poaching by cattle on these lower altitude, moderately steep grasslands, produced numerous hoof shaped patches of bare ground, into which ruderal annuals (e.g. *Euphrasia officinalis* agg.) and ruderal perennials (that could tolerate some degree of grazing and trampling, such as *Cerastium fontanum*, *Bellis perennis*, *Ranunculus acris*, *Trifolium repens* and *Potentilla erecta*) could spread. The increase in gaps within the vegetation may also have benefited the seed regeneration of *Holcus lanatus*.

The intensity of grazing within a grassland can affect the balance between the survival and clonal spread of certain species, and the establishment of seedlings from the seed bank (Bullock *et al.*, 1994). Grazing encourages the clonal growth of fast growing perennial grasses such as *Agrostis capillaris*, however, if the grazing intensity is high enough these dominant grasses can be suppressed with the resultant appearance of gaps within the sward which allows seedlings to establish from both the seed rain and soil seed bank (Bullock *et al.*, 1994). The speed at which change occurs depends upon factors such as the presence of a seed bank or seed rain which contains novel species, and the degree to which the perennial grass species continue to dominate the seed rain (Bullock *et al.*, 1994). Annual and biennial species with short life-histories rely on the availability of gaps within the sward for seed germination to occur, followed by rapid growth which gives them a competitive advantage over their neighbouring species (Bullock *et al.*, 1994). The absence of gaps for seedling recruitment, or the absence of seed within the soil seed bank or seed rain, will limit the abundance of annual species. The population size of some clonal perennial species such as *Cerastium fontanum* is also controlled by the establishment of seedlings within gaps (Bullock *et al.*, 1994).

In this study the winter-green, perennial grass, *Festuca rubra*, increased in all three CG10b sample stands. Previous studies have observed large increases in the cover of *Festuca rubra* under reduced grazing (Ball, 1974; Buttenschøn and Buttenschøn, 1982a; Hill *et al.*, 1992). This would suggest that the grazing pressure in all three enclosures has reduced. This is contrary to what the increase in *Luzula multiflora* within the U5c community indicates. This suggests that it is the temporal and spatial variations in grazing pressure rather than changes in overall annual stocking rate that are important. Different species in different communities have responded in different ways to the changes in seasonal grazing pressure.

There were no major changes within the U10a community, however the minor increases in *Agrostis* spp., *Anthoxanthum odoratum*, *Galium saxatile* and *Vaccinium vitis-idaea* within Enclosure 1 are perhaps an initial move towards a more grass dominated U4e *Festuca ovina* - *Agrostis capillaris* - *Galium saxatile* (*Vaccinium myrtillus* - *Deschampsia flexuosa*) grassland under the higher sheep stocking rate. The cattle within Enclosure 3 rarely ventured on to this high level moss-heath community and their influence upon the vegetation is difficult to gauge, however the small changes that did occur within Enclosure 3 were similar to those observed within the enclosure with the low sheep stocking rate (Enclosure 2) suggesting that the cattle had minimal effect. Previous studies have indicated that an increase in the perennial grass *Deschampsia flexuosa* is normally associated with a decline in grazing pressure (Rawes, 1981; Hill *et al.*, 1992). Within this study *Deschampsia flexuosa* increased in all three enclosures, however the trampling and grazing sensitive *Cladonia* species declined in all three enclosures, suggesting that seasonal grazing pressure had increased rather than decreased within this montane community. This clearly illustrates the difficulty of comparing the responses of individual species to changes in management on different sites.

4.6.3 CHANGES IN SPECIES COVER AND SWARD HEIGHT

Prior to 1994 the enclosures were unfenced and formed part of a large 282.5 hectare block of land which included a 60 hectare area of improved *Festuca - Agrostis* grassland (Chapter 2). This improved grassland also contained the main site used for supplementary feeding. The area that later became Enclosure 1 was furthest away from this improved grassland and therefore likely to be subject to a lower overall grazing pressure than the other two enclosures, which probably explains its higher 1994 U5c and U5b mean summer sward surface heights.

Following the establishment of the experimental stocking rates, the spring and summer mean sward heights of the U5c and U5b communities were consistently higher within the enclosure with the lowest stocking rate. The height of the *Nardus stricta* within this enclosure was also consistently higher. Stocking rate therefore had an impact upon the vegetation structure. The vegetation within the U5b and U5c communities, including the *Nardus stricta*, was being grazed significantly more in the two enclosures with the higher stocking rates. The enclosure containing the summer grazing cattle consistently had the lowest U5c mean summer sward surface height. Grant *et al.* (1985) and Hodgson *et al.* (1991) showed that cattle grazing *Nardus stricta* dominated swards consistently ingest more *Nardus stricta* than do sheep, and that there is an inverse relationship between the proportion of *Nardus stricta* in their diet and the height of the preferred grasses between the *Nardus stricta* tussocks. Although there was indirect evidence that the cattle were grazing the U5c *Nardus stricta* community within Enclosure 3 in the form of lower sward heights, there was no evidence of a reduction in the cover of *Nardus stricta*. On the contrary, the cover of *Nardus stricta* increased significantly within Enclosure 3, whereas in the sheep only enclosures the cover of *Nardus stricta* showed no significant overall increase. The opposite of this was observed by Grant *et al.* (1996b) and Common *et al.* (1998) who had shown that summer grazing cattle could significantly reduce the cover of *Nardus stricta* within grasslands dominated by the species, whereas under sheep grazing Grant *et al.* (1996b) observed an increase in the cover of *Nardus stricta* even when more preferred grasses were in short supply. There are however difficulties in comparing the results from Grant *et al.* (1996b) and Common *et al.* (1998) with this study, as they used inclined point quadrats to estimate species cover whereas the present study used vertical sward stick measurements. This methodological difference will have influenced the results, as the sward stick is a mini-quadrat rather than a point quadrat. The cover of the narrow leaved, tussock forming *Nardus stricta* tends to be overestimated using the sward stick method. Nevertheless, it is unlikely that this methodological difference would produce conflicting results.

In a plot scale study also carried out at Kirkton Farm, Hulme *et al.* (1999) examined vegetation changes within a *Festuca ovina - Agrostis capillaris - Nardus stricta* grassland under four different grazing management regimes. The management involved maintaining sward heights of 3, 4.5 and 6 cm using Scottish Blackface wethers, plus the complete exclusion of grazing livestock (Hulme *et al.*, 1999). Grazing only occurred between May and October. Over the six years of the experiment, changes in species composition were small, with few species gained or lost, and most of the observed changes were due to shifts in the abundance of the dominant species. Maintenance of a short sward (3 - 4.5 cm) resulted in an increase in the dominance of *Nardus stricta* and a reduction in *Molinia caerulea*, whereas the 6 cm treatment did not result in expansion of *Nardus stricta* (Hulme *et al.*, 1999). Exclusion of the sheep resulted in an increase in the cover of grazing-intolerant species such as *Molinia caerulea* and ericoid shrubs, and a decline in species associated with short turf and heavy grazing (*Agrostis capillaris*, *Anthoxanthum odoratum*, *Carex pilulifera* and *Nardus stricta*) (Hulme *et al.*, 1999). The three maintained sward heights were all lower than the summer inter-tussock sward heights measured within the three Kirkton Face enclosures, suggesting that the grazing pressures in the experiment carried out by Hulme *et al.* (1999) were higher. Although the vegetation types were similar and the experiments were carried out on the same farm it is difficult to compare the results from the two experiments, since Hulme *et al.* (1999) used small 0.3 ha plots, which were grazed by wethers during the summer only. Stock numbers were also adjusted at weekly intervals to maintain the required sward heights. This grazing management was very different from that established within the Kirkton Face enclosures and failed to replicate what happens on commercial hill farms. Nevertheless, under the highest stocking rate

(Enclosure 3) the cover of *Molinia caerulea* did decline significantly within the U5b community. A decline in *Molinia caerulea* under cattle grazing was also observed by Common *et al.* (1998) within a *Nardus stricta* dominated grassland, and Grant *et al.* (1996a) within a grassland initially dominated by *Molinia*. Davies (1987) observed a disappearance of *Molinia caerulea* from grassland initially dominated by the species when grazed by wethers at stocking rates of both 5 and 15 sheep ha^{-1}.

Both the U5c and U5b communities showed an initial rapid decline in mean summer sward surface height followed by a stabilisation under all three treatments. This decline in sward height was coupled with a change to a more uniform, less tussocky grassland. It is likely that due to the slow dynamics of these upland grasslands, the single year when the treatments were similar was not sufficiently long enough for them to reach equilibrium with their new environment (Hill *et al.*, 1992). The decline in the summer sward surface height during the first three years was therefore probably a response to the change from the pre-1994 management to the all year round grazing established within all three enclosures thereafter. It is possible that the animals grazing the much larger area of pasture available to them prior to the erection of the fences were more selective, avoiding the taller more tussocky species, such as *Nardus stricta*, and concentrating on the inter-tussock vegetation.

The general reduction in the mean summer sward height and the *Nardus stricta* height within the U5b community, may have allowed the once hidden *Juncus squarrosus* plants to become more evident within the sward as they showed no decline in height. As the ability of the sward stick platform to intercept the *Juncus squarrosus* increased, there was a resultant increase in the recorded cover of the species. It is impossible to determine from the sward stick data whether there was an actual increase in the number of *Juncus squarrosus* plants. *Juncus squarrosus* has a low competitive ability due to its slow growth rate, shade intolerance and the way its foliage is held close to the ground (Welch, 1966). Under a no-grazing situation this inability to grow upwards means that it gets shaded-out by taller species (such as *Deschampsia flexuosa* and *Calluna vulgaris*), and overwhelmed by accumulating litter (Welch, 1966), therefore declining in cover, as was observed by Marrs *et al.* (1988) and Hill *et al.* (1992). However, under situations in which grazing and trampling create a shorter sward (as observed in all three enclosures in this study), it can successfully compete with other species (Welch, 1966). Marrs *et al.* (1988) also observed a decline in the cover of *Juncus squarrosus* under a free-ranging sheep stocking rate of 1.4 sheep/ha (0.112 LU/ha) (50% higher than Enclosure 1). This illustrates the problem of comparing overall trends in species change in sites which have different species compositions, spatial distributions and structures (Miles, 1987), and which are subject to different environmental conditions (i.e. climate, soils, hydrology, altitude, slope, aspect, geographical location, native herbivores, seed rain and seed bank). Other factors may also effect how the vegetation responds, such as past environmental and management conditions, short-term cyclical changes in the weather, or changes in the performance of individual plants due to their age or life history (Miles, 1987; Ball, 1974; Clary and Holmgren, 1987). Perhaps the greatest difficulty when comparing the changes observed by Marrs *et al.* (1988) with those observed in this study is the problem of stocking densities. Overall stocking rates which encompass large and varied areas (both in terms of vegetation types and topography) can be very misleading, as they do not represent the actual grazing pressure imposed on the particular vegetation patch that has been monitored.

The year to year variation in mean spring sward surface heights were probably related to management factors or variations in the weather. All the sheep from the enclosures were removed during January and February 1996 due to the severe weather conditions, and this is probably responsible for the peak in sward heights in 1996. The reason for the peak in 1998 is less clear, since none of the animals were removed over the winter period, and soil and air temperatures in March and April were not significantly higher in 1998 than in any other year. However, the total number of days when 75 % of the enclosure area was covered with snow was lower in 1998 than in any of the previous 3 years (31 days compared with 46, 54 and 64 days). Therefore, the sward in 1998 may not have been crushed as much. In addition to this the U5b and U5c communities were covered with a light snowfall for seven days at the beginning of April 1998, which would have reduced the grazing impact on this vegetation prior to the measurement of the first set of sward heights. April snow cover was recorded on a maximum of only 2 days in the previous 3 years.

The summer grazing cattle had a significant impact on the height of the M6d community and its major constituent *Juncus acutiflorus*. The cattle appeared to have an immediate impact following their introduction into the enclosure in June 1995. Year to year variations in the height of the M6d community within Enclosure 3 were probably due to differences in the grazing behaviour of the cattle, as different animals were used each year. The cattle appeared to utilise the M6d community in 1995 and 1996 to a greater extent than in 1997 and 1998. There was no evidence of grazed *Juncus acutiflorus* within the two sheep only enclosures, and the annual variations in mean summer sward surface height are therefore unlikely to be grazing related. It is not possible to determine why the ungrazed *Juncus acutiflorus* was so much higher in 1998 than in the previous years. The large increase in the cover of *Juncus acutiflorus* within Enclosure 3 suggests that the cattle grazing and its associated trampling and poaching were actually stimulating the growth and spread of this species, rather than reducing it.

4.7 Conclusions

Vegetation always responds to management change, but this response may be gradual or rapid, subtle or clear (Miles, 1987). Any temporal stability within vegetation patches is only relative, as vegetation is constantly changing through time as individuals die and are replaced (although the rate at which this change occurs can vary greatly) (Miles, 1987). Extrapolating which changes are due to the dynamic nature of the vegetation and which are in response to the imposed treatments is therefore extremely difficult, particularly when only minor changes are observed. To add to this, changes due to weather fluctuations may partially obscure changes caused by alterations in grazing management (Ball, 1974; Clary and Holmgren, 1987). Within the monitoring period (1994 - 1998) the summer of 1995 was a climatic anomaly as outlined in Chapter 2. It had a significantly higher mean summer maximum temperature than in any other year. It also had the highest maximum June, July and August temperatures and the lowest June and August rainfall totals. It is likely that this warmer, drier summer would have had an effect on the vegetation. Different species will have responded to this climatic anomaly in different ways and at different rates. Some of the responses will have been immediate (i.e. the death of individual plants), whilst others will have been longer term (e.g. increased or decreased seed set and germination).

Although there was little evidence of changes in species composition or frequency, structural changes in the swards were observed, clearly indicating the differences between the treatments and the period before the trial was established.

The three grazing treatments had little impact on the species composition of the U5c, CG10b or U10a communities, although cattle grazing did appear to affect the calcareous grasslands to a certain extent. Cattle grazing did not however have an observed impact on the composition of the *Nardus stricta* dominated swards.

Certain species, which appeared to show clear trends within one community type, showed the opposite response in the other communities, and few species followed similar trends to those reported from other sites. Very few additional species appeared within any of the sample stands. Whether there is potential for novel species to invade the communities in the future is very much dependent upon the seed rain and soil seed bank (Bullock *et al.*, 1994), but these factors were not examined in this study. A summary of the main responses of the vegetation to the three grazing treatments is given in Table 4.19.

The difference between the three grazing treatments appears to have been insufficient to cause any major divergence in the species compositions of any of the monitored communities in the short term. It is possible that the different grazing intensities may have resulted in boundary changes between shorter and more tussocky swards, and in the fine-scale patterning within the grasslands (Bakker *et al.*, 1983). This monitoring of boundaries requires further study.

Table 4.19 - A summary of the impact of grazing treatment on species composition, structure and cover, within the monitored vegetation types

Enclosure	Grazing Treatment	Impact on vegetation
1	All year round grazing by **sheep** at an annual stocking rate of **0.074** LU ha^{-1}	1) Limited, minor changes in species frequency and cover within the U5c community. 2) Increase in ruderal and grazing tolerant species within the CG10b grassland. 3) Minor changes in species frequency within the U10a community suggesting initial move towards a more grass dominated U4e community. 4) U5c and U5b swards becoming shorter, more homogeneous and less tussocky. 5) Significant increase in the cover of *Juncus squarrosus* within the U5b community.
2	All year round grazing by **sheep** at an annual stocking rate of **0.051** LU ha^{-1}	1) Limited, minor changes in species frequency within the U5c, CG10b and U10a communities. 2) U5c and U5b swards becoming shorter, more homogeneous and less tussocky. 3) Significantly higher U5c and U5b mean summer sward surface heights than in the other two enclosures. 4) Significant increase in the cover of *Juncus squarrosus* within the U5b community.
3	All year round grazing by **sheep** at an annual stocking rate of **0.046** LU ha^{-1}, plus summer grazing **cattle** at **0.185** LU ha^{-1} from mid June to late September	1) Limited, minor changes in species frequency within the U5c and U10a communities. 2) Increase in ruderal and grazing tolerant species within the CG10b grassland. 3) Increase in bare ground within the CG10b grassland. 4) U5c and U5b swards becoming shorter, more homogeneous and less tussocky. 5) Significant increase in the cover of *Nardus stricta* within the U5c community. 6) Significant increase in the cover of *Juncus squarrosus* within the U5b community. 7) Significantly lower M6d mean summer sward surface heights than in the other two enclosures. 8) Significant increase in the cover of *Juncus acutiflorus* within the M6d community.

CHAPTER 5 – THE ABOVE-GROUND BIOMASS OF INDIGENOUS GRASSLAND AND MIRE COMMUNITIES

5.1 Summary

1) The mean monthly above-ground biomass values of three plant communities (U5c, U5b and M6d) were estimated within the three study enclosures.
2) The methodology involved harvesting strips of vegetation *in situ*, sub-sampling, sorting, drying and weighing.
3) Mean above-ground biomass values from all the communities varied significantly through the seasons.
4) Mean summer biomass values varied from year to year. The vegetation within all three enclosures responded in a similar manner over time, with significantly higher summer and spring biomass levels in 1996 compared with 1994 and 1995.
5) The enclosure with summer grazing cattle had significantly lower U5c and M6d mean above-ground biomass values than the other two enclosures.
6) The mean above-ground biomass of the U5b community was significantly lower in the enclosure with the higher sheep stocking rate than in the other two enclosures.
7) Over a period of four years the U5c community within Enclosure 2 (sheep stocking rate of 0.051 LU ha^{-1}) became shorter, denser and more structurally homogeneous, with an increased biomass of both bryophytes and dead material.
8) Regression equations, R^2 values and results of significance tests were obtained for the relationships between sward height and biomass within the U5 grasslands.

5.2 Introduction

Approximately 15 % of mainland Britain lies above 244 m and has a rainfall of more than 1270 mm (Rawes and Welch, 1969). This upland area generally supports low densities of domestic herbivores, in particular sheep. These upland grazing systems support a range of vegetation community types, which vary in species composition and productivity, and hence in the seasonal food resource they offer to large grazing animals (Hunter, 1962; Gordon, 1989a; 1989b). The spatial distribution of these different vegetation patches can thus have a major influence on the foraging behaviour of free-ranging herbivores (Senft *et al.*, 1987; Gordon and Illius, 1992; Hester *et al.*, 1999). The nutrient flows and community dynamics within these patches are affected by the grazing, trampling, defecation and urination of the herbivores (Hester *et al.*, 1999). Differences in the size, foraging behaviour and plant species preferences of different species and breeds of herbivore can result in different impacts on the vegetation (Gordon, 1989a; 1989b; Grant *et al.*, 1996b). Alterations to the grazing management system at a particular site can therefore have major impacts on the species composition, sward structure, sward height, and standing live and dead biomass of the vegetation (Miles, 1987). These changes could have beneficial or detrimental impacts in terms of agricultural production, nature conservation, landscape value or recreational use of the land.

Other factors can also effect species composition and productivity within upland vegetation types. Climatic anomalies, such as unusually dry or hot summers, or plant damaging weather events such as floods or severe gales, can cause short-term changes in productivity or much longer-term changes in species composition (Clary and Holmgren, 1987). Temporal, spatial and quantitative changes in the damage caused by native herbivores and plant diseases can also have major direct and indirect impacts on the vegetation (Clary and Holmgren, 1987). They not only affect the ability of the vegetation to tolerate further grazing, but may also lead to changes in the foraging behaviour of the domestic herbivores, therefore affecting communities not directly damaged.

The Kirkton Face study site is composed of a complex mosaic of vegetation patches with different species compositions and structures (see Chapter 4).

The aim of the work described in this chapter was:

1) To obtain mean monthly above-ground biomass values (i.e. total live vascular-plant material, main vascular plant species and species groups, bryophytes, dead standing material and litter) for the U5c, U5b and M6d communities, under the three different grazing systems.
2) To determine whether there was any significant difference in the above-ground biomass of the sampled communities between the three enclosures, prior-to and following the establishment of the experimental stocking rates.
3) To determine whether there was a seasonal change in the amount of above-ground biomass.
4) To determine whether there was any year-to-year variation in the above-ground biomass, particularly in early spring prior to the onset of growth and during mid-summer when biomass is likely to be at its maximum.
5) To obtain mean monthly above-ground biomass values (i.e. total live vascular-plant material, main vascular plant species and species groups, bryophytes, dead standing

material and litter) for the U4d *Festuca ovina - Agrostis capillaris - Galium saxatile* (*Luzula multiflora - Rhytidiadelphus loreus*) community, within Enclosure 2.

6) To determine the relationships between standing biomass and sward surface height for the U5c and U5b communities, in order to obtain regression equations that could be incorporated into the Hill Grazing Management Model (Armstrong *et al.*, 1997a) (Chapter 7).

5.3 Materials and methods

5.3.1 METHODOLOGIES FOR ESTIMATING ABOVE-GROUND BIOMASS

An estimate of the biomass of a species present at a certain point in time can be calculated using the total dry matter (gDM m^{-2}) and the proportion of the dry matter comprising the particular species (i.e. the percentage dry weight). Three methods can be used to determine percentage dry weight ('t Mannetje, 1978):

1) Direct measurement (i.e. the harvesting, sorting, drying and weighing of a sample);

2) Visual estimation;

3) Indirect estimation.

The first method is the most labour intensive, but it is the most accurate on a per unit area basis. However, because of the time required to carry out this method, the number of samples that can be processed is limited, which can result in poor estimates of percentage dry weights, with some species never being sampled.

Subjective visual estimation can only be carried out effectively by trained observers, and the results obtained from different observers and at different times may not be comparable due to operator bias (Frame, 1993). This method allows numerous estimates to be made rapidly for subsequent analyses, but it cannot be used to obtain precise measurements (Frame, 1993). Visual estimation is most appropriate for homogeneous swards with simple botanical compositions (Frame, 1993). It is therefore of limited value in complex indigenous grasslands and mires such as those found within the study site.

The total above-ground biomass of a sward can be estimated indirectly based on measurements of sward height (Bircham, 1981) or electronic capacitance (Vickery *et al.*, 1980), or by the use of weighted disc instruments (e.g. automatic rising plate meters (Earle and McGowan, 1979)) or point quadrats (Jonasson, 1988). However, in order to estimate percentage dry weights of individual species or groups of species other methodologies for indirect estimation have been developed, such as the dry-weight-rank (DWR) method ('t Mannetje and Haydock, 1963; Jones and Hargreaves, 1979). Another method, which involves some harvesting in conjunction with indirect estimations, is the comparative yield estimate (CYE) (Haydock and Shaw, 1975; Kelly and McNeill, 1980; Friedel *et al.*, 1988; Hofstede *et al.*, 1995). This semi-destructive technique provides quick and reproducible biomass data with limited damage to the vegetation. It uses a double sampling procedure based on the comparison of the dry matter yield in a quadrat with that of a series of standard reference quadrats (Haydock and Shaw, 1975).

Although both the DWR and CYE methods could have been used in this study, the more accurate, though time consuming, direct method of harvesting all the samples was used.

5.3.2 FIELD METHODS

5.3.2.1 *Vegetation types sampled*

The following vegetation types were sampled from each of the three enclosures:

1) U5c *Nardus stricta - Galium saxatile* (*Carex panicea - Viola riviniana*) grassland, between 400 - 450 m;

2) *Juncus squarrosus* rich U5b *Nardus stricta - Galium saxatile* (*Agrostis canina - Polytrichum commune*) grassland, between 450 - 520 m;

3) M6d *Carex echinata - Sphagnum recurvum* (*Juncus acutiflorus*) mire, between 360 - 400 m;

A fourth community was sampled from Enclosure 2 only:

4) U4d *Festuca ovina - Agrostis capillaris - Galium saxatile* (*Luzula multiflora - Rhytidiadelphus loreus*) grassland containing some species more typical of a U10a *Carex bigelowii - Racomitrium lanuginosum* (*Galium saxatile*) moss-heath, at approximately 580 m.

5.3.2.2 *Sampling methodology*

The patches of vegetation from which the samples were harvested, were subjectively chosen to be both extensive and homogeneous. The patches also had to have similar species compositions across the three enclosures (where appropriate), and be located at similar altitudes.

Strips of vegetation (11 cm x 155 cm) were harvested at monthly intervals from each of the communities (Table 5.1). Each cut was taken to ground level, using AL-KO 6 rechargeable garden shears (AL-KO International, Consett, County Durham, UK). All the cut material, plus any litter within the cut strip, was placed into clearly labelled plastic bags. The dates on which sampling occurred, the number of enclosures sampled and the number of samples per enclosure are shown in Table 5.1

Table 5.1 - Biomass sampling dates, the number of enclosures sampled and the number of samples per enclosure.

NVC	Year	Date of Harvest												Number of enclosures sampled	Number of samples per enclosure
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
U5c	1994				12	18	15	15	11	8	5	3	1	3	3
	1995	*	*	*	18	19	15	12	9	5	4	10	12	3	4 from May
	1996	*	*	5	3	3	4	8	7	4	5	*	*	3	4
	1997	*	*	*	8	9	6	8	12	18	23	*	*	Enc. 2 only	4
	1998	*	*	*	1	29		7	31	29				Enc. 2 only	4
U5b	1994				12	18	15	13	10	7	5	2	1	3	3
	1995	*	*	*	18	19	15	12	9	5	4	10	12	3	4 from May
	1996	*	*	5	2	2	4	8	5					3	4
M6d	1995					16	19	26	22	21		9	7	3	4
	1996	*	*	12	11	15	25	30	28					3	4
U4d	1997	*	*	*	16	14	16	17	14	18	15	13	*	Enc. 2 only	4

* Herbage samples were not collected during these months due to snow cover, ice or ground frost.

5.3.3 Laboratory and analytical methods

Sub-samples were taken using the method described by Grant (1993). Each herbage sample was thoroughly mixed, and any clumps of vegetation were teased apart. Any stones, animal faeces or lumps of soil were removed and if necessary the sample was washed and sieved to remove other soil particles. The sample was then divided into quarters, and the diagonally opposite quarters were recombined. One of the two portions was set aside and the other was re-mixed. The procedure was repeated a further two times to produce a sub-sample of between 12.5 and 20 % of the original. Some of the sub-samples were stored at 4°C for immediate sorting, whilst the remainder were stored in a deep freeze at -18°C for later analysis.

Each sub-sample was sorted into live and dead fractions, and the live fraction was sorted into individual species. An attempt was made to sort the dead fraction into litter and standing dead material, however this was found to be extremely difficult and almost certainly inaccurate. Root material within the litter layer was not removed and therefore the dead fraction did contain some live root material. The sorted material plus the portion of the bulk sample set aside, were dried in an electric drying oven at 80°C for 24-48 hours until completely dry. The dried material was weighed on an electronic balance (Oertling GC32) and the values recorded. The dry weight values of the sorted material were used to determine the proportion of each species within the sub-sample. Dry biomass values (in gDM m^{-2}) for each species were estimated by multiplying each proportion value with the total dry biomass value, this figure was then converted into a value in gDM m^{-2} by using the area of each herbage cut (Equation 5.1). Mean monthly biomass values were calculated for each community within each enclosure.

Equation 5.1 - Equation for determining the dry biomass (in gDM m^{-2}) of individual species within the sward.

$$B_a = [(BSS_a / BSS_t) * BS_t] * (1 / AS)$$

Where:

B_a = Biomass in gDM m^{-2} of species ***a***

BSS_a = Biomass in gDM of species ***a*** within the **sub-sample**

BSS_t = Total biomass of the **sub-sample** in gDM

BS_t = Total biomass of the **sample** in gDM

AS = Area of the **sample** cut in m^2

5.3.4 STATISTICAL ANALYSIS

Since the data on above-ground biomass was unbalanced within and between treatments and had missing values, a variance-component model was fitted by Residual Maximum Likelihood (REML) to calculate means and standard errors of difference (Genstat 5 Committee, 1993). The Wald test which has a Chi squared distribution, was used to test the fixed effect of enclosure (pre and post-trial establishment), on total above-ground biomass, live vascular-plant biomass, bryophyte biomass and dead biomass of each of the communities (Buist and Engel, 1993). Tests for statistically significant differences between values were made by subtracting one value from another and dividing the result by the standard error of difference produced by REML, which is comparable to the least significant difference test (Snedecor and Cochran, 1980).

In order to determine whether there was any year to year variation or consistent trend in above-ground biomass values under the three grazing regimes, two key periods were examined; early spring prior to the onset of growth when live biomass was at its lowest, and summer when live biomass was at its highest.

Within both the U5b and U5c communities the early spring minima in both live biomass and live sward surface height (Chapter 4) occurred in either April or May. Therefore the biomass data from these two months was combined and used in the analyses. Spring biomass data for the U5c and U5b communities was available for 1995 and 1996 from all three enclosures. Additional spring biomass data for the U5c community within Enclosure 2 was available from 1997 and 1998.

Because of yearly variations in the climate, the peak in live biomass did not always occur in the same month in different years, therefore a mean summer biomass value for each year was calculated. For the U5c community data from July, August and September were used in the analyses. Because the sampling of the U5b community finished in August 1996, the mean summer biomass values were calculated using only the July and August values from each year. Summer biomass data for the U5c and U5b communities was available for 1994, 1995 and 1996, from all three enclosures. Additional summer biomass data for the U5c community within Enclosure 2 was available from 1997 and 1998.

Sampling of the M6d community ceased in August 1996, therefore only July and August values were used in the analyses. M6d summer biomass data was available for 1995 and 1996 from all three enclosures.

A variance-component model was fitted by Residual Maximum Likelihood (REML) to calculate means and standard errors of difference (Genstat 5 Committee, 1993). The Wald test was used to test the fixed effects and interactions of year and treatment on the summer and early spring above-ground biomass values (live vascular-plant biomass, dead biomass and bryophyte biomass) of each of the communities (Buist and Engel, 1993).

5.3.5 RELATIONSHIP BETWEEN SWARD HEIGHT AND ABOVE-GROUND BIOMASS

An important function of the Hill Grazing Management Model (Armstrong *et al.*, 1997a) is its ability to predict sward height from standing biomass values. This was considered important because of the role sward height plays in the prediction of herbage intake and diet selection by sheep (Hodgson, 1985; Armstrong *et al.*, 1997a; 1997b). The regression equations embedded within the current model, which calculate sward height from biomass values for indigenous grasslands, were derived from data collected from an *Agrostis - Festuca* sward and a *Molinia* sward (Armstrong *et al.*, 1997a). Neither of these relationships were suitable for making inferences about *Nardus stricta* dominated grasslands, as the structure and rates of production and senescence of *Nardus stricta* grasslands are very different from those of *Agrostis - Festuca* and *Molinia* grasslands (Job and Taylor, 1978).

For the grazed U5c and U5b swards, data on sward height and biomass have been used to derive relationships between the two variables using linear and non-linear regression analyses (Genstat 5 Committee, 1993). In order to determine the most statistically valid and biologically sensible equations to use within the modified version of the Hill Grazing Management Model (see Chapter 7) a number of regression analyses were carried out using mean values of total biomass, live biomass and live vascular plant biomass, together with their associated mean sward height and mean live sward height values. The mean biomass values were calculated using data from each enclosure on each sampling date from April 1995 to August 1996 (i.e. each biomass value is the mean of 3 or 4 herbage samples). The corresponding mean sward height values were obtained using a HFRO sward stick (Barthram, 1986). On each sampling date, thirty sward height measurements were taken from within a 15 m radius of each herbage cut (i.e. each mean sward surface height value was derived from 90 (3 x 30) or 120 (4 x 30) sward height measurements). Due to the seasonal variation in the proportion of live and dead material and the structure of the sward, the number of sward stick contacts with live material (within the 90 or 120 measurements), varied between months and between enclosures. Therefore the number of measurements used to calculate the mean monthly live sward surface heights was not fixed.

5.4 Results

5.4.1 Species composition

5.4.1.1 *Numbers of vascular plant species found within the sub-samples*

The numbers of vascular plant species identified within the sorted sub-samples are shown in Table 5.2. Lists of all the vascular plant species identified within the sub-samples are given in Appendix 5.1.

Table 5.2 - Numbers of vascular plant species found within the herbage samples

Community	Enclosure	Number of Vascular Plant Species					
		Gramineae	Cyperaceae and Juncaceae	Ericaceae and Empetraceae	Forbs	Pteridophyta	**Total**
U5c	1	9	16	1	27	3	56
	2	11	17	1	17	3	49
	3	11	12	3	20	2	48
	All	**14**	**19**	**3**	**28**	**3**	**67**
U5b	1	8	14	3	15	2	42
	2	11	18	3	17	1	50
	3	11	16	5	14	1	47
	All	**13**	**18**	**5**	**20**	**2**	**58**
M6d	1	10	15	0	24	1	50
	2	12	16	0	24	0	52
	3	9	15	0	21	0	45
	All	**15**	**17**	**0**	**26**	**1**	**59**
U4d	2	9	5	3	8	0	25

A total of 67 species were identified within the U5c samples compared with 58 within the U5b samples. Forty-nine species were found in samples from both of these communities. The main difference between the two communities was in the higher biomass of *Juncus squarrosus*, *Vaccinium myrtillus* and *Deschampsia flexuosa* within the U5b community. Species indicative of areas flushed by moderately base-rich water were found within samples from both the U5c and U5b communities (e.g. *Thalictrum* *alpinum*, *Persicaria vivipara* and *Selaginella selaginoides*). Fifty-nine species of vascular plant were identified within the M6d samples, including some species indicative of calcareous flushing (e.g. *Saxifraga aizoides*, *Carex dioica* and *Parnassia palustris*). Only 25 species of vascular plant were identified within the U4d samples. The U4d samples were taken from an exposed ridge-top site, which lacked any calcareous flushing. Seventy-two percent of the species found in the U4d samples were also recorded in samples from the other three communities.

The mean number of vascular plant species per sample was higher in the M6d community than in the other three communities (Table 5.3). The total number of species within the U4d community was much lower than in the U5c and U5b communities, however the mean number of species per sample was the same (i.e. 11) (Table 5.3).

Table 5.3 - Mean number of vascular plant species per sample

Community	Enclosure	Mean Number of Species Per Sample	Range	Standard Deviation
U5c	1	12	4 - 23	3.2
	2	11	6 - 21	2.6
	3	11	6 - 20	2.3
	All	**11**	**4 - 23**	**2.75**
U5b	1	11	4 - 17	2.6
	2	11	5 - 21	3.2
	3	10	6 - 18	2.6
	All	**11**	**4 - 21**	**2.8**
M6d	1	15	6 - 25	4.0
	2	13	5 - 23	3.7
	3	13	5 - 21	3.6
	All	**14**	**5 - 25**	**3.8**
U4d	2	11	8 - 15	1.6

5.4.1.2 *Comparison between the numbers of species recorded within the U5c community using two different methods*

More species were recorded within the sorted U5c sub-samples than within the 32 m^2 permanent quadrat sample stands (Chapter 4 and Table 5.4). The sorted sub-samples from each enclosure only represented an area of approximately 6.4 m^2 of vegetation (i.e. 20% of the sample stand area), however, the random nature and wide spatial and temporal coverage of the areas from which the samples were taken, resulted in a higher number of recorded species. Both methods indicated that the U5c grassland within Enclosure 1 had a higher plant species richness than the U5c grasslands within the other two enclosures, and that the U5c grassland within Enclosure 3 had the lowest plant species richness.

Table 5.4 - The number of species within the U5c grasslands as determined using two different methods

	Number of species recorded within the sorted U5c sub-samples (approx. 6.4 m^2)	Number of species recorded within the U5c fixed quadrat sample stand (32 m^2)
Enclosure 1	56	39
Enclosure 2	49	37
Enclosure 3	48	22
All Enclosures	67	53

5.4.2 ABOVE-GROUND BIOMASS OF THE U5C *NARDUS STRICTA* - *GALIUM SAXATILE* (*CAREX PANICEA* - *VIOLA RIVINIANA*) GRASSLAND

5.4.2.1 *Biomass differences between the three enclosures prior to the establishment of the trial stocking rates*

There were no significant differences between the U5c mean biomass values from the three enclosures prior to the establishment of the trial stocking rates in August 1994 (Table 5.5).

Table 5.5 - Enclosure effects on mean above-ground biomass values within the U5c grasslands prior to the establishment of the trial stocking rates. Data from May 1994 to August 1994 were used in the analyses.

(**NS** $P > 0.05$, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$).

	Mean Biomass (gDM m^{-2})			Enclosure Effects (df = 2)	
	Enc. 1	Enc. 2	Enc. 3	Wald	*P*
Total above-ground biomass	375.1	386.9	428.5	2.7	**NS**
Live vascular plant biomass	157.5	140.9	171.2	2.6	**NS**
Live *Nardus stricta* biomass	73.5	52.9	59.2	4.4	**NS**
Live biomass of grasses (excluding *N. stricta*)#	48.6	37.7	49.4	1.7	**NS**
Bryophyte biomass	51.9	59.1	62.9	0.5	**NS**
Dead biomass (litter and dead standing material)	165.7	186.9	194.4	1.7	**NS**

Data was normalised by square root transformation. Means are for the un-transformed values.

5.4.2.2 *Biomass differences between the three enclosures following the establishment of the trial stocking rates*

There were significant differences between the U5c mean biomass values from the three enclosures following the establishment of the trial grazing regimes (Table 5.6). Enclosure 3, which was grazed by sheep and summer cattle, had significantly lower mean live vascular plant biomass, mean live *Nardus stricta* biomass and mean live other grass species biomass, than the two sheep only enclosures (L.S.D. tests, $P < 0.05$). Enclosure 3 had the lowest mean monthly live vascular plant biomass values in 11 of the 12 sampled months following the introduction of the cattle in June 1995. Mean above-ground biomass values from the two sheep only enclosures were not significantly different during the trial period (L.S.D tests, $P > 0.05$).

Table 5.6 - Treatment effects on mean above-ground biomass values within the U5c grasslands following the establishment of the trial stocking rates. Data from September 1994 to August 1996 were used in the analyses. (NS $P > 0.05$, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$).

	Mean Biomass (gDM m^{-2})			Treatment Effects (df = 2)	
	Enc. 1	Enc. 2	Enc. 3	Wald	P
Total above-ground biomass	573.0	603.3	544.1	8.6	*
Live vascular plant biomass	173.1	168.5	140.1	21.1	***
Live *Nardus stricta* biomass	64.9	56.9	41.2	16.1	***
Live biomass of grasses (excluding *N. stricta*)#	71.0	71.1	52.2	20.3	***
Bryophyte biomass	64.9	72.5	76.3	2.2	NS
Dead biomass (litter and dead standing material)	335.0	362.4	327.7	6.9	*

Data was normalised by square root transformation. Means are for the un-transformed values.

5.4.2.3 *Seasonal changes in above-ground biomass within the U5c community*

The amounts of live and dead above-ground biomass varied temporally in response to the processes of production, senescence, translocation, decomposition and grazing. Figure 5.1 shows the seasonal variation in above-ground biomass of the U5c community within Enclosure 1, as an example. Similar seasonal patterns to those shown in Figure 5.1 were observed in Enclosures 2 and 3.

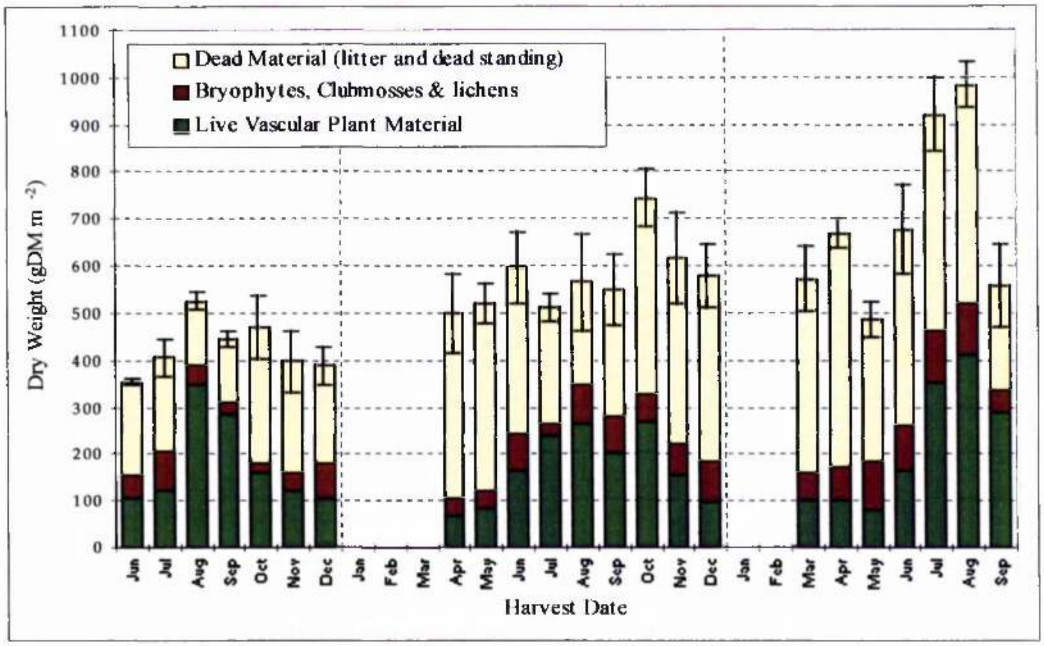


Figure 5.1 - The seasonal variation in above-ground biomass of the grazed U5c community within Enclosure 1 (0.074 LU ha^{-1}). Monthly means from June 1994 to September 1996 are shown. The standard error bars (± 1 S.E.) relate to the total above-ground biomass.

Live vascular plant biomass was at a minimum in early spring, prior to the onset of growth (Table 5.7 and Figure 5.1). Rapid production during the early summer resulted in maximum live vascular plant biomass being achieved in late summer, prior to the main period of senescence (Table 5.7 and Figure 5.1). Dead biomass peaked in early spring following winter senescence and litterfall. High rates of decomposition during the summer resulted in minimum values of dead biomass being recorded in late summer, before the onset of rapid autumn senescence (Table 5.7 and Figure 5.1).

Table 5.7 - Mean monthly maximum and minimum above-ground biomass values of the U5c grasslands within the three study enclosures during the trial period (September 1994 to August 1996).

Enclosure	**Total Above-ground** Biomass (gDM m^{-2})		**Live** Biomass (gDM m^{-2})		**Live Vascular Plant** Biomass (gDM m^{-2})		**Dead** Biomass (gDM m^{-2})	
	Mean Max.	Mean Min.	Mean Max.	Mean Min.	Mean Max.	Mean Min.	Mean Max.	Mean Min.
Enclosure 1 (0.074 LU ha^{-1} sheep only)	**983** (Aug 96)	**388** (Dec 94)	**521** (Aug 96)	**104** (Apr 95)	**412** (Aug 96)	**68** (Apr 95)	**483** (Apr 96)	**107** (Sep 94)
Enclosure 2 (0.051 LU ha^{-1} sheep only)	**987** (Jul 96)	**343** (Dec 94)	**488** (Aug 96)	**122** (Dec 94)	**370** (Aug 96)	**103** (Apr 95)	**565** (Apr 96)	**137** (Sep 94)
Enclosure 3 (0.096 LU ha^{-1} sheep plus summer cattle)	**932** (Jul 96)	**362** (Sep 95)	**456** (Jul 96)	**128** (Apr 95)	**330** (Aug 96)	**53** (Apr 95)	**576** (Apr 96)	**191** (Jul 94)
All Enclosures (± 1 S.E.)	**946.7** *± 66.0* (Jul 96)	**372.0** *± 19.8* (Dec 94)	**483.1** *± 27.8* (Aug 96)	**127.7** *± 13.2* (Apr 95)	**370.5** *± 23.5* (Aug 96)	**74.6** *± 11.2* (Apr 95)	**541.3** *± 25.7* (Apr 96)	**152.7** *± 13.0* (Sep 94)

5.4.2.4 *Seasonal changes in the biomass of the main species and species groups within the U5c community*

Since there were no significant differences between the mean live vascular plant biomass values from the two sheep only enclosures (Enclosures 1 and 2), data from these two enclosures were combined to produce Figure 5.2, which shows the mean monthly live above-ground biomass values of the main species and species groups within the U5c community during 1995. Although the U5c community was visually dominated by *Nardus stricta*, this species never constituted more than 47 % of the live vascular plant biomass in any month (Figure 5.2). During 1995 the mean dry weight of live *Nardus stricta* ranged from less than 30 gDM m^{-2} in May and December, up to 96 gDM m^{-2} in July. The mean biomass of other grass species peaked in September (115.6 gDM m^{-2}), and exceeded that of *Nardus stricta* from August through to December (Figure 5.2).

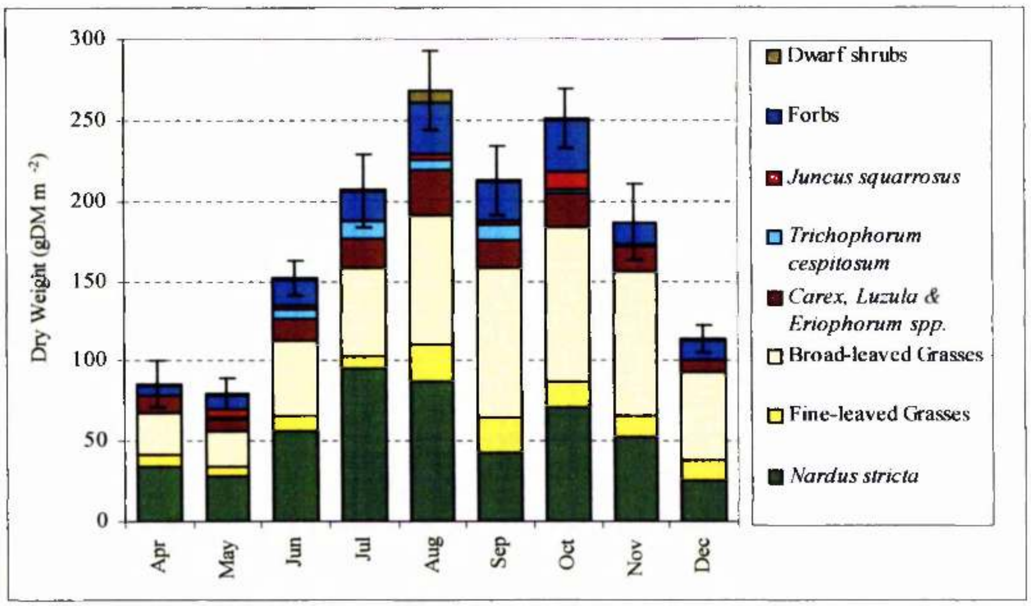


Figure 5.2 - Seasonal changes in the biomass of the main vascular plant species and species groups within the grazed U5c community during 1995. Data from both Enclosures 1 and 2 have been used to derive the monthly means. The standard error bars (± 1 S.E.) relate to the total live vascular plant biomass.

Litter and dead standing material accounted for over 60% of the above-ground biomass during the winter and spring, and even in August dead material formed over 42% of the biomass (Figure 5.3). The amount of dead standing *Nardus stricta* was greater than the amount of live standing *Nardus stricta* in all months apart from July and August. In April and May over 75% of the standing *Nardus stricta* biomass was dead material.

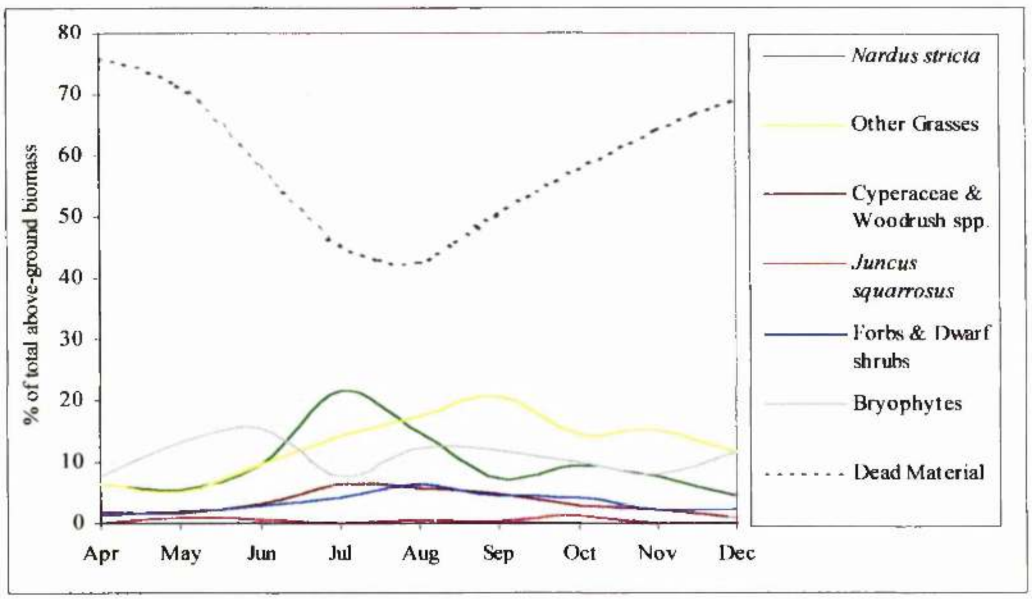


Figure 5.3 - The seasonal change in percentage composition of the grazed U5c community during 1995. The data are expressed in terms of percentages of the total above-ground biomass. Data from both Enclosures 1 and 2 have been used to derive the percentage values.

5.4.2.5 *Annual variations in the mean spring biomass values of the U5c community within the three enclosures*

All three enclosures showed significantly higher mean bryophyte biomass values in spring 1996 compared with spring 1995 (Table 5.8 and Figure 5.4). The mean dead biomass values within Enclosures 2 and 3 were also significantly higher in spring 1996 than in spring 1995 (L.S.D. tests $P < 0.05$) (Figure 5.4).

Table 5.8 - Treatment and year effects on mean spring above-ground biomass values within the U5c grasslands. April and May data from 1995 and 1996 have been used in the analyses.

(NS $P > 0.05$, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$).

	Treatment (df = 2)		Year (df = 1)		Treatment x Year (df = 2)	
	Wald statistic	*P*	Wald statistic	*P*	Wald statistic	*P*
Live vascular plant biomass	6.4	*	1.6	**NS**	0.2	**NS**
Bryophyte biomass	3.8	**NS**	7.8	**	0.4	**NS**
Dead biomass (litter and dead standing material)	2.9	**NS**	11.8	***	5.7	**NS**

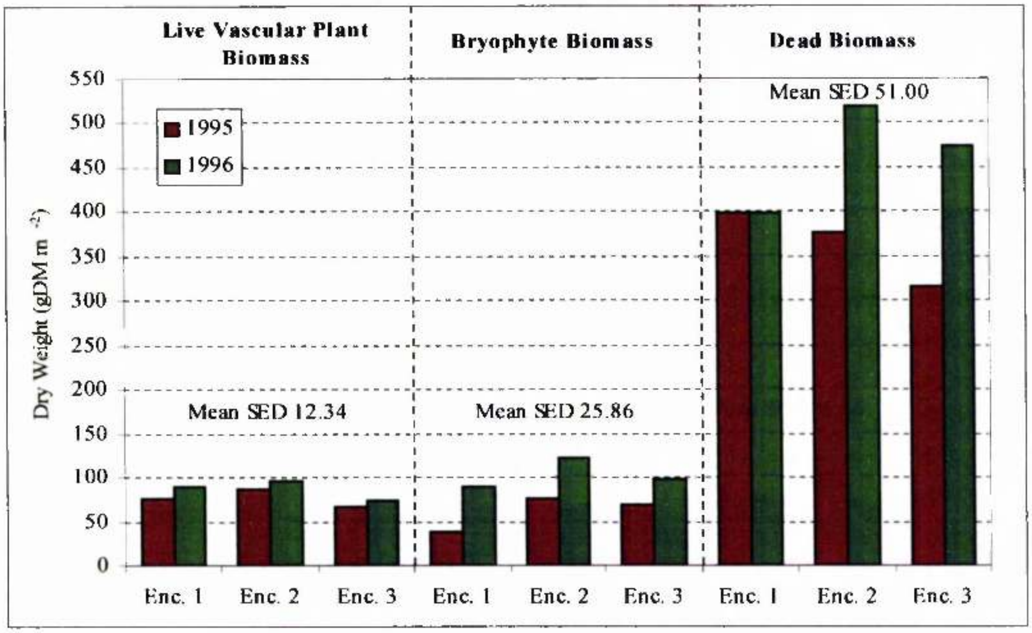


Figure 5.4 - Mean spring above-ground biomass values of the U5c community within all three enclosures during 1995 and 1996. Data from both April and May have been used to derive the spring means.

Additional mean spring biomass data was collected from Enclosure 2 in 1997 and 1998 and this is shown in Figure 5.5. The mean spring live biomass and bryophyte biomass values increased steadily over the period 1994 to 1998 (fixed effect of year: live biomass, Wald = 22.5, df = 3, $P < 0.001$; bryophyte biomass, Wald = 10.9, df = 3, $P < 0.01$). Mean spring dead biomass peaked in 1996 and then declined over the next two years to below its 1995 value.

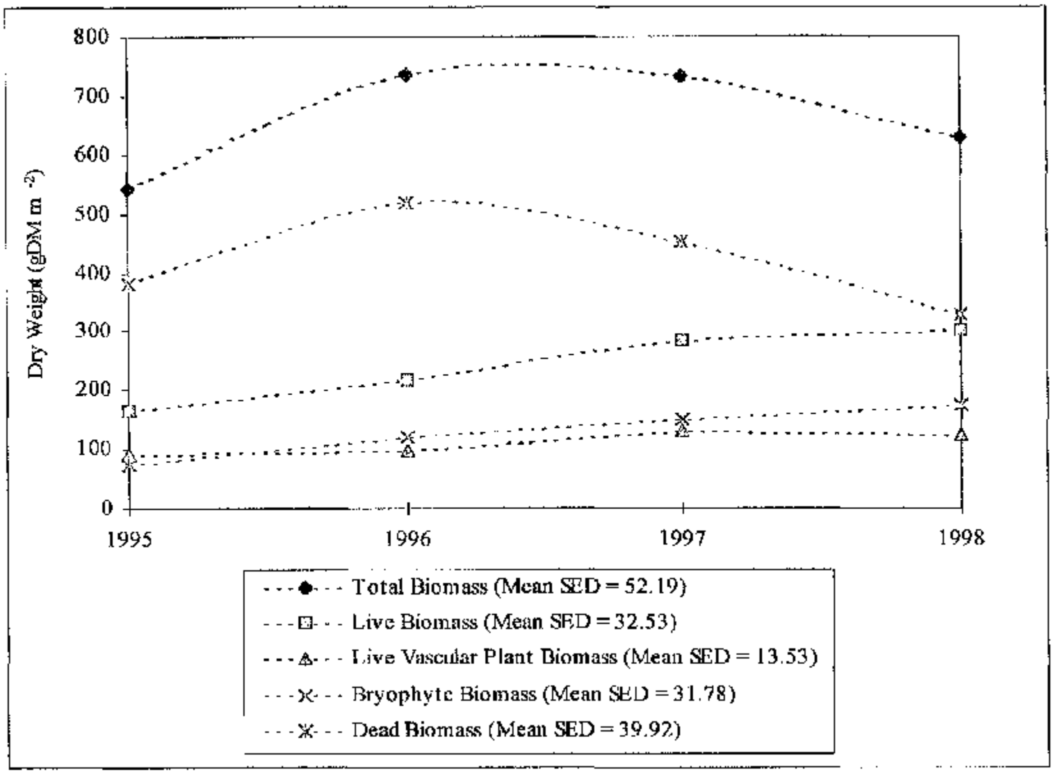


Figure 5.5 - Changes in the mean spring biomass values of the U5c community within Enclosure 2 (0.051 LU ha^{-1}) from 1995 to 1998. Data from both April and May have been used to derive the spring means.

5.4.2.6 *Annual variations in the mean summer biomass values of the U5c community within the three enclosures*

Analysis of the summer biomass data showed that the mean values for live vascular plant biomass, bryophyte biomass and dead biomass were significantly higher in 1996 than in 1994 and 1995 in all three enclosures (Table 5.9 and Figure 5.6).

Table 5.9 - Treatment and year effects on mean summer above-ground biomass values within the U5c grasslands. July, August and September data from 1994, 1995 and 1996 have been used in the analyses.

(**NS** $P > 0.05$, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$).

	Treatment (df = 2)		Year (df = 2)		Treatment x Year (df = 4)	
	Wald statistic	*P*	Wald statistic	*P*	Wald statistic	*P*
Live vascular plant biomass	6.5	*	62.4	***	2.7	**NS**
Live *Nardus stricta* biomass	8.3	*	21.0	***	3.5	**NS**
Bryophyte biomass	2.2	**NS**	16.7	***	1.2	**NS**
Dead biomass (litter and dead standing material)	0.4	**NS**	92.6	***	3.6	**NS**

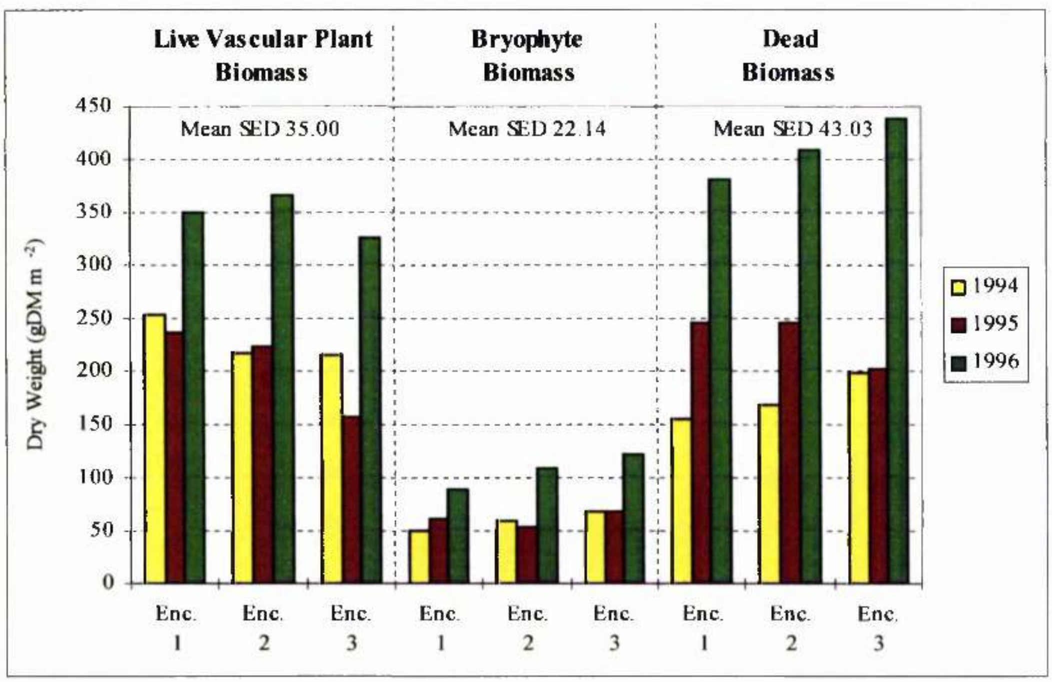


Figure 5.6 - Changes in the mean summer above-ground biomass values of the U5c community within all three enclosures during 1994, 1995 and 1996. Data from July, August and September have been used to derive the summer means.

Within Enclosure 2 the mean summer total above-ground biomass rose sharply from 447 gDM m^{-2} in 1994 to reach a peak of 883 gDM m^{-2} in 1996, when mean live vascular plant biomass and dead biomass values were at their highest (Figure 5.7). The mean summer bryophyte biomass continued to increase over the sampling period resulting in over three times the amount of bryophyte dry matter in 1998 than there was in 1994. The mean summer dead biomass doubled between 1994 and 1996 and then declined steadily. There was significantly more bryophyte biomass and dead biomass in 1998 than in 1994 (L.S.D. tests, $P < 0.05$), however the amount of live vascular plant material was not significantly higher (L.S.D. test, $P > 0.05$).

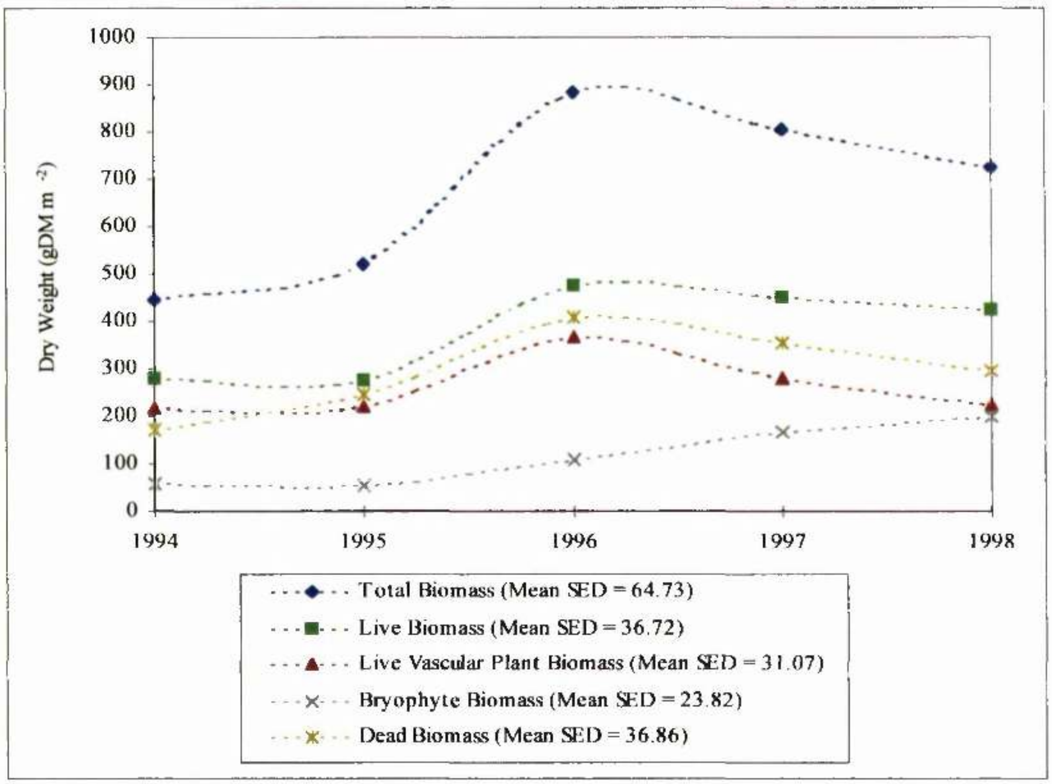


Figure 5.7 - Changes in the mean summer above-ground biomass of the U5c community within Enclosure 2 (0.051 LU ha^{-1}) from 1995 to 1998. Data from July, August and September have been used to derive the summer means.

5.4.3 ABOVE-GROUND BIOMASS OF THE U5B *NARDUS STRICTA - GALIUM SAXATILE* (*AGROSTIS CANINA - POLYTRICHUM COMMUNE*) GRASSLAND

5.4.3.1 *Biomass differences between the three enclosures prior to the establishment of the trial stocking rates*

Prior to the establishment of the trial stocking rates, there were no significant differences between the three enclosures in the mean above-ground biomass, live biomass and live vascular plant biomass values of the U5b grasslands (Table 5.10). There were however significant differences in the composition of the U5b vegetation (Table 5.10).

Table 5.10 - Enclosure effects on mean above-ground biomass values within the U5b grasslands, prior to the establishment of the trial stocking rates. Data from May 1994 to August 1994 were used in the analyses. (**NS** $P > 0.05$, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$).

	Mean Biomass (gDM m^{-2})			Enclosure Effects (df = 2)	
	Enc. 1	Enc. 2	Enc. 3	Wald	*P*
Total above-ground biomass	393.1	451.0	469.5	1.5	**NS**
Live vascular plant biomass	163.2	178.9	156.7	0.8	**NS**
Dead biomass (litter and dead standing material)	196.1	211.5	214.6	0.5	**NS**
Bryophyte biomass	33.8	60.6	98.2	5.2	**NS**
Live *Nardus stricta* biomass	46.3	61.0	29.4	7.5	*
Live biomass of other grass species	10.6	41.0	24.0	13.0	**
Live biomass of sedge species	52.9	16.4	16.8	31.4	***
Live biomass of dwarf shrubs	1.1	5.5	18.5	8.3	*
Live *Juncus squarrosus* biomass #	33.9	28.0	44.1	0.7	**NS**

Data was normalised by square root transformation. Means are for the un-transformed values.

5.4.3.2 *Biomass differences between the three enclosures following the establishment of the trial stocking rates*

Over the period September 1994 to August 1996 the mean total above-ground biomass, bryophyte biomass and dead biomass values were significantly lower in Enclosure 1 than in Enclosures 2 and 3 (L.S.D tests, $P < 0.05$) (Table 5.11). Enclosure 2, which had the lowest stocking rate, had a significantly higher mean live vascular plant biomass than both Enclosures 1 and 3 (L.S.D tests, $P < 0.05$) (Table 5.11).

Table 5.11 - Treatment effects on mean above-ground biomass values within the U5b grasslands, following the establishment of the trial stocking rates. Data from September 1994 to August 1996 were used in the analyses. (**NS** $P > 0.05$, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$).

	Mean Biomass (gDM m^{-2})			Treatment Effects (df = 2)	
	Enc. 1	Enc. 2	Enc. 3	Wald	*P*
Total above-ground biomass	623.7	750.1	741.7	35.0	***
Live vascular plant biomass	199.0	234.4	205.5	17.6	***
Dead biomass (litter and dead standing material)	374.3	432.2	428.1	18.8	***
Bryophyte biomass	50.4	83.5	108.2	31.5	***
Live *Nardus stricta* biomass #	49.9	50.9	41.3	3.7	**NS**
Live biomass of other grass species #	18.0	40.8	35.4	65.4	***
Live biomass of sedge species #	24.3	16.7	7.4	31.6	***
Live biomass of forbs #	6.6	12.4	5.9	25.0	***
Live *Juncus squarrosus* biomass #	77.1	71.3	51.0	10.0	**

Data was normalised by square root transformation. Means are for the un-transformed values.

5.4.3.3 *Seasonal changes in above-ground biomass within the U5b community*

The seasonal variation in above-ground biomass of the U5b community within Enclosure 1 is shown in Figure 5.8 as an example. Similar seasonal patterns were observed in Enclosures 2 and 3. Live vascular plant biomass was at its lowest in early spring and reached a peak in late summer (Figure 5.8 and Table 5.12). The biomass of dead material peaked in early summer and again in autumn (Figures 5.8). The first peak in dead biomass was due to the senescence of old *Juncus squarrosus* leaves, which had remained green throughout the winter.

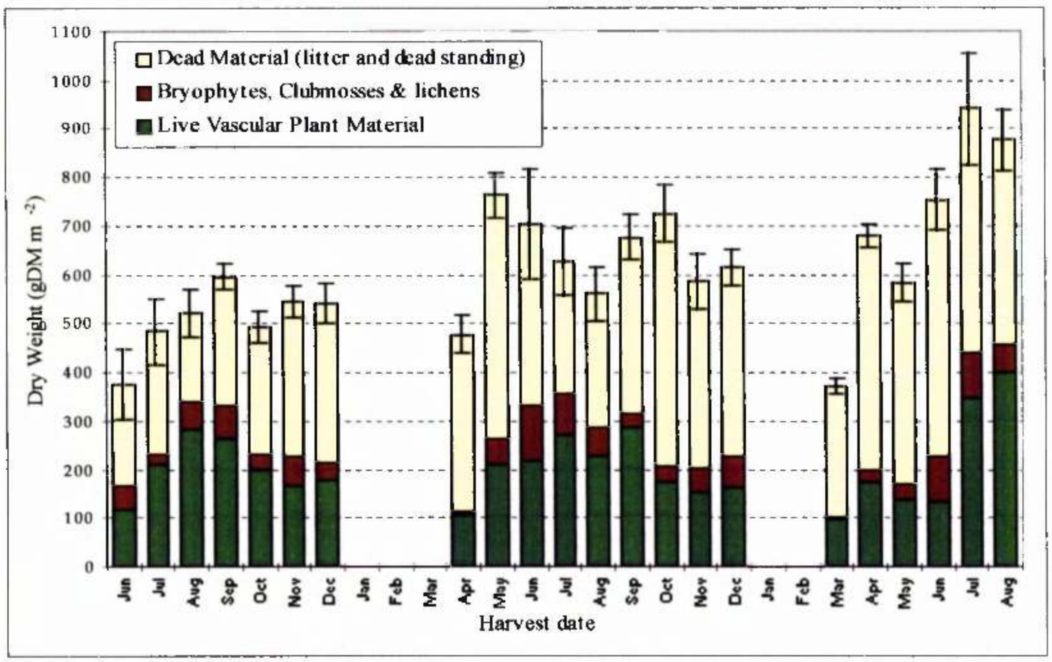


Figure 5.8 - The seasonal variation in above-ground biomass of the grazed U5b community within Enclosure 1 (0.074 LU ha^{-1}). Monthly means from June 1994 to August 1996 are shown. The standard error bars (± 1 S.E.) relate to the total above-ground biomass.

Table 5.12 - Mean monthly maximum and minimum above-ground biomass values of the U5b grasslands within the three study enclosures during the trial period (September 1994 to August 1996).

Enclosure	**Total Above-ground** Biomass (gDM m^{-2})		**Live** Biomass (gDM m^{-2})		**Live Vascular Plant** Biomass (gDM m^{-2})		**Dead** Biomass (gDM m^{-2})	
	Mean Max.	Mean Min.	Mean Max.	Mean Min.	Mean Max.	Mean Min.	Mean Max.	Mean Min.
Enclosure 1 (0.074 LU ha^{-1} sheep only)	**941** (Jul 96)	**373** (Mar 96)	**455** (Aug 96)	**103** (Mar 96)	**399** (Aug 96)	**98** (Mar 96)	**530** (Jun 96)	**263** (Oct 94)
Enclosure 2 (0.051 LU ha^{-1} sheep only)	**1175** (Jul 96)	**477** (Dec 94)	**575** (Jul 96)	**206** (Nov 95)	**491** (Aug 96)	**132** (Apr 95)	**714** (May 96)	**226** (Sep 94)
Enclosure 3 (0.096 LU ha^{-1} sheep plus summer cattle)	**1084** (Oct 95)	**426** (Dec 94)	**468** (Jul 96)	**197** (Nov 94)	**345** (Jul 96)	**110** (May 95)	**709** (Oct 95)	**229** (Dec 94)
All Enclosures (± 1 S.E.)	**1036.3** *± 67.1* (Jul 96)	**481.9** *± 85.5* (Dec 94)	**492.3** *± 31.6* (Jul 96)	**193** *± 23.1* (Mar 96)	**405.7** *± 28.7* (Aug 96)	**138.0** *± 17.0* (Apr 95)	**583** *± 47.4* (May 96)	**260.6** *± 15.6* (Sep 94)

5.4.3.4 *Seasonal changes in the biomass of the main species and species groups within the U5b community*

Because of the limited number of samples and the variation in species composition within the U5b community, data from all three enclosures were combined to provide a more realistic picture of the seasonal changes that occur within a grazed U5b community (Figure 5.9). Mean monthly live *Nardus stricta* biomass peaked in August (81.9 gDM m^{-2}), while the maximum mean monthly biomass of other grass species occurred in September (71.0 gDM m^{-2}) (Figure 5.9). The mean monthly biomass of live *Juncus squarrosus* remained above 59 gDM m^{-2} from April to December, and did not vary significantly over this period (fixed effect of month: Wald = 4.7, df = 8, $P > 0.05$). The biomass of live *Juncus squarrosus* exceeded that of *Nardus stricta* in all months.

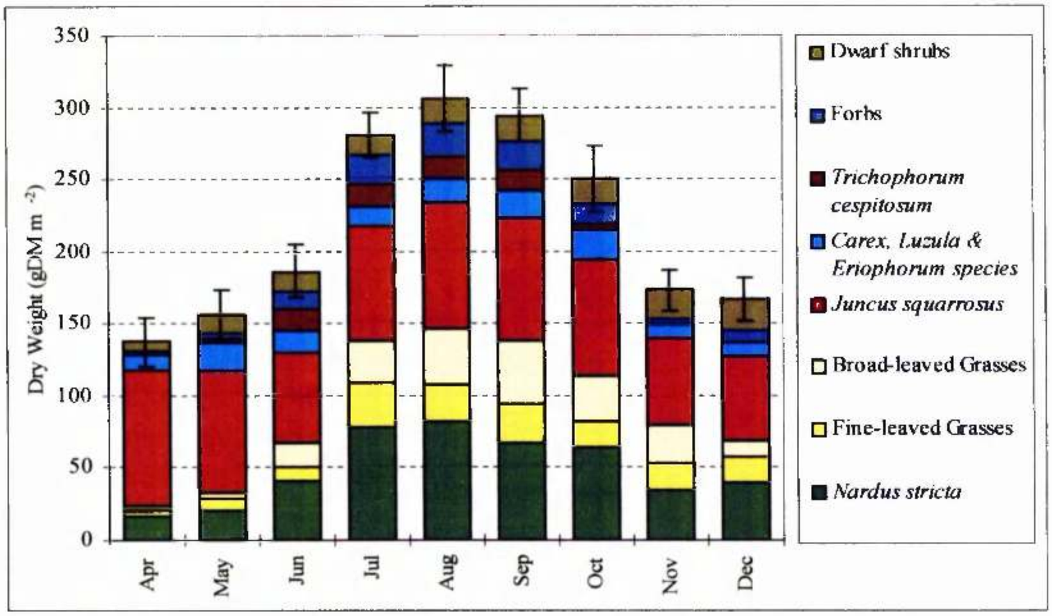


Figure 5.9 - Seasonal changes in the biomass of the main vascular plant species and species groups within the grazed U5b community. Data from all three enclosures have been used to derive the monthly means. The standard error bars (± 1 S.E.) relate to the total live vascular plant biomass.

5.4.3.5 *Annual variations in the mean spring biomass values of the U5b community within the three enclosures*

Enclosures 2 and 3 showed a similar pattern of significantly higher mean spring dead biomass values in 1996 compared with 1995, whereas Enclosure 1 showed no significant difference between years (Table 5.13 and Figure 5.10). There were no significant differences between years in the mean live vascular plant biomass or bryophyte biomass values in any of the enclosures (Table 5.13 and Figure 5.10).

Table 5.13 - Treatment and year effects on mean spring above-ground biomass values within the U5b grasslands. April and May data from 1995 and 1996 have been used in the analyses.

(**NS** $P > 0.05$, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$).

	Treatment (df = 2)		Year (df = 1)		Treatment x Year (df = 2)	
	Wald statistic	*P*	Wald statistic	*P*	Wald statistic	*P*
Live vascular plant biomass	1.5	**NS**	0.1	**NS**	1.0	**NS**
Bryophyte biomass	21.1	***	1.2	**NS**	1.2	**NS**
Dead biomass (litter and dead standing material)	5.4	**NS**	20.7	***	10.1	**

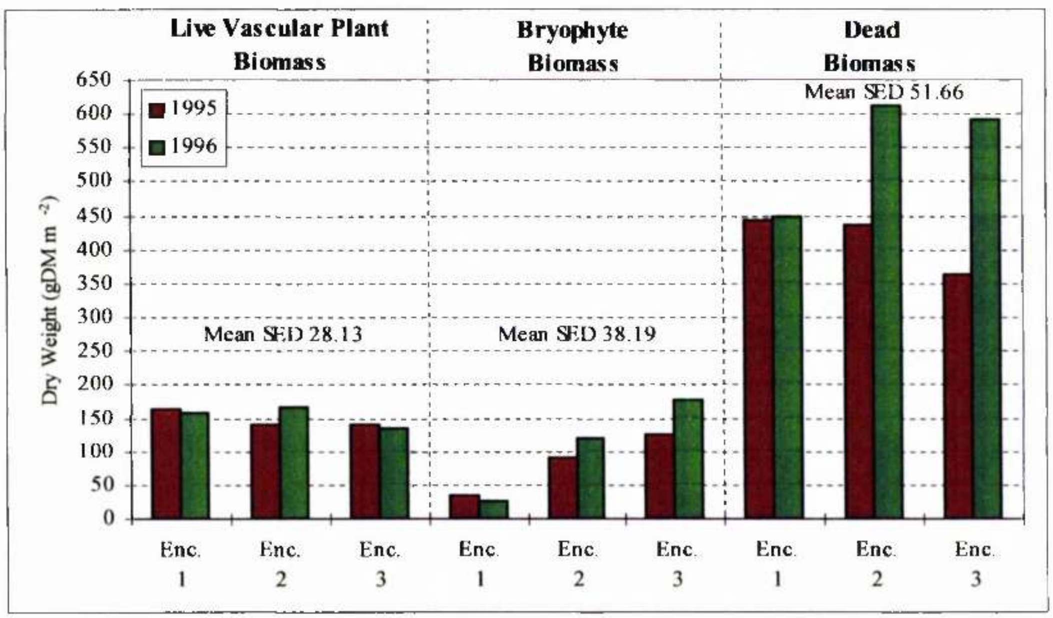


Figure 5.10 - Mean spring above-ground biomass values of the U5b community within all three enclosures during 1995 and 1996. Data from both April and May have been used to derive the spring means.

5.4.3.6 *Annual variations in the mean summer biomass values of the U5b community within the three enclosures*

Analysis of the summer biomass data showed that the mean live vascular plant biomass, mean biomass of grasses (excluding *Nardus stricta*) and mean dead biomass values were significantly higher in 1996 than in 1994 within all three enclosures (Table 5.14 and Figure 5.11).

Table 5.14 - Treatment and year effects on mean summer above-ground biomass values within the U5b grasslands. July and August data from 1994, 1995 and 1996 have been used in the analyses.

(**NS** $P > 0.05$, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$).

	Treatment (df = 2)		Year (df = 2)		Treatment x Year (df = 4)	
	Wald statistic	*P*	Wald statistic	*P*	Wald statistic	*P*
Live vascular plant biomass	17.2	***	41.1	***	4.9	**NS**
Live *Nardus stricta* biomass	9.8	**	1.0	**NS**	8.5	**NS**
Live biomass of other grasses	25.1	***	15.7	***	1.7	**NS**
Bryophyte biomass	6.9	*	0.2	**NS**	2.1	**NS**
Dead biomass (litter and dead standing material)	5.8	**NS**	62.1	***	2.5	**NS**

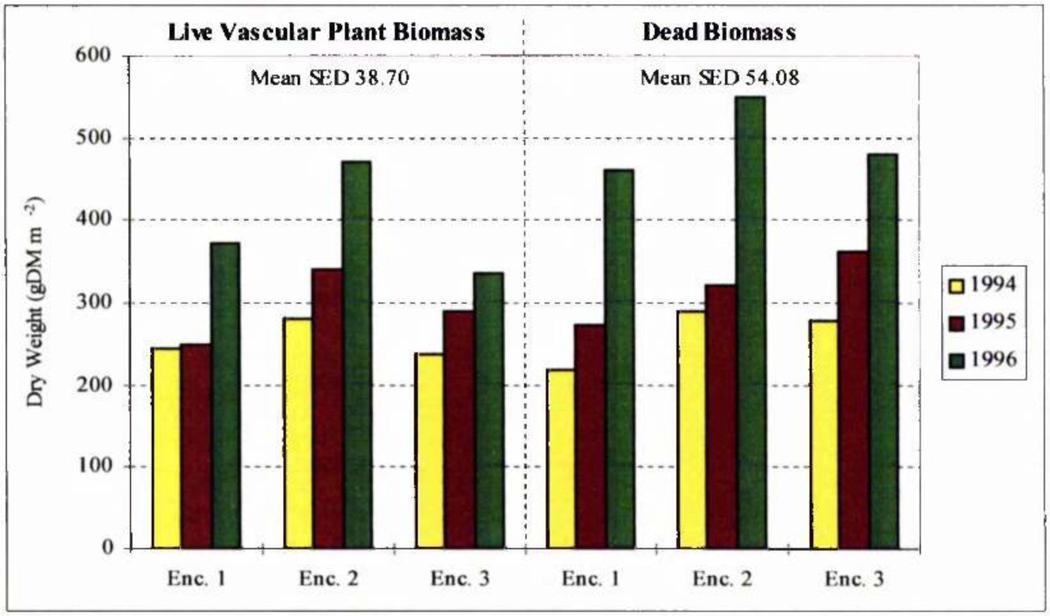


Figure 5.11 - Changes in the mean summer live vascular plant biomass and dead biomass values of the U5b community within all three enclosures during 1994, 1995 and 1996. Data from July and August have been used to derive the summer means.

5.4.3.7 *Comparison between the two U5 grasslands*

The U5b grassland, which contained a much higher proportion of the winter-green rush *Juncus squarrosus*, had significantly higher mean summer and spring live vascular plant biomass and dead biomass values than the U5c grassland (Table 5.15). The mean summer and spring bryophyte biomass values of the two communities were not significantly different (Table 5.15).

Both communities showed rapid growth from May to August, with mean live vascular plant biomass values doubling over this period. In 1995 the live vascular plant biomass in both communities peaked in mid-summer and again in autumn. The autumn peak corresponded with a secondary period of vegetative growth, following a period in late summer dominated by reproductive growth.

Table 5.15 - Differences between the two U5 *Nardus stricta - Galium saxatile* grasslands in the amounts of mean spring and summer above-ground biomass. April and May data from 1995 and 1996 have been used in the spring analyses. July and August data from 1994, 1995 and 1996 have been used in the summer analyses.

(NS $P > 0.05$, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$).

		Mean Biomass (gDM m^{-2})		Community Effect (df = 1)	
		U5c	U5b	Wald statistic	*P*
Spring	Live vascular plant biomass	81.9	150.3	60.7	***
	Bryophyte biomass	81.8	95.6	0.8	**NS**
	Dead biomass (litter and dead standing material)	413.4	482.7	9.6	**
	Total above-ground biomass	577.1	728.7	24.7	***
Summer	Live vascular plant biomass	264.9	314.8	12.3	***
	Bryophyte biomass	83.6	89.2	0.3	**NS**
	Dead biomass (litter and dead standing material)	288.2	359.1	18.6	***
	Total above-ground biomass	636.6	763.0	17.4	***

5.4.4 ABOVE-GROUND BIOMASS OF THE M6D *CAREX ECHINATA - SPHAGNUM RECURVUM (JUNCUS ACUTIFLORUS)* MIRE

The biomass of the M6d community was not measured in the pre-trial period (i.e. before August 18th 1994), and therefore it is not known whether there were any significant differences between the enclosures prior to the establishment of the trial stocking rates.

5.4.4.1 *Biomass differences between the three enclosures following the establishment of the trial stocking rates*

The mean live vascular plant biomass and mean live *Juncus acutiflorus* biomass were significantly lower in the enclosure containing the summer grazing cattle, than in the sheep only enclosures (L.S.D. tests, $P < 0.05$) (Table 5.16). However, mean bryophyte biomass was significantly higher in the cattle grazed enclosure (L.S.D. test, $P < 0.05$). Enclosure 2, which had the lowest annual stocking rate, had a significantly higher mean dead biomass than the other two enclosures (L.S.D. tests, $P < 0.05$) (Table 5.16).

Table 5.16 - Treatment effects on mean above-ground biomass values within the M6d mire community, following the establishment of the trial stocking rates. Data from May 1995 to August 1996 were used in the analyses. (**NS** $P > 0.05$, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$).

	Mean Biomass ($gDM\ m^{-2}$)			Treatment Effects (df = 2)	
	Enc. 1	Enc. 2	Enc. 3	Wald	*P*
Total above-ground biomass	578.1	622.9	580.8	3.0	**NS**
Live vascular plant biomass	197.2	183.7	139.8	29.2	***
Live *Juncus acutiflorus* biomass #	60.19	66.59	33.21	21.1	***
Live biomass of grasses (including *N. stricta*)#	51.78	44.42	52.48	2.4	**NS**
Dead biomass (litter and dead standing material)	263.3	313.2	258.0	11.2	**
Bryophyte biomass	117.6	126.0	183.0	10.1	**

Data was normalised by square root transformation. Means are for the un-transformed values.

5.4.4.2 *Seasonal changes in above-ground biomass within the M6d community*

The seasonal variation in above-ground biomass of the M6d community within Enclosure 1 is shown in Figure 5.13 as an example. Live vascular plant biomass was at its lowest in early spring and reached a peak in late summer (Figure 5.12 and Table 5.17). The biomass of dead material followed a contrasting pattern with a maximum in spring and a minimum in late summer (Figure 5.12 and Table 5.17). Similar seasonal patterns were observed for the M6d community within Enclosures 2 and 3.

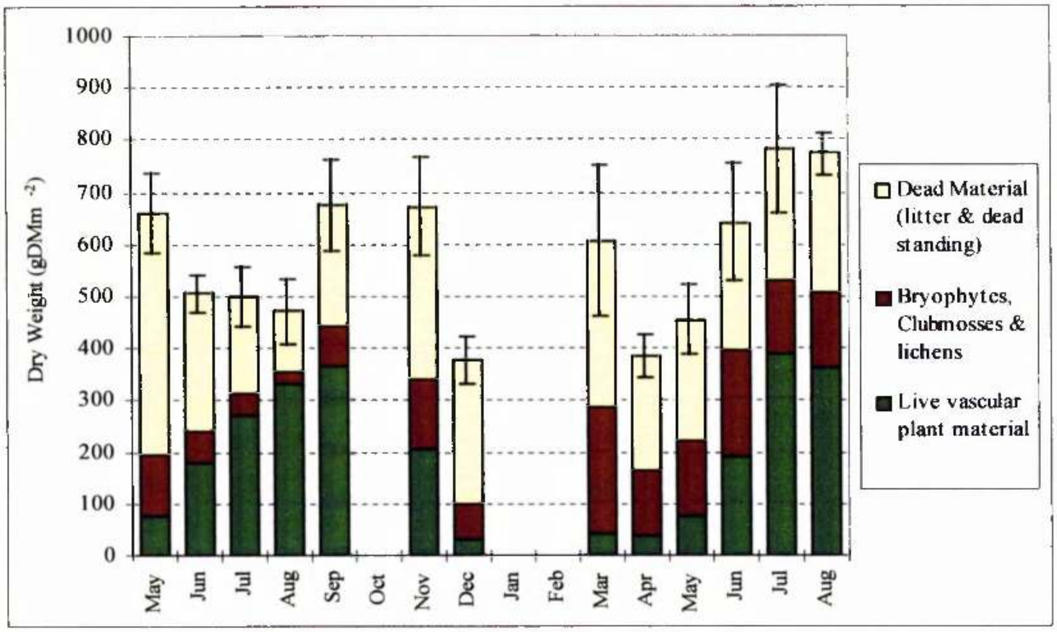


Figure 5.12 - The seasonal variation in above-ground biomass of the M6d community within Enclosure 1 (0.074 LU ha^{-1}). Monthly means from May 1995 to August 1996 are shown. The standard error bars (± 1 S.E.) relate to the total biomass.

Table 5.17 - Mean monthly maximum and minimum above-ground biomass values of the M6d mire community within the three enclosures, between May 1995 and August 1996.

Enclosure	**Total Above-ground** Biomass (gDM m^{-2})		**Live** Biomass (gDM m^{-2})		**Live Vascular Plant** Biomass (gDM m^{-2})		**Dead** Biomass (gDM m^{-2})	
	Mean Max.	Mean Min.	Mean Max.	Mean Min.	Mean Max.	Mean Min.	Mean Max.	Mean Min.
Enclosure **1** (0.074 LU ha^{-1} sheep only)	**784** (Jul 96)	**379** (Dec 95)	**531** (Jul 96)	**100** (Dec 95)	**388** (Jul 96)	**32** (Dec 95)	**465** (May 95)	**119** (Aug 95)
Enclosure **2** (0.051 LU ha^{-1} sheep only)	**817** (Aug 96)	**425** (Dec 95)	**566** (Sep 95)	**107** (Dec 95)	**355** (Aug 95)	**31** (Apr 96)	**468** (Mar 96)	**121** (Jul 95)
Enclosure **3** (0.096 LU ha^{-1} sheep plus summer cattle)	**805** (Jul 96)	**422** (May 96)	**505** (Jul 96)	**176** (Nov 95)	**290** (Sep 95)	**38** (Apr 96)	**384** (May 95)	**96** (Aug 95)
All Enclosures (± 1 S.E.)	**792.2** *± 20.3* (Aug 96)	**411.2** *± 29.4* (Apr 96)	**502.4** *± 39.6* (Jul 96)	**154** *± 40.3* (Dec 95)	**331.1** *± 26.5* (Sep 95)	**35.3** *± 3.6* (Apr 96)	**408.2** *± 29.3* (May 95)	**120.8** *± 11.1* (Aug 95)

5.4.4.3 *Seasonal changes in the biomass of the main species and species groups within the M6d community*

Since there were no significant differences between the mean live vascular plant biomass values from the two sheep only enclosures (Enclosures 1 and 2), data from these two enclosures were combined to produce Figure 5.13, which shows the mean monthly live above-ground biomass values of the main vascular plant species and species groups within the M6d community.

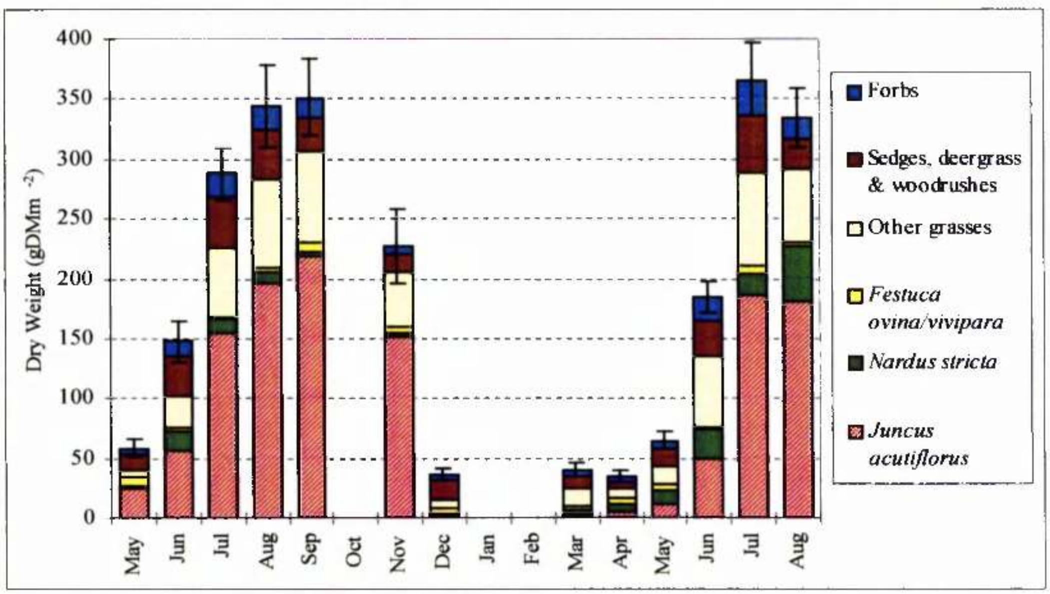


Figure 5.13 - Seasonal changes in the biomass of the main vascular plant species and species groups within the M6d mire community. Data from both Enclosures 1 and 2 have been used to derive the monthly means. The standard error bars (± 1 S.E.) relate to the total live vascular plant biomass.

5.4.4.4 *Annual variations in the mean summer biomass values of the M6d community within the three enclosures*

Analysis of the summer biomass data showed that the mean bryophyte biomass and dead biomass values were significantly higher in 1996 than in 1995, in all three enclosures, but the mean live vascular plant biomass values were not significantly higher (Table 5.18 and Figure 5.14). Mean summer live vascular plant biomass and live *Juncus acutiflorus* biomass values were significantly lower in the sheep and cattle grazed enclosure compared with the sheep only enclosures, whereas mean summer bryophyte biomass was significantly higher in the sheep and cattle grazed enclosure (Table 5.18 and Figure 5.14).

Table 5.18 - Treatment and year effects on mean summer above-ground biomass values within the M6d mire community. July and August data from 1995 and 1996 have been used in the analyses.

(**NS** $P > 0.05$, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $0.001 \geq P$).

	Treatment (df = 2)		Year (df = 1)		Treatment x Year (df = 2)	
	Wald statistic	*P*	Wald statistic	*P*	Wald statistic	*P*
Live vascular plant biomass	26.3	***	0.4	**NS**	4.0	**NS**
Live *J. acutiflorus* biomass	11.1	**	0.3	**NS**	1.5	**NS**
Live biomass of grasses	0.7	**NS**	5.7	*	0.7	**NS**
Bryophyte biomass	12.6	**	22.8	***	1.8	**NS**
Dead biomass	1.4	**NS**	95.9	***	6.2	*

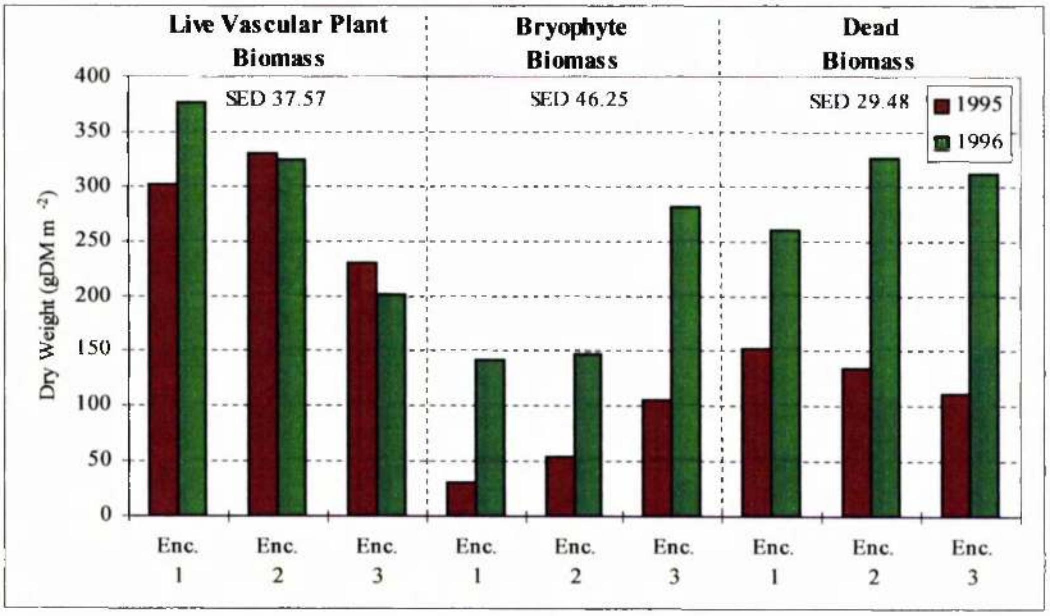


Figure 5.14 - Changes in the mean summer live vascular plant biomass, bryophyte biomass and dead biomass values of the M6d community within all three enclosures during 1995 and 1996. Data from July and August have been used to derive the summer means.

5.4.5 ABOVE-GROUND BIOMASS OF THE U4D *FESTUCA OVINA - AGROSTIS CAPILLARIS - GALIUM SAXATILE* (*LUZULA MULTIFLORA - RHYTIDIADELPHUS LOREUS*) GRASSLAND

Data for the U4d community was only collected from Enclosure 2, between April and November 1997.

5.4.5.1 *Seasonal changes in above-ground biomass within the U4d community*

Mean live vascular plant biomass peaked in July and was at a minimum in April (Table 5.19 and Figure 5.15). Live biomass exceeded dead biomass in all months. The maximum mean bryophyte biomass was recorded in June. Bryophytes formed between 28% (October) and 62% (April) of the monthly mean live biomass (Figure 5.15). Mean monthly total dead biomass values did not vary significantly through the year (main effect for month; Wald = 7.0, df = 7, $P > 0.05$).

Table 5.19 - Mean monthly maximum and minimum above-ground biomass values of the U4d grassland within Enclosure 2, between April and November 1997.

Enclosure	**Total Above-ground** Biomass (gDM m^{-2}) (± 1 S.E.)		**Live** Biomass (gDM m^{-2}) (+ 1 S.E.)		**Live Vascular Plant** Biomass (gDM m^{-2}) (± 1 S.E.)		**Dead** Biomass (gDM m^{-2}) (± 1 S.E.)	
	Mean Max.	Mean Min.	Mean Max.	Mean Min.	Mean Max.	Mean Min.	Mean Max.	Mean Min.
Enclosure **2** (0.051 LU ha^{-1} sheep only)	**673.3** ± *67.0* (Jul 97)	**429.8** ± *32.3* (Oct 97)	**459.3** ± *65.5* (Jul 97)	**267.5** ± *32.0* (Oct 97)	**281.6** ± *33.4* (Jul 97)	**120.9** ± *7.8* (Apr 97)	**240.7** ± *12.8* (Apr 97)	**162.4** ± *4.79* (Oct 97)

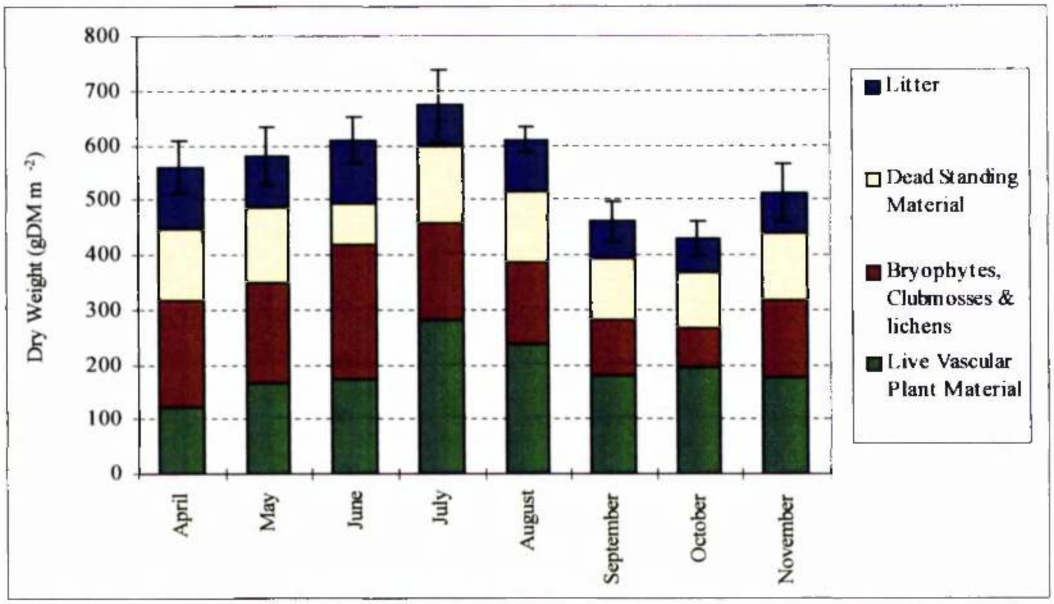


Figure 5.15 - The seasonal variation in above-ground biomass of the grazed U4d community within Enclosure 2 (0.051 LU ha^{-1}). Monthly means from April to November 1997 are shown. The standard error bars (± 1 S.E.) relate to the total biomass.

5.4.5.2 *Seasonal changes in the biomass of the main species and species groups within the U4d community*

The biomass of grasses peaked in August and again in October. Between 39% (July) and 75% (October) of the mean monthly live vascular plant biomass was composed of grasses excluding *Nardus stricta*. Forbs formed over 19 % of the live vascular plant biomass in every month (Figure 5.16). *Galium saxatile* accounted for 68% of the forb biomass, with *Alchemilla alpina* accounting for a further 22%.

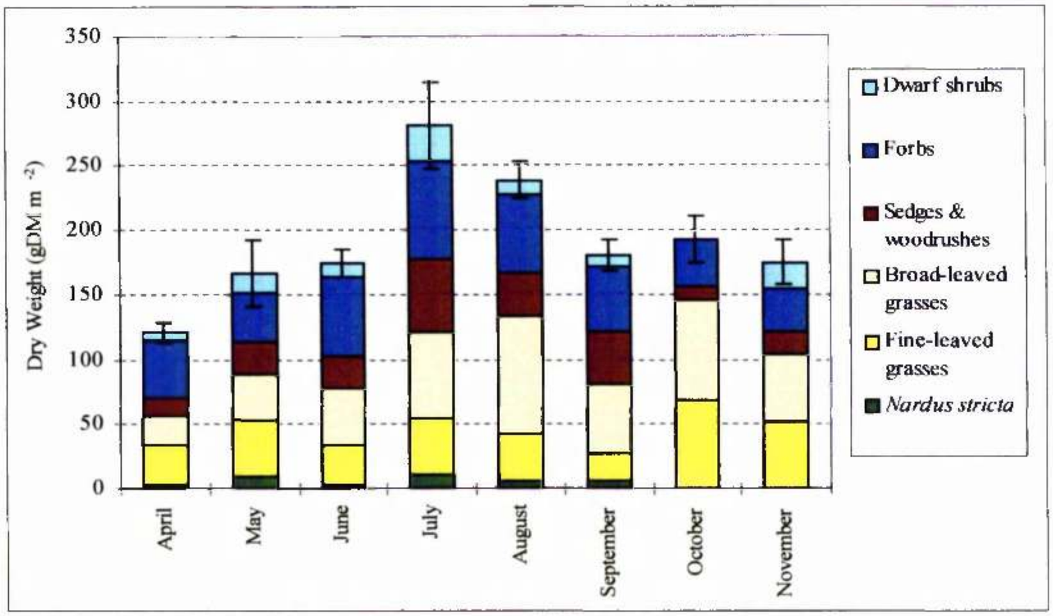


Figure 5.16 - Seasonal changes in the biomass of the main vascular plant species and species groups within the grazed U4d community within Enclosure 2 (0.051 LU ha^{-1}). Monthly means from April to November 1997 are shown. The standard error bars (± 1 S.E.) relate to the total live vascular plant biomass.

5.4.6 Relationship between sward surface height and above-ground biomass

The simple linear relationships between mean sward surface height and mean total above-ground biomass were significant in both the U5c and U5b communities (U5c, $F_{1, 57}$ = 7.08, $P < 0.05$; U5b, $F_{1, 46}$ = 8.43, $P < 0.005$), however both the R^2 values obtained from these regression analyses were less than 0.15. Total above-ground biomass contains both bryophyte and litter biomass, which have little or no effect on sward surface height. By using mean live vascular plant biomass rather than total biomass these elements can be removed, producing more robust relationships that are biologically meaningful and statistically valid. The relationships between; (1) mean sward surface height and mean live vascular plant biomass, and (2) mean **live** sward surface height and mean live vascular plant biomass, were found to be non-linear in both the U5c (Figures 5.17 and 5.18) and U5b communities (Figures 5.19 and 5.20). Best-fit trendlines were obtained using logistic curve equations. All four relationships were highly significant (Table 5.20).

Table 5.20 - Regression equations, R^2 values and significance tests (ANOVA) for the relationships between sward height and biomass within the U5 grasslands.

NVC	Relationship	v_1 *df*	v_2 *df*	*F*	*P*	R^2	Regression Equation
U5c	Mean sward height v mean live vascular plant biomass	3	55	40.96	<0.001	0.674	$y = 5.043 + 11.74 / (1 + \text{Exp}(-0.001745 * (x - 1064)))$
U5c	Mean **live** sward height v mean live vascular plant biomass	3	55	70.54	<0.001	0.782	$y = 2.63 + 13.11 / (1 + \text{Exp}(-0.002594 * (x - 1292)))$
U5b	Mean sward height v mean live vascular plant biomass	3	44	23.81	<0.001	0.593	$y = 10.65 + 7.54 / (1 + \text{Exp}(-0.00222 * (x - 2287)))$
U5b	Mean **live** sward height v mean live vascular plant biomass	3	44	56.27	<0.001	0.779	$y = 2.49 + 16.54 / (1 + \text{Exp}(-0.001378 * (x - 2045)))$

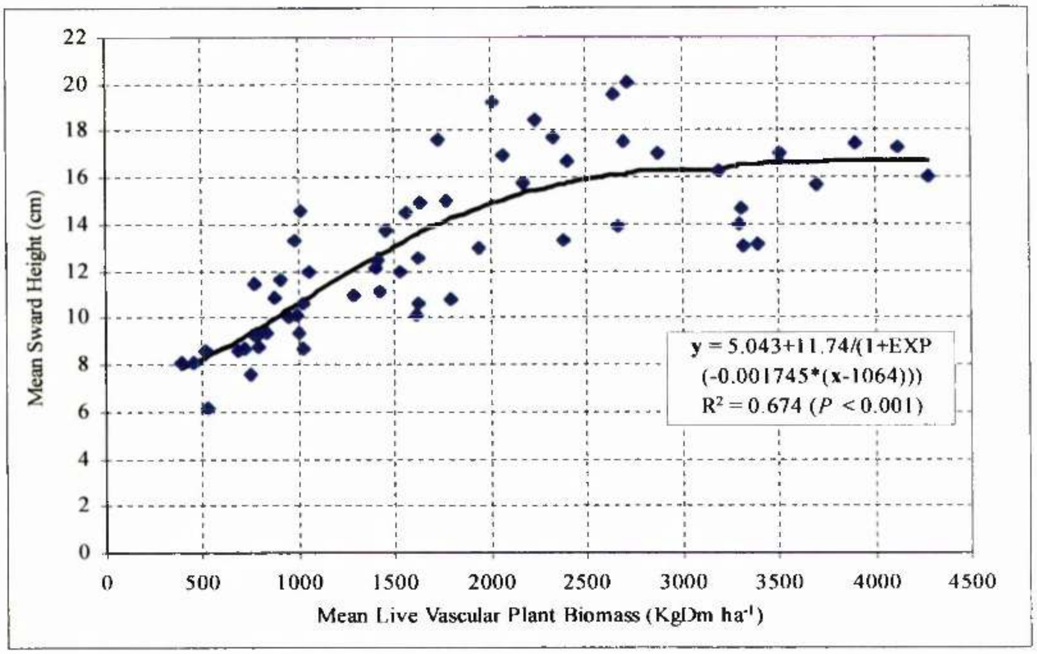


Figure 5.17 - The relationship between mean sward surface height and mean live vascular plant biomass within the **U5c** community (logistic curve fitted).

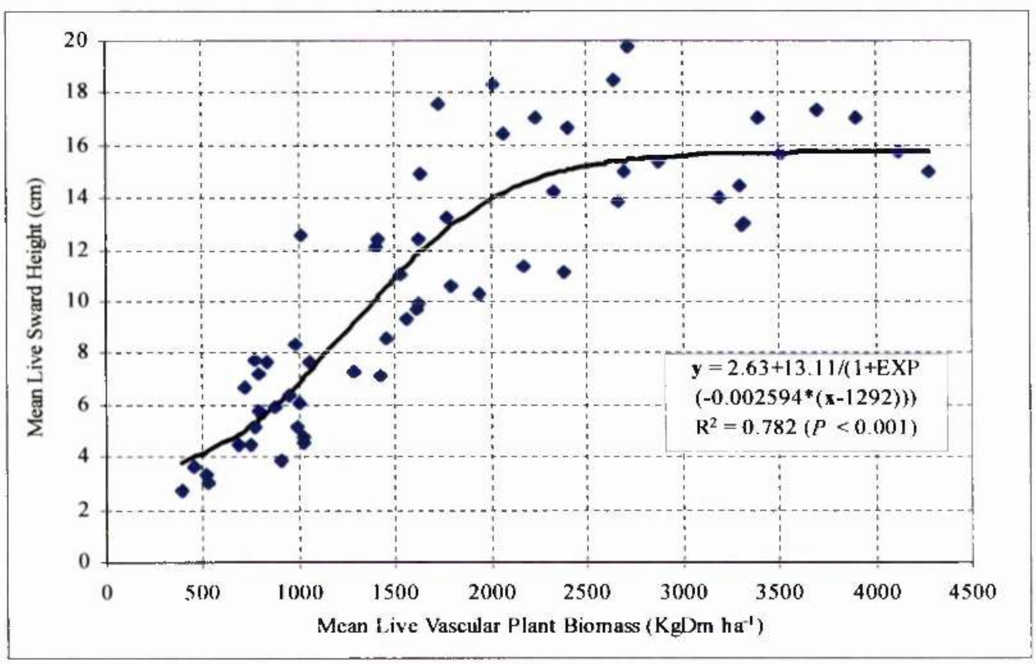


Figure 5.18 - The relationship between mean **live** sward surface height and mean live vascular plant biomass within the **U5c** community (logistic curve fitted).

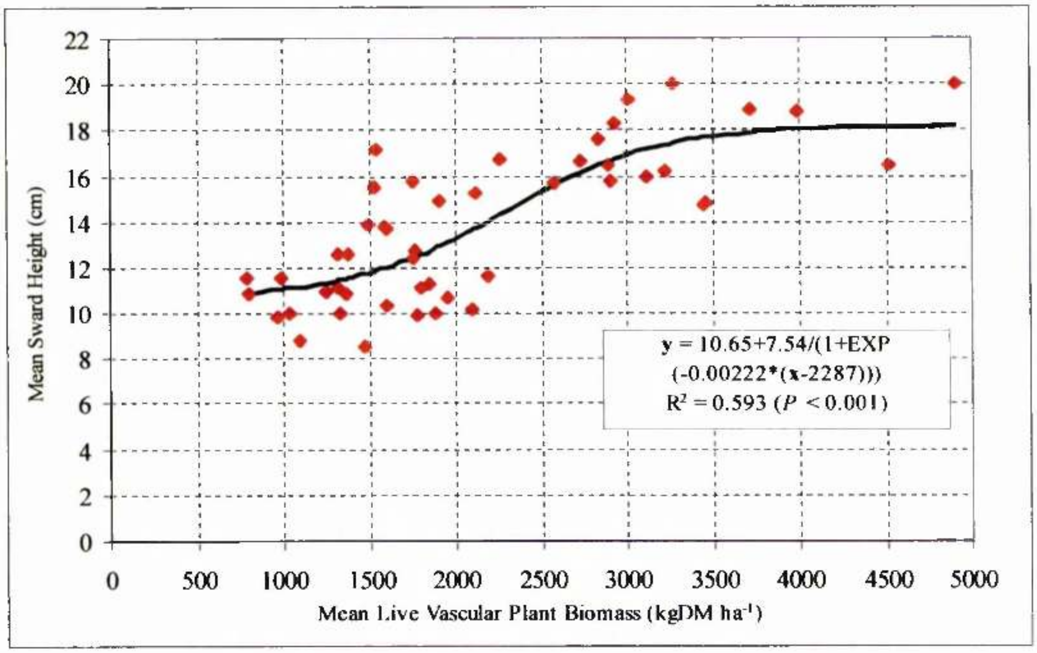


Figure 5.19 - The relationship between mean sward surface height and mean live vascular plant biomass within the **U5b** community (logistic curve fitted).

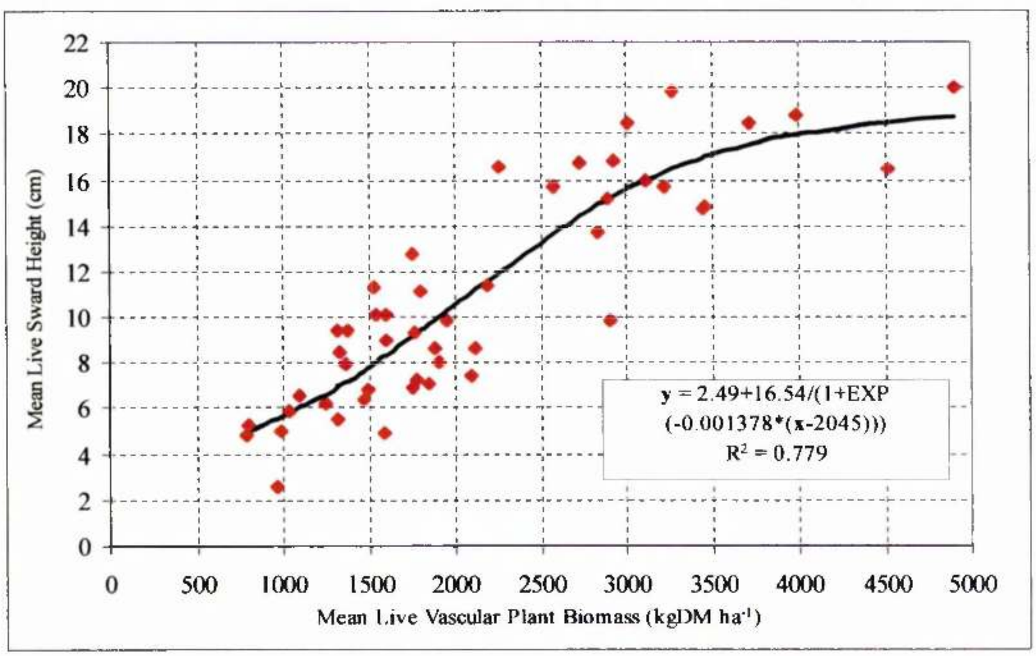


Figure 5.20 - The relationship between mean **live** sward surface height and mean live vascular plant biomass within the **U5b** community (logistic curve fitted).

5.5 Discussion

5.5.1 SELECTION OF VEGETATION TYPES

The U5c, U5b and M6d communities were chosen because they are not fully represented within the current MLURI Hill Grazing Management Model (Armstrong *et al.*, 1997a), and were abundant within the site. The two U5 communities cover 52% of the study area and are the two main *Nardus stricta* dominated communities (Chapter 3). The M6d community, which is dominated by *Juncus acutiflorus*, covers 9.6% of the study site and is the main community occupying the lower part of the enclosures, below 400 m. The U4d community was sampled, as it was necessary to collect data from a community type (i.e. *Festuca - Agrostis* grassland) that was present within the current model, so that the model could be tested and evaluated (see Chapter 7). It was not possible to sample this community in all three enclosures due to a lack of time and resources.

5.5.2 SAMPLING METHODODOLOGY

The sampling sites were not accessible by vehicle and therefore it was impractical to use a sampling method involving the cutting of turves which would then have required transportation to the laboratory for clipping and sorting (Perkins *et al.*, 1978; Ford and Wilson, 1994). Therefore, the herbage samples were harvested *in situ*.

Various methods of harvesting herbage samples *in situ* from indigenous grasslands have been used in the past, including cutting to ground level (Gordon, 1989a), cutting to a known height above ground level (Rawes, 1963; Rawes and Welch, 1969; Perkins *et al.*, 1978), and cutting along the upper surface of the litter horizon (Job and Taylor, 1978). It was decided that the herbage should be cut to ground level in order to collect as much of the above-ground biomass as possible, and because of the difficulty in trying to cut to a certain height above ground level. The absence of a clear upper surface to the litter horizon meant that the method used by Job and Taylor (1978) could not be used in this study. There was a compact soil surface beneath all four of the communities that were sampled, giving a definite ground level along which the herbage could be cut. This was not the case for an M17 *Scirpus cespitosus - Eriophorum vaginatum* blanket mire community that was sampled in 1994. The saturated peat substrate and surface *Sphagnum* layer meant that there was no definitive ground level, making the harvest of this community in a consistent manner almost impossible. For this reason the sampling of this community ceased after only four harvests and the data is not presented in this thesis.

Initially three samples were harvested each month from the U5c and U5b communities within each enclosure, however due to the large variances that were found, the number of samples was increased to four per community per enclosure in May 1995. Since the M6d and U4d communities were harvested after May 1995 the number of samples per month per enclosure was set at four.

Nardus stricta normally forms discrete tussocks (Chadwick, 1960), and the pasture in which it occurs is therefore normally a mosaic of tussocks and inter-tussock areas. However, within the U5b and U5c grasslands that were sampled on the Kirkton Face the *Nardus stricta* does not form large discrete tussocks, but a dense interlocking sward of relatively small plants intimately mixed with the other grass, sedge and herb species, with only a very limited inter-tussock area. It was therefore not practical to adopt the system used by Grant *et al.* (1985) in which three separate sward components:

tussock; hollow; and intermediate, were surveyed and sampled. Therefore, a single sample was harvested which encompassed the range of species and structures.

5.5.3 PROBLEMS AND LIMITATIONS OF THE *IN SITU* HARVESTING METHODOLOGY

1) The *Nardus stricta* grasslands within the study site were heterogeneous, with small-scale spatial variations in species composition and structure (Chapters 3 and 4). Because of the remote location of the sampling sites and the physical limitations in the amount of material that could be harvested and removed from the hill by a single person, the number of samples per enclosure per community per month was limited to a maximum of four. This also produced the maximum number of sub-samples that could be sorted within the four-week period between sampling dates. Unfortunately due to time constraints and limited resources it was not possible to sample and sort all four communities in a single month. The limited sample sizes were therefore unavoidable, but inevitably resulted in high variance levels within the biomass data. Nevertheless, useful and usable data were produced.
2) Overestimates of above-ground biomass may have occurred due to soil contamination and the presence of root material within the litter layer, although procedures to reduce the amount of soil contamination were carried out through the physical removal of large particles and the washing of some samples. The washing and sieving of the samples created problems in itself, as small particles of litter and live material were also lost in the process.
3) The collection of winter data was hampered by snow cover, which varied from year-to-year preventing samples from being collected in some months. At other times frozen litter horizons prevented all the material from being collected. This would

have resulted in under-estimates of the biomass. There were also problems experienced while collecting herbage samples during windy weather, when small amounts of the cut material were lost before they could be placed into sample bags. It was not thought however that these losses were significant.

4) Extrapolating biomass values from percentage dry weight figures obtained from a sub-sample also results in errors, although the procedure for obtaining the sub-samples removed any subjectivity and reduced bias, and was carried out in a consistent and repeatable manner (Grant, 1993). Once trained, the identification and separation of individual species from the samples could be done rapidly and accurately, with very few items left unidentified. The process of cutting and mixing the sample meant that the separation of dead standing material from litter was much more difficult to accomplish and almost certainly inaccurate.

Smeaton and Winn (1981) carried out a number of experiments to determine important sources of error associated with the estimation of standing biomass by cutting to ground level, within hill pastures in New Zealand. They found that small quadrats (0.125 m^2) were almost as effective as larger quadrats (0.25 m^2) with only 3-12 % more cuts required to achieve the same precision. Variation due to type of cutting machine was not significant, but differences between the cutters (i.e. persons doing the cutting) were found to be highly significant. These significant differences were found in both the green and dead fractions as well as in the total biomass. They also showed that bias was not constant, as there was variation in the bias between some individual cutters from one trial to another. Smeaton and Winn (1981) could not account for the large differences between cutters as they were not discernible by eye, however it was assumed that they were due to differences in cutting height. They also found that subjective sampling gave estimates of biomass which were not significantly different from those determined by random selection but had smaller associated standard errors.

In order to reduce cutter error the author harvested almost all the U5c, U5b and M6d samples, while a colleague harvested all the U4d samples. Within cutter variation will inevitably have occurred as a result of differences in the slope of the sampling sites, variations in weather conditions and tiredness. It is also possible that there may have been a temporal bias, due to increased experience in the use of the machinery and the sampling methodology.

Although there were limitations in the harvesting methods used in the present study, they were the most appropriate, practical and potentially accurate methods that could have been used given the remote location of the site and the time constraints involved.

5.5.4 TREATMENT EFFECTS

Comparisons between the three treatments are problematical, due to methodological errors, lack of replicates, small sample sizes, large variances and the limited pre-trial data set. However, the analyses appeared to show that grazing by sheep and summer cattle resulted in significantly lower U5c and M6d mean live vascular plant biomass values, compared with sheep only grazing. The mean biomass values of both *Nardus stricta* and the other grass species within the U5c community were also significantly lower in the enclosure grazed by both sheep and cattle. The cattle were rarely observed grazing above the 500 m contour and appeared to spend most of their time grazing on these two communities at the base of the enclosure. Cattle are generally un-selective within a plant community and will graze tussocky vegetation, such as *Nardus stricta* and *Molinia caerulea* and taller species such as *Juncus acutiflorus*, whereas sheep tend to graze selectively from the base of the sward avoiding the tussock species (Buttenschøn and Buttenschøn, 1982b; Grant *et al.*, 1985; Hodgson *et al.*, 1991; Common *et al.*, 1998).

The enclosure with the lower sheep stocking rate (0.051 LU ha^{-1}) had a significantly higher U5b mean live vascular plant biomass compared with the enclosure with the high sheep stocking rate (0.074 LU ha^{-1}). Sheep stocking rate had no significant effect upon the mean live vascular plant biomass of the M6d or U5c communities (although monthly mean values tended to be higher under the lower stocking rate), or on the mean biomass of either *Nardus stricta* or of the other grass species within the U5c community. Sheep stocking rate did however have a significant effect upon the amount of above-ground biomass within the U5b community. This community contained less *Nardus stricta* and more *Juncus squarrosus* than the U5c community, and contained a greater amount of winter green material.

5.5.5 CLIMATIC AND TEMPORAL EFFECTS

Under all three treatments, mean summer live and dead biomass values were consistently higher in 1996 compared with the previous two years. Mean spring biomass values also tended to be higher in 1996 than in 1995. A combination of climatic, management and biological factors may have been responsible for these consistent increases across all treatments and communities.

As outlined in Chapter 2, the grazing management of the site prior to the erection of the fences was very different to the all year round grazing during the trial period, and the change in the vegetation within all three enclosures may have been in response to this change in grazing management.

Another management factor which may have influenced both spring and summer biomass in 1996 was the removal of all the sheep from the three enclosures for a period of 39 days between the 26/01/96 and 05/03/96 due to severe weather conditions. This may have contributed to the build up of dead material observed in spring 1996, since the dead and senescing live material were not being consumed.

Temperature and rainfall figures varied over the trial period (Chapter 2 and Appendix 2.1). The summer of 1995 had very low June (37.1 mm) and August (27.2 mm) rainfall totals, and maximum temperatures in excess of 25.1 ^{o}C on 15 days (a temperature not achieved in the other years). These high summer temperatures and low rainfall figures resulted in two periods when there was likely to be a soil water deficit on the moderately steep, freely drained slopes dominated by *Nardus stricta*, which may have led to a lower than average biomass production. Rainfall between December 1995 and March 1996 was 473 mm, which was less than half the rainfall in any of the other winter periods. During this period there were only 3 days when rainfall exceeded 25 mm compared with between 15 and 24 days in the other years. This lower winter rainfall total and lower number of extreme rainfall days would have resulted in less surface runoff, leading to a reduction in the amount of litter and dead material transported out of the system. 1996 had a moderate summer rainfall with no drought period (263 mm between June and August), and a higher mean September temperature (12^{o}C) than any other year, allowing higher production rates later on in the season. This may have been partially responsible for the higher vascular plant biomass values recorded in the summer of 1996.

The mean summer sward surface height values of the U5c community within Enclosure 2 declined from 1995 to 1997, whereas the mean summer biomass figures increased over this period. The summer sward was becoming shorter, but denser, with significantly more bryophyte biomass and dead material within the lower layers of the sward. The sward was becoming more homogeneous and less structurally diverse.

5.5.6 IMPACT OF NATIVE HERBIVORES

A number of native herbivore species occurred within the study site, and the grazing of these species will have had an impact upon the standing biomass. Temporal changes in the population sizes of particular species as a response to the altered management or simply due to cyclical patterns in population numbers could have had an impact on the vegetation. Unfortunately, none of the native herbivore populations were monitored during the experiment. Mountain hares (*Lepus timidus*) and red deer (*Cervus elaphus*) were present in small numbers on the ridge and were occasionally seen grazing within the fenced area. The main native mammalian herbivores within the enclosures appeared to be field voles (*Microtus agrestis*), which were present in large numbers, their burrows and tracks being clearly visible within the grassland. Vole densities appeared to vary according to the type and structure of the vegetation and the soil type. Evidence of their presence in the form of runs, burrows, droppings and grazed vegetation, was more obvious within the drier grasslands with tall, rank, tussocky vegetation, and a thick litter layer, than within the shorter more heavily grazed grasslands or mire communities. A single 10 m^2 quadrat located in an area of *Nardus stricta* grassland at an altitude of 590 m within the study area was found to contain 89 vole burrow entrance holes. Hansson (1977) suggested that *Microtus agrestis* requires a habitat with at least 80-90 % of the ground surface covered by litter or lush green vegetation. Work by Hill *et al.* (1992) on hill pastures in North Wales showed that in the absence of sheep grazing, voles became the dominant herbivore causing large year-to-year variation in herbage biomass. Hill *et al.* (1992) suggested that an increase in the vole population caused an increase in the abundance of pleurocarpous mosses in a *Festuca ovina* - *Nardus stricta* grassland. They also suggested that vole grazing was the main cause for an increase in *Agrostis vinealis* at the expense of *A. capillaris* within an *Agrostis* - *Festuca* grassland which had been protected from sheep grazing, and that voles may also have been partly responsible for the limited cover of forbs within pastures from which sheep had been excluded (Hill *et al.*, 1992). It has been suggested by Summerhayes (1941) that the network of tunnels created by *Microtus agrestis* may also affect the drainage of a site.

Very large numbers of antler moth larvae (*Cerapteryx graminis*), which feed on native coarse grasses (Carter, 1982), were present within the *Nardus stricta* grasslands in 1998, with up to 30 larvae m^{-2} recorded. The small brown adult moths were abundant for a short period during August and September. Though present in other years they were not as abundant and had a more restricted spatial distribution. Leatherjackets (larvae of craneflies, *Tipula* spp.) were also very abundant within the grassland. These soil-dwelling larvae feed mainly on root tissue, but will consume accessible leaf material (Lewis and Hopkins, 2000). Large numbers of slugs are also present within the grassland communities. The number of slugs appeared to vary from year to year and their distribution within the vegetation types was not uniform. Slugs lay their eggs in clusters and also have relatively poor dispersal ability, which leads to a characteristically aggregated population distribution (Lutman, 1978). Vegetation structure and the palatability of the plant species also influences slug distribution (Lutman, 1978). Work carried out by Lutman (1978) on an *Agrostis - Festuca* grassland at Llyn Llydaw in North Wales, gave an estimated annual consumption by slugs of 304 kJ m^{-2} (16.3 g m^{-2}). Feeding intensity was at its highest from mid-October to April, the period when plant productivity was at its lowest (Lutman, 1978). No attempt was made to determine the grazing impact of either the invertebrate or wild vertebrate herbivores within this present study.

5.5.7 Use of the relationship between sward surface height and above-ground biomass

The derived relationships between sward surface height and above-ground biomass for the two *Nardus stricta*-dominated grasslands will be used in a modified version of the Hill Grazing Management Model, extending its applicability to sites with large areas of wet, acid grassland (Chapter 7). These relationships will also provide farmers with a means of obtaining estimates of the available forage resources within *Nardus stricta*-dominated grasslands by simply taking sward height measurements. This could lead to a more efficient and informed use of these grassland types.

5.5.8 Comparison with other published work

Mean maximum total biomass and live biomass values of over 950 gDM m^{-2} and 450 gDM m^{-2} respectively, were recorded for both the U5c and U5b grasslands within the Kirkton Face study site (Table 5.21). These values are twice those determined by Job and Taylor (1978), and Rawes and Welch (1969) from similar communities (Table 5.21). Job and Taylor (1978) used a technique in which the sward was clipped along the upper surface of the litter horizon, while Rawes and Welch (1969) harvested the sward at a set height above the soil surface. Both these methodologies result in some biomass (both live and dead) being left *in situ* and unrecorded, resulting in lower above-ground biomass values. The sampling sites used in these two studies were also at a higher altitude (50 - 250 m higher) than the Kirkton Face sampling sites (Table 5.21) and at lower latitudes where summer day lengths are shorter. Grazing intensity, which is perhaps the most important influence on above-ground biomass, was not consistent across all the sites (Table 5.21).

The live biomass values obtained by Grant *et al.* (1985) from a sheep and cattle grazed *Nardus stricta* grassland were comparable with those obtained from the Kirkton Face study site, while the total biomass values were considerably greater (Table 5.21). Grant *et al.* (1985) measured the above-ground biomass of both tussock and inter-tussock vegetation by collecting turves from both areas, which were then clipped to soil level in the laboratory. This ensured that the two structurally distinct elements of the vegetation were sampled and that all the above-ground biomass was harvested. The sampling site used by Grant *et al.* (1985) was however, 150 m lower than the Kirkton Face sampling site, increasing the likelihood of higher productivity.

There appeared to very limited published information on the biomass of *Juncus acutiflorus* dominated mires, however the maximum standing crop obtained by de Leeuw and Bakker (1986) from a sheep grazed *J. acutiflorus* community in the Netherlands was comparable with that obtained from the Kirkton Face study site (Table 5.21).

The mean maximum live biomass value of the U4d community was higher than previously published values for similar communities (Table 5.22). Differences in methodology, in particular harvesting techniques, and differences in species composition, geographical location, environmental conditions and grazing management may account for these discrepancies (Table 5.22).

5.6 Conclusions

Even with a limited number of samples, direct harvesting together with the sorting of sub-samples provides the most accurate method for determining the above-ground biomass of indigenous grasslands. The total above-ground biomass and the proportion of live and dead material varied depending on the type of vegetation, the time of year, and the grazing management. The vegetation within all three enclosures responded in a similar manner over time, with significantly higher summer and spring biomass levels in 1996 compared to 1995. Over the trial period the *Nardus stricta*-dominated grasslands became shorter, denser and more homogeneous under all three grazing treatments. It is thought that these temporal changes were due to both management and climatic factors.

The *Nardus stricta*-dominated grasslands, especially the U5c community, formed an important forage resource, with relatively large amounts of green vascular plant biomass present within the sward, particularly during the summer and autumn. The U5c grasslands within the study site also contained comparable amounts of *Festuca ovina* and *Agrostis capillaris* to those found within the U4d community, clearly indicating the grazing value of these relatively species-rich *Nardus stricta*-dominated grasslands. The grazing value of the U5c and U5b communities is much reduced during the winter months, due to the high proportion of dead standing and litter material, in particular dead standing *Nardus stricta* which dominates the upper layers of the sward, although some live material does persist throughout the winter, mainly at the base of the tussocks.

Table 5.21 - Some published above-ground biomass values for *Nardus stricta*, *Juncus squarrosus* and *Juncus acutiflorus* communities

Vegetation Type	Altitude (m)	Location	Total Biomass ($gDM\ m^{-2} \pm 1$ S.E.)		Live Biomass ($gDM\ m^{-2} \pm 1$ S.E.)		Live Vascular Plant Biomass ($gDM\ m^{-2} \pm 1$ S.E.)		Grazing	Sampling Method	Reference
			Max.	Min.	Max.	Min.	Max.	Min.			
Nardus - Festuca - Agrostis (U5c)	425m	Crianlarich, Perthshire	**987** ± 106 (Jul)	**343** ± 38 (Dec)	**488** ± 65 (Aug)	**122** ± 26 (Dec)	**370** ± 50 (Aug)	**103** ± 18 (Apr)	All year round sheep grazing (0.051 LU ha^{-1})	Harvested *in situ* to ground level.	Present study (Enc. 2)
Nardus - Juncus squarrosus (U5b)	475m	Crianlarich, Perthshire	**1175** ± 108 (Jul)	**477** ± 69 (Dec)	**575** ± 59 (Jul)	**206** ± 8 (Nov)	**491** ± 54 (Aug)	**132** ± 31 (Apr)	All year round sheep grazing (0.051 LU ha^{-1})	Harvested *in situ* to ground level.	Present study (Enc. 2)
Juncus acutiflorus mire (M6d)	380m	Crianlarich, Perthshire	**817** ± 26 (Aug)	**425** ± 49 (Dec)	**566** ± 91 (Sep)	**107** ± 28 (Dec)	**355** ± 48 (Aug)	**31** ± 4 (Apr)	All year round sheep grazing (0.051 LU ha^{-1})	Harvested *in situ* to ground level.	Present study (Enc. 2)
Nardus - Festuca - Poa	525 m	Mid Wales (Plynlimon)	**310** (Aug)	**100** (May)	**195** (Aug)	**50** (May)			Pasture improved with surface treatment, and grazed by both sheep and cattle.	Harvested *in situ* to the upper surface of the litter horizon.	Job and Taylor (1978)
Festuca - Agrostis-/ Nardus	670 m	Mid Wales (Plynlimon)	**305** (Aug)	**170** (May)	**220** (Aug)	**36** (May)			Uncontrolled grazing by sheep	Harvested *in situ* to the upper surface of the litter horizon.	Job and Taylor (1978)
Nardus grassland	260 - 280m	Cleish Hills, Fife	**1770** ± 190 (Oct) tussock 2470± 95, inter-tuss. 1330± 130		**560** ± 140 (Jul) tussock 1010± 80, inter-tuss. 240± 5				Controlled sheep and cattle grazing	Turves cut from tussock and between tussock areas, taken to the laboratory where they were clipped at soil level and sorted.	Grant *et al.* (1985) and Hodgson *et al.* (1991)
Nardus stricta community	549 m	North East England (Moor House NNR)	**502** Autumn		**256** Autumn	**136** Early Spring			Sheep grazing April to October	Harvested *in situ*. Cuts taken 2cm from ground level.	Rawes and Welch (1969)
Juncus squarrosus community	549 m	North East England (Moor House NNR)	**550** Autumn		**275** Autumn	**139** Early Spring			Sheep grazing April to October	Harvested *in situ*. Cuts taken 2cm from ground level.	Rawes and Welch (1969)
Juncus acutiflorus mire	-	Westerholt, Netherlands	**830** (Oct)						Controlled sheep grazing (3 sheep ha^{-1})	Harvested *in situ* to the upper surface of the litter horizon.	de Leeuw and Bakker (1986)

Table 5.22 - Some published above-ground biomass values for *Festuca / Agrostis* grasslands

Vegetation Type	Altitude (m)	Location	Total Biomass (gDM $m^{-2} \pm 1$ S.E.)		Live Biomass (gDM $m^{-2} \pm 1$ S.E.)		Live Vascular Plant Biomass (gDM $m^{-2} \pm 1$ S.E.)		Grazing	Sampling Method	Reference
			Max.	Min.	Max.	Min.	Max.	Min.			
Festuca - Agrostis - Galium saxatile (U4d)	580m	Crianlarich, Perthshire	**673** ± 67 (Jul)	**430** ± 32 (Oct)	**459** ± 66 (Jul)	**268** ± 32 (Oct)	**282** ± 33 (Jul)	**121** ± 8 (Apr)	All year round sheep grazing (0.051 LU ha^{-1})	Harvested *in situ* to ground level.	Present study (Enc. 2)
Species poor *Agrostis - Festuca* grassland	No Data	Rhum	**~295** Autumn excludes mosses	**~190** Spring excludes mosses			**~160** Summer	**~40** Winter	Uncontrolled grazing by red deer, cattle, ponies and goats.	Harvested *in situ* to ground level.	Gordon (1989a)
Forb rich *Agrostis - Festuca* grassland	310 m	North East Scotland (Cabrach)	**510** (Sept)	**300** (March)	**300** (Sept)	**120** (March)	**240** (Sept)	**60** (March)	Limited grazing by sheep and cattle	Turves cut and transported to the laboratory where they were clipped to ground level and sorted.	Ford and Wilson (1994)
Festuca-/ Agrostis alluvial grassland	518 m	North East England (Moor House NNR)			**55** (Aug)	**18.5** (June)			Heavy summer grazing by sheep	Vegetation cut 0.5 inches off the ground, *in situ*.	Rawes (1963)
Agrostis - Festuca grassland	240 - 250m	Cleish Hills, Fife	**660** ± 35 (Jul)		**290** ± 30 (Jul)				Controlled sheep and cattle grazing	Turves cut and taken to the laboratory where they were clipped at soil level and sorted.	Grant *et al.* (1985)
Agrostis - Festuca grassland	488 m	North Wales (Llyn Llydaw)	**962** (Sept)	**725** (April)	**289** ± 15 (Sept)	**167** (April)			Mainly summer grazing sheep	Turves cut and transported to the laboratory, clipped to ground level, plus *in situ* clipped quadrats (cut 1-2 cm above soil)	Perkins *et al.* (1978)
Festuca - Agrostis - Danthonia grassland	420 m	Mid Wales (Plynlimon)	**190** (Aug)	**128** (May)	**100** (Aug)	**40** (May)			Partially controlled sheep grazing	Harvested *in situ* to the upper surface of the litter horizon.	Job and Taylor (1978)

CHAPTER 6 – THE ABOVE-GROUND PRODUCTION AND OFFTAKE OF INDIGENOUS GRASSLAND AND MIRE COMMUNITIES

6.1 Summary

1) The production and utilisation of four vegetation types were estimated using an exclosure cage technique.
2) Production values ranged from 2 tonnes ha^{-1} for a montane *Festuca vivipara* - *Agrostis capillaris* grassland, to approximately 4 tonnes ha^{-1} for a species rich *Nardus stricta* grassland. These values were comparable with those obtained by Job and Taylor (1978) and Perkins *et al.* (1978) for similar upland vegetation types in Wales.
3) Production of vascular plant biomass was highest in June and July, with little or no production during the winter months.
4) The U5c grassland had a two peak pattern of growth with maximum production in early summer and a secondary peak in autumn.
5) In the U5c community total production of *Nardus stricta* was lower than that of the other combined grass species. The peak in daily production rate of *Nardus stricta* occurred in June, while that of the other grasses occurred in July. The relative growth rate of broad and fine-leaved grasses was higher than that of *Nardus stricta*. Bryophyte production occurred mainly in spring and autumn with little growth during summer when peak vascular plant production occurred.
6) The *in vitro* DM digestibility of green *Nardus stricta* was found to be comparable with that of *Festuca ovina* and *Agrostis capillaris*. Live *Juncus squarrosus* had a very low DM digestibility.

7) Offtake of green material from the U5c community was higher than from the U5b community, with utilisation rates of over 60 % within Enclosures 1 and 3. Enclosure 2 had the lowest estimated offtake from the U5c community (12.6 % utilisation). The enclosure containing the summer grazing cattle had the highest estimated offtake of the U5c, U5b and M6d communities.

8) Under the higher stocking rates of Enclosures 1 and 3 the offtake of live *Nardus stricta* from the U5c community was only slightly lower than the offtake of the inter-tussock vegetation.

9) There are many limitations with the use of cages in estimating production in grazed swards and there are numerous sources of error, however they are the only practical means of obtaining approximate production values for upland vegetation types in remote field sites.

6.2 Introduction

The processes involved in the transfer of nutrients and plant material within a hill grassland system, include production, senescence, litterfall, translocation, decomposition and grazing (Job and Taylor, 1978). Temporal variations in the rates of these processes lead to seasonal gains and losses in above-ground live and dead standing material and litter (Rawes and Welch, 1969; Job and Taylor, 1978). These fundamental processes, in particular production and grazing, determine how the vegetation develops over time (Job and Taylor, 1978).

The dry matter production of hill vegetation types is dependent upon a number of factors. These include key determinants such as the species composition and structure of the vegetation, together with environmental and management factors. Climate, soil conditions (nutrient status, pH, moisture content) and grazing management all affect production (Hopkins, 2000). Production is also indirectly affected by altitude, which directly affects climate, influencing temperature, precipitation, wind-speed and light intensity (Hopkins, 2000). In mountainous regions another important factor influencing production is aspect, which affects light intensity, temperature, and soil moisture content, all major determinants of photosynthetic rate and consequently leaf growth (Rorison *et al.*, 1986; Parsons and Chapman, 2000). In Britain the main climatic variable determining plant productivity is temperature (Grant, 1968; Grace, 1988; Hopkins, 2000), which declines by between 0.6 and 1.0°C per 100 m rise in altitude (Grace, 1988). The rates of enzyme-controlled processes such as photosynthesis and respiration are temperature dependent, hence the rates of growth and senescence vary both diurnally and seasonally (Hopkins, 2000). Grace (1988) concluded that in Britain a 1°C rise in temperature increased plant productivity by about 10 %, providing other factors were not limiting. Below a threshold soil temperature of approximately 6°C there is however very little growth of temperate grasses (Smith, 1984; Hopkins, 2000). In much of upland Scotland (including West Perthshire) soil temperatures remain below 6°C from mid-December through to mid-April, giving a relatively short growing season (Chapter 2). The main soil nutrient factors limiting production in hill vegetation systems are the supply of available Nitrogen and Phosphorus (Harrison *et al.*, 1994). Plant production is also affected by soil pH, which influences the build up of toxic ions (e.g. Aluminium and Manganese) and the availability of some nutrients (Hopkins, 2000). Each plant species is adapted to a particular range of soil pH, temperature and nutrient levels.

Information on the primary production of semi-natural grasslands and mires in upland Britain is rather limited (Milton, 1940; Milton and Davies, 1947; Rawes and Welch, 1969; Forrest and Smith, 1975; Job and Taylor, 1978; Perkins *et al.*, 1978; Newbould, 1981; Davies, 1987; Common *et al.*, 1991), and there is very little data from western Scotland (Tiley *et al.*, 1986). The estimates of production that are available have been obtained using a variety of field and analytical techniques (Frame, 1993; Job and Taylor, 1978; Perkins *et al.*, 1978). The variety of methodologies used in previous studies, and the fact that the study sites had different species compositions, climates, altitudes, lengths of growing season, day lengths, soil conditions and management histories, have led to wide variations in estimated production values for what appear to be similar vegetation types. The Kirkton Face study site consists of three enclosures each with a different grazing regime (see Chapter 2 for details). The enclosures contain a mosaic of vegetation types with different species compositions and structures, occurring over a wide range of altitudes, and soil types (Chapter 3). The work reported in this chapter describes the annual and seasonal productivity of a range of these vegetation types, and compares the values against published production values for similar vegetation types from other sites in upland Britain.

Birch wood macro-fossils found within the peat deposits of the Kirkton Face study site (personal observations) indicate that there has been a major loss of organic material from this system through deforestation, as a result of climatic deterioration and/or clearance by man (Moore, 1977; Birks, 1988; Dickson, 1994; Smout, 1997). Organic material and nutrients continue to be lost from the system through grazing and the subsequent removal of stock, a process that has been happening in the area for over 200 years (Watson, 1932). Nutrients are also lost in the form of solutes and suspended material in drainage water, through the physical removal of organic material by wind transportation, and through peat erosion (Crisp, 1966; Job and Taylor, 1978). These nutrient losses are partially compensated by inputs from precipitation, weathering processes and supplementary animal feed (Crisp, 1966). It is not known whether the inputs fully compensate for the losses. Therefore, the system may not be in equilibrium, and may be experiencing a progressive degradation of its nutrient reserves, which will influence the species composition and productivity of the vegetation in the future.

As described in Chapters 4 and 5, grazing has an important influence on the composition, structure and biomass of the sward. The diet which a herbivore selects is determined by a range of plant and animal factors, but is largely dependent upon what is available and the requirements of the animal (Gordon and Iason, 1989). Plant factors that affect diet selection include, the species composition and structure (e.g. height and density) of the sward, and the spatial distribution of the different species and plant parts within the sward, in particular the distribution and availability of more preferred species

(Milne *et al.*, 1982; Grant *et al.*, 1985; Milne, 1991; Gordon and Illius, 1992). An array of grazing related plant attributes also influence diet selection, including the digestibility, nutritional value, fibre content and silica content of the plant material, and the levels of plant secondary metabolites within the plant material (Arnold, 1964; Hughes *et al.*, 1964; Grant *et al.*, 1985; Reichardt *et al.*, 1987; Hodgson *et al.*, 1991). There are also a number of animal functional attributes that affect diet selection and foraging behaviour, including body size; the morphology, size and function of the digestive tract; the size, shape and structure of the mouthparts; and the method of biting (Grant *et al.*, 1985; Gordon and Illius, 1988; 1992; Illius and Gordon, 1993).

Small animals have relatively higher metabolic energy requirements per unit body weight than larger animals, and require higher quality (lower fibre content) diets in order to survive (Bell, 1970; Jarman, 1974). Larger herbivores tend to have bigger mouthparts and are therefore less able to select individual species, live material, or the more nutritious plant parts, than smaller herbivores (Grant *et al.*, 1985; Gordon and Illius, 1988; 1992). Sheep mouthparts differ from those of cattle, in that sheep have narrow jaws, with thin mobile lips, whilst cattle have wide jaws, with thick, relatively immobile lips and protractile tongues (used for grasping herbage) (Grant *et al.*, 1985). These differences allow sheep to be more selective and allow them to utilise proportionally more live material than cattle (Grant *et al.*, 1985; 1987).

Large ruminants also have larger rumens and longer food retention times within the gut, than small ruminants, which allows them to utilise a more fibrous diet (Demment and van Soest, 1985; Gordon and Illius, 1988). Large animals also have higher foraging costs than small animals, and may therefore need to be less selective in order to contain these costs (Murray, 1991).

The dietary preferences of domestic ruminants are strongly influenced by learning (Provenza and Balph, 1987). Between-breed differences in the diet selection of sheep have been observed by Osoro *et al.* (1999), however Key and MacIver (1980) comparing cross-fostered and naturally reared lambs of two breeds, found that subsequent diet selection by the lamb was more related to the diet selection of the rearing dam rather than to its breed.

The herbage intake rates of sheep and cattle are also dependent upon a range of factors, including the digestibility of the vegetation (Allison, 1985; Armstrong *et al.*, 1986; Hodgson *et al.*, 1991); the time of year (Hodgson *et al.*, 1991; Wallis de Vries and Daleboudt, 1994); the sward height and structure (Hodgson, 1981; Forbes and Hodgson, 1985; Penning, 1986; Illius *et al.*, 1987; Burlison *et al.*, 1991; Wallis de Vries and Daleboudt, 1994); the physiological state and body condition of the animal (Arnold and Birrell, 1977; Doney *et al.*, 1981); and the time spent foraging (Rook, 2000).

The grazing distribution patterns of free-ranging ruminants are affected by abiotic factors such as slope, distance to water and exposure, and by biotic factors such as the distribution and proportion of different vegetation types, and the quantity and quality of forage within these different vegetation types (Hunter, 1962; Gordon and Illius, 1992; Bailey *et al.*, 1996; Hester *et al.*, 1999). In heterogeneous environments grazing ruminants have been shown to use a range of available food resources, rather than just the single source that provides the highest daily intake rate (Illius *et al.*, 1987; Wallis de Vries and Daleboudt, 1994). Observations on the distribution of South Country Cheviot sheep on a hillside in South-East Scotland (Hunter, 1962) indicated that although there was strong selection for the vegetation types with the highest nutritional value, the flock as a whole used all the vegetation types. Social interactions between individuals, and home-range behaviour have also been shown to influence the grazing location of sheep (Hunter and Milner, 1963; Hewson and Wilson, 1979; Lawrence and Wood-gush, 1988). Herbivores also show seasonal patterns in the grazing utilisation of different vegetation types, and these seasonal patterns of use differ between species (Osborne, 1984; Gordon, 1989b). As part of the present study, information on the grazing utilisation of a range of vegetation types (with different species compositions, structures, biomasses, and spatial distributions) has been gathered from the three study enclosures, which are subject to three different grazing regimes.

The main aims of the work described in this chapter were:

1) To obtain monthly estimates of above-ground vascular plant production for the grazed U5c, U5b, U4d and M6d communities, using an exclosure cage technique (Rawes and Welch, 1969; Job and Taylor, 1978). This data could then be used in a modified version of the MLURI Hill Grazing Management Model (Armstrong *et al.*, 1997a; 1997b) (Chapter 7).
2) To determine seasonal growth patterns and rates of production for the key species and species groups within the communities.
3) To obtain estimates of the annual offtake of green material from the different plant communities under the three different management regimes, using an exclosure cage technique.

6.3 Material and methods

6.3.1 FIELD AND LABORATORY TECHNIQUES

An exclosure cage technique (Milner and Hughes, 1968; 't Mannetje, 1978; Job and Taylor, 1978) was used to measure the production and offtake from four plant communities:

(1) U5c *Nardus stricta - Galium saxatile* (*Carex panicea - Viola riviniana*) grassland;

(2) U5b *Nardus stricta - Galium saxatile* (*Agrostis canina - Polytrichum commune*) grassland:

(3) M6d *Carex echinata - Sphagnum recurvum* (*Juncus acutiflorus*) mire;

(4) U4d *Festuca ovina - Agrostis capillaris - Galium saxatile* (*Luzula multiflora - Rhytidiadelphus loreus*) grassland.

The exclosure cages were positioned on the same patches of vegetation used for the above-ground biomass measurements (see Chapter 5). The robust, portable, wire mesh cages were 1.55 x 1.0 x 1.0 m in size, with a mesh size of 10 cm^2. The cages were held in place by metal pegs, and were suitable for the exclusion of both sheep and cattle, being tall enough to enclose all the vegetation.

A strip of vegetation (11 cm x 155 cm) was harvested to ground level at monthly intervals from inside and outside each exclosure cage, using AL-KO 6 rechargeable garden shears (AL-KO International, Consett, County Durham, UK). Both the inside and outside cuts were taken approximately 50 cm from the cage wall. Each strip of cut material was placed into a clearly labelled plastic bag. After each harvest the cages were moved to new locations within the sampling patch. Care was taken to ensure that the cages were not placed onto areas that had already been sampled, and that the species composition and vegetation structure at the new site was as similar as possible to the previous site. The dates on which sampling occurred, the number of enclosures sampled and the number of cages per enclosure are shown in Table 6.1. The methodologies used for sub-sampling and sorting the vegetation and the analytical methods used for calculating above-ground biomass values are outlined in Chapter 5.

Table 6.1 - Sampling dates, the number of enclosures sampled and the number of cages per enclosure.

		Date of Harvest									Number of enclosures sampled	Number of cages per enclosure
NVC	**Year**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**		
U5c	1995	18	19	15	12	9	5	4	10	12	3	3 in April, 4 from May
U5b	1995	18	19	15	12	9	5	4	10	12	3	3 in April, 4 from May
M6d	1995		16	19	26	22	21		9	7	3	4
	1996	11	15	25	30						3	4
U4d	1997	16	14	16	17	14	18	15	13		Enc. 2 only	4

Note – Cages were sited on the U5c and U5b communities on the 9th February 1995, and were not moved until the first cuts had been taken on the 18th April.

6.3.2 METHODS FOR CALCULATING ANNUAL NET PRIMARY PRODUCTION

The amount of above-ground net primary production (NPP) of a grazed grassland during a specified period of time (t) can be determined using Equation 6.1.

Equation 6.1

$$NPP = \Delta SB + L + G + R + T$$ (Milner and Hughes, 1968; Perkins *et al.*, 1978)

Where:

ΔSB = change in total standing biomass;

L = losses of standing material into the litter layer;

G = plant losses due to grazing;

R = material respired during plant metabolism;

T = material translocated to the roots.

Grazing can be removed from the equation by harvesting one set of samples from an area freely accessible to grazing animals at the start of the specified time period, and another set from inside an exclosure cage at the end of the specified time period. Respiration and translocation rates cannot be measured easily in the field, and therefore these losses had to be excluded from the production calculations (Equation 6.2).

Equation 6.2

$$NPP = (SBC_{t2} - SBG_{t1}) + L \qquad \text{(Perkins } et\ al.\text{, 1978; Job and Taylor, 1978)}$$

Where:

SBG_{t1} = standing biomass at the beginning of the sampling period from an area freely accessible to grazing animals (i.e. outside the exclosure cages at $time_1$);

SBC_{t2} = standing biomass at the end of the sampling period ($time_2$) from an area caged since $time_1$;

L = losses of standing material into the litter layer.

Accurate measurement of litterfall is extremely difficult and was considered impractical, due to the problems associated with collecting the material in a dense sward (Job and Taylor, 1978). The change in the amount of litter over the monitoring period cannot be used to estimate litterfall as this does not take into account decomposition and losses due to wind and water transport, neither of which were measured. This lack of data on rates of litterfall can be partially overcome by separating the biomass into live standing vascular plant material, live bryophytes, dead standing material and litter fractions, and making an assumption that over the short periods of time involved (i.e. four weeks) losses due to litterfall only occur from the dead standing component (Job and Taylor, 1978).

In order to estimate the annual net primary production of the vascular plant component the growing season was split into two periods: Period 1 - mid-April to mid-July; and Period 2 - mid-July to mid-November. At the start of the growing season (Period 1) growth is likely to be vigorous, leading to a net increase in live vascular plant material, whereas the rate of senescence is likely to be slight (Job and Taylor, 1978). At the same time pre-existing dead material is being shed from the standing dead fraction into the litter fraction, leading to a net loss of dead standing material. Monthly production over this period is therefore most appropriately estimated using the change in live vascular plant biomass (Equation 6.3), which is likely to be greater than the change in total standing vascular plant biomass.

Equation 6.3

$$NPP_t = \mathrm{BLC}_{t2} - \mathrm{BLG}_{t1} \qquad \text{(Job and Taylor, 1978)}$$

Where:

NPP_t = monthly net primary production;

BLG_{t1} = mean live vascular plant biomass of samples harvested from a grazed area at the start of the enclosure period (i.e. taken from outside the exclosure cages at $time_1$);

BLC_{t2} = mean live vascular plant biomass of samples harvested from an area enclosed over the specified time period (i.e. taken from inside the exclosure cages at $time_2$).

In the period from mid-July to mid-November (Period 2) the rate of senescence increases (i.e. material is being lost from the green fraction and is entering the dead standing fraction), but production continues to occur (i.e. green material is still being added to the standing biomass). In order to account for this, the monthly change in mean total standing vascular plant biomass was used as an estimate of monthly production (Equation 6.4), but only if it was greater than the change in mean live vascular plant biomass.

Equation 6.4

$$NPP_t = \mathrm{BTC}_{t2} - \mathrm{BTG}_{t1} \qquad \text{(Job and Taylor, 1978)}$$

Where:

NPP_t = monthly net primary production;

BTG_{t1} = mean total standing vascular plant biomass of samples harvested from a grazed area at the start of the enclosure period (i.e. taken from outside the exclosure cages at $time_1$);

BTC_{t2} = mean total standing vascular plant biomass of samples harvested from an area enclosed over the specified time period (i.e. taken from inside the exclosure cages at $time_2$).

Individual values of production for each time period were then summed to give a total annual NPP value for the vascular plant component. Since it is possible to have periods when the change in live vascular plant biomass and the change in total standing vascular plant biomass are both negative, only the positive monthly production values were used in the calculations. An assumption was made that no significant production occurred between mid-November and mid-April.

The production for each time period was converted into an average daily production rate, which was then used to calculate production for each calendar month. This was thought to be the most appropriate way to graphically show the seasonal variation in production.

Since the live biomass component was separated into species, it was possible to estimate monthly production values for individual species or groups of species. The dead standing biomass was not completely sorted and therefore the annual production value could only be estimated using the monthly changes in live standing material. Therefore, production during periods of high senescence was probably under-estimated.

6.3.3 GROWTH RATES

The relative growth rates (RGR) of the main components within the three grassland communities were calculated using the following formula:

Equation 6.5

$$RGR = [\log_e(BLC_{t2} / BLG_{t1})] / T \qquad \text{(Rawes and Welch, 1969)}$$

Where:

BLC_{t2} = final live biomass inside cage;

BLG_{t1} = initial live biomass outside cage;

T = time in days between harvests.

6.3.4 RANDOM ERROR ADJUSTMENTS

Singh *et al.* (1984), Lauenroth *et al.* (1986) and Biondini *et al.* (1991) have shown that random errors associated with field estimates of net primary production (NPP) can result in a positive bias and thus an overestimation in NPP. Equations have been developed by Sala *et al.* (1988) that relate the calculated NPP to the actual NPP, and estimate the size of the overestimation. A computer program containing the algorithms needed to adjust the calculated NPP values to correct the overestimation has been developed by Biondini *et al.* (1991). The program only uses significant increments in biomass between consecutive dates ($P < 0.05$). Production is assumed to be zero during periods when non-significant increments and negative values are obtained. The computer program was not used to adjust all the production values in this study, but its use was simply evaluated, by comparing the adjusted annual production values with the unadjusted values, for each of the four community types.

6.3.5 METHODS FOR CALCULATING OFFTAKE

Monthly offtake of live vascular plant material by grazing livestock can be estimated using Equation 6.5:

Equation 6.5

$$G = BLC_{t2} - BLG_{t2}$$ (Milner and Hughes, 1968; Job and Taylor, 1978)

Where:

G = live vascular plant biomass consumed by the grazing livestock over the grazing period;

BLC_{t2} = mean live vascular plant biomass of samples harvested from an area enclosed over the specified time period (i.e. taken from inside the exclosure cages at *time*$_2$).

BLG_{t2} = mean live vascular plant biomass of samples harvested from an area grazed over the same specified time period (i.e. taken from outside the exclosure cages at *time*$_2$).

Summing the individual monthly offtake values produces an annual offtake value. Because of the relatively small amounts of material removed by the sheep and the heterogeneous nature of the swards (resulting in high variance estimates), the grazed and ungrazed biomass distributions overlapped. This large overlap in the distributions, coupled with the small sample sizes used to calculate the mean values, frequently resulted in negative offtake values being recorded. In order to lessen this random error and reduce over-estimation, both positive and negative values were used in the calculation. The offtake values of live *Nardus stricta*, *Juncus squarrosus* and inter-tussock vegetation were also calculated. Utilisation rates were calculated by dividing the estimated annual production values by the estimated annual offtake values.

Residual Maximum Likelihood (REML) was used to determine whether the mean live vascular plant biomass within the cages was significantly higher than that outside the cages (Genstat 5 Committee, 1993).

6.3.6 DATA USED IN THE CALCULATION OF ABOVE-GROUND PRODUCTION VALUES

Since there were no significant differences between the two sheep grazed enclosures in the above-ground vascular plant biomass values of either the U5c or the M6d communities (see Chapter 5), the data from both enclosures were combined. This combined data was used in the calculation of the production values. The resultant production values for the two communities therefore represent production under a management system of all year round, light to moderate sheep grazing (0.051 - 0.074 LU ha^{-1}). Although there was a significant difference between the U5b above-ground vascular plant biomass values within the three enclosures (see Chapter 5), the small sample sizes and large within enclosure variability in biomass values and percentage compositions, meant that production values calculated for each individual enclosure were subject to a high degree of error. By using data from all three enclosures a more appropriate estimate of production for this heterogeneous community under continuous grazing (0.051 - 0.096 LU ha^{-1}) was calculated.

Bryophytes were excluded from the main calculations and dealt with separately. This was done mainly because of their spatial heterogeneity, which led to increased variation in the data. Perkins *et al.* (1978) also showed that the pattern of bryophyte growth within an *Agrostis-Festuca* grassland was different to that of the vascular plant species, tending to be low during the dry summer months when the biomass of vascular plants was high.

6.3.7 TESTING THE EFFECT OF THE EXCLOSURE CAGES

Two tests were carried out to determine whether the exclosure cages directly affected net herbage accumulation, and whether grazing behaviour within the immediate vicinity of the cages was affected. This information was used to determine whether the biomass values obtained from inside the cages needed adjusting prior to the calculation of the monthly production and offtake values.

6.3.7.1 *Test 1: effect upon net herbage accumulation*

The first test looked for significant differences between the mean biomass harvested from inside the cages and that harvested from outside the cages, in a no grazing situation. The test was carried out within a 3 ha fenced enclosure, which was 0.5 km south-west of the main study site. Domestic stock were excluded from the enclosure. Nine exclosure cages were placed randomly onto a U5 *Nardus stricta - Galium saxatile* grassland at an altitude of between 350 - 400 m, in May. Herbage samples were harvested from inside and outside the cages in June and July, giving a total of thirty-six samples. The samples, which were not sorted, were oven-dried and weighed. A variance-component model was fitted by Residual Maximum Likelihood

(REML) to calculate means and standard errors of difference (Genstat 5 Committee, 1993). The Wald test was used to test the fixed effect of caging on total above-ground biomass (Buist and Engel, 1993). Month and cage identity were fitted as random effects within the model.

6.3.7.2 *Test 2: effect upon grazing behaviour*

The second test determined whether the location of the cut in relation to the cage affected the biomass values obtained (i.e. did the cages attract or repel the grazing animals, resulting in increased or decreased offtake from the areas immediately surrounding the cages). The cages on the U5c community within Enclosure 2 were used. From May to September, two herbage samples were harvested per month from within a 1 m zone of each of the four cages, and two samples were harvested from a distance of over 5 m from each cage, giving a total of 80 samples. The un-sorted samples were oven-dried and weighed. A variance-component model was fitted by REML to calculate means and standard errors of difference (Genstat 5 Committee, 1993). The Wald test was used to test the fixed effect of distance from cage on total above-ground biomass (Buist and Engel, 1993). Month was fitted as a random effect.

6.3.8 *IN VITRO* DRY MATTER DIGESTIBILITIES

Dried samples of green and dead standing material of a number of species (i.e. *Nardus stricta*, *Juncus squarrusos*, *Trichophorum cespitosum*, *Agrostis capillaris*, *Festuca ovina/vivipara*, *Anthoxanthum odoratum* and *Molinia caerulea*) were analysed for *in vitro* DM digestibility (Tilley and Terry, 1963), at the Scottish Agricultural College's laboratories at Auchincruive.

6.4 Results

6.4.1 TESTING THE EFFECT OF THE EXCLOSURE CAGES

6.4.1.1 *Test 1: effect upon net herbage accumulation*

Analysis of the data from inside and outside the exclosure cages, in a no grazing situation, indicated that mean above-ground biomass was significantly higher inside (787.2 gDM m^{-2}) than outside the cages (736.6 gDM m^{-2}) (Wald = 4.4, df = 1, $P < 0.05$).

In order to account for this apparent cage effect, the biomass values from inside the cages, for the U5c, U5b and M6d communities, were reduced by **6.43%** over the peak growing period of mid-June to mid-October. The peak period of growth for the U4d community was assumed to be shorter, due to its higher altitude and exposed position. Therefore the caged biomass values of the U4d community were reduced by **6.43%** between mid-July and mid-September only. Assumptions were made that the cages have a consistent effect throughout the peak of the growing season, and that this positive effect occurs equally in all the communities.

6.4.1.2 *Test 2: effect upon grazing behaviour*

There was no significant difference between the mean above-ground biomass of samples harvested from areas adjacent to the cages (within 1 m) and those harvested from areas over 5 m from the cages (Wald = 0.6, df = 1, $P > 0.05$). There was no statistical evidence that the cages within Enclosure 2 either attracted or deterred the sheep, and therefore there was no further adjustment of the data.

6.4.2 Estimates of above-ground production

6.4.2.1 *U5c and U5b communities*

The production of live vascular plant material during 1995 within the U5c community was estimated to be 408.9 gDM m^{-2} compared with 347.9 gDM m^{-2} for the U5b community. Both communities showed peaks in production in early to mid-summer and again in September (Figure 6.1).

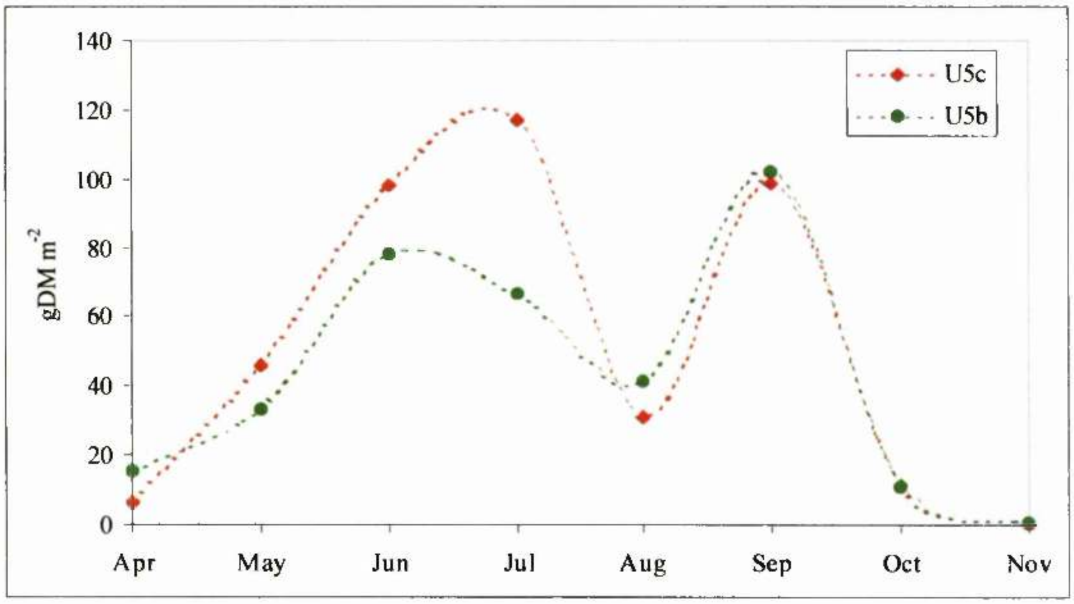


Figure 6.1 - Estimated monthly production of the U5c and U5b communities during the 1995 growing season. The monthly production values have been adjusted for cage effects (Section 6.4.1.1), but have not been adjusted for random errors.

In the U5c community, peak production of *Nardus stricta* occurred in June with a secondary peak in September (Figures 6.2 and 6.3). The other grass species showed only a single peak in production during July (Figures 6.2 and 6.3). Annual production of

Nardus stricta was estimated to be 120.4 gDM m^{-2} compared with 158.2 gDM m^{-2} for the other grass species (Figure 6.2). Bryophyte production was estimated to be 104.0 gDM m^{-2} with peaks in production during May and July.

Within the U5c community the broad-leaved grasses grew at a faster rate than the fine-leaved grasses, which in turn grew faster than *Nardus stricta* (Table 6.2). Despite the variability, growth rates were generally higher in the early part of the season.

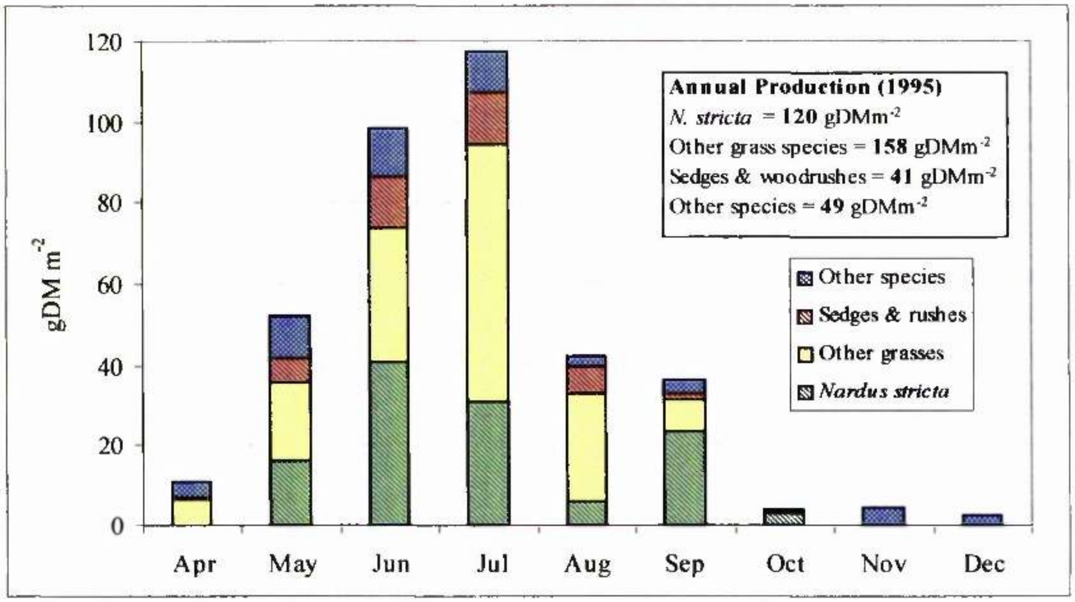


Figure 6.2 - Estimated monthly production of the main species and species groups within the U5c community during the 1995 growing-season. Production values have been estimated using the increments in mean live biomass only. The monthly production values have been adjusted for cage effects (Section 6.4.1.1), but have not been adjusted for random errors.

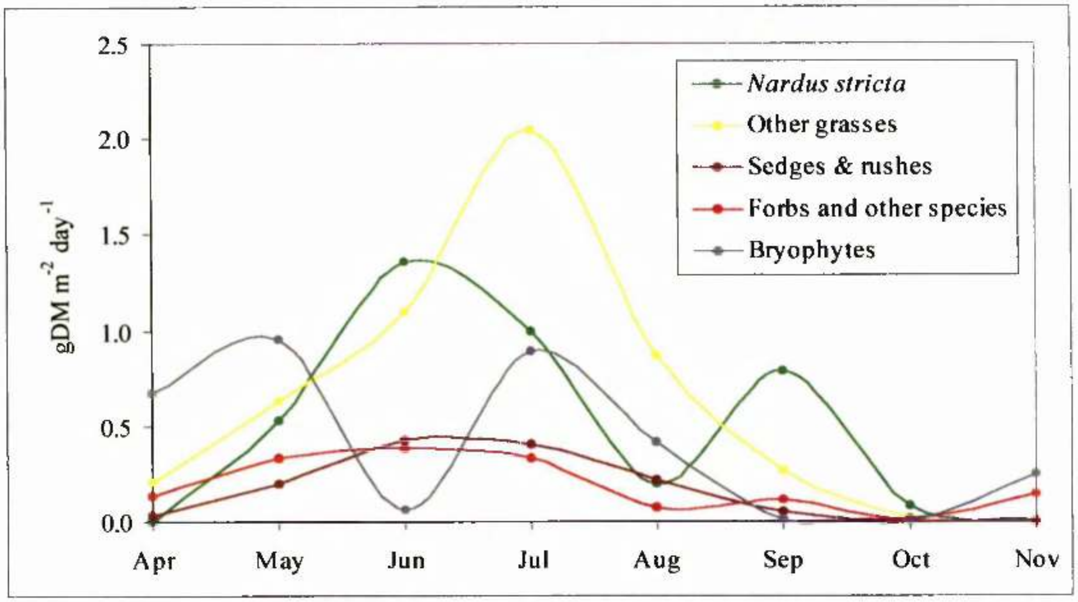


Figure 6.3 - Estimated daily production of selected species and species groups within the U5c community during the 1995 growing season.

Table 6.2 - Seasonal variation in the relative growth rates (RGR) of selected components within the U5c grassland

	18th April - 18th May	19th May - 14th June	15th June - 11th July	12th July - 8th August	9th Aug - 4th Sept	5th Sept - 4th Oct	Average RGR over the season
Broad-leaved grasses	0.0060	0.0107	0.0060	0.0108	0.0023	0.0022	0.0063
Fine-leaved grasses	0.0017	0.0044	0.0153	0.0156	0	0	0.0062
Nardus stricta	0	0.0126	0.0085	0.0031	0	0.0072	0.0052
Sedges and rushes	0.0024	0.0087	0.0072	0.0047	0.0018	0.0005	0.0042

Within the U5b community the peak in production of *Nardus stricta* also occurred in June (Figure 6.4 and 6.5), with *Juncus squarrosus* production peaking in July (Figure 6.4 and 6.5). Growth of *Trichophorum cespitosum* only occurred between April and July, reaching a peak in June (Figure 6.4 and 6.5). Bryophyte production was estimated to be 86 gDM m^{-2} with maximum production occurring in May and November (Figure 6.5).

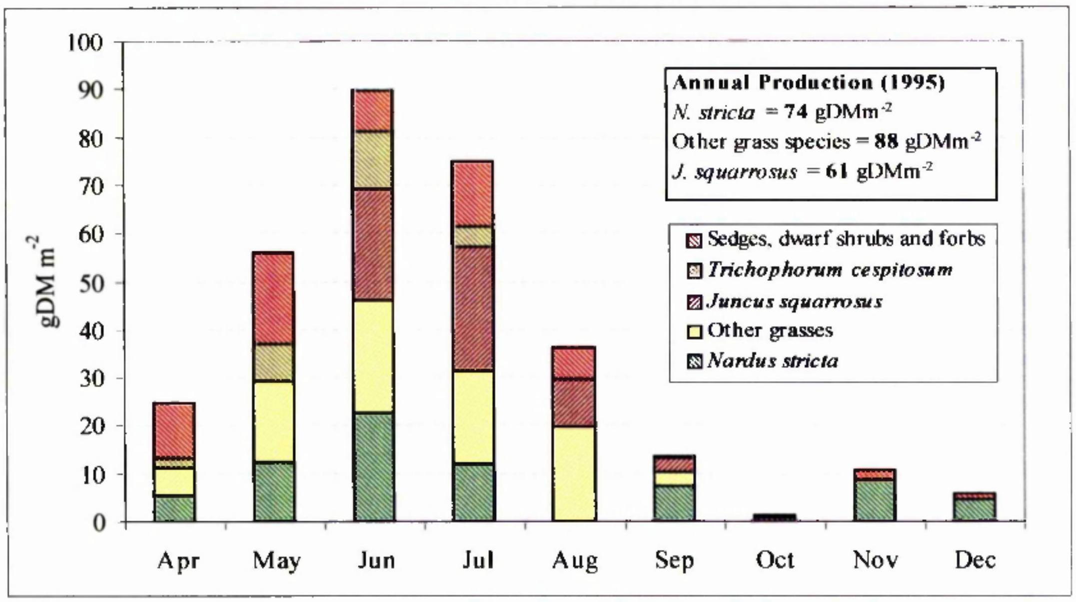


Figure 6.4 - Estimated monthly production of the main species and species groups within the U5b community during the 1995 growing-season. Production values have been estimated using the increments in mean live biomass only. The monthly production values have been adjusted for cage effects (Section 6.4.1.1), but have not been adjusted for random errors.

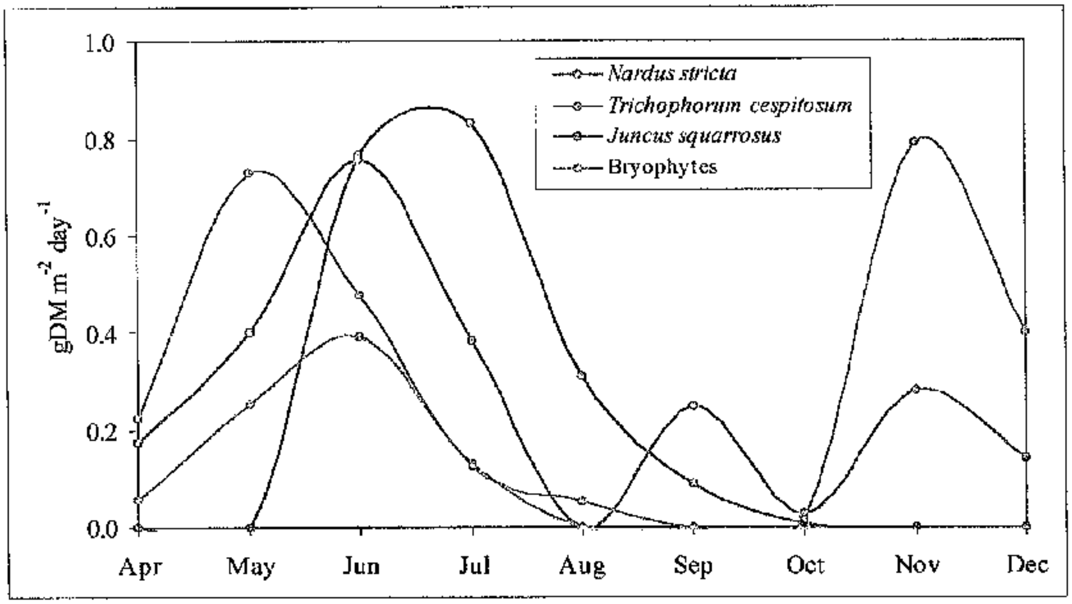


Figure 6.5 - Estimated daily production of selected species within the U5b community during the 1995 growing season.

Trichophorum cespitosum had a higher mean relative growth rate than any other species (Table 6.3). Its growth rate was particularly high in the early part of the season (Table 6.3). Although the U5b grassland was at a higher altitude than the U5c grassland the growth rate of both the fine and broad-leaved grasses was higher within the U5b community.

Table 6.3 - Seasonal variation in the relative growth rates (RGR) of selected components within the U5b grassland

	18th April - 18th May	19th May - 14th June	15th June - 11th July	12th July - 8th August	9th Aug - 4th Sept	5th Sept - 4th Oct	Average RGR over the season
Nardus stricta	0.0082	0.0068	0.0086	0	0	0.0018	0.0042
Juncus squarrosus	0	0	0.0077	0.0025	0.0012	0.0003	0.0019
Trichophorum cespitosum	0.0333	0.0226	0.0079	0	0	0	0.0106
Fine-leaved grasses	0.0174	0.0129	0.0152	0	0.0054	0	0.0085
Broad-leaved grasses	0.0119	0.0161	0.0076	0.0063	0.0031	0	0.0075

6.4.2.2 *M6d community*

The annual production of live vascular plant material within the M6d community was estimated to be 310.2 gDM m^{-2} (mid-May 1995 to mid-May 1996). Peak summer production was higher in 1996 than in 1995 (Figure 6.6). Growth occurred between mid-April and the end of September with the main peak in production during July (Figure 6.6). Bryophyte production was estimated to be 162.2 gDM m^{-2}, with peak production rates in September (2.02 gDM m^{-2} day^{-1}) and April (1.35 gDM m^{-2} day^{-1}), and little or no production during June or July. Annual production of *Juncus acutiflorus* was estimated to be 189.1 gDM m^{-2} with grasses producing a further 61.6 gDM m^{-2}. Rapid senescence began in mid-August and by early November virtually all the *Juncus acutiflorus* had died back.

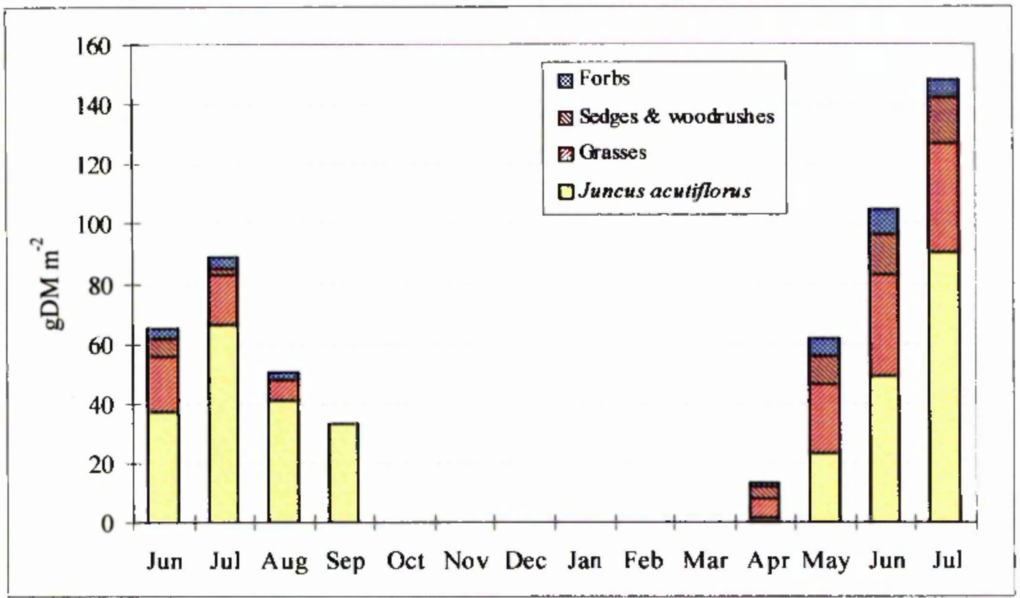


Figure 6.6 - Estimated monthly production of the main species and species groups within the M6d community during the period June 1995 to July 1996. Production values have been estimated using the increments in mean live biomass only. The monthly production values have been adjusted for cage effects (Section 6.4.1.1), but have not been adjusted for random errors.

6.4.2.3 *U4d community*

The U4d community, which was between 60 and 220 m higher than the other studied vegetation types, had the lowest estimated above-ground vascular plant production of the four communities, at 188.2 gDM m^{-2}. However, this value increased to 289.3 gDM m^{-2} if the annual productions of the four species groups were combined (Figure 6.7). Production of the U4d community reached a maximum in July with a secondary peak in October (Figure 6.7). From April to July the combined production of forbs, dwarf shrubs, sedges and woodrushes exceeded that of grasses, however there was little growth of these former species after July (Figure 6.7). The annual production of fine-leaved grasses (including *Nardus stricta*) was 44.9 gDM m^{-2} compared with 111.0 gDM m^{-2} for the broad-leaved grasses. The relative growth rate of the broad and fine-leaved grasses (excluding *Nardus* stricta) was lower in the U4d grassland than in the U5c and U5b grasslands (Table 6.4). The total annual production of bryophytes was 120.0 gDM m^{-2}, with maximum production in early summer and a secondary peak in late autumn.

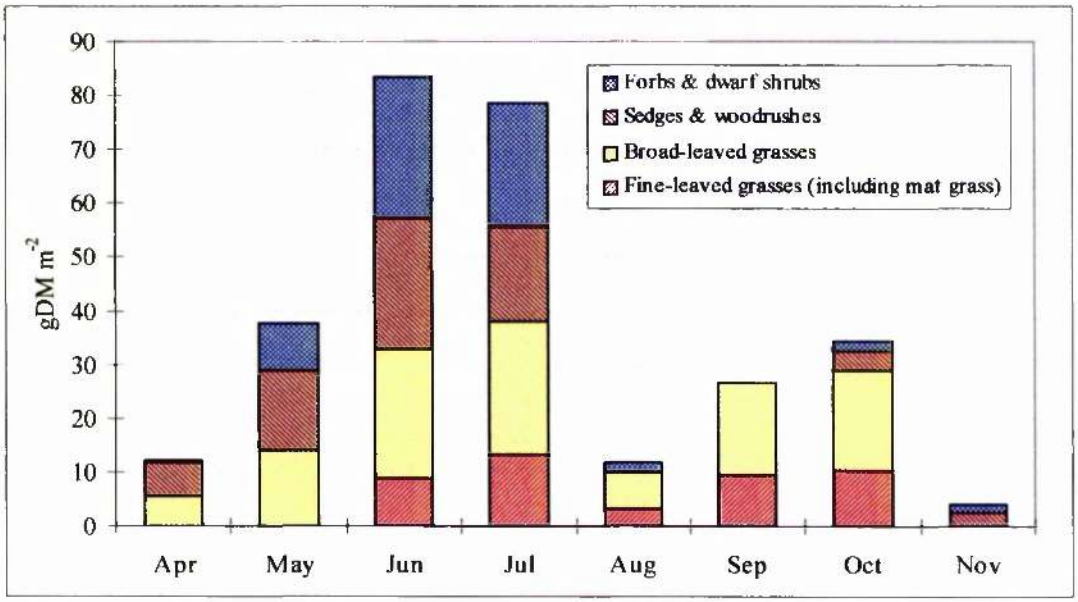


Figure 6.7 - Estimated monthly production of the main species and species groups within the U4d community during the 1997 growing-season. Production values have been estimated using the increments in mean live biomass only. The monthly production values have been adjusted for cage effects (Section 6.4.1.1), but have not been adjusted for random errors.

Table 6.4 - Seasonal variation in the relative growth rates (RGR) of selected components within the U4d grassland during the 1997 growing-season

	16th April - 14th May	15th May - 16th June	17th June - 17th July	18th July - 14th Aug	15th Aug - 18th Sept	19th Sept - 15th Oct	Average RGR over the season
Fine-leaved grasses	0	0	0.0045	0.0054	0	0.0134	0.0039
Broad-leaved grasses	0.0059	0.0051	0.0079	0.0030	0	0.0080	0.0050
Sedges and woodrushes	0.0096	0.0070	0.0126	0	0	0	0.0049

6.4.3 ABOVE-GROUND PRODUCTION VALUES ADJUSTED FOR RANDOM ERROR FACTORS

The random error adjusted production values for the four communities, calculated using the computer program developed by Biondini *et al.* (1991), are shown in Table 6.5. The adjusted value for the U5b community is less than half the unadjusted value.

Table 6.5 - Estimated above-ground vascular plant production of the U5c, U5b, M6d and U4d communities, before and after adjustment for random error factors.

NVC type	Annual above-ground vascular plant production (gDM m^{-2})	
	Values unadjusted for random errors	Values adjusted using the computer program developed by Biondini *et al.* (1991)
U5c	408.9	317.5
U5b	347.7	137.5
M6d	340.4	180.5
U4d	188.2	125.7

6.4.4 *IN VITRO* DRY MATTER DIGESTIBILITIES

Table 6.6 shows the seasonal DM digestibilities of a range of species from the study site. The mean DM digestibility of *Nardus stricta* (mean D-value (April to September) = 0.50) was found to be higher than that of *Festuca ovina/vivipara* (mean D-value (April to September) = 0.47) and only slightly lower than that of *Agrostis capillaris* (mean D-value (April to September) = 0.54).

Table 6.6 - *In vitro* dry matter digestibility values

		D-Value					
		April	**May**	**June**	**July**	**Aug**	**Sep**
Grasses	*Nardus stricta* green	0.483	0.498	0.565	0.522	0.472	0.453
	Nardus stricta dead			0.157			
	Agrostis capillaris green	0.563	0.595	0.596	0.495	0.519	0.483
	Festuca ovina/vivipara green	0.471	0.511	0.530	0.462	0.439	0.381
	Anthoxanthum odoratum green		0.734	0.712	0.672		0.598
	Molinia caerulea green				0.569	0.481	0.457
Other Species	*Juncus squarrosus* green	0.179	0.156	0.193	0.145	0.128	0.118
	Juncus squarrosus dead			0.075			
	Trichophorum cespitosum green			0.566	0.540	0.490	0.430
	Trichophorum cespitosum dead		0.178				

6.4.5 OFFTAKE OF LIVE VASCULAR PLANT MATERIAL

The difference between the mean live vascular plant biomass harvested from within the cages and that harvested from outside the cages was not always positive. This is illustrated in Figure 6.8 for the U5c grassland.

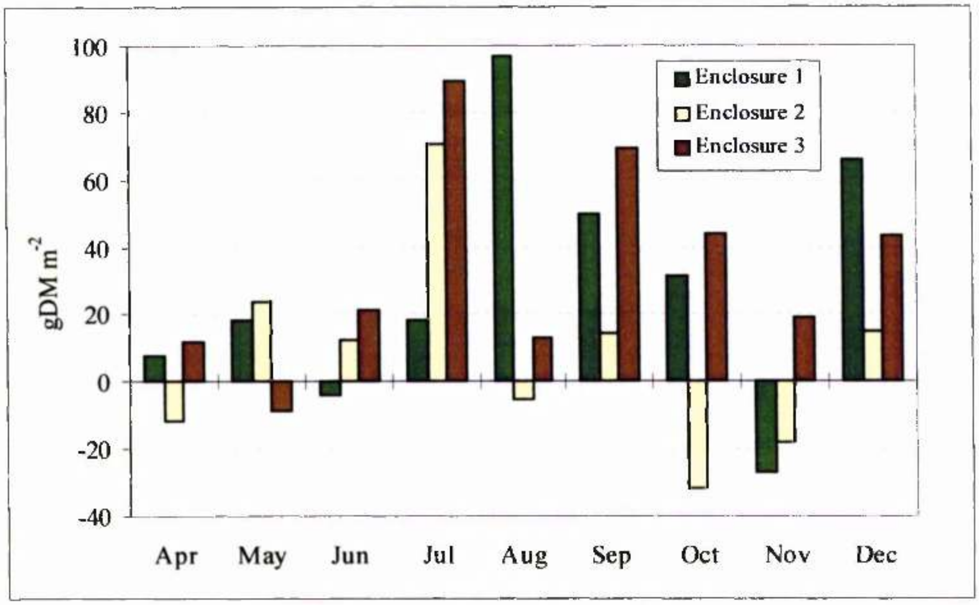


Figure 6.8 - The difference between the mean live vascular plant biomass of the U5c community within the exclosure cages (un-grazed) and that outside the exclosure cages (open to grazing) during 1995.

REML analysis of the data indicated that the overall mean live vascular plant biomass of the U5c grassland was significantly higher inside than outside the exclosure cages within Enclosures 1 and 3 (Enclosure 1, Wald = 6.6, df = 1, $P < 0.05$; Enclosure 3, Wald = 15.5 df = 1, $P < 0.001$), but not within Enclosure 2 (Wald = 0.5, df = 1, $P > 0.05$). The overall mean live vascular plant biomass of the M6d mire community was significantly higher inside than outside the cages within the cattle and sheep grazed enclosure (Enclosure 3, Wald = 4.0, df = 1, $P < 0.05$), but was not significantly higher within the two sheep only enclosures. For the U5b and U4d communities there was no significant difference between the overall mean live vascular plant biomass inside the cages compared with outside the cages in any of the sampled enclosures (Wald $\leq$ 0.3, df = 1, $P > 0.05$), although the mean inside values were consistently higher.

The estimated offtake of live vascular plant material from the U5c community was higher than from the U5b community (Table 6.7). In all three enclosures the offtake from the U5c community tended to be highest in the summer (mid-June to mid-September), and lowest in October and during the late winter/early spring period. Enclosure 2, which had the lowest stocking rate, had the lowest estimated offtake from the U5c community. The annual offtake from the U5b grassland was similar across all three enclosures. The enclosure containing the summer grazing cattle (Enclosure 3) had the highest estimated offtake of the U5c and M6d communities. There was no recorded utilisation of the M6d community within either of the sheep only enclosures (Table 6.7). Within Enclosure 2 the offtake from the U4d community was much lower than that from the two *Nardus stricta* communities, which had comparable offtakes.

Table 6.7 - Estimated annual offtake and percentage utilisation of live vascular plant material. Offtake values have been calculated using the sum of all positive and negative monthly 'offtake' values of live vascular plant material.

		U5c (mid-February to mid-December 1995)	U5b (mid-February to mid-December 1995)	U4d (mid-April to mid-November 1997)	M6d (mid-May 1995 to mid-May 1996)
Enclosure 1 0.074 LU ha^{-1}	offtake (gDM m^{-2})	258.3	51.3	No	< 0
	Utilisation (%)	63.2 %	14.8 %	Data	0 %
Enclosure 2 0.051 LU ha^{-1}	offtake (gDM m^{-2})	70.0	67.5	15.2	< 0
	Utilisation (%)	17.1 %	19.4 %	8.1 %	0 %
Enclosure 3 0.096 LU ha^{-1}	offtake (gDM m^{-2})	302.2	67.2	No	56.1
	Utilisation (%)	73.9 %	19.3 %	Data	16.5 %

Under the higher stocking rates of Enclosures 1 and 3, the offtake of live *Nardus stricta* from the U5c community was only slightly lower than the offtake of the inter-tussock vegetation (Table 6.8). Offtake of both *Nardus stricta* and inter-tussock vegetation from the U5c community was highest in Enclosure 3. Under the low sheep stocking rate of Enclosure 2 the estimated offtakes of *Nardus stricta* and inter-tussock vegetation were considerably lower than those estimated for Enclosures 1 and 3 (Table 6.8). Offtake of *Juncus squarrosus* from the U5b community was only recorded from Enclosure 3, the enclosure containing the summer grazing cattle.

Table 6.8 - Estimated offtake of live *Nardus stricta* and inter-tussock vegetation from the U5c community during 1995 (mid-February to mid-December). Values have been calculated using the sum of all positive and negative monthly 'offtake' values.

	Annual offtake (gDM m^{-2})	
	Nardus stricta	Inter-tussock Vegetation*
Enclosure 1 (0.073 LU ha^{-1})	**89.6** (highest offtake in July, August, November and December)	**136.1** (highest offtake between July and September)
Enclosure 2 (0.052 LU ha^{-1})	**17.4** (offtake between May and September, no winter offtake)	**66.6** (highest offtake between May and July)
Enclosure 3 (0.103 LU ha^{-1})	**118.3** (highest offtake in June, September and November)	**141.5** (highest offtake between June and October)

* The inter-tussock vegetation was composed of broad and fine-leaved grasses (excluding *Nardus stricta* and *Molinia caerulea*), sedges (excluding *Carex nigra* and *Carex echinata*), woodrushes and forbs.

Note - The sum of the *Nardus stricta* and inter-tussock offtakes from Enclosure 2 was greater than the total offtake value given in Table 6.7. This was due to the method of calculation.

6.5 Discussion

6.5.1 CAGE EFFECTS

Exclosure cages affect net herbage accumulation (Milner and Hughes, 1968) and therefore the production and offtake values obtained from experiments using them are subject to some degree of cage effect error. Previous experiments comparing net herbage accumulation from inside and outside exclosure cages have shown both positive and negative effects (Milner and Hughes, 1968; 't Mannetje, 1978; Marsh, 1978; Frame, 1993). The size and shape of cage, type of mesh, length of time the sward is protected, and the time of year, all influence the micro-environment within the cages (e.g. temperature, air flow, humidity and light intensity). The micro-environmental conditions determine the rates of production, senescence, litterfall and decomposition, and hence affect net herbage accumulation (Parsons *et al.*, 1984; Frame, 1993). The production of swards under continuous stocking differs from that of swards released from grazing. Under continuous stocking the removal of plant material by the herbivore has a marked effect on shoot growth (Parsons *et al.*, 1984). There is an intimate relationship between growth and intake that is dependent upon the presence of the grazing animals (Parsons *et al.*, 1983). The net herbage accumulation inside an exclosure cage depends upon the extent to which an increase in photosynthesis and growth is offset by an increase in the rate of senescence (Parsons *et al.*, 1984). There are also seasonal differences in the rate of photosynthesis and loss of tillers following the removal of grazing that do not occur under continuous stocking (Parsons *et al.*, 1984). The rate of net herbage accumulation within a cage also depends upon the initial leaf area index (LAI) of the sward (Parsons *et al.*, 1983; 1984). Parsons *et al.* (1984) showed that in a perennial ryegrass sward of low

LAI there is a large increase in photosynthesis after caging and net herbage accumulation continues for more than 5 weeks. Whereas in less closely grazed swards with a greater LAI and rates of photosynthesis close to a maximum, ceiling yields are reached in less than 5 weeks and thus the rate of accumulation calculated over the regrowth period is lower (Parsons *et al.*, 1984). Cages can also trap material that would otherwise have been lost through wind transportation or surface water run-off, leading to an increase in the litter component. This study showed that under a no-grazing situation the total above-ground biomass of a U5 grassland was significantly higher inside than outside the cages during the summer months, suggesting that production is increased within the cage micro-environment. The use of unadjusted biomass values would have resulted in over-estimates of production and offtake. Therefore, in order to reduce this cage effect it was considered appropriate to reduce the U5c and U5b caged biomass values by 6.43 % from mid-June to mid-October. The same adjustment factor and time period were used for the M6d community. The U4d caged biomass values were only adjusted between mid-July and mid-September, due to the higher altitude and exposed position of this grassland relative to the other communities, which would have led to a shorter growing period. Although both the M6d and U4d communities are structurally and compositionally distinct from the U5 grasslands (see Chapters 4 and 5) it was thought more appropriate to use an adjustment factor rather than to leave the values un-adjusted. These two communities were absent from the ungrazed enclosure in which Test 1 was carried out and therefore no specific adjustment factors could be calculated.

The rate of growth and the structural characteristics of a sward are altered when herbivores are removed (Frame, 1993). By removing large herbivores not only is the effect of grazing removed, but the effects of trampling, dung deposition and urine input are also removed (Frame, 1993). Trampling can cause physical damage to individual plants and cause soil compaction, which reduces the air content within the soil and impedes water flow and root penetration, resulting in reduced above and below-ground production (Brown and Evans, 1973; Frame, 1976). Calculations made using the exclosure cage method will always over-estimate the amount of grazed vegetation since losses due to trampling are included (de Leeuw and Bakker, 1986). Trampling damage caused by the summer grazing cattle within Enclosure 3 was clearly evident in the form of increased bare ground and localised poaching, which may have reduced production outside the cages during June to September. Although the study showed that there was no significant difference between the above-ground biomass adjacent to the cages compared with that harvested some distance away, the vegetation immediately surrounding cages that had been static for over 12 months showed clear evidence of increased damage (Plate 6.1). Cages left un-moved for long periods were used as 'scratching posts' by the grazing animals, leading to increased trampling damage and possibly higher offtake from the area adjacent to the cages.

The cages also excluded wild herbivores such as mountain hares and red deer that were observed in small numbers feeding within the study area, and therefore the calculated offtake values may have included material grazed by these animals. Grazing by wild herbivores may also explain some of the difference between the biomass inside and outside the exclosure cages measured in Test 1 (Section 6.4.1.1), however no hares or deer were observed in the enclosure used for this test.

Plate 6.1 - Damaged U5c vegetation surrounding an exclosure cage left un-moved for over 12 months

6.5.2 METHODS FOR CALCULATING PRODUCTION

There are many problems associated with the measurement of herbage production in indigenous hill plant communities. The vegetation is composed of a complex mix of grasses, sedges, rushes, annual and perennial herbs and dwarf shrubs, all of which have different seasonal patterns of growth and senescence. In some species growth and senescence occur simultaneously (e.g. *Agrostis capillaris* and *Festuca ovina*), although the rates of the two processes and the balance between them varies seasonally, whereas others (such as *Trichophorum cespitosum*, *Molinia caerulea* and *Juncus acutiflorus*) are much more seasonal, with growth occurring for only a short period in summer, followed by a separate period of senescence leading to complete die back in autumn (Grant and Hodgson, 1986). The presence of storage organs and the recycling of nutrients also varies between species. This variation in morphology, physiology and seasonality of growth mean that estimates of herbage production based on sequences of cuts have major limitations.

There are also a number of limitations with the method used to calculate above-ground net primary production:

1) The values of dead standing material are subject to a high degree of error, because of the difficulty in separating dead standing material from litter (see Chapter 5).
2) An assumption is made that before mid-July the rate of senescence is negligible.
3) An assumption is made that losses due to litterfall only occur from the dead standing component.
4) At certain times of year when production, senescence and litterfall are occurring contemporaneously, production can only be approximately derived using the change in total standing vascular plant biomass.
5) Random errors associated with field estimates of net primary production (NPP) can result in a positive bias and thus an overestimation in NPP.

The rationale behind the computer program developed by Biondini *et al.* (1991), for adjusting net primary production, is based on the premise that NPP is not the sum of the differences between Biomass_{time2} - Biomass_{time1}, but only the sum of the positive differences. In the calculation of NPP, a value of zero is assigned each time a negative difference value is calculated (something which could occur by chance alone), whereas, when the difference is positive, NPP is assigned that positive value. Therefore, estimates of NPP are not normally distributed, but have a distribution formed from a combination of two discrete distributions: one with mass of zero, and another with a truncated normal distribution (Biondini *et al.*, 1991). Although many of the methodological problems outlined earlier, lead to under-estimation of NPP, this statistical artefact results in an overestimation of NPP (Biondini *et al.*, 1991). Biondini *et al.* (1991) concluded that adjustment for overestimation did not guarantee an accurate estimate of NPP, but removed an unnecessary source of error. The concept of overestimation of NPP is tenable and should be taken into consideration. However, evaluation of the computer program developed by Biondini *et al.* (1991) indicated that the program was inappropriate in situations where there were few significant monthly increments in biomass (which was the case for the U5b, M6d and U4d samples). The differences between the adjusted and unadjusted NPP estimates were considered to be unacceptably large (e.g. a difference of 210.2 gDM m^{-2} between the adjusted and unadjusted U5b NPP). The computer program was therefore not used to adjust all the production data.

Although there are many limitations with the exclosure cage technique and the method of calculating NPP, the production values obtained from this study are believed to be reliable estimates. More accurate estimates of herbage production on continuously grazed swards can be obtained using tissue turnover and carbon exchange methods (Davies, 1993a; 1993b), however these techniques are unsuitable for remote field sites, are time consuming and are inappropriate for complex communities with many species.

6.5.3 *IN VITRO* DRY MATTER DIGESTIBILITIES

The DM digestibility values obtained indicate that live *Nardus stricta* has a digestibility comparable with that of *Festuca ovina/vivipara* and *Agrostis capillaris*. These results show that live *Nardus stricta* cannot be regarded as of negligible nutritive value. *Nardus stricta* swards however have a higher proportion of dead material than *Festuca - Agrostis* swards and this material is of very low digestibility. The proportion of live and dead material and the position of the dead material in the sward vary throughout the year. This will affect the digestibility of the material grazed by the animals. Unlike

Nardus stricta the DM digestibility of live *Juncus squarrosus* was found to be extremely low. The D-values for *Juncus squarrosus* were considerably lower than those obtained by Grant and Campbell (1978), while the D-values for *Trichophorum cespitosum* and *Molinia caerulea* were comparable with those obtained by Grant *et al.* (1976) (Table 6.9). The *in vitro* digestibility values of live broad-leaved and fine-leaved grasses within an *Agrostis* - *Festuca* grassland determined by Eadie and Black (1968) were considerably higher than the *Festuca* and *Agrostis* values obtained in this study (Table 6.9). Eadie and Black (1968) also estimated the *in vitro* digestibility of a *Nardus stricta* dominated grassland over the winter and spring period, obtaining digestibility values of green material ranging from 0.63 to 0.69 (Eadie and Black, 1968).

Table 6.9 - A comparison between the *in vitro* dry matter digestibilities of green material from the Kirkton Face enclosures (marked in red) with those from two published sources.

	May	June	July	Aug	Sep	Reference
Molinia caerulea			0.569	0.481	0.457	
Molinia caerulea	0.670	0.646	0.525	0.493	0.466	Grant *et al.*, 1976
Trichophorum cespitosum		0.566	0.540	0.490	0.430	
Trichophorum cespitosum	0.666	0.642	0.525	0.493	0.466	Grant *et al.*, 1976
Juncus squarrosus	0.156	0.193	0.145	0.128	0.118	
Juncus squarrosus *	0.329		0.258		0.264	Grant and Campbell, 1978
Agrostis capillaris	0.595	0.596	0.495	0.519	0.483	
Broad-leaved grasses	0.73					Eadie and Black, 1968
Festuca ovina/vivipara	0.511	0.530	0.462	0.439	0.381	
Fine-leaved grasses	0.68					Eadie and Black, 1968
Nardus stricta	0.498	0.565	0.522	0.472	0.453	
Nardus stricta grassland (45% *Nardus stricta*, 51.5% broad and fine-leaved grasses)	0.69					Eadie and Black, 1968

* Mean value from three years

6.5.4 CALCULATED OFFTAKE VALUES

The offtake values calculated using the cage method are likely to be over-estimates since trampling damage, preferential grazing of the vegetation surrounding the cages and changes in the rate of production within the cages are likely to have resulted in a positive bias (see 6.5.1). The small sample sizes (only four per month) and large standard errors (in excess of 20 gDM m^{-2} for the U5c community) are also likely to have reduced the accuracy of the results, however I believe the methodology does provide acceptable estimates of offtake that can be used to look at differences between communities and grazing management.

The results indicate that sheep actively grazed all three of the grassland communities, and that under the low stocking rate the utilisation of the two *Nardus stricta* communities was similar. However, offtake from the *Festuca ovina - Agrostis capillaris* grassland was much lower than from the *Nardus stricta* grasslands, despite its higher digestibility. The patches of *Festuca ovina - Agrostis capillaris* grassland that were sampled were limited in size, and were at a higher altitude and in a more exposed position than the sampled *Nardus stricta* grasslands. It appeared that size of patch and spatial location were more important in determining the foraging patterns and use of these particular vegetation types than digestibility. Increasing the sheep stocking rate or adding summer grazing cattle resulted in a substantial increase in estimated offtake from the U5c community, but no increased offtake from the U5b community. The animals appeared to be selecting the more digestible U5c community, which had a higher proportion of *Agrostis capillaris*, *Festuca ovina* and *Nardus stricta*, rather than the U5b community with its high proportion of relatively indigestible *Juncus squarrosus*. Within Enclosures 1 and 3 the estimated offtake of the U5c inter-tussock vegetation was over twice that of Enclosure 2, however the offtake of *Nardus stricta* was over five times that of Enclosure 2. Under the higher stocking rate, the sheep appeared to be changing their foraging behaviour, no longer preferentially grazing the more digestible inter-tussock vegetation. In all three enclosures, offtake from the U5c community was highest in mid-summer, when the proportion of live vascular plant material within the sward was at its highest. There was little offtake from the U5c community during the autumn senescence, when dead standing material (in particular *Nardus stricta*) was very abundant within the sward. There was also very little offtake from the U5c community during the late winter/early spring when the amount of live vascular plant material within the sward was at a minimum and the proportion of litter and dead standing material within the sward was at its highest (Chapter 5).

Armstrong *et al.* (1986) showed that the digestibility of *Nardus stricta* grasslands was lower than that of *Agrostis - Festuca* grasslands, and that the voluntary intake of *Nardus stricta* grasslands, by Scottish blackface wethers, was lower than that from *Agrostis - Festuca* grasslands. Diet selection studies using sheep and cattle have shown that *Nardus stricta* has a very low preference ranking compared with other grass species, with both sheep and cattle preferentially grazing inter-tussock grasses (Grant *et al.*, 1985). The diets of cattle grazing *Nardus stricta*-dominated pastures consistently contained more live *Nardus stricta* leaf material and dead material than those of sheep grazing the same sward (Grant *et al.*, 1985). Whereas, the diets of the sheep consistently contained more broad and fine-leaved grasses, and a higher proportion of leaf material, from the inter-tussock vegetation, than did the cattle diets (Grant *et al.*, 1985). Grant *et al.* (1985) showed that the proportion of *Nardus stricta* in the diets of both sheep and cattle grazing *Nardus*-dominated pastures, increased as the live aboveground biomass of the inter-tussock areas decreased. This rate of increase was much greater for the cattle than the sheep, indicating that the cattle switched to the taller more accessible parts of the sward, once the more preferred areas had been grazed too short to allow intake to be maintained at the current rate (Grant *et al.*, 1985; Hodgson *et al.*, 1991). Further studies by Grant *et al.* (1996b) in which *Nardus stricta* utilisation was estimated in terms of the fraction of tillers and leaves that were grazed, found that under similar sward conditions cattle utilised more *Nardus stricta* than did sheep. Armstrong and Hodgson (1986) studying the grazing of a range of indigenous hill plant communities by sheep and cattle, showed that in general sheep tended to maintain diet digestibility at the expense of intake rate, whereas cattle tended to maintain intake rate at the expense of digestibility. They observed that sheep tended to graze lower within the sward strata than cattle, and selected diets containing a higher proportion of live grass-leaf and forb material, and a lower proportion of seed-head and stem material than the cattle (Armstrong and Hodgson, 1986; Grant and Hodgson, 1986). Armstrong *et al.* (1997) studying groups of non-lactating sheep and cattle grazing *Nardus*-dominated pastures during the growing season, found that the diet of cattle generally contained more *Nardus stricta*, dead material, sedges and rushes, but less fine-leaved grasses and forbs, than the diet of sheep. The digestibility of the sheep diet tended to be higher than the digestibility of the cattle diet (Armstrong *et al.*, 1997). Armstrong *et al.* (1997) also found that the pasture grazed by the cattle had a greater stock-carrying capacity than the pastures grazed by the sheep, and that the carrying capacity of the sheep grazed pasture was higher when the inter-tussock sward height was maintained at 3.5 cm rather than 4.5 cm.

The offtake values obtained from the present study indicate only a slightly higher offtake of *Nardus stricta* from the U5c community in the cattle grazed enclosure, and no preferential offtake of other grass species compared to *Nardus stricta* except at the low sheep stocking rate. The live biomass of broad and fine-leaved grasses (excluding *Nardus stricta*) within the U5c grassland was however not significantly higher in the enclosure with the low sheep stocking rate compared with the enclosure with the high sheep stocking rate. Although, it was significantly higher in the enclosure with the low sheep stocking rate compared with the enclosure containing both sheep and cattle (Chapter 5).

Three possible factors contributing towards the relatively high offtake of *Nardus stricta* from the U5c grasslands have been identified:

(1) The *Nardus stricta* grasslands studied in this project lack distinct tussock and inter-tussock areas, limiting the ability of the sheep to actively select from within the dense, inter-locking sward.

(2) The digestibility of live *Nardus stricta* collected from within the study site was found to be comparable with that of *Festuca ovina* and *Agrostis capillaris*.

(3) The Scottish Blackface sheep used in this study had spent their entire adult lives grazing within the enclosures and had been almost entirely restricted to swards dominated by *Nardus stricta*.

Offtake of green material from the *Juncus acutiflorus*-dominated M6d community, and of live *Juncus squarrosus* from the U5b community, was much higher in the cattle and sheep grazed enclosure than in the sheep only enclosures, indicating the greater readiness of cattle to graze the tall, tough and fibrous components of the sward (Grant *et al.*, 1985; Hodgson *et al.*, 1991). In a comparative study of diet selection, Grant *et al.* (1985), showed that the diet of cattle, grazing a *Molinia*-dominated grassland, contained a higher proportion of *Juncus* species than did the diet of sheep grazing a similar community. Grant *et al.* (1985) did however note, that of the three species of *Juncus* found within the sward (*J. conglomeratus, J. effusus, J. acutiflorus*) the species most readily eaten by the sheep was *Juncus acutiflorus*. In a sheep-grazed grassland mosaic in the Netherlands, de Leeuw and Bakker (1989) noted that *Juncus acutiflorus* was grazed in the spring before the shoots became too tall, and again from September onwards when the standing material died back and newly developing shoots were exposed. In the present study no net offtake of green material was recorded from the M6d mire community within either of the two sheep only enclosures. This lack of recorded net annual offtake is almost certainly due to the inaccuracy of the technique used, rather than to the complete avoidance of this community by the grazing sheep.

6.5.5 COMPARISON WITH OTHER PUBLISHED WORK

Some published annual production values obtained from grassland sites in upland Britain are shown in Table 6.10. The production value for the *Nardus stricta* grassland (U5c) obtained from this study (408.9 gDM m^{-2}) was similar to those estimated by Job and Taylor (1978) for *Nardus stricta* grasslands at comparable altitudes in mid-Wales (356 - 436 gDM m^{-2}). It was however considerably higher than that given by Rawes and Welch (1969) for a *Nardus stricta* grassland in the North Pennines. At the sampling site in the North Pennines, grasses (excluding *Nardus stricta*) contributed only 15 % of the total dry matter production (Rawes and Welch, 1969), compared with almost 50 % in the U5c grasslands of the Kirkton Face. The *Nardus* grasslands at these two sites clearly had different species compositions. The relatively species-rich *Nardus stricta*-dominated grasslands which have developed on the base-rich Dalradian mica-schists of the study site, are also likely to be more productive than those found on the acidic granites, Torridonian sandstones, and Moine gneisses and schists, which occur to the north west of the Breadalbane range (Ratcliffe and Thompson, 1988; Rodwell, 1992).

Rawes and Welch (1969) also measured the productivity of a *Juncus squarrosus* community in the North Pennines. The total annual production value of 343 gDM m^{-2} recorded by Rawes and Welch (1969) is within 5 gDM m^{-2} of the value calculated for the Kirkton Face U5b grassland.

Production data from a semi-natural, hill grassland (a mosaic of *Festuca ovina*, *Agrostis capillaris*, *Nardus stricta*, *Juncus* spp. and *Molinia caerulea*) adjacent to the Kirkton Face study site was collected by Tiley *et al.* (1986) during the growing seasons of 1981 to 1985. Herbage growth was measured under cages at 3 weekly intervals from the end of April to the end of October each year. The herbage was harvested using a reciprocating blade mower set to cut at a height of 2.5 cm above the ground. After each harvest the cages were moved to new locations where the sward had been pre-trimmed down to the sampling height. Annual dry matter yields of between 2.19 and 4.05 tonnes ha^{-1} were obtained (mean of 3.64 tonnes ha^{-1}), which are comparable with the U5c and U5b production estimates obtained in 1995 from the present study.

A study by Grant *et al.* (1996c) looking at leaf growth and senescence of *Nardus stricta* found that peak growth occurred in June and July (4 - 5 mm $tiller^{-1}$ day^{-1}), and the rate of senescence was low until early autumn when it reached 6 mm per tiller per day. The rate of lamina extension of *Nardus stricta* was found to be less than half that of *Agrostis capillaris* within the same sward (Grant *et al.*, 1996c). The periods of peak growth and senescence of *Nardus stricta* were the same as those recorded in the present study.

The production value obtained for the U4d grassland (188.2 gDM m^{-2}) was lower than the values given by Job and Taylor (1978), Perkins *et al.* (1978) and Harrison *et al.* (1994) for comparable *Festuca ovina - Agrostis capillaris* grasslands, however Rawes (1963) obtained a very similar production value of 174 gDM m^{-2} for an *Agrostis - Festuca* grassland at an altitude of 555 m (Table 6.10).

6.6 Conclusions

By adjusting the production and offtake values, to account for cage effects, the reliability and accuracy of the exclosure cage method can be improved. Although there are many limitations with the use of cages in estimating production and offtake in grazed swards, and there are numerous sources of error, they are the only practical means of obtaining approximate production and offtake values for hill vegetation types in remote field sites (Parsons *et al.*, 1984).

A relatively high production value of over 4.0 tonnes ha^{-1} was estimated for the *Nardus stricta*-dominated U5c community. The production of the U5c grassland was greater than that of the U5b, U4d and M6d communities. The U4d community which occurred at the highest altitude and in the most exposed position had the lowest net primary production, which was less than half that of the U5c community. The patterns and rates of growth varied between the different communities.

The results indicate that the utilisation of the different vegetation types was not related to a single factor, but appeared to be dependent upon the species of herbivore; the abundance and spatial location of the vegetation type; and the digestibility, biomass and structure of the sward.

Table 6.10 - Some published annual production values for *Nardus stricta, Juncus squarrosus* and *Festuca / Agrostis* grasslands

Vegetation Description	Location	Altitude (m)	Production ($gDM\ m^{-2}$)	Reference	Grazing
Nardus - Festuca - Agrostis (U5c)	Crianlarich	425	**409**	Present study	Controlled sheep grazing
Nardus - Juncus squarrosus (U5b)	Crianlarich	475	**348**	Present study	Controlled grazing
Festuca - Agrostis (U4d)	Crianlarich	580	**188**	Present study	Controlled sheep grazing
Nardetum	Moor House NNR, North Pennines	550	**193**	Rawes and Welch (1969)	Summer grazing sheep (April - October)
Nardus stricta, Festuca ovina, Poa pratensis, Holcus lanatus, Lolium perenne, Anthoxanthum odoratum, Carex binervis, Trifolium repens	Plynlimon, Mid-Wales	525	**436**	Job and Taylor (1978)	Sheep and cattle, some pasture improvement
Festuca ovina, Danthonia decumbens, Nardus stricta, Agrostis capillaris, Deschampsia flexuosa, Vaccinium myrtillus, Potentilla erecta	Plynlimon, Mid-Wales	440	**364**	Job and Taylor (1978)	Uncontrolled grazing by sheep
Festuca ovina, Agrostis canina, Nardus stricta, Vaccinium myrtillus, Anthoxanthum odoratum Deschampsia flexuosa, Calluna vulgaris	Plynlimon, Mid-Wales	670	**357**	Job and Taylor (1978)	Uncontrolled grazing by sheep
Festuca ovina, Juncus squarrosus, Agrostis canina, Deschampsia flexuosa, Nardus stricta, Vaccinium myrtillus, Anthoxanthum odoratum.	Plynlimon, Mid-Wales	565	**286**	Job and Taylor (1978)	Uncontrolled grazing by sheep
Agrostis capillaris - Festuca ovina, Festuca ovina - Nardus stricta, Juncus spp. - *Molinia caerulea* mosaic	Crianlarich, West Perthshire	300 - 400	**364**	Tiley *et al.* (1986)	Controlled sheep grazing plus autumn cattle
Juncetum squarrosi	Moor House NNR, North Pennines	550	**343**	Rawes and Welch (1969)	Summer grazing sheep (April - October)
Festuca - Agrostis alluvial grassland	Moor House NNR, North Pennines	518	**274**	Rawes (1963)	Summer grazing sheep (April - October)
Agrosto-Festucetum	Moor House NNR, North Pennines	555	**174**	Rawes and Welch (1969)	Summer grazing sheep (April - October)
Festucetum	Moor House NNR, North Pennines	840	**54**	Rawes and Welch (1969)	Summer grazing sheep (April - October)
Festuca ovina, Danthonia decumbens, Agrostis capillaris, Deschampsia flexuosa, Vaccinium myrtillus, Nardus stricta, Luzula campestris	Plynlimon, Mid-Wales	420	**356**	Job and Taylor (1978)	Partially controlled sheep grazing
Moderately herb-rich *Agrostis - Festuca* grassland	Llyn Llydaw, North Wales	488	**271**	Perkins *et al.* (1978)	Summer grazing sheep (April to October)
Agrostis capillaris - Festuca ovina grassland on well drained un-fertilised brown earth above limestone pavement grykes (hollows)	Moor House NNR, North Pennines	480	**225 - 363**	Harrison *et al.* (1994)	Summer grazing sheep (April - October)
Agrostis capillaris - Festuca ovina grassland on well drained un-fertilised brown earth above limestone pavement grykes (hollows)	Moor House NNR, North Pennines	639	**193 - 238**	Harrison *et al.* (1994)	Summer grazing sheep (April - October)

CHAPTER 7 – TESTING, EVALUATION AND MODIFICATION OF THE HILL GRAZING MANAGEMENT MODEL

7.1 Summary

1) The overall aim of this chapter was to test and evaluate the Macaulay Land Use Research Institute's Hill Grazing Management Model, and to modify and re-evaluate the model if required.

2) Before the model could be evaluated it was necessary to check the accuracy of the measured offtake values. This was done by calculating the total metabolisable energy (ME) used by the sheepflock within Enclosure 2, and the total estimated ME content of the measured green offtake, and then comparing the two values.

3) The ME content of the green offtake was higher than the estimated total ME used by the sheepflock, but was within acceptable limits. Although there are major limitations with the use of the exclosure cage technique for estimating offtake, the results indicate that acceptable values of offtake can be obtained using this method.

4) The original MLURI Hill Grazing Management Model (HGMM) was then tested and evaluated using data from Enclosure 2.

5) The HGMM under-estimated the production, green biomass, sward height and offtake of inter-tussock material from the *Nardus stricta* grasslands. The model assumes that *Nardus stricta* is not utilised, however the exclosure cage data collected in this study showed that this was not the case (Chapter 6).

6) The metabolisable energy content of the offtake predicted by the HGMM was lower than the amount required to maintain the sheepflock at the levels of performance recorded.

7) The HGMM was therefore modified to allow the input of data from the U5c and U5b communities. The modified model was then tested and evaluated using data from Enclosure 2.

8) The modified HGMM under-estimated the green biomass, dead biomass and sward height of the U5b community, indicating that the rates of senescence and litterfall set within the model were not appropriate for this community type. The predictions for the U5c community were much closer to the measured values.

9) The modified HGMM predicted higher offtake from the *Nardus stricta* grasslands and higher total offtake of live and dead material than the original unmodified HGMM. However, the predicted offtake from the U5b grassland remained lower than the measured value. Although the ME content of the offtake was higher than that predicted by the original model it remained lower than the total ME required to maintain the sheepflock at the levels of performance recorded.

10) The modified model was also tested using a large-scale independent data set. The modified model under-estimated the offtake during pregnancy and early lactation. It did however predict a higher total offtake and a higher offtake from the *Nardus stricta* grasslands than the un-modified model.

11) The modifications significantly improved elements of the vegetation sub-model by predicting reasonably well the green and dead biomass, and sward height of the U5c grassland. The full inclusion of the U5c and U5b vegetation types into the model results in a slight improvement in the model's offtake predictions and improves its

applicability for use in the north and west of Britain where these communities are widespread and abundant. However, the modified model still significantly under-estimates offtake particularly in the early part of the year.

12) The algorithms within the offtake sub-model appear to be inadequate, resulting in weak predictions, particularly during the first half of the year.

13) New grazing decision support tools need to have fully integrated animal and plant sub-models.

7.2 Introduction

Numerous models have been produced which simulate the grazing of domestic livestock (Gordon and Hutchings, 1993), predicting animal energy requirements (reviewed in Wallach *et al.*, 1984), intake (e.g. Demment and Laca, 1993; Finlayson *et al.*, 1995), and foraging behaviour (e.g. Illius, 1986; Focardi and Marcellini, 1995; Newman *et al.*, 1995), as well as herbage growth (e.g. Johnson and Parsons, 1985; Lauenroth *et al.*, 1986; Rice, 1986; Hutchings, 1991) and vegetation dynamics (e.g. Parsons *et al.*, 1991; Sanderson and Rushton, 1995; Birch *et al.*, 1997; 2000; Palmer and Hester, 2000). By combining a range of these models, computer based decision support systems have been created, which are designed to assist farmers and land managers in their practical grazing management (e.g. Hill Grazing Management Model (Armstrong *et al.*, 1997a; 1997b), GRAZPLAN (which includes the GrassGro and GrazFeed decision support systems) (Donnelly *et al.*, 1997; Freer *et al.*, 1997; Moore *et al.*, 1997; Clarke *et al.*, 2000), HillDeer (Partridge *et al.*, 1999), HILLPLAN (Milne and Sibbald, 1998)).

The Macaulay Land Use Research Institute's Hill Grazing Management Model (HGMM) is a computer model designed to assist grazing management decision-making on hill farms in the UK (Milne, 1998). The model requires information on (a) the site location; (b) the area and cover of each of the main hill vegetation types: *Calluna vulgaris* moorland (newly burnt, pioneer, building, mature, degenerate, blanket bog and suppressed); *Agrostis - Festuca* grassland; *Festuca - Agrostis* grassland (including its cover within the other vegetation types); *Nardus stricta*-dominated grassland; *Molinia caerulea*-dominated grassland (burnt and un-burnt); (c) the mean altitude of the heather and combined indigenous grassland vegetation types; (d) the area of reseeded pasture, together with its altitude, soil type, management and rate of fertilizer application; (e) the mean live weight of the breeding ewes and the number of ewes on the hill each month (Armstrong *et al.*, 1997a; 1997b). The HGMM has two main components; a model that uses published data to predict the herbage resource available to the grazing livestock, and an intake and foraging behaviour model that uses data provided by the vegetation model to predict offtake from each vegetation type (Armstrong *et al.*, 1997a; 1997b). The information provided by the model has to be interpreted by the user to assess whether the sheep stocking rate will influence the productivity of the vegetation, lead to vegetation change or cause animal welfare problems. The HGMM has been widely used by researchers to predict heather moorland utilisation (e.g. Simpson *et al.*, 1998), and by landowners, conservation bodies and government agencies to set stocking rates that meet animal production or conservation objectives. Armstrong *et al.* (1997a; 1997b) have however identified a number of weaknesses in the model and gaps in the knowledgebase. One of the main weaknesses is the limited range of vegetation types. Although the model does include *Nardus stricta* grassland it is only considered in terms of the species-poor *Festuca* - *Agrostis* growing between the *Nardus stricta* tussocks. The offtake studies carried out as part of this thesis have shown that *Nardus stricta* is utilised by grazing animals and should not be ignored (Chapter 6). Communities dominated by *Juncus squarrosus*, *Trichophorum cespitosum*, *Eriophorum* spp. and *Vaccinium myrtillus* are not included in the model at all. If this model or similar new models are to be of any value on sites with a high proportion of *Nardus stricta* or *Juncus squarrosus* dominated grassland, such as Kirkton Farm, data on the production and digestibility of these communities must be included.

No matter how complex models become they can never represent the system completely. Models can only incorporate the current quantitative knowledge that is available (Rice, 1986). In any model the numerous components and relationships that form the knowledgebase must be simplified, and those relationships that are highly complex or poorly understood may need to be combined or omitted (Rice, 1986). By testing and evaluating models, any areas where data are currently deficient are highlighted, and any processes that are poorly defined are exposed (Rice, 1986). Research can then be carried out to increase our understanding of these processes, leading to improvements in the predictive ability of the model and subsequent re-evaluation. The development of models is dependent on this constant process of evaluation, improvement and re-evaluation.

The aims of this chapter were:

1) To test and evaluate the HGMM decision support tool;
2) To modify the model to improve its predictive ability for sites with high proportions of *Nardus stricta* and *Juncus squarrosus* dominated grassland, using data collected from the study site;
3) To test and re-evaluate the modified version of the model.

7.3 Are the offtake values determined using the exclosure cages valid estimates?

7.3.1 INTRODUCTION

Before the Hill Grazing Management Model could be tested it was necessary to determine whether the offtake values, determined using the exclosure cages, were valid estimates. If the measured values were unreliable, evaluation of the model would have been impossible. Data from Enclosure 2 were used in this validation since this was the only enclosure from which data on the production and utilisation of the U4d *Festuca ovina - Agrostis capillaris - Galium saxatile* community was collected.

The amount of offtake can be estimated indirectly by calculating the total metabolisable energy (ME) requirements of the grazing animals based on their measured performance. A computer model developed by Conington *et al.* (in prep.), henceforth known as the Hill Sheep Model (HSM), calculates the energy use of a sheepflock based on body weights, weight changes, the physiological state of the animals and the digestibility of the food source. The HSM estimates the ME required for maintenance and production using a comprehensive set of algorithms that have been developed using up-to-date information on sheep metabolism. This model was used to calculate the total ME required to maintain the recorded levels of performance of the sheepflock within Enclosure 2 during 1995. The model does not take into account supplementary feed allowances, and therefore the energy content of the supplementary feed given to the sheep between January and April was calculated and deducted from the total ME value. The measured offtake values determined using the exclosure cages

(Chapter 6) were converted into ME, and the total ME content of the measured offtake was then compared with the calculated flock requirements.

7.3.2 UTILISATION OF METABOLISABLE ENERGY

The total annual utilisation of metabolisable energy by the sheepflock (based on the measured performance of the animals) calculated by the HSM was 93.28 GJ (Figure 7.1).

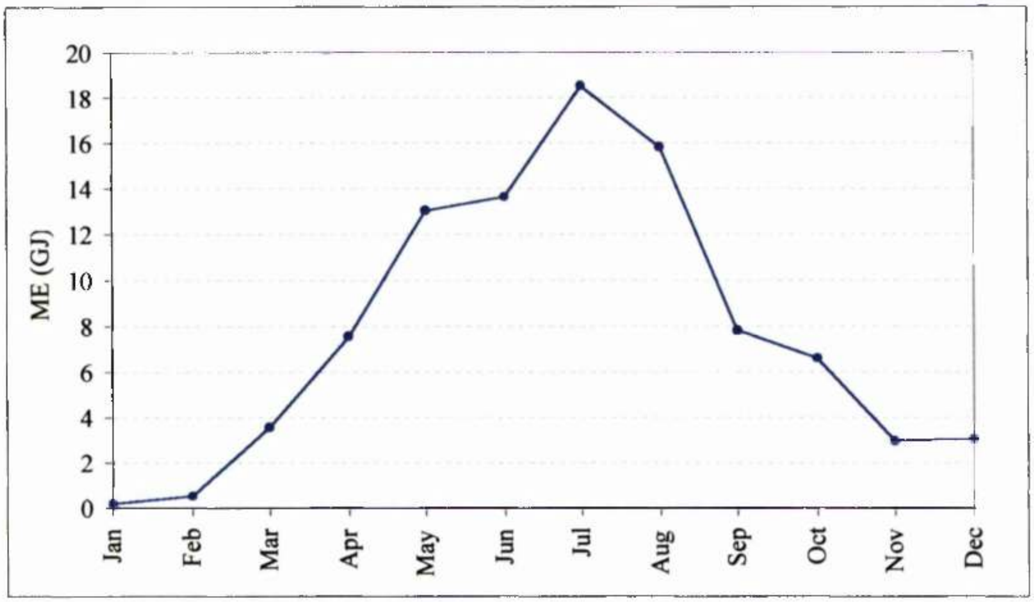


Figure 7.1 - Estimated monthly utilisation of ME by the sheepflock within Enclosure 2

The very low ME values predicted for January and February suggest that the HSM is under-estimating the utilisation of the pasture during this period. These low net figures are mainly due to the large weight loss of the animals during the winter. Whilst the use of body resources to meet the metabolic needs of the sheep is likely to be high, the animals clearly did not stop grazing over this period and therefore the figures are almost certainly erroneous.

The HSM does not include any additional requirement for energy due to cold stress. Maintenance of a core body temperature of 39°C is crucial to a sheep's survival (Duncan, 1998). This is achieved by balancing their metabolic heat production (through physiological and behavioural mechanisms) against the energy they lose to the environment (Christopherson and Young, 1986; Duncan, 1998). The digestion process produces heat and is one of the main mechanisms for maintaining body temperature. Within the range of temperatures known as the thermo-neutral zone an animal can maintain its body temperature without additional energy expenditure by adjusting evaporative heat loss (Duncan, 1998). Below the lower critical temperature (LCT), which is the lower limit of the thermo-neutral zone, an animal must increase its metabolic heat production by mobilising energy reserves, in order to balance the heat lost to the environment (Duncan, 1998). The LCT for an adult sheep with a fleece depth of 20-30 cm has been estimated to be –20°C in still air conditions (Slee, 1987). Animals that have a low food intake have a much higher LCT than well fed animals since the process of digestion produces heat, maintaining body temperature (Duncan, 1998). The amount of thermal insulation (i.e. the thickness of the fleece and the depth of subcutaneous fat), together with climatic factors, such as wind speed and precipitation, also influence LCT (Duncan, 1998). Sheep in windy conditions or with wet fleeces have higher LCT's than sheep in still conditions with dry fleeces (Joyce and Blaxter, 1964; Joyce *et al.*, 1966). Although adult hill sheep are well adapted to cold conditions (Duncan, 1998), the cold, wet and windy climate of the study site (Chapter 2) is likely to have resulted in the lower critical temperature being reached on some days during the winter period, thus requiring additional energy use to maintain body temperature. The animals must have been grazing during this period (and were observed doing so) in order to maintain their body temperatures. Therefore, the negative and very low ME offtakes over the winter period must be inaccurate, and the overall utilisation of ME calculated by the HSM (based on animal performance) must be an under-estimate. However, the error is unlikely to be large as the cold stress period coincides with the months when there were the fewest animals in the flock (i.e. no lambs or hoggs) and the lowest levels of production. It is difficult to assess how many days the effective temperature was below the LCT during 1995. However, if as an example it is assumed that the effective temperature was 1.5°C below the LCT on 25 % of the days during the winter (November to March) and that for every degree below the LCT each ewe needed to increase heat production by approximately 395 KJ day^{-1} (Christopherson and Young, 1986), then the total amount of additional energy expenditure by the sheepflock to maintain homeothermy would have been approximately 0.52 GJ.

Despite the problems caused by cold stress, the offtake calculated by the HSM, which uses current data on sheep metabolism, can be considered to be the best estimate available.

7.3.3 ME CONTENT OF THE GREEN OFFTAKE

The ME content of the green offtake from the four sampled communities was estimated to be 113.86 GJ in total (Table 7.1). This value assumes that offtake from the four sampled communities is the same throughout their range. The value does not include offtake of dead material or offtake from the un-sampled communities. The total offtake and ME content of dead material was assumed to be low, due to its low digestibility. The total offtake from the other plant communities was also assumed to be low due to their limited cover and/or low digestibilities. As outlined in Chapter 6, offtake values are likely to have been over-estimated using the cage technique.

Table 7.1 - Conversion of offtake values into total metabolisable energy (ME)

	Offtake (kgDM ha)	Area (ha)	Total Offtake (kgDM)	DM Digestibility (%)	OM Digestibility (%)	ME (MJ kg^{-1})	**Total ME (GJ)**
U5c	700	6.04	4228	62.8	62.9	9.87	41.73
U5b	675	13.10	8840	48.6	47.8	7.50	66.29
U4d	152	3.69	561	66.0	66.3	10.41	5.84
M6d	0	3.24	0	48.6	47.8	7.50	0
						Total	**113.86**

The annual mean DM digestibility values have been calculated using the figures given in Table 7.5 together with the monthly percentage biomass values of the components.
The digestibility of the M6d community is assumed to be comparable with that of the U5b community.
OM digestibility is assumed to equal DM digestibility minus 0.037 divided by 0.94 (MAFF *et al.*, 1975).
ME (MJ kg^{-1} of DM) is assumed to equal 0.0157 times OM digestibility (g kg^{-1} of DM).

The total ME of the green biomass removed by the sheep from the four sampled communities was 20.58 GJ greater than the total ME used by the sheep as predicted by the HSM. Although the measured offtake exceeds the predicted value, the difference (≈20 %) is within acceptable limits. The measured offtake values from Enclosure 2 can therefore be used with confidence to test and evaluate the Hill Grazing Management Model. Although there are major limitations with the use of the exclosure cage technique for estimating offtake (Chapter 6), the results from Enclosure 2 indicate that acceptable values can be obtained using this method.

7.4 Testing the published Hill Grazing Management Model

Data from Enclosure 2 were used to test and evaluate the HGMM. Before the model could be tested the NVC vegetation types identified in the enclosure had to be converted into appropriate vegetation types for the model, and the percentage covers of the main vegetation components within the communities had to be estimated.

7.4.1 Conversion of community types

Each one of the twenty-two NVC community types within Enclosure 2 (Chapter 3) was placed into the most appropriate HGMM vegetation type (Figure 7.2). Some NVC communities could not be classified into appropriate HGMM vegetation types and were therefore placed into an un-classified group.

7.4.2 Calculation of percentage cover values

The percentage cover values of *Nardus stricta* and inter-tussock vegetation (i.e. grasses (excluding *Nardus stricta* and *Molinia caerulea*), sedges (excluding *Carex echinata* and *Carex nigra*), woodrushes and forbs) within the U5c and U5b grasslands were calculated using the sward stick data described in Chapter 4. Data from July, August and September 1995 were used to calculate mean summer percentage cover values. The percentage cover of inter-tussock vegetation was assumed to be equivalent to the percentage cover of *Festuca - Agrostis* grassland as used in the model. The percentage cover values of *Nardus stricta*, *Festuca - Agrostis*, *Calluna vulgaris* and *Molinia caerulea* within the other NVC communities were visually estimated in the field (Table 7.2).

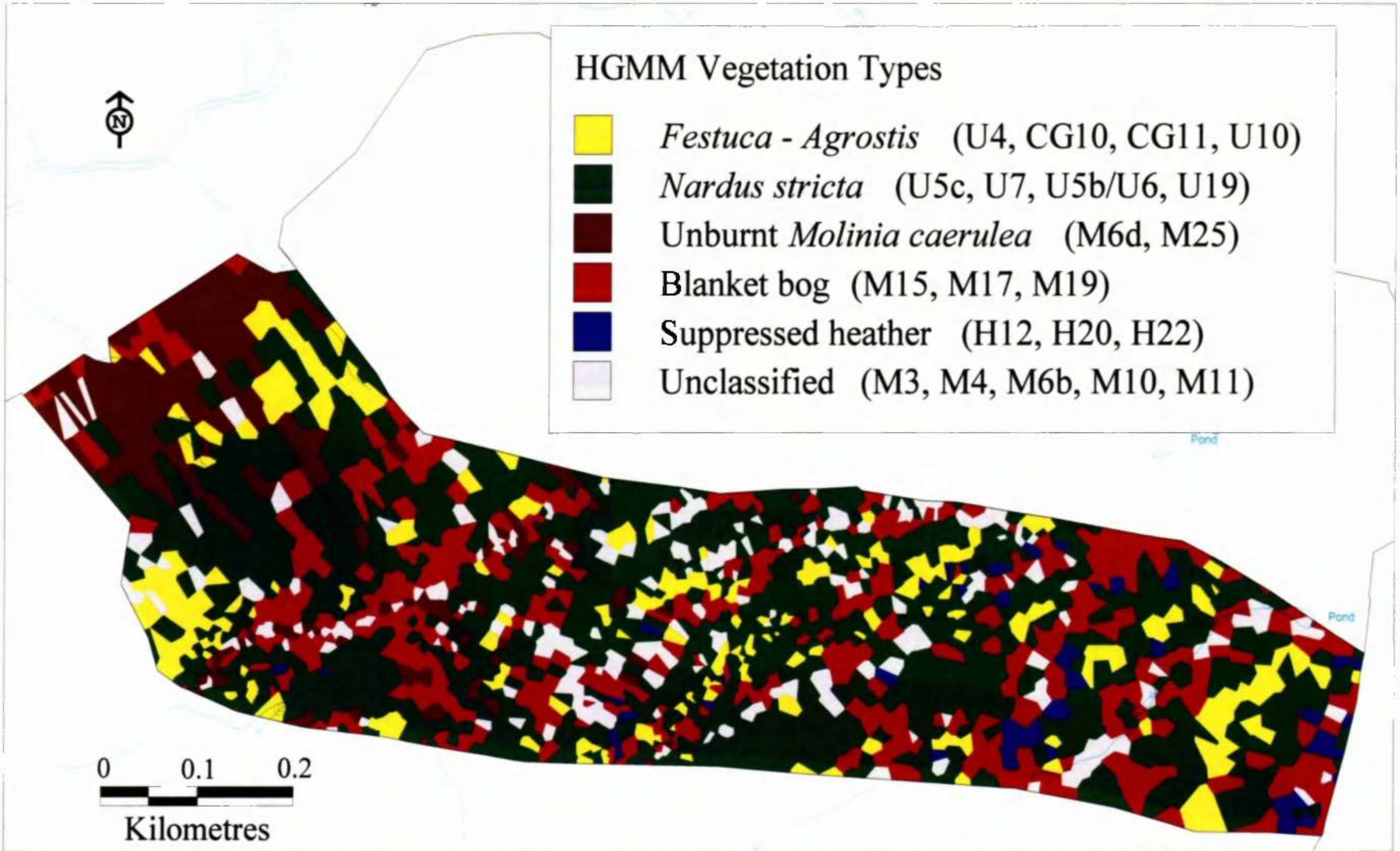


Figure 7.2 - Map of the MLURI Hill Grazing Management Model Vegetation Types found within Enclosure 2

Table 7.2 - Conversion of NVC types within Enclosure 2 into HGMM vegetation types and revised areas for input into the model

NVC Community Type	Area (ha)	Model Vegetation Type	Model Input Data	Revised Area (ha)
U5c	6.037	*Nardus stricta* (44.2% cover), *Festuca/Agrostis* (30.8% cover)		
U5b / U6	13.096	*Nardus stricta* (41.4% cover), *Festuca/Agrostis* (27.5% cover)		
U7	0.185	*Nardus stricta* (44.2% cover), *Festuca/Agrostis* (30.8% cover)		
U19	0.140	*Nardus stricta* (20% cover), *Festuca/Agrostis* (30% cover)	*Nardus stricta* (42.13% cover), *Festuca/Agrostis* (28.58% cover)	19.458
U4	1.777	*Festuca/Agrostis* (100% cover)		
CG10	0.071	*Festuca/Agrostis* (80% cover)		
CG11	0.789	*Festuca/Agrostis* (80% cover)		
U10	1.635	*Festuca/Agrostis* (75% cover)	*Festuca/Agrostis* (100% cover)	3.691
H12	0.891	Suppressed *Calluna vulgaris* (60% cover)		
H20	0.015	Suppressed *Calluna vulgaris* (5% cover)		
H22	0.020	Suppressed *Calluna vulgaris* (5% cover)	Suppressed *Calluna vulgaris* (57.92% cover)	0.926
M15	0.981	Blanket Bog - *Calluna vulgaris* (5% cover), *Festuca/Agrostis* (3% cover)		
M17	6.735	Blanket Bog - *Calluna vulgaris* (5% cover), *Festuca/Agrostis* (2% cover)		
M19	1.023	Blanket Bog - *Calluna vulgaris* (40% cover), *Festuca/Agrostis* (0% cover)	Blanket Bog - *Calluna vulgaris* (9.1% cover), *Festuca/Agrostis* (1.88% cover)	8.739
M25	0.602	Unburnt *Molinia caerulea* (30% cover), *Festuca/Agrostis* (5% cover)		
M6d	3.238	Unburnt *Molinia caerulea* (12% cover), *Festuca/Agrostis* (5% cover)	Unburnt *Molinia caerulea* (14.82% cover), *Festuca/Agrostis* (5% cover)	3.84
M3	0.232	Unclassified		
M4	0.561	Unclassified		
M6b	1.668	Unclassified		
M10	0.515	Unclassified		
M11	0.566	Unclassified	Unclassified	3.542
Total Area	**40.777**		**Revised Total Area**	**40.196**

7.4.3 DATA ENTRY INTO THE HILL GRAZING MANAGEMENT MODEL

The un-modified HGMM (Version 1.01) computer program was run using the data shown in Table 7.3.

Table 7.3 - Model input data

Information Required by the HGMM	**Input Data**
Zone	5
Location	Upland
Side	West
Mean altitude of heather communities (calculated using GIS)	564 m
Blanket Bog - Area	8.739 ha
Blanket Bog - Cover of *Calluna vulgaris*	9.1 %
Blanket Bog - Cover of *Festuca/Agrostis*	1.88 %
Suppressed Heather - Area	0.926 ha
Suppressed Heather - Cover of *Calluna vulgaris*	57.92 %
Mean altitude of indigenous grassland communities	500 m
Festuca/Agrostis - Area	3.691 ha
Festuca/Agrostis - Cover	100 % (fixed)
Nardus stricta community - Area	19.458 ha
Nardus stricta community - Cover of *Nardus stricta*	42.13 %
Nardus stricta community - Cover of *Festuca/Agrostis*	28.58 %
Unburnt *Molinia caerulea* community - Area	3.84 ha
Unburnt *Molinia caerulea* community - Cover of *Molinia caerulea*	14.82 %
Unburnt *Molinia caerulea* community - Cover of *Festuca/Agrostis*	5.0 %
Average ewe weight	46.8 kg
Ewe Numbers (January to December)*	13, 22, 22, 27, 27, 26, 27, 25, 22, 22, 22, 36

* The HGMM assumes that all ewes produce a single lamb. There is no provision for the inclusion of hoggs (yearling un-mated ewes) in the model. It would have been inappropriate to ignore the presence of the hoggs or to have given them a value equivalent to a ewe, therefore each hogg was allocated a value of 0.66 of a ewe.

7.5 Comparison between the published Hill Grazing Management Model predictions and the measured values

7.5.1 STATISTICAL ANALYSES

A Mean Square Prediction Error (MSPE) analysis was carried out to determine the accuracy of the model predictions, and what proportion of any error was due to bias, slope or random effects. For each of the model predictions the observed values were plotted against the predicted values and a linear regression analysis was carried out.

7.5.2 *FESTUCA - AGROSTIS* GRASSLAND

The production, green biomass, sward height and green offtake values predicted by the un-modified HGMM for the *Festuca - Agrostis* grassland within Enclosure 2 were compared with the measured values obtained from the U4d *Festuca ovina - Agrostis capillaris - Galium saxatile* community.

The predicted annual production value of 227.4 gDM m^{-2} was over 20 % more than the measured annual production value (188.2 gDM m^{-2}). The model predicted much higher production rates in May and August, and lower production rates in June and July than the measured rates (Figure 7.3). There was a large mean prediction error most of which was due to random effects (Table 7.4 and Figure 7.4). This indicates that the production algorithm within the model does not predict well the monthly production of the U4d *Festuca ovina - Agrostis capillaris - Galium saxatile* community. The error cannot easily be corrected because most of it was due to random effects.

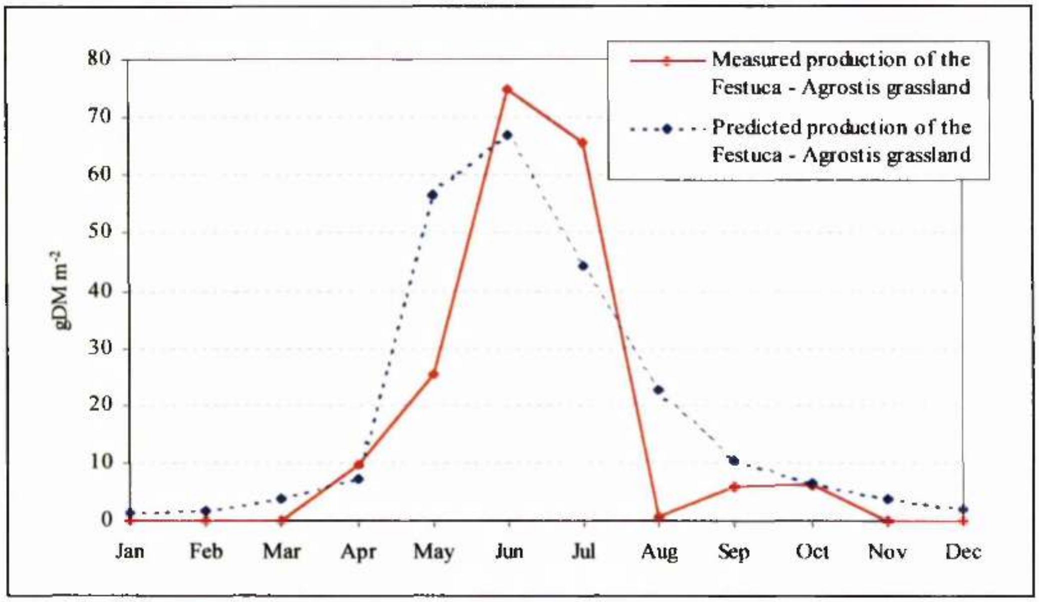


Figure 7.3 - Production of the *Festuca - Agrostis* grassland as predicted by the un-modified HGMM and the measured production of the U4d community within Enclosure 2.

Table 7.4 - MSPE analysis of the model predictions for the *Festuca - Agrostis* grassland.

Observed versus Predicted	Mean Square Prediction Error (MSPE)	Mean Prediction Error (MPE)	MPE as % of actual mean	% of total MSPE		
				Bias	Slope	Random
Production *Festuca-Agrostis* Grassland	254.91	15.97	**67.9 %**	4.9 %	0.01 %	95.1 %
Green Biomass *Festuca-Agrostis* Grassland	15080.92	122.80	**64.2 %**	94.7 %	0.01 %	5.3 %
Sward Height *Festuca-Agrostis* Grassland	0.89	0.94	**19.6 %**	71.3 %	0.2 %	28.5 %

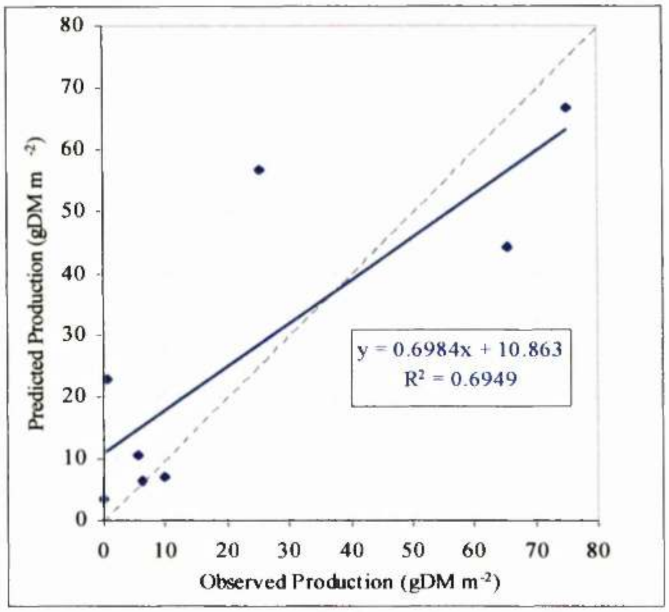


Figure 7.4 - Observed versus predicted production values of the *Festuca - Agrostis* grassland (April to November).

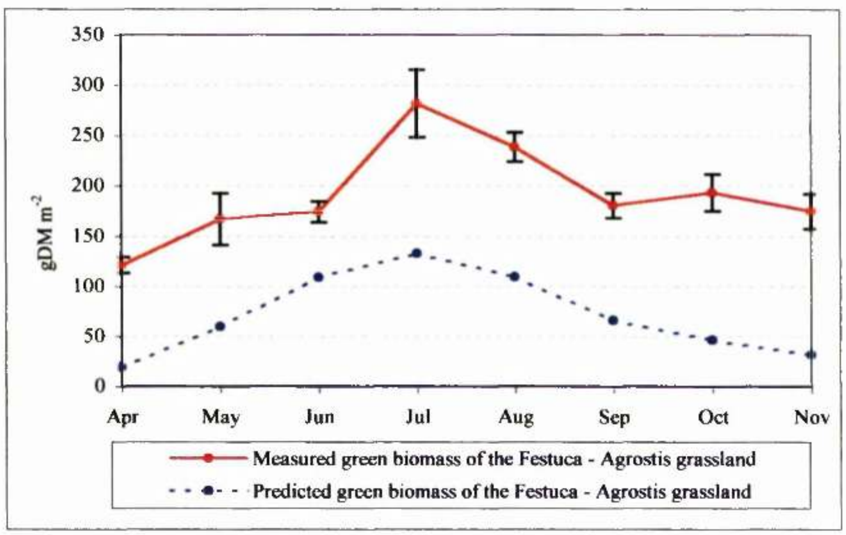


Figure 7.5 - Measured live vascular plant biomass of the U4d *Festuca - Agrostis* grassland (± 1 S.E.) compared with the predicted green biomass of the *Festuca - Agrostis* grassland.

The predicted green biomass values of the *Festuca - Agrostis* grassland were considerably lower than the measured values (Figures 7.5). There was a large mean prediction error most of which was due to bias effects (Table 7.4). The predictions of the model were consistently lower than the measured green biomass values (Figure 7.6).

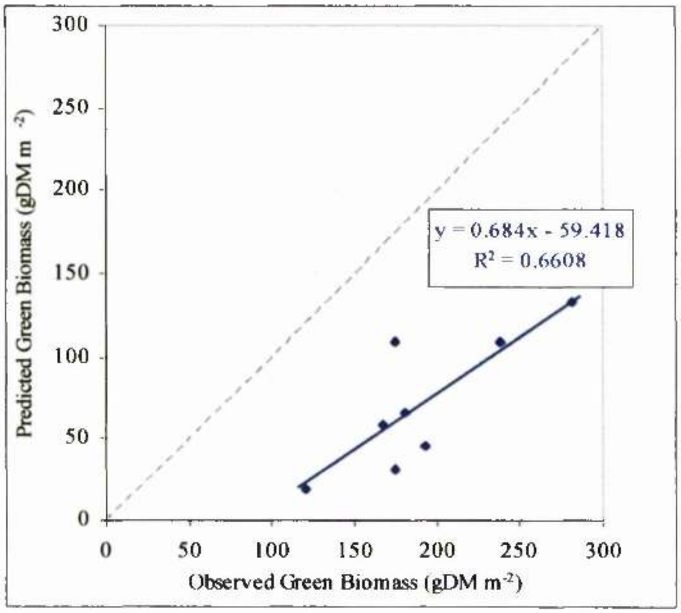


Figure 7.6 - Observed versus predicted green biomass values of the *Festuca - Agrostis* grassland.

The predicted sward height values of the *Festuca - Agrostis* grassland were also consistently lower than the measured values (Figures 7.7 and 7.8). The mean prediction error was low (Table 7.4). Most of the error was due to bias effects, although random effects were also important (Table 7.4).

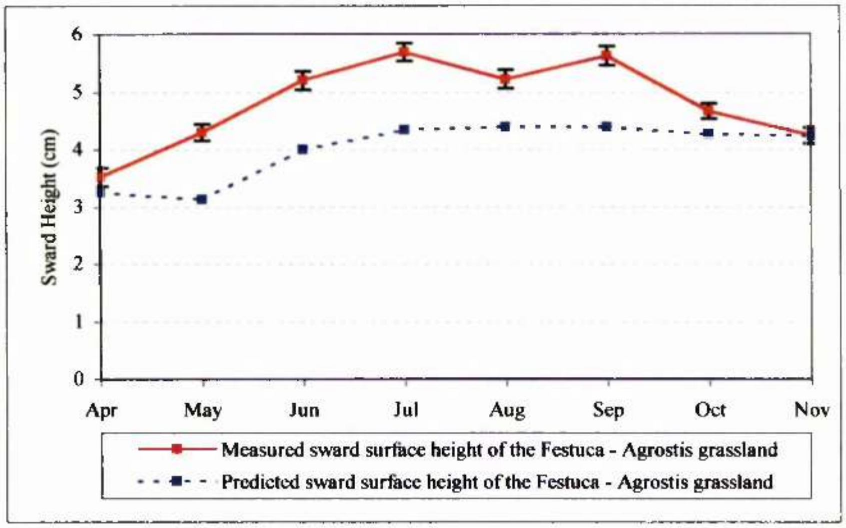


Figure 7.7 - Measured sward surface height of the U4d *Festuca - Agrostis* grassland (± 1 S.E.) compared with the predicted sward height of the *Festuca - Agrostis* grassland.

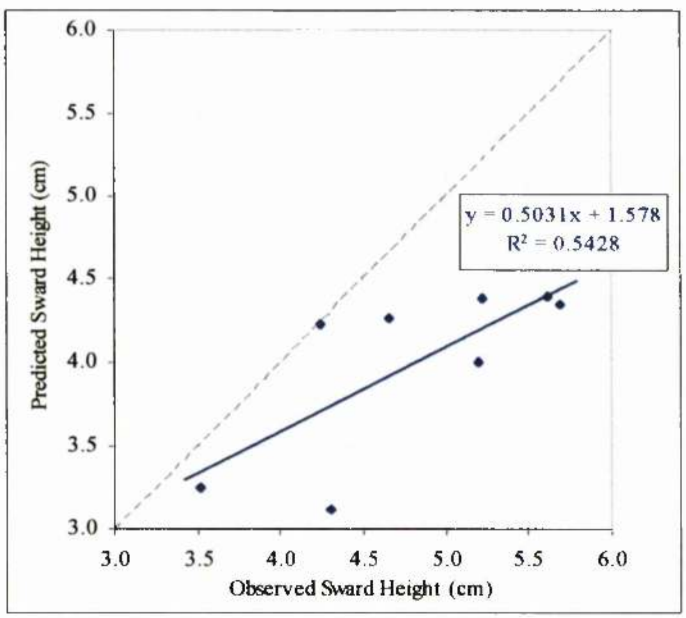


Figure 7.8 - Observed versus predicted sward surface height values of the *Festuca - Agrostis* grassland.

The un-modified model predicted an annual offtake of green material from the *Festuca - Agrostis* grassland of 87.2 gDM m^{-2}, which was nearly six times the measured offtake from the U4d community (15.2 gDM m^{-2}) (Chapter 6).

7.5.3 INTER-TUSSOCK VEGETATION

An annual production of 65.0 gDM m^{-2} was predicted by the model for the *Festuca - Agrostis* inter-tussock vegetation within the '*Nardus*' grassland. This value was less than a third of the measured production of the inter-tussock vegetation within the U5c community (208.6 gDM m^{-2}) (Figure 7.9).

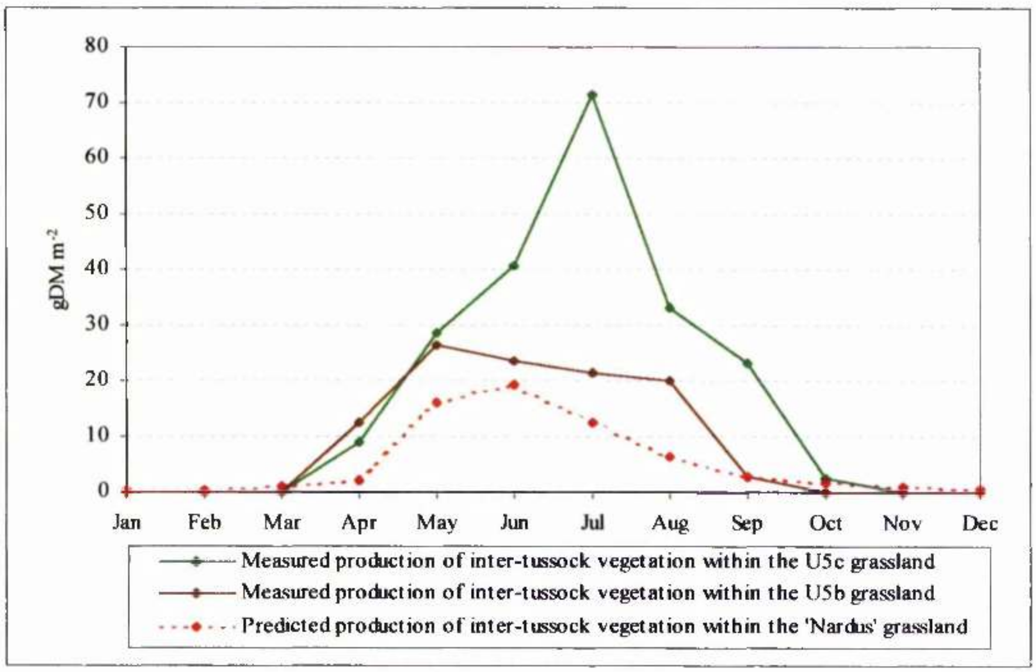


Figure 7.9 - Measured production of inter-tussock vegetation within the U5c and U5b grasslands compared with the predicted production of inter-tussock *Festuca - Agrostis* within the '*Nardus*' grassland.

The mean prediction error for the production of the U5c inter-tussock vegetation was very high (Table 7.5). The error was due mainly to bias and random effects. The predicted production values of the inter-tussock vegetation within both the U5c and U5b grasslands were consistently lower than the measured values (Figure 7.10).

Table 7.5 - MSPE analysis of the model predictions for the production of the inter-tussock vegetation.

Observed versus Predicted	Mean Square Prediction Error (MSPE)	Mean Prediction Error (MPE)	MPE as % of actual mean	% of total MSPE		
				Bias	Slope	Random
Production of the U5c inter-tussock vegetation (April - Nov)	656.10	25.61	**98.3** %	47.5 %	12.3 %	40.2 %
Production of the U5b inter-tussock vegetation (April - Nov)	62.84	7.93	**59.3** %	45.9 %	8.5 %	45.7 %

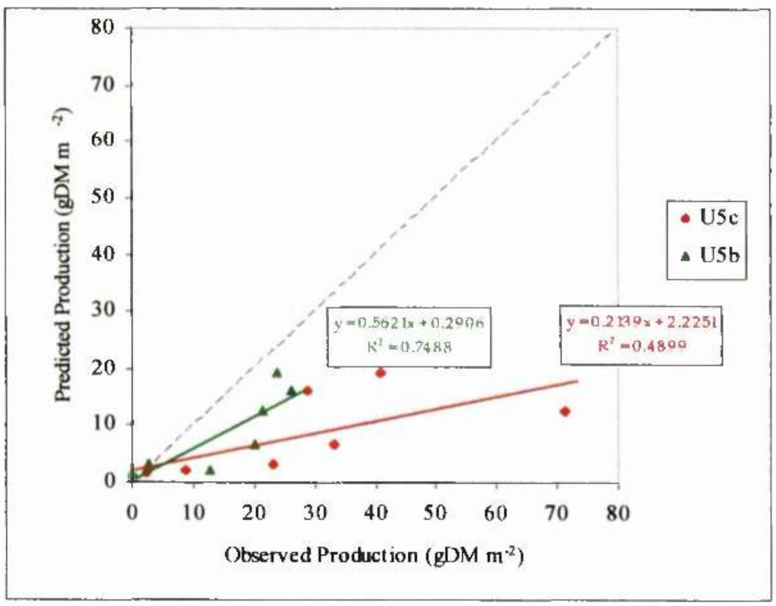


Figure 7.10 - Observed versus predicted production values of the inter-tussock vegetation within the '*Nardus*' grasslands (April to November).

The predicted green biomass values of the *Festuca - Agrostis* component of the '*Nardus*' grassland were also considerably lower than the measured values for the U5c and U5b inter-tussock vegetation (Figures 7.11 and 7.12). The model predicted a maximum green biomass in July of 40.7 gDM m^{-2}, whereas the harvested material indicated that peak inter-tussock green biomass occurred much later in the season during September and October, when values of over 140 gDM m^{-2} were recorded for the U5c inter-tussock vegetation.

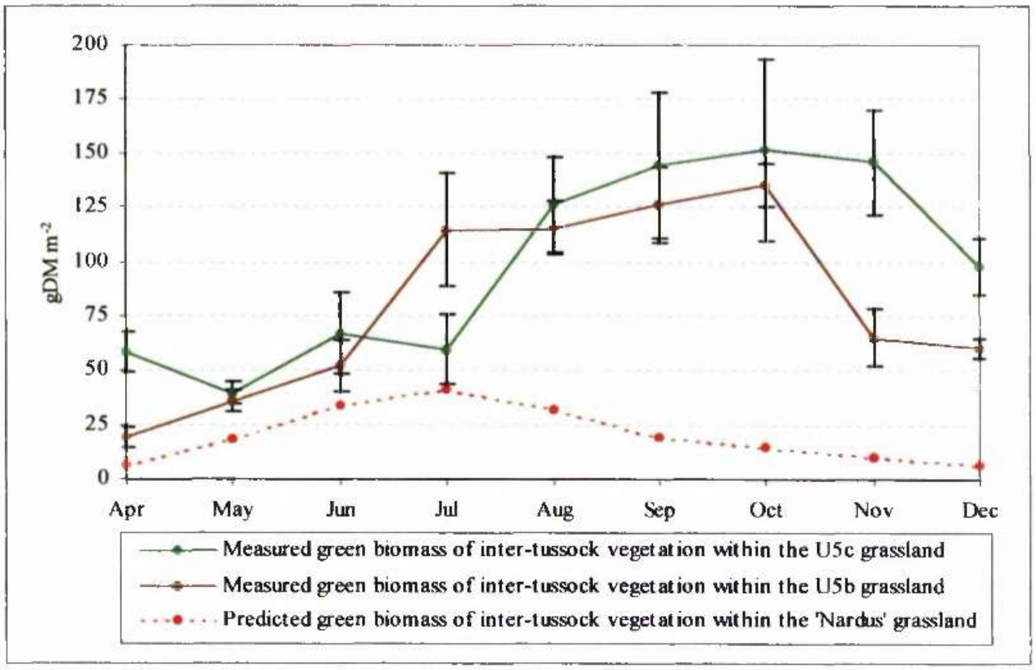


Figure 7.11 - Measured green vascular plant biomass of the inter-tussock vegetation within the U5c and U5b grasslands (± 1 S.E.) compared with the predicted green biomass of the inter-tussock *Festuca - Agrostis* component of the '*Nardus*' grassland.

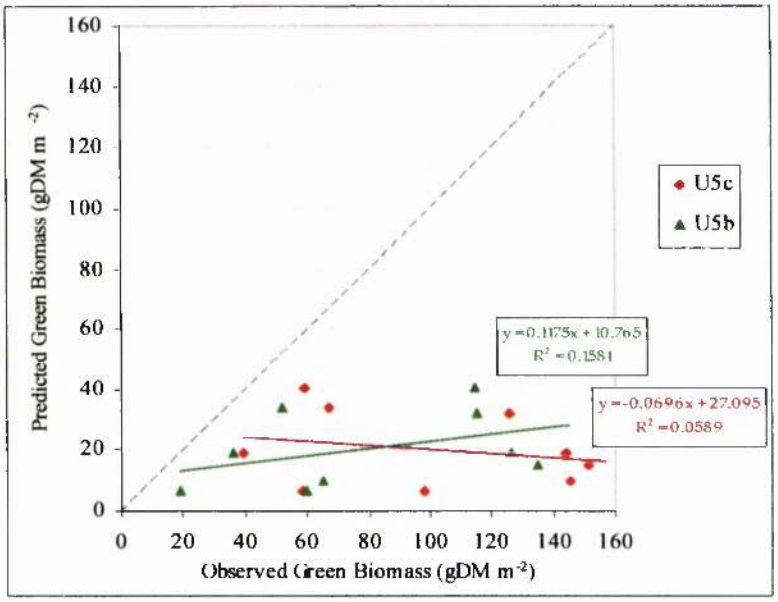


Figure 7.12 - Observed versus predicted green biomass of the inter-tussock vegetation within the '*Nardus*' grasslands.

The mean prediction errors for the green biomass of both the U5c and U5b inter-tussock vegetation were very high (Table 7.6). The errors were due mainly to bias and random effects. The predicted green biomass values were consistently lower than the measured values (Figures 7.12). The production, senescence and litterfall algorithms for the inter-tussock vegetation are all weak and inadequate.

Table 7.6 - MSPE analysis of the model predictions for the green biomass of the inter-tussock vegetation.

Observed versus Predicted	Mean Square Prediction Error (MSPE)	Mean Prediction Error (MPE)	MPE as % of actual mean	% of total MSPE		
				Bias	Slope	Random
Green biomass of the U5c inter-tussock vegetation	8298.65	91.10	**92.1 %**	72.3 %	6.4 %	21.4 %
Green biomass of the U5b inter-tussock vegetation	5013.90	70.81	**88.0 %**	69.9 %	0.4 %	29.7 %

The inter-tussock sward heights predicted by the model were considerably lower than the measured heights, particularly during the summer and autumn (Figure 7.13). The summer inter-tussock sward heights were four times higher than those predicted by the model (Figure 7.13).

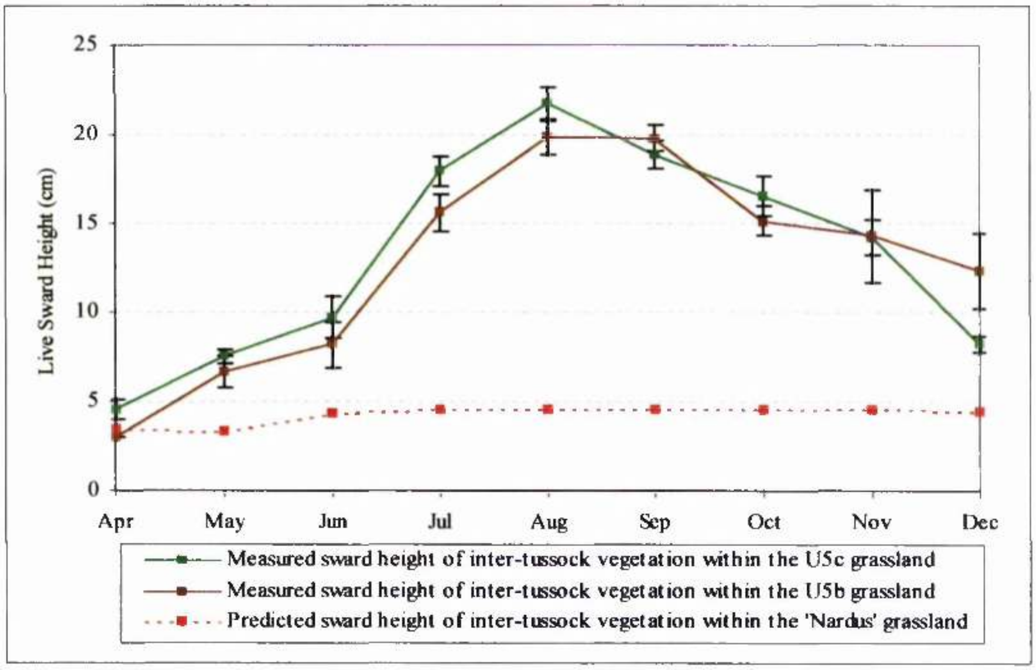


Figure 7.13 - Measured sward surface height of the inter-tussock vegetation within the U5c and U5b grasslands (± 1 S.E.) compared with the predicted sward height of the inter-tussock *Festuca - Agrostis* component of the '*Nardus*' grassland.

The mean prediction errors for the inter-tussock sward heights of both the U5c and U5b communities were high (Table 7.7). The errors were due mainly to bias and slope effects (Table 7.7 and Figure 7.14).

Table 7.7 - MSPE analysis of the model predictions for the sward height of the inter-tussock vegetation.

Observed versus Predicted	Mean Square Prediction Error (MSPE)	Mean Prediction Error (MPE)	MPE as % of actual mean	% of total MSPE		
				Bias	Slope	Random
Sward Height of the U5c inter-tussock vegetation	108.51	10.42	**78.6 %**	72.3 %	15.1 %	12.7 %
Sward Height of the U5b inter-tussock vegetation	98.09	9.90	**77.6 %**	71.5 %	19.4 %	9.2 %

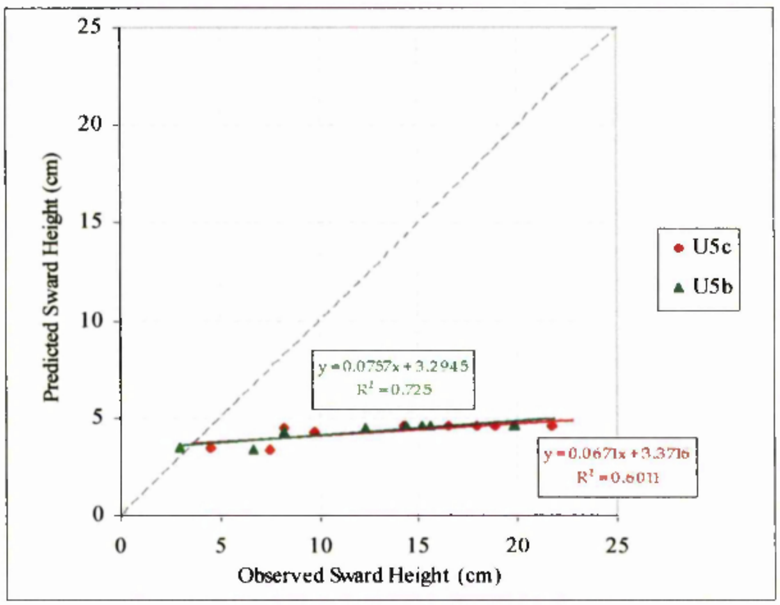


Figure 7.14 - Observed versus predicted sward surface height of the inter-tussock vegetation within the '*Nardus*' grasslands.

The model predicted an annual offtake of live inter-tussock vegetation from within the '*Nardus*' grassland of 18.2 gDM m^{-2}. The offtakes of live inter-tussock vegetation from the U5c and U5b grasslands obtained using the exclosure cage technique were estimated to be 66.6 gDM m^{-2} and 18.3 gDM m^{-2} respectively. This would give a mean offtake of live inter-tussock vegetation from the '*Nardus*' grasslands of 33.5 gDM

m^{-2}, which is almost double the predicted value. The mean offtake of all live vascular plant material from the '*Nardus*' grasslands (i.e. including *Nardus stricta*) was estimated to be 68.3 gDM m^{-2}, which is nearly four times the predicted offtake from the community.

The model predicted an annual offtake of green material from the unburnt *Molinia* grassland of 4.66 gDM m^{-2}. There was no measured offtake of live material from this vegetation type (i.e. the M6d community).

Conversion of the total monthly offtake values predicted by the un-modified model into metabolisable energy gave a total annual ME value of 76.30 GJ (the metabolisable energy content of the winter supplementary feed has been removed from this figure). This is 16.98 GJ lower than the amount predicted by the HSM. The HSM predicted much higher energy utilisation between March and August than the HGMM. During this period the measured offtake of *Nardus stricta* was at its highest (Chapter 6).

7.6 Are the predictions of the un-modified model valid?

The model over-estimated the offtake of live material from the *Festuca - Agrostis* community, but under-estimated the offtake of live material from the *Nardus stricta* dominated communities. The biomass and sward height of the *Festuca - Agrostis* community, and the production, biomass and sward height of the inter-tussock vegetation, were all under-estimated. The offtake values calculated using the cage technique indicated that the animals were grazing the *Nardus stricta*. The assumption by the model that *Nardus stricta* is not grazed is clearly false. In order to improve the validity of the model it required modification. The grazing animals must be given the opportunity to utilise the *Nardus stricta*, *Juncus squarrosus* and *Trichophorum cespitosum*, as well as the fine and broad-leaved grasses within the U5c and U5b grasslands. In order to do this, data for the U5c and U5b communities have been incorporated into the model. Separate tussock and inter-tussock data were not used in the modified model, due to the structural nature of the sward, which is a dense interlocking mix of plants, lacking distinct tussock and inter-tussock areas (Chapters 4 and 5).

7.7 Modification of the Hill Grazing Management Model

7.7.1 ALTERATIONS TO THE FORTRAN MODEL

A number of sub-routines were modified and additional sub-routines were added to the FORTRAN version of the HGMM (Table 7.8), in order to allow data for the U5c and U5b communities to be entered.

Table 7.8 - Model sub-routines that were amended

Sub-routine	Function
INTRO	Introduction to the model
MODEL	Main module for the model program
ICALC2	Indigenous grassland calculations
OFFTAKE3	Offtake calculations
BITE9	Bite size and weight, and digestibility of grassland calculations
BIOMASS	Biomass calculations
YRLOOP1	Daily and monthly loop calculations
INPUT	Read input file
OUTPUT	Write to output file

Modifications to the FORTRAN model were carried out by D. Arnot (Computing Department, SAC Auchincruive)

7.7.2 DATA REQUIRED FOR THE MODIFIED MODEL

The following data for the U5c and U5b communities were required to modify the model:

1) Total annual production values;
2) Monthly proportions of production;
3) Sward height biomass relationships;
4) Monthly live and dead digestibilities;
5) Bite rates.

7.7.3 ADJUSTMENT OF THE PRODUCTION DATA

The production data from the Kirkton Face study site required adjustment before it could be entered into the model. The sampling site was at an altitude of approximately 500 m within Temperature Zone 5 (Meteorological Office, 1975). The monthly production data needed to be adjusted to sea-level within Temperature Zone 7 before it could be entered into the model.

To adjust the observed production values, the altitude of the grassland was first adjusted to its equivalent in Temperature Zone 7 using Equation 7.1 (Lance, 1987, Armstrong *et al.*, 1997a).

Equation 7.1

$$A_T = L(A + Z)$$

where:

L = adjustment factor for the difference in the rate of change of temperature with altitude (lapse rate).

A = unadjusted altitude (m);

Z = adjustment factor for temperature zone.

For indigenous grasslands within Zone 5; $L = 1.06$ and $Z = 162.02$

The monthly production values were then adjusted to sea-level using the following correction factors:

1) April to October values were multiplied by 4.63;
2) May to June values were multiplied by 1.0;
3) July to September values were multiplied by 3.23.

The correction factors were calculated by running the model using a test set of data and comparing monthly production values predicted for a *Festuca - Agrostis* grassland at sea-level and at the adjusted altitude of the Kirkton Face site (701.7 m).

7.7.4 SWARD HEIGHT BIOMASS RELATIONSHIPS

The logistic curve regression equations for the relationship between mean sward surface height and mean live vascular plant biomass were used in the modified model (see Chapter 5).

7.7.5 BITE RATES

Bite rates were assumed to be constant and were set at 50 bites min^{-1}, which was the average sheep bite rate measured on a *Nardus stricta* community between May and November by Hodgson *et al.* (1991).

7.7.6 CALCULATION OF MONTHLY DRY MATTER DIGESTIBILITIES

The monthly dry matter digestibilities of the live and dead material within the U5c and U5b grasslands (Table 7.10) were calculated using the dry matter digestibility figures given in Table 7.9. Digestibility values determined for a *Nardus stricta* grassland by Eadie and Black (1968) were used for the combined *Nardus stricta* and inter-tussock fraction of the grassland, with data from Grant and Campbell (1978) used for the green *Juncus squarrosus* and *Trichophorum cespitosum* fractions. Both these sources were used by Armstrong *et al.* (1997b) in the original model. The study site DM digestibilities of *Festuca ovina* and *Agrostis capillaris* (Chapter 6) were not used, as they were considerably lower than the Eadie and Black (1968) figures used in the original model. Since the live *Nardus stricta* digestibilities from the study site were comparable with those for *Festuca ovina* and *Agrostis capillaris* it would have been inappropriate to use the study site *Nardus stricta* values within the modified model. The dry matter digestibilities for *Calluna vulgaris* were the same as those used in the original model.

Table 7.9 - Dry Matter digestibilities of the grassland components

	Nardus stricta grassland		*Juncus squarrosus*		*Trichophorum cespitosum*		*Calluna vulgaris*
	Live[2]	Dead[2]	Live[3]	Dead[1]	Live[3]	Dead[1]	Live[4]
Jan	0.63	0.28	0.264	0.075	0	0.178	0.41
Feb	0.64	0.27	0.264	0.075	0	0.178	0.41
Mar	0.63	0.3	0.264	0.075	0	0.178	0.41
Apr	0.63	0.3	0.329	0.075	0.675	0.178	0.41
May	0.69	0.32	0.329	0.075	0.675	0.178	0.56
Jun	0.69	0.32	0.329	0.075	0.675	0.178	0.56
Jul	0.69	0.32	0.258	0.075	0.645	0.178	0.56
Aug	0.63	0.3	0.258	0.075	0.645	0.178	0.48
Sep	0.63	0.3	0.264	0.075	0.484	0.178	0.46
Oct	0.63	0.28	0.264	0.075	0.484	0.178	0.46
Nov	0.63	0.28	0.264	0.075	0.484	0.178	0.46
Dec	0.63	0.25	0.264	0.075	0.484	0.178	0.41

[1] *in vitro* DM digestibilities of material collected from the Kirkton Face study site.
[2] From Eadie and Black (1968). The samples of *Nardus stricta* grassland on which the *in vitro* digestibility determinations were carried out had a mean composition of 45 % *Nardus stricta*, 38 % broad-leaved grasses, 13.5 % fine-leaved grasses, and 3.7 % other species. This species composition was very similar to that of the U5c grassland (Chapter 5).
[3] From Grant and Campbell (1978)
[4] From Milne (1974)
Digestibility values for live and dead material have been interpolated for months not given in the source references.

7.8 Testing the modified Hill Grazing Management Model

7.8.1 LIMITATIONS OF USING THE ENCLOSURE DATA SET TO TEST THE MODEL

It is not normally appropriate to test a model using data that has been used to create it, and therefore there are limitations in using the data from the enclosures to validate the modified model. However, only a relatively small amount of information was incorporated into the model (i.e. production, digestibility and sward height-biomass relationships for the U5c and U5b communities). It was therefore possible to use the enclosure data to find out whether the senescence and litterfall algorithms for the indigenous grasslands that are embedded in the model were appropriate for the U5c and U5b communities. These algorithms affect the amounts of green and dead biomass and also the sward height. Since the algorithms associated with the offtake of live and dead material were not modified, it was also possible to use the enclosure data to test how well the modified model predicted offtake from the U5c, U5b and *Festuca* - *Agrostis* communities.

7.8.2 DATA ENTRY INTO THE MODIFIED MODEL

Data from Enclosure 2 were used to test and evaluate the modified model. Data for the U5c and U5b communities were entered into the model via an EXTRA.IN file (Table 7.10). Additional information on the site location, the areas and composition of the other vegetation types, and the average weight and number of sheep, were entered directly into the front-end of the model (Table 7.11).

Table 7.10 - Additional input data for the modified model (entered in the EXTRA.IN file)

Area and percentage cover of the two communities

	Area (ha)	Percentage cover
U5c community	6.285	100
U5b community	13.096	100

Total annual production values adjusted to temperature Zone 7 and 0 metres above sea level

	Production (kg ha^{-1})
U5c community	10245.297
U5b community	9138.857

Monthly proportion of total annual production

	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec
U5c community	0	0	0	0.0296	0.0448	0.0960	0.3699	0.0970	0.3113	0.0515	0	0
U5b community	0	0	0	0.0785	0.0361	0.0856	0.2343	0.1459	0.3601	0.0562	0.0022	0.0011

Mean monthly dry matter digestibilities of the live and dead fractions of the two communities

	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec
U5c - live vascular material	0.621	0.606	0.597	0.627	0.662	0.671	0.679	0.618	0.616	0.590	0.627	0.626
U5c - dead material	0.276	0.267	0.297	0.300	0.315	0.318	0.312	0.298	0.298	0.268	0.279	0.249
U5b - live vascular material	0.515	0.430	0.426	0.408	0.488	0.504	0.542	0.524	0.463	0.514	0.526	0.484
U5b - dead material	0.239	0.220	0.243	0.219	0.256	0.289	0.273	0.271	0.239	0.228	0.250	0.218

Sward height biomass relationships

	Relationship	Regression Equation
U5c community	Mean sward height v mean live vascular plant biomass	$y = 5.043 + 11.74 / (1 + \exp(-0.001745 * (x - 1064)))$
U5b community	Mean sward height v mean live vascular plant biomass	$y = 10.65 + 7.54 / (1 + \exp(-0.00222 * (x - 2287)))$

Bite rates

	Bites min^{-1}
U5c community	50
U5b community	50

Table 7.11 - Input data for the modified model (entered into the model's front-end input data interface)

Information required by the modified HGMM	**Input Data**
Zone	5
Location	Upland
Side	West
Mean altitude of heather communities (calculated using GIS)	564 m
Blanket Bog - Area	8.739 ha
Blanket Bog - Cover of *Calluna vulgaris*	9.1 %
Blanket Bog - Cover of *Festuca/Agrostis*	1.88 %
Suppressed Heather - Area	0.926 ha
Suppressed Heather - Cover of *Calluna vulgaris*	57.92 %
Mean altitude of indigenous grassland communities	500 m
Festuca/Agrostis - Area	3.691 ha
Festuca/Agrostis - Cover	100 % (fixed)
Unburnt *Molinia caerulea* community - Area	3.84 ha
Unburnt *Molinia caerulea* community - Cover of *Molinia caerulea*	14.82 %
Unburnt *Molinia caerulea* community - Cover of *Festuca/Agrostis*	5.0 %
Average ewe weight	46.8 kg
Ewe Numbers (January to December)*	13, 22, 22, 27, 27, 26, 27, 25, 22, 22, 22, 36

* The HGMM assumes that all ewes produce a single lamb. There is no provision for the inclusion of hoggs (yearling un-mated ewes) in the model. It would have been inappropriate to ignore the presence of the hoggs or to have given them a value equivalent to a ewe, therefore each hogg was allocated a value of 0.66 of a ewe.

7.9 Comparison between the modified Hill Grazing Management Model predictions and the measured values

7.9.1 STATISTICAL ANALYSES

A Mean Square Prediction Error (MSPE) analysis was carried out to determine the accuracy of the model predictions, and what proportion of any error was due to bias, slope or random effects. For each of the model predictions the observed values were plotted against the predicted values and a linear regression analysis was carried out.

7.9.2 GREEN BIOMASS OF THE U5C AND U5B COMMUNITIES

The predicted green biomass values of the U5c and U5b communities tended to be lower than the measured values (Figure 7.15). The predictions for the U5c community were closer to the measured values than the predictions for the U5b community (i.e. the mean prediction error for the U5c community was lower than that for the U5b community). The mean prediction error for the U5c community was relatively low, and was due mainly to random effects, although bias and slope effects were also important (Table 7.12). The mean prediction error for the U5b community was due mainly to bias effects (Table 7.12 and Figure 7.16).

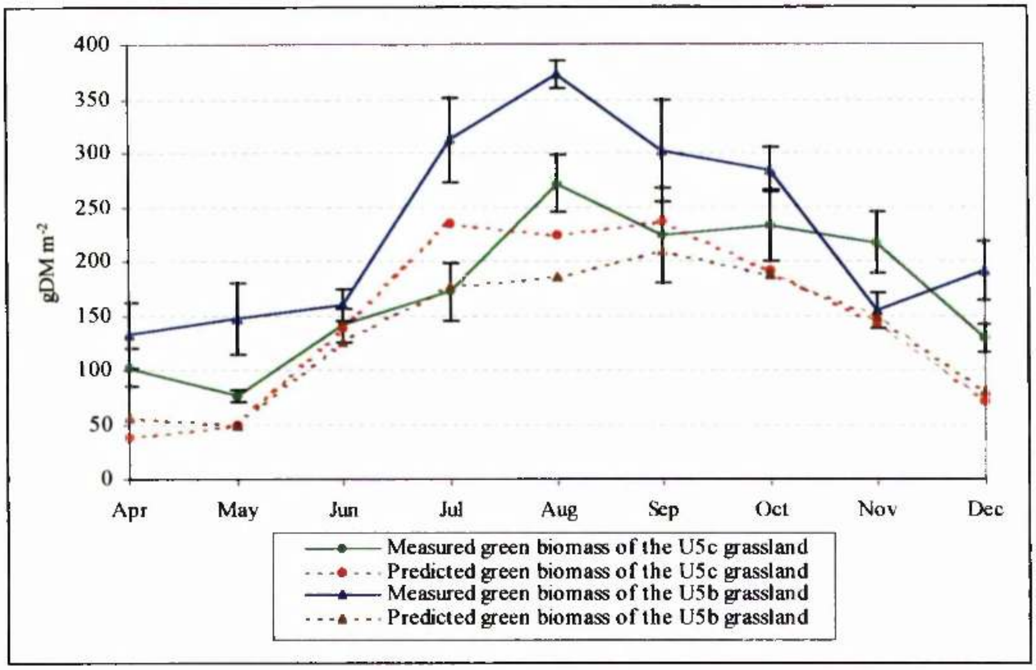


Figure 7.15 - Predicted and measured green biomass values of the U5c and U5b communities (± 1 S.E.).

Table 7.12 - MSPE analysis of the model predictions for the green biomass of the U5c and U5b communities.

Observed versus Predicted	Mean Square Prediction Error (MSPE)	Mean Prediction Error (MPE)	MPE as % of actual mean	% of total MSPE		
				Bias	Slope	Random
Green biomass of the U5c community	2432.17	49.32	**28.3 %**	27.4 %	22.4 %	50.2 %
Green biomass of the U5b community	11137.47	105.53	**46.3 %**	75.3 %	1.3 %	23.4 %

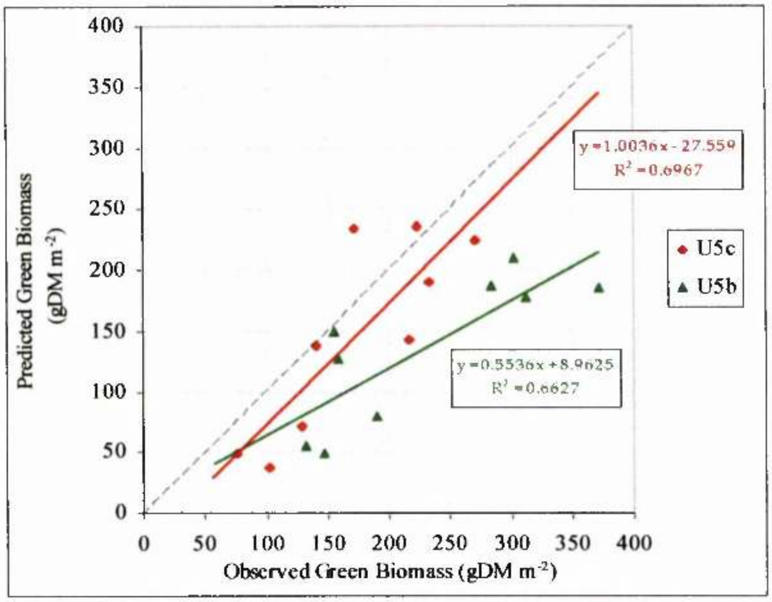


Figure 7.16 - Observed versus predicted green biomass values of the U5c and U5b communities.

7.9.3 DEAD STANDING BIOMASS OF THE U5C AND U5B COMMUNITIES

The model predicted well the dead standing biomass of the U5c community during the spring and summer, however it over-estimated the values during the autumn and winter (Figure 7.17). The predicted dead standing biomass values of the U5b community were lower than the measured values in all months apart from December (i.e. there was a strong bias effect) (Figure 7.18 and Table 7.13).

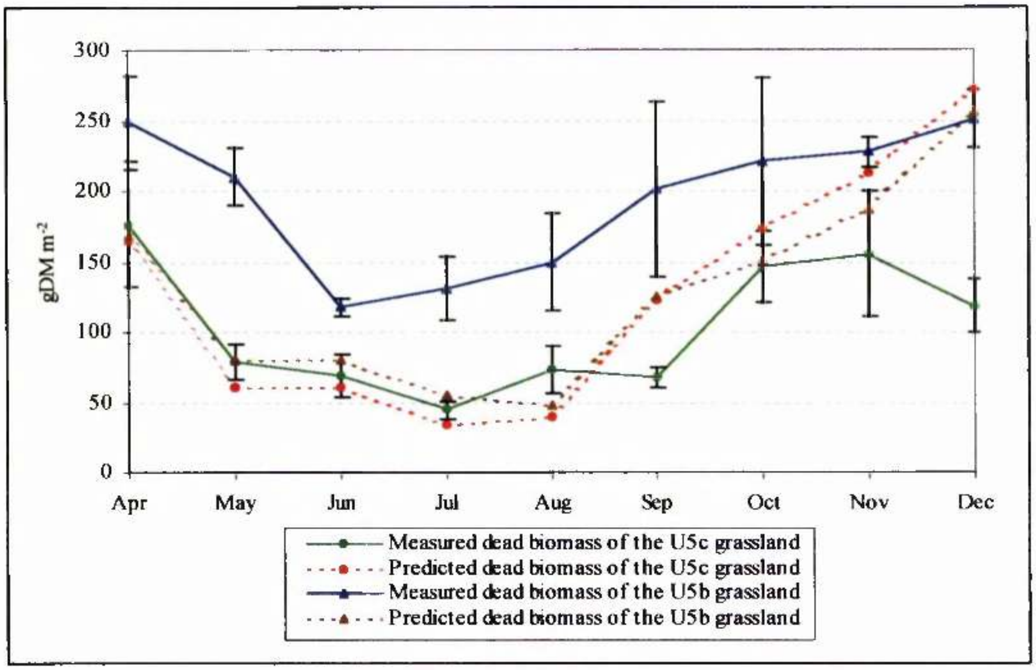


Figure 7.17 - Predicted and measured dead standing biomass values of the U5c and U5b communities (± 1 S.E.)

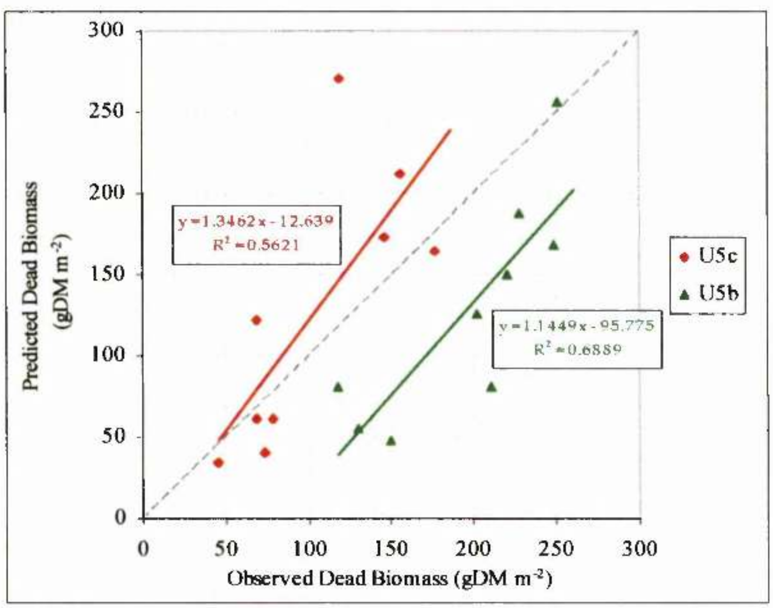


Figure 7.18 - Observed versus predicted dead standing biomass values of the U5c and U5b communities.

Table 7.13 - MSPE analysis of the model predictions for the dead standing biomass of the U5c and U5b communities

Observed versus Predicted	Mean Square Prediction Error (MSPE)	Mean Prediction Error (MPE)	MPE as % of actual mean	% of total MSPE		
				Bias	Slope	Random
Dead standing biomass of the U5c community	3528.64	59.4	57.5 %	13.7 %	61.6 %	24.7 %
Dead standing biomass of the U5b community	5929.72	77	39.4 %	74.6 %	12.5 %	12.9 %

7.9.4 SWARD HEIGHTS OF THE U5C AND U5B COMMUNITIES

The sward surface heights predicted by the modified model tended to be lower than the measured heights for both the U5c and U5b communities (i.e. there were strong bias effects) (Figures 7.19 and 7.20). This was expected since the model uses the predicted green biomass values to calculate the predicted sward surface heights.

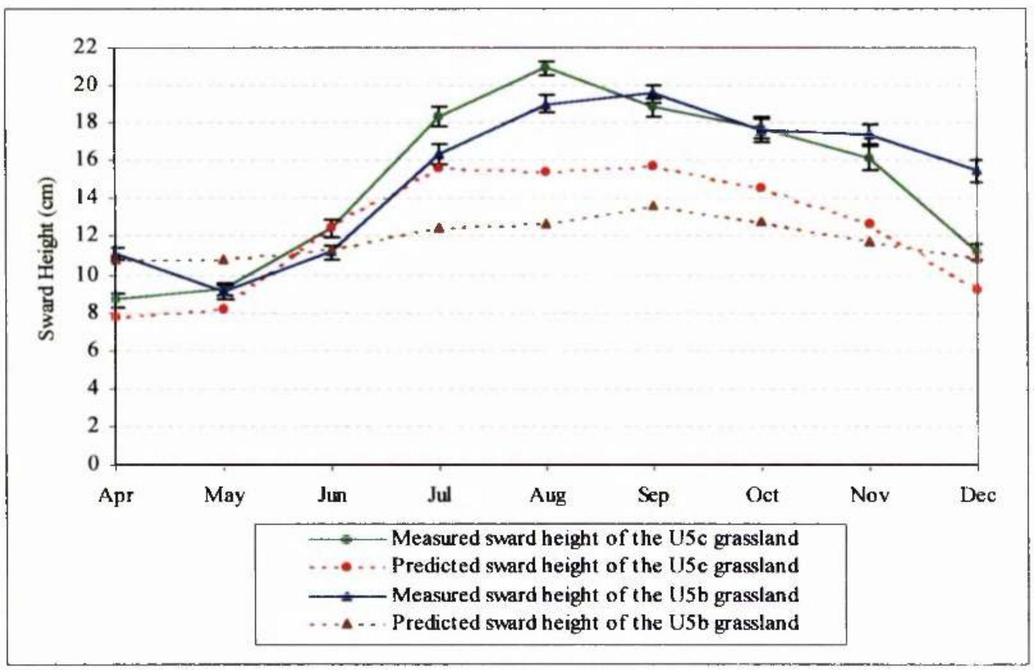


Figure 7.19 - Predicted and measured sward surface heights of the U5c and U5b communities (± 1 S.E.)

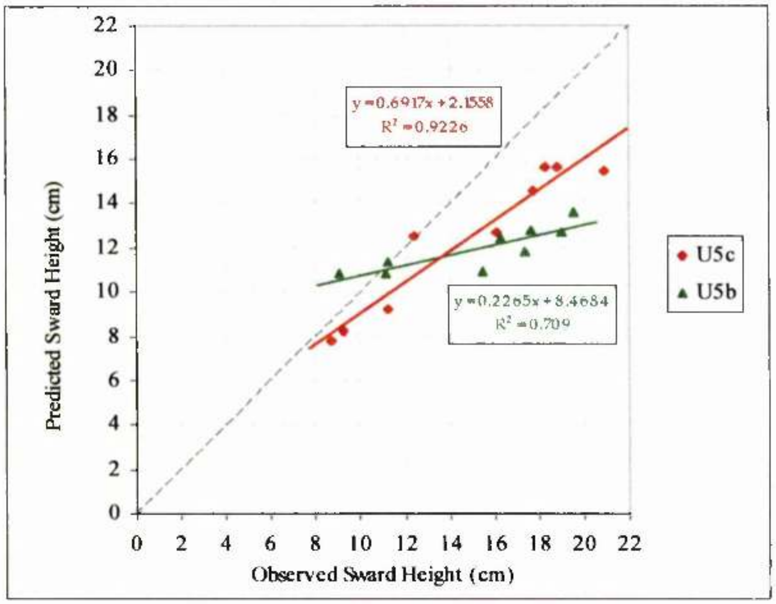


Figure 7.20 - Observed versus predicted sward surface height values of the U5c and U5b communities.

The mean prediction error for the U5c sward height was relatively low, with most of the error due to bias effects (Table 7.14). The MPE for the U5b community, which was due mainly to bias and slope effects, was also relatively low, but was slightly larger than the MPE for the U5c community (Table 7.14).

Table 7.14 - MSPE analysis of the model predictions for the sward height of the U5c and U5b communities

Observed versus Predicted	Mean Square Prediction Error (MSPE)	Mean Prediction Error (MPE)	MPE as % of actual mean	% of total MSPE		
				Bias	Slope	Random
Sward Height of the U5c community	8.29	2.88	**19.41 %**	67.9 %	13.7 %	18.4 %
Sward Height of the U5b community	18.75	4.33	**28.50 %**	54.6 %	24.1 %	21.3 %

7.9.5 Offtake from the U5c, U5b and *Festuca - Agrostis* communities

By running the modified model with the U5c and U5b production, digestibility and bite rate values, annual green offtakes of 71.8 gDM m^{-2} and 4.0 gDM m^{-2} respectively were predicted for the two community types. The predicted offtake of green material from the U5c community was slightly greater than the measured value, whereas the predicted offtake of green material from the U5b community was only 6 % of the measured value (Table 7.15). The modified model predicted a green offtake from the *Festuca - Agrostis* community that was 10.4 gDM m^{-2} less than the prediction of the original un-modified model, but remained considerably greater than the measured value (Table 7.15). The modified model predicted a total offtake of live and dead material that was 774 kgDM greater than the un-modified model (Table 7.16). The predicted offtake of live and dead material from the *Nardus stricta* grasslands also increased from 4196 kgDM to 5540 kgDM (Table 7.17).

Table 7.15 - Comparison between the measured and predicted offtakes from the *Nardus stricta*, *Festuca - Agrostis* and un-burnt *Molinia* vegetation types.

	Measured value	**Un-modified** model prediction	**Modified** model prediction
Offtake of live material from the *Festuca - Agrostis* grassland (gDM m^{-2})	15.2	87.2	76.8
Offtake of live material from the *Nardus* grassland (U5c and U5b) (gDM m^{-2})	70.0 (U5c) 67.5 (U5b)	18.2	71.8 (U5c) 4.0 (U5b)
Offtake of live material from the unburnt *Molinia* grassland (gDM m^{-2})	0.0	4.7	4.1

Table 7.16 - Total offtake from Enclosure 2 predicted by the original and modified models.

	Offtake (kgDM)												
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	**Total**
Original Model	205	318	372	403	475	1133	1593	1208	769	705	531	713	**8425**
Modified Model	199	312	361	732	649	1218	1595	1132	735	684	682	901	**9199**

Table 7.17 - Total offtake from the different vegetation types within Enclosure 2 as predicted by the original and modified models.

	Total Offtake (kgDM)	
	Original HGMM	**Modified HGMM**
Blanket bog heather	169.6	154.0
Suppressed heather	39.4	35.1
Green *Festuca - Agrostis*	3217.0	2833.3
Dead *Festuca - Agrostis*	507.6	373.9
Green un-burnt *Molinia*	56.6	47.7
Dead un-burnt *Molinia*	0.01	0.01
Green *Festuca - Agrostis* within *Nardus* grassland	3542.1	
Dead *Festuca - Agrostis* within *Nardus* grassland	654.0	
Green U5c grassland		4515.2
Dead U5c grassland		480.9
Green U5b grassland		523.3
Dead U5b grassland		20.3
Green *Festuca - Agrostis* within blanket bog	83.1	79.5
Dead *Festuca - Agrostis* within blanket bog	10.4	7.3
Green *Festuca - Agrostis* within un-burnt *Molinia*	122.2	111.3
Dead *Festuca - Agrostis* within un-burnt *Molinia*	22.6	16.6

Conversion of the total monthly offtake values predicted by the modified model into metabolisable energy gave a total annual ME value of 82.98 GJ (the metabolisable energy content of the winter supplementary feed has been removed from this figure). This is 6.68 GJ greater than that predicted by the original un-modified model, but is still 10.30 GJ lower than the ME calculated by the HSM, and 30.88 GJ lower than the estimated ME of the measured live offtake (Figure 7.21).

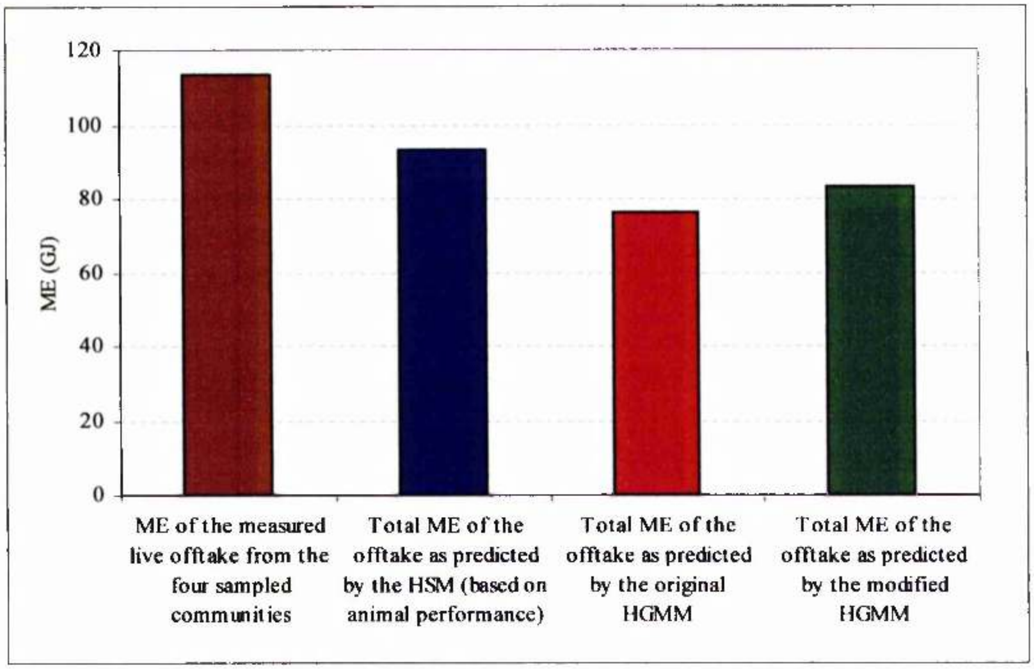


Figure 7.21 - The estimated ME of the live offtake from the four sampled communities measured using the exclosure cage technique, and the total ME of the offtake utilised by the sheepflock as predicted by the three models.

Modification of the model increased the predicted ME content of the offtake during April and May, although the May value (6.84 GJ) remained considerably lower than the value calculated by the HSM (13.08 GJ) (Figure 7.22).

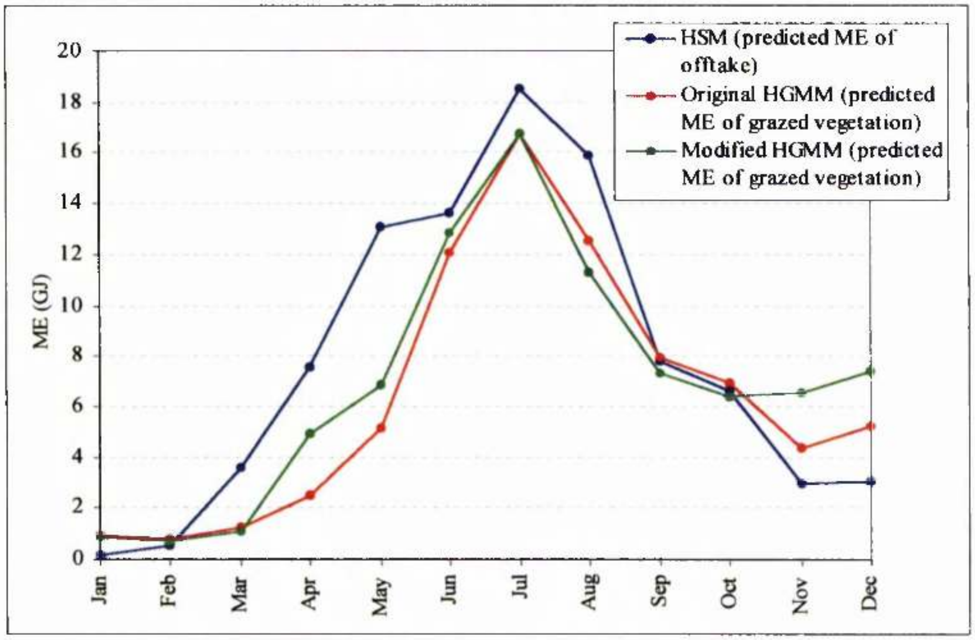


Figure 7.22 - Comparison between the monthly ME values predicted by the three models.

7.9.6 TESTING THE ORIGINAL AND MODIFIED MODELS USING DATA FROM ENCLOSURE 1

The original and modified models were also run using data from Enclosure 1 (i.e. sheep numbers, areas of vegetation types etc.). The total annual offtake of live and dead material (from Enclosure 1) predicted by the modified model was 1468 kgDm greater than that predicted by the unmodified model (i.e. 14285 kgDM compared with 12817 kgDM). The modified model predicted a total annual offtake from the *Nardus stricta* grasslands of 9733 kgDM, while the original model predicted an offtake of only 7304 kgDM. The modified model predicted an annual offtake of live material from the U5c community (in terms of gDM m^{-2}) of 74.8 gDM m^{-2}, and an offtake of live material from the U5b community of 4.2 gDM m^{-2}. Both these values were considerably lower than the offtake values measured using the exclosure cage technique (Chapter 6).

7.10 Testing the original and modified models using an independent data set

7.10.1 The independent data set

It is normally inappropriate to test and validate a model using data that has been used to construct it, and therefore it was important to test the modified model using an independent data set. Information gathered from the Gleann a'Chlachain, an 850 ha hirsel adjacent to the main study site, was used to test both the un-modified and modified models. It was deemed impractical to collect offtake figures from this site using the cage technique as it would have required a very large number of additional herbage cuts. Therefore in order to test the two versions of the model, the ME content of the predicted offtakes were compared with the ME required to achieve the recorded levels of animal performance.

The Hill Sheep Model was used to calculate the total ME required to attain the recorded levels of performance of the sheepflock within Gleann a'Chlachain, during 1995/96. This method appears to provide a robust means of accurately assessing actual animal offtake. Data on the number and mean body weights of ewes, lambs and hoggs, together with information on weight changes, the physiological state of the ewes, and the estimated mean monthly digestibility of the food source, were used to run the HSM.

The vegetation of the Gleann a'Chlachain was mapped using a simple field-based mapping technique, which involved traversing the site and sketching boundaries between vegetation types on to a large-scale field map. Although this mapping technique is not as accurate as the one used to map the enclosures (Chapter 3), it is the standard method of vegetation mapping that would be employed by most users of the Hill Grazing Management Model. The vegetation was classified into the most appropriate HGMM vegetation type, except the *Nardus* grassland, which was split into U5c and U5b NVC community types. The percentage cover of *Calluna vulgaris* and *Festuca - Agrostis* within the blanket bog, and the percentage cover of *Molinia caerulea* and *Festuca - Agrostis* within the un-burnt *Molinia* vegetation type, were estimated in the field. Sward stick data from the main study site was used to estimate the cover of *Festuca - Agrostis* within the *Nardus* grassland. Areas of scree, bare ground, standing water and moss-dominated heath were left un-classified. The vegetation map was digitised (Figure 7.23) and the area of each vegetation type was calculated.

The M17 *Trichophorum cespitosum* mire community, which occupied much of the base of the glen, was classified as blanket bog with 10 % *Calluna vulgaris* cover, however this community could equally have been classified as un-burnt *Molinia* grassland with 10 % cover of *Molinia caerulea*. This illustrates two major problems of the model, namely the limited number of vegetation types and the need to try and classify all the major communities into what may be inappropriate vegetation types. Almost 250 hectares of land were classified as a mosaic of *Nardus* grassland with patches of *Festuca - Agrostis*. It was estimated that the patches of *Festuca - Agrostis* covered approximately 10 % of the area, although the actual figure could have been anywhere between 5 and 20 %. These difficulties in classifying vegetation types and in estimating areas can have major impacts on the offtake predictions of the model.

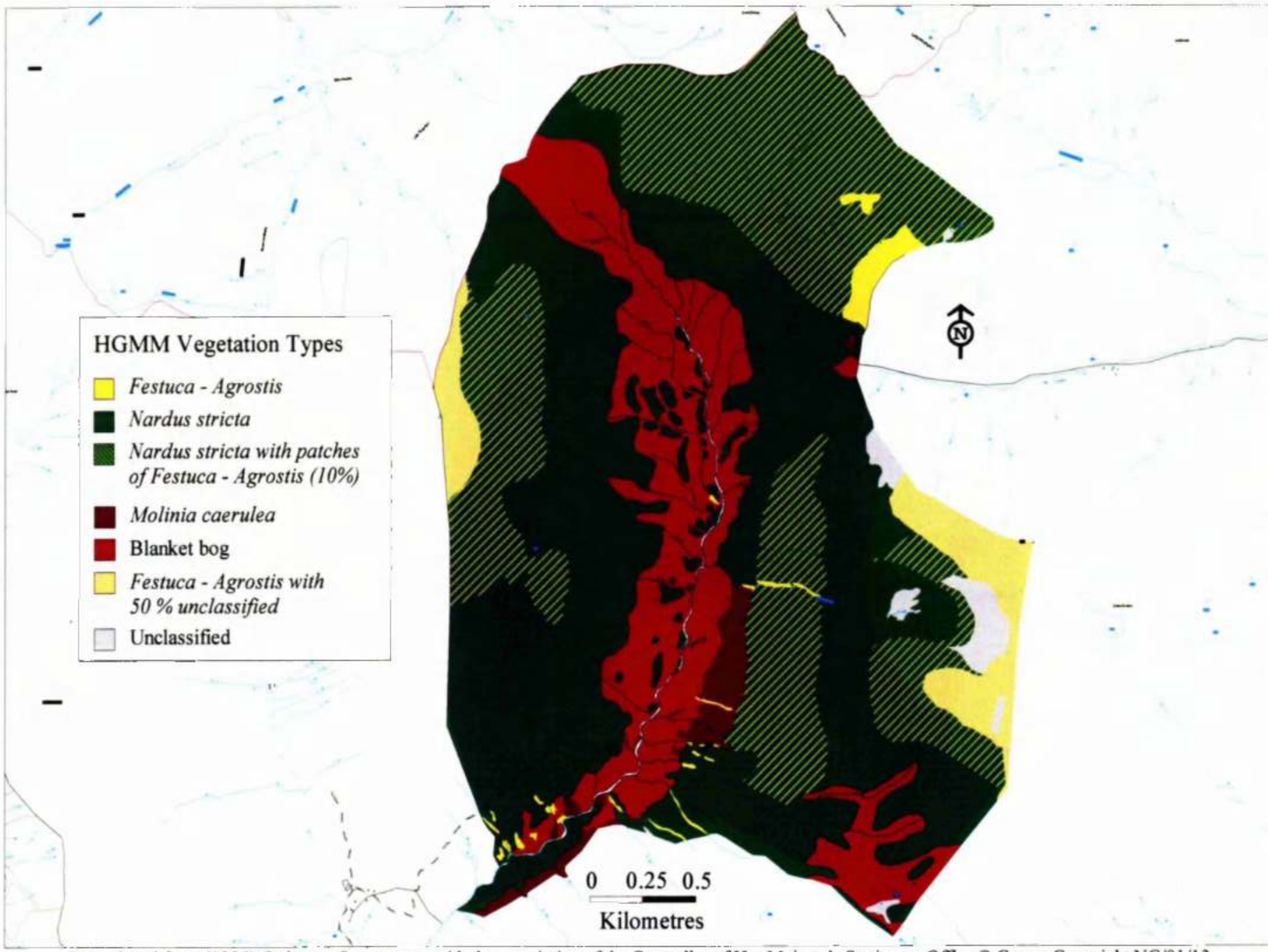


Figure 7.23 - Map of the MLURI Hill Grazing Management Model vegetation types found within Gleann a'Chlachain

7.10.2 RUNNING THE MODEL USING THE INDEPENDENT DATA SET

The two versions of the HGMM were run using the data shown in Table 7.18.

Table 7.18 - Model input data for Gleann a'Chlachain

Information Required by the Models	Input Data - Published model	Input Data - Modified model
Zone	5	5
Location	Upland	Upland
Side	West	West
Mean altitude of heather communities	450 m	450 m
Blanket Bog - Area	145.25 ha	145.25 ha
Blanket Bog - Cover of *Calluna vulgaris*	10.0 %	10.0 %
Blanket Bog - Cover of *Festuca/Agrostis*	1.0 %	1.0 %
Mean altitude of indigenous grassland	600 m	600 m
Festuca/Agrostis - Area	55.33 ha	55.33 ha
Festuca/Agrostis - Cover	100 % (fixed)	100 % (fixed)
Nardus stricta community - Area	575.87 ha	
Nardus stricta community - Cover of *Nardus stricta*	42.96 %	
Nardus stricta community - Cover of *Festuca/Agrostis*	29.14 %	
U5c Community - Area		366.09 ha
U5b Community - Area		209.78 ha
Unburnt *Molinia caerulea* community - Area	15.98 ha	15.98 ha
Unburnt *Molinia caerulea* community - Cover of *Molinia caerulea*	25.0 %	25.0 %
Unburnt *Molinia caerulea* community - Cover of *Festuca/Agrostis*	5.0 %	5.0 %
Average ewe weight	45.75 kg	45.75 kg
Ewe Numbers (January to December) *	587, 587, 515, 586, 622, 622, 622, 615, 587, 587, 587, 603	587, 587, 515, 586, 622, 622, 622, 615, 587, 587, 587, 603

* The HGMM assumes that all ewes produce a single lamb. There is no provision for the inclusion of hoggs (yearling un-mated ewes) in the model. It would have been inappropriate to ignore the presence of the hoggs or to have given them a value equivalent to a ewe, therefore each hogg was allocated a value of 0.66 of a ewe.

7.10.3 THE MODEL PREDICTIONS USING THE INDEPENDENT DATA SET

The modified model predicted a higher total offtake and a higher offtake from the *Nardus* grasslands than the un-modified model (Table 7.19). Both versions of the model considerably underestimated the offtake required to obtain the actual recorded performance levels in the first half of the year (Figure 7.24). The total daily grazing times predicted by both models for the winter and spring periods were short, particularly those predicted by the modified model (Table 7.20). The intake rates over the winter period predicted by the modified model from the U5c and U5b grasslands (0.95 gDM minute^{-1} and 0.74 gDM minute^{-1} respectively) were much higher than the intake rates from the *Nardus* inter-tussock vegetation predicted by the original model (0.35 gDM minute^{-1}).

Table 7.19 - Total offtake from the different vegetation types within Gleann a'Chlachain as predicted by the original and modified models.

	Total Offtake (Tonnes DM)	
	Original HGMM	**Modified HGMM**
Blanket bog heather	10.52	5.93
Festuca - Agrostis	53.22	28.06
Un-burnt *Molinia*	0.36	0.19
Festuca - Agrostis within *Nardus* grassland	109.48	
U5c grassland		157.69
U5b grassland		5.91
Festuca - Agrostis within blanket bog	2.14	1.24
Festuca - Agrostis within un-burnt *Molinia*	0.52	0.31
Total (green and dead material)	**176.23**	**199.33**

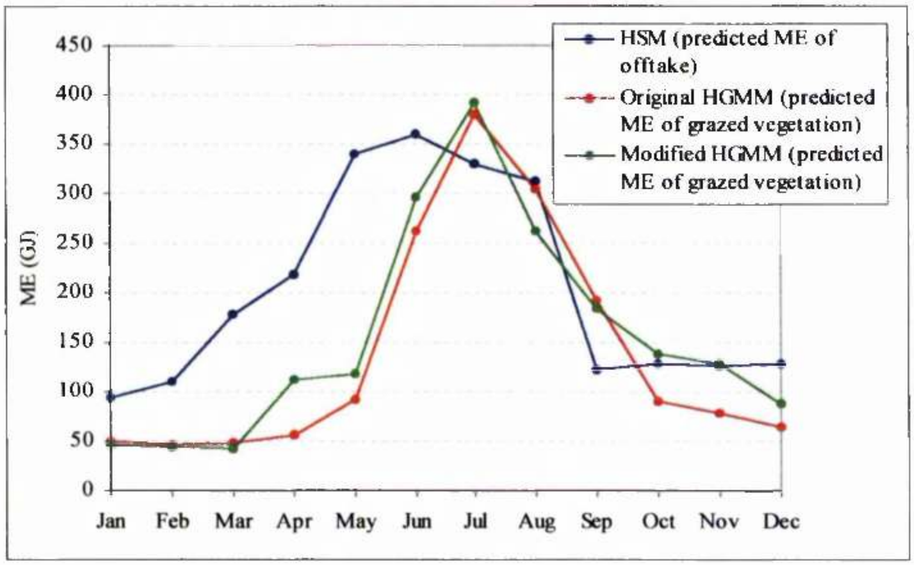


Figure 7.24 - Comparison between the monthly ME values predicted by the three models for the Gleann a'Chlachain data.

Table 7.20 - Total daily grazing times as predicted by the original and modified models.

Month	Total Daily Grazing Time (Hours)	
	Original Model	**Modified Model**
January	7.24	3.44
February	7.65	3.89
March	8.51	3.87
April	13.0	13.0
May	13.0	13.0
June	13.0	10.0
July	10.01	7.3
August	10.10	6.40
September	13.0	7.13
October	13.0	6.35
November	10.97	6.03
December	9.16	4.60

7.11 Does modification improve the model?

The modifications significantly improved elements of the vegetation sub-model by predicting reasonably well the green and dead biomass, and sward height of the U5c grassland. The modified model did however under-estimate the green biomass, dead biomass and sward height of the U5b community, indicating that the rates of senescence and litterfall set within the model were inappropriate for this community type and require modification. The under-estimates of biomass were probably due to the large proportion of winter-green *Juncus squarrosus* that was present within the U5b community.

The full inclusion of the U5c and U5b grasslands into the model resulted in a slight improvement in the offtake predictions. Modification not only increased the total offtake, but also increased the offtake from the *Nardus stricta* grasslands. Predicted offtake from the U5b community was however considerably lower than the observed value. In the model, dry matter intake from a particular community type is dependent upon the relative potential intake of digestible dry matter available from that community and on the relative area of the community (Armstrong *et al.*, 1997b). The U5b grassland had the largest area of any vegetation type within the enclosures, but it had a relatively low digestibility, due to its high proportion of *Juncus squarrosus* a species with a very low DM digestibility (Chapter 6; Grant and Campbell, 1978). Within the foraging algorithm, potential intake of digestible dry matter has a greater influence on community selection than area (Armstrong *et al.*, 1997b). This resulted in the very low predicted offtake from the U5b community. The foraging algorithm appears to require modification, possibly by increasing the relative area weighting.

Although modification resulted in an increase in total offtake, the modified model still significantly under-estimated offtake compared with that required to attain the measured performance levels, particularly in the winter and spring. During the early part of the year the predicted dry matter digestibility of the offtake was very low, which limited both the potential daily DM intake and the total grazing time. Using the independent data set the modified model predicted total grazing times of less than four hours a day over the winter period. Since it is highly unlikely that the animals grazed for such a short period there is clearly a problem with the intake sub-model during this part of the year, and it requires modification if the predictions are to improve. The largest difference between the offtake predicted by the HGMM (both modified and un-modified versions) and the offtake required to attain the measured performance levels was in May, when available biomass and DM digestibility limited daily DM intake. From June to October the ME of the offtake predicted by the modified HGMM was similar to that predicted by the HSM, suggesting that over this period the intake sub-model was more robust.

The modifications have improved the model's applicability for use in the north and west of Britain where the U5c and U5b communities are widespread and abundant. The modified model is however probably unsuitable for sites where *Nardus stricta* grasslands have developed over highly acidic bedrock, as the composition and productivity of these grasslands is likely to be different from the grasslands found within the study site (Chapter 6). The modified model may also be of limited value in situations where the sward has developed distinct tussock and inter-tussock areas, which allows the animals to be more selective in their grazing choice.

7.12 Further improvements to the model

There are limitations to what further improvements could be made to the HGMM without completely re-writing the program, but possibilities include:

1) Altering the rates of senescence and litterfall for the U5b community to improve the biomass predictions.
2) Adding production and sward height data for the montane U4d community obtained from this study. The production and sward height algorithms for the *Festuca - Agrostis* grassland are not suitable for the montane U4d community with it's high content of sedges, forbs, dwarf shrubs and bryophytes.
3) Adding production, sward height and digestibility data for additional plant communities such as the abundant *Trichophorum cespitosum* dominated mire communities, *Vaccinium myrtillus* and *Empetrum nigrum* heaths, and *Eriophorum vaginatum* dominated mires.
4) The use of a comprehensive set of DM digestibility values from a single source determined using a standard and consistent methodology.
5) Improving the intake and foraging behaviour sub-model. Removing some of the constraints on intake, in particular digestibility, may improve the intake predictions of the model. I.A.R. Hulbert (personal communication) has been gathering information on the grazing location of the sheep within Enclosure 2, using Global Positioning System (GPS) collars fitted to the animals. Data on the daily and seasonal foraging behaviour of the animals has been collected. This data will be combined with the GIS vegetation map of Enclosure 2 (Chapter 3) to determine the relative utilisation of the different vegetation types. The

information obtained will be used to improve the foraging algorithm within the model.

6) The option to input mean altitude data for each of the vegetation types.
7) The use of daily climate data obtained from the site or the nearest Meteorological Office weather station, rather than the use of average climate data.

7.13 Development of new grazing models for British hill farming systems

There are a number of important factors that influence production, foraging behaviour, choice of grazing location and intake rate that are not included within the HGMM. These factors, which should be taken into account within new grazing models, include:

1) The spatial pattern of vegetation patches within heterogeneous landscapes (Clarke *et al.*, 1995a; 1995b; Bailey *et al.*, 1998; Hester and Baillie, 1998; Hester *et al.*, 1999; Palmer and Hester, 2000).
2) The distribution and availability of supplementary feed, water, snow-lie, shade and shelter (Powell, 1997; Bailey *et al.*, 1998; Waterhouse, 1999).
3) Social interactions, home-range behaviour and shepherding (Hunter and Milner, 1963; Hewson and Wilson, 1979; Lawrence and Wood-Gush, 1988; Scott *et al.*, 1995; Sibbald *et al.*, 1998).
4) The season and time of day (Hunter, 1962; Hunter and Milner, 1963; Hewson and Wilson, 1979).
5) Environmental conditions (temperature, rainfall, wind-speed, exposure and topography), which affect both the movement of grazing animals and their net

energy balance (which alters the intake required to maintain body weight and condition) (Coughenour, 1991; Armstrong and Robertson, 2000).

6) Grazing competition between different species of herbivore (e.g. sheep and red deer (Osborne, 1984; Hester *et al.*, 1999)).

New grazing models developed for British hill farms will need to include other livestock species such as cattle, horses and goats, together with native herbivores such as red deer (e.g. HILLDEER, Partridge *et al.*, 1999), as well as more detailed information on the age and sex of the animals, their physiological state, body weight, seasonal weight changes and energy requirements. New models will need to have fully integrated animal and plant sub-models.

Grazing management decision support tools are increasingly required to have multiple goals and a wide range of end-users, including farmers, conservationists and local and regional government. Many of these end-users want spatial models that can be used within a GIS environment. They also want additional information on the impacts of grazing management on vegetation dynamics, community change, sward structure, biodiversity, and farm and regional economics. New grazing management decision support tools will need to address these issues.

The Macaulay Land Use Research Institute is currently designing and creating a new farm-scale grazing management decision support tool for hill farms called HILLPLAN that will aid research on rural land-use and provide support in decision-making to farmers and government (Milne and Sibbald, 1998). HILLPLAN simulates the grazing of both sheep and cattle on hill and upland pastures. It predicts the impact of grazing on the vegetation and the effect of the grazing management on the productivity of the livestock (Milne and Sibbald, 1998). The models within HILLPLAN use the latest concepts and contain up-to-date information. It should therefore have greater predictive ability in simulating management effects on vegetation and on annual productivity at the farm-scale than the current Hill Grazing Management Model (Milne, 1998). However, until the model has been released and tested it is not known whether it will produce accurate predictions for hill farms with high proportions of *Nardus stricta* dominated grassland. It is likely that there will be problems with the HILLPLAN model due to lack of appropriate data for some vegetation types. The data collected for this thesis will be an important resource that can be used to test, evaluate and possibly improve HILLPLAN in the future.

Whilst grazing models have considerable potential as decision support tools, the results here demonstrate that there may be many and wide-ranging differences between observed data collected from well-characterised sites and predictions made by these models. There is a clear need to use any model with caution, especially where the data is limited or of poor quality, or where the vegetation differs markedly from that within the model.

CHAPTER 8 – GENERAL DISCUSSION AND CONCLUSIONS

8.1 Study design and choice of study site

The choice of whether to use large-scale non-replicated enclosures or small replicated plots has to be based on a balance between available resources (e.g. land, fencing, time, equipment and personnel) and the applicability and credibility of the resulting data. By using large enclosures not only did the livestock have access to a range of plant communities and therefore a choice in their grazing decisions, but they could also be managed in a way that was closer to a 'real' hill-farm management system than would have been possible using small plots. Monitoring of the ewe weights and body conditions showed that the ewes could be kept in the enclosures all year-round without compromising their performance or welfare (Appendix 2.6). The lambing performance figures for all three plots were comparable with those of sheep grazing hill pastures elsewhere on the farm. Mean weight gains of over half a kilogram per day were recorded for the cattle over the summer grazing period (Appendices 2.6 and 2.7). This clearly indicates that the enclosures were productive systems and representative of management at a larger farm-scale. The system-scale enclosures also contained sufficient numbers of ewes and lambs to allow the establishment of a full-flock age structure, enabling the animals to gain effective, long-term experience of the enclosures. This avoided some of the problems associated with small plots using small numbers of animals, which have no prior knowledge of the plots.

There were however some problems with the livestock management within the enclosures, of which the main one was the use of 'bought-in' bullocks as summer grazers. This was found to be a mistake, as the behaviour of the animals varied considerably from year-to-year depending on where they had come from. In some years the animals also caused damage to the fences and entered the other enclosures. With hindsight the use of 'home-bred' suckler cows with calves would have been a more sensible choice, although the number of cows and calves would have been low (no more than seven).

A major drawback of using the large-scale enclosures was the lack of replication. However, replication was judged impractical in terms of both cost and time. Finding comparable areas of land to be used as replicates at the same scale (i.e. 40 ha each) would also have been extremely difficult. The Kirkton Face hillside was only large enough for the establishment of three enclosures that were of a similar size, had comparable topographies and altitudinal ranges, and had similar vegetation types (including areas and spatial distributions). The areas on either side of the study site were not suitable, as the topographies and vegetation of these areas were not comparable with those of the enclosures. Although the enclosures were very similar in terms of size, topography and vegetation cover, there were differences, and therefore some of the variation in the biomass, structure, productivity and utilisation data collected from the three enclosures may have been due to these physical and spatial differences, rather than management differences.

If replication had been possible, the data would undoubtedly have been statistically more robust, but the increased data collection time would have reached unmanageable levels. Replication would only have been possible if the enclosures had been smaller (e.g. 20 hectares rather than 40 hectares) and data collection had concentrated on one community type (e.g. the U5c *Nardus stricta* grassland). However, it would not have been possible to adequately test, evaluate and modify the Hill Grazing Management Model if data from only one vegetation type had been collected.

Replicated grazing studies carried out within small plots (e.g. Grant *et al.*, 1985; Hulme *et al.*, 1999) tend to produce more statistically robust data than un-replicated system-scale studies, and can provide detailed information on diet selection, intake and vegetation dynamics. However, if the vegetation within these small plots does not represent what is available to the free-ranging animals, and the management regime does not represent 'real-life', which is almost always the case, then the results and conclusions from these studies will have limited value to those who manage the hills and uplands. It is considered essential that grazing studies include a range of scales from small plot to large system. Models provide the link between the two extremes, but it is only through the use of system-scale data that models can be fully tested.

8.2 Methodologies used in the study

The technique used to map the enclosures produced a detailed vegetation map that was considerably more accurate than a simple field-based sketch map would have been. It was only through the production of this detailed vegetation map that accurate data on the areas of each vegetation type could be obtained. This highly accurate data was necessary for the testing and modification of the Hill Grazing Management Model. There are however some drawbacks with this mapping technique in that it requires at least two surveyors and is extremely time consuming. A much more rapid technique using a handheld GPS unit could be used for any future mapping, since in May 2000 the

US Government removed the in-built error from the GPS signals (known as selective availability) significantly improving the accuracy of hand held GPS units.

The vegetation map is currently being used in a foraging behaviour study that is running in parallel to the study described in this thesis. A number of ewes within Enclosure 2 have been fitted with GPS collars. The GPS will provide information on the location of the ewes within the enclosure. The location data will then be overlain onto the digitised vegetation map. This will provide information on the use of the different vegetation types at different times of the day and night and at different times of the year. This location data coupled with the production and utilisation data (provided by this study) will help to improve our knowledge of the grazing behaviour of hill sheep on indigenous semi-natural hill vegetation, and provide a test for the foraging behaviour algorithms within the HGMM and HILLPLAN.

The heterogeneity of hill grasslands, both in terms of species composition and structure, inevitably leads to large variations in the amount of above-ground biomass over very small distances. The high standard deviations of the biomass data indicate that the number of samples harvested and sorted was probably too low. However, it was not possible to harvest or sort anymore vegetation due to a lack of time and resources. I believe that the field and laboratory methods used to determine above-ground biomass, and the number of samples collected, provided the most accurate information possible in the circumstances, and that the values obtained were reasonable estimates of the above-ground biomass. As discussed earlier, it may have been more appropriate to have concentrated on one community type (e.g. the U5c grassland) and to have collected herbage samples over a single year. In this way the number of monthly herbage cuts could have been increased from 4 per community per enclosure to 16 or more. This would have reduced variance levels and produced more robust biomass, production and offtake data. However, given the reduced data set (i.e. just one community type) and the considerable year-to-year variation, the test of the HGMM would not have been as valid.

As outlined in Chapter 6 there are many problems associated with the use of exclosure cages to estimate the net primary production and utilisation of grazed pastures. They are however believed to be the only practical means of obtaining this type of data from semi-natural hill-grasslands in remote field sites. The exclosure cage technique has been widely used by researchers in the UK to obtain production data from hill grasslands (Rawes and Welch, 1969; Perkins *et al.*, 1978). Job and Taylor (1978) used this technique to estimate the production of a range of indigenous hill grassland communities, including *Festuca* - *Agrostis* and burnt and un-burnt *Molinia* grasslands. The data published by Job and Taylor (1978) was used by Armstrong *et al.* (1997a) in the development of the Hill Grazing Management Model. Since the production data for the indigenous hill grasslands used in the HGMM was obtained using an exclosure cage technique, it was thought appropriate to use a similar technique in this present study.

An attempt was made to improve the accuracy of the production estimates by adjusting the biomass data to account for some of the cage effects. The method used to calculate the production values also attempted to take into consideration the seasonal changes in the rates of production, senescence and litterfall. Comparison with published production data for similar plant communities suggests that the values given in this thesis are reasonable estimates. The offtake values obtained from this study were almost certainly less accurate than the production values. Highly accurate estimates of offtake from heterogeneous hill grasslands grazed by relatively low numbers of free-ranging herbivores cannot be obtained using an exclosure cage technique. However, by comparing the estimated energy content of the measured offtake from Enclosure 2 with the energy required by the animals to attain their measured productivity and performance, the data was deemed sufficiently accurate to test the HGMM.

There are a number of techniques to determine diet selection and intake that could have been used in this study, however none of these methods were deemed practical. The use of oesophageally-fistulated animals to determine diet selection (Grant *et al.*, 1985) was thought to be impractical and unacceptable due to the large size of the hill enclosures and the lack of daily inspection. The technique of n-alkane analysis could have been used to determine the intake and species composition of the ingested herbage (Mayes *et al.*, 1986; Dove, 1992). However, this procedure is costly and time-consuming (Jones and Moseley, 1993). The cuticular wax of each species has a characteristic n-alkane composition, and this also varies between different parts of the plant, and with the age of the plant (Jones and Moseley, 1993). Considerable calibration of the different plant species would have been required, using housed sheep. Such work would have been a complete study in itself. The limitations of the n-alkane analysis technique mean that it is probably not an appropriate method to use in hill pastures containing numerous plant species, such as those found on the study site.

Because of the relative stability of the hill grasslands in terms of species composition, it was necessary to use a vegetation monitoring method that was capable of detecting small changes in species composition between observations. The nested quadrat methodology developed by Critchley and Poulton (1998), which optimises precision and scale, reduces observer variation, and allows areas to be monitored rapidly and consistently, was thought to be the most appropriate monitoring method to use. The results indicate that the technique was effective in detecting minor changes in the vegetation. However, one of the limitations of the methodology used in this study was the very limited area of vegetation that was monitored. The use of sample stands also meant that the quadrats were concentrated in particular areas. It would have been more appropriate to have had smaller sample stands or individual quadrats randomly distributed within the chosen community types throughout the enclosures. This would have reduced the risk of bias associated with using single sample stands for each community within each enclosure.

The objective and consistent manner in which the sward height data was collected (using a HFRO sward stick) meant that the data was robust, and that the changes observed were real.

The field and laboratory techniques used in this study were thought to be the most appropriate for this type of system-scale study, being a compromise between the need for accurate, credible and usable data, and the finite amount of time and resources available.

8.3 The vegetation of the study site

The study site contained a complex mosaic of vegetation community types, varying in species composition, structure, biomass, productivity and nutritive value. This vegetation mosaic has developed through the interaction of environmental, biological, historical and management factors. Variations in soil type, drainage, slope, aspect and microclimate across the study site have affected the distribution of species, resulting in a highly complex and often patchy distribution of species and community types.

Although the present day environmental factors have tended to determine the distribution of the species, and the geographical location, geology and long-term environmental history have determined the regional flora, it has been the management of the site that has been the key factor determining what species are actually present today. The principal management factor, over the last 200 years, has been the large-scale grazing of sheep.

The study site contained a rich diversity of plant species and community types. The main vegetation types were semi-natural grasslands dominated by *Nardus stricta* and *Juncus squarrosus*, and mire communities dominated by *Juncus acutiflorus* and *Trichophorum cespitosum*. Smaller patches of more species-rich calcicolous-grassland and base-rich flushes were scattered throughout the site. Because of the underlying base-rich geology (i.e. Dalradian mica-schist) and the altitude of the site, many of the communities, including the *Nardus stricta*-dominated grasslands, contained calcicolous and arctic-alpine species.

The species compositions of the monitored vegetation types were not static over time, as plant communities are dynamic systems in which the vegetation is constantly changing as individuals die and are replaced (Miles, 1987). Any change in management will alter the dynamics and relative stability of the community and will lead to change, however the changes may take place over a long time period, and may be only minor in nature (Miles, 1987). Only minor changes in species composition were observed in the monitored communities, indicating that these vegetation types, which are dominated by grazing tolerant, long-lived perennial grasses, show very little response in the short-term to relatively minor changes in grazing pressure. It was difficult to determine whether the observed changes in species composition were due to alterations in the grazing management or to climatic fluctuations, or simply to the dynamic nature of the communities. The introduction of summer grazing cattle did lead to an increase in ruderal and grazing tolerant species within the calcicolous grassland, and to an increase in the area of bare ground, which will provide potential sites for new colonisation. However, reducing the number of sheep did not result in any major changes in species composition. Under all three grazing regimes the cover of *Juncus squarrosus* increased significantly, and the *Nardus stricta* grasslands became shorter, more homogeneous and less tussocky. This change in sward structure across all three enclosures suggests that the grazing regime that existed on the site prior to the commencement of the project was very different from the grazing regimes imposed during the trial. It is difficult to assess what the historical grazing regime was on the site prior to the establishment of the enclosures since the study site formed part of a much larger grazed area. It is likely however that the grazing of the study site area was much more variable and seasonal in nature prior to the start of the study. This clearly shows one of the problems that can arise in grazing studies when areas of previously un-enclosed land are not given time to reach equilibrium with the imposed baseline stocking rate, before the trial stocking rates are imposed. It is particularly notable that these effects were found in a system scale study using large enclosures. It is likely that small plots would exhibit this effect even more. Since the vegetation types are dominated by long-lived perennial species that respond relatively slowly to change, less than a year of the baseline stocking-rate was clearly not long enough. Unfortunately the practicalities of short-term grazing studies meant that a longer baseline period was simply not possible.

In conclusion, a reduction in sheep numbers has little impact on species composition over the short-term. Grazing by cattle and sheep has more of an impact, but the effects remain relatively minor. The grasslands dominated by *Nardus stricta* appear to be extremely stable under the range of grazing treatments tested. Changes in the structure of the sward appear to be more important than changes in species composition.

8.4 Production and offtake

The work described in this thesis has shown that the U5c *Nardus stricta* grasslands of the study site are relatively species-rich and contain a number of species more typical of montane or calcicolous grasslands. These grasslands also contain a large proportion of fine and broad-leaved grasses (other than *Nardus stricta*), and have relatively high production rates, producing large amounts of green biomass (with a moderately high digestibility) during the summer. The intake of herbage from these grasslands over the summer months is potentially high. They are however much less valuable as a forage resource during the autumn and winter, due to the build-up of large amounts of dead standing material and litter, in particular dead standing *Nardus stricta* which has a very low digestibility. The utilisation of these grasslands and of the *Nardus stricta* within them varied depending on the grazing management and the time of year. Under the low sheep stocking rate, the sheep appeared to be more selective, utilising proportionately less *Nardus stricta* and more inter-tussock vegetation, than under the higher sheep stocking rate and mixed sheep and cattle treatments. The U5b grasslands, dominated by *Juncus squarrosus* and *Nardus stricta*, were less productive than the U5c grasslands but contained more live and dead biomass throughout the year. *Juncus squarrosus*, which has a very low digestibility, formed a high percentage of the biomass within the U5b grasslands. The amounts of fine and broad-leaved grasses within the U5b sward also tended to be lower than those within the U5c grassland. Less green material was grazed from the U5b grasslands than from the U5c grasslands. Increasing the stocking rate did not result in increased utilisation of the U5b community. Offtake from the *Juncus acutiflorus*-dominated mire community was only recorded from the sheep and cattle grazed enclosure, indicating the greater readiness of the cattle to eat the taller, fibrous, less digestible swards.

This study has provided a data set on the productivity, biomass and utilisation of *Nardus stricta, Juncus squarrosus* and *Juncus acutiflorus* dominated communities that is unique. It clearly demonstrates and provides data on the intake of *Nardus stricta,* which published models have failed to take into account. The data set fills some of the gaps in our knowledge that existed regarding these hill community types.

8.5 Management implications

Hill farmers are under pressure from the UK Government and nature conservation bodies to change the way that they graze their hill-pastures, no longer regarding them as simply a forage resource, but managing them for multiple-objectives, including nature conservation, landscape enhancement, archaeological conservation, recreation and animal production (Meuret and Dumont, 2000, Sibbald *et al.*, 2000). The implementation of agri-environment schemes, designed to provide environmental and nature conservation benefits at the farm-level, and changes in the livestock support payments given to farmers in the Less Favoured Areas, are the driving forces behind these changes in management (Sibbald *et al.*, 2000, SERAD, 2000e). The principal management prescription for hill farms is a reduction in breeding ewe numbers. The question remains as to whether this is the most appropriate and effective means of increasing biodiversity and obtaining these multiple-objectives. One of the main objectives of these agri-environment schemes for hill farms is an increase in the area of heather moorland. The work presented in this thesis indicates that in the short term, reducing the number of ewes (i.e. extensification) has very little impact on the species composition of hill grasslands; it does not result in an increase in the cover of dwarf shrubs and has only minor effects on the structure and biomass of these grasslands. Entering into a short-term management agreement (under an agri-environment scheme) to reduce sheep numbers is unlikely to result in any major environmental benefits if *Nardus stricta* and *Juncus squarrosus* dominate the hill vegetation. Mixed sheep and cattle grazing appeared to have more of an impact on the composition, structure and biomass of the vegetation than simply a reduction in sheep numbers. However it is very difficult to determine whether these changes actually resulted in an increase in biodiversity. Creating structural diversity is perhaps the key to improving the biodiversity of these grasslands, through an increase in the number of invertebrate species (Dennis *et al.*, 1997). In order to do this, other management options such as summer only grazing, rotational grazing, mixed livestock grazing or further reductions in sheep numbers may be more effective management options. A further reduction in sheep numbers on the *Nardus stricta*-dominated grasslands of the study site would probably lead to greater structural diversity in the vegetation. However, the build up of dead material and the increase in *Molinia caerulea* that is likely to occur under very low grazing pressures, may lead to a decline in the total number of vascular plant species. Further research is required on the impact of different management options on the structural diversity, vascular plant species diversity and overall biodiversity of these *Nardus stricta*-dominated grasslands.

Although heather moorland has been given a far higher conservation and landscape value than any of the hill grasslands (Thompson *et al.*, 1995), it is important to stress that these grasslands can be species-rich and structurally diverse, and form part of a historic, cultural landscape. The replacement of the *Nardus stricta*-dominated grasslands found on the study site with heather moorland would inevitably lead to a considerable reduction in the number of vascular plant species, and almost certainly a reduction in the overall biodiversity. Rather than trying to encourage the development of blanket heather moorland through the reduction of sheep numbers, more emphasis should be put on active management to create habitat mosaics in which grassland, heathland, mire, scrub and woodland are all integral parts. Developing management prescriptions to achieve these habitat mosaics will require much more research, at a range of scales.

I do not think that highly prescriptive agri-environment schemes with rigid rules are the most effective way of increasing biodiversity and improving the environment of hill farms. I believe that a much more flexible scheme in which specific management options are developed for individual farms would be more effective. This would require a detailed environmental audit to be carried out on each participating farm, together with the production of a conservation management plan specifically tailored for that premises. This would allow the conservation management plan to be set within a much more local or regional context, taking into consideration species or communities identified within local biodiversity action plans. Whether modelling and the use of decision support tools can assist in this process is discussed in the next section.

8.6 The role of modelling

This study has shown that the published Hill Grazing Management Model (Armstrong *et al.*, 1997a; 1997b) does not produce accurate predictions when used on a site with a large proportion of *Nardus stricta*-dominated vegetation. It over-estimated offtake of the *Festuca - Agrostis* community and under estimated the offtake of live material from the *Nardus stricta*-dominated communities. It also under-estimated the biomass and sward height of the *Festuca - Agrostis* community, and the production, biomass and sward height of the inter-tussock vegetation.

Modification of the model using data on the production, sward height and digestibility of the U5c and U5b grasslands significantly improved elements of the vegetation sub-model and resulted in a slight improvement in the model's offtake predictions. Estimated offtake from the U5 communities increased, while offtake from the *Festuca - Agrostis* community decreased. The improvements in the offtake predictions were relatively minor and the modified model continued to under-estimate total offtake, particularly during the late winter and spring. Further development of both the vegetation biomass sub-model and in particular the foraging and intake sub-model is required. More information is needed on the foraging behaviour of sheep and on the factors that determine the selection of vegetation types. The use of GPS collars to track sheep within Enclosure 2 will hopefully provide some of this information. Additional information on the digestibility of the different hill plant species and communities throughout the year is also required, together with improved information on the relationship between the digestibility and daily DM intake of these vegetation types.

The inclusion of the two U5 *Nardus stricta*-dominated communities into the model has improved the model's applicability for use on sites where these communities are abundant, however there remains some doubt about the accuracy of the offtake predictions. Due to the limitations and inaccuracies of the model I do not believe that it is an appropriate tool to use as a sole guide for the setting of stocking rates on hill farms for conservation purposes. I do however agree with Armstrong *et al.* (1997b) that the model is a useful educational and research tool for illustrating the hill grazing system, and has served to identify a number of gaps in our knowledge of these grazing systems.

The Macaulay Land Use Research Institute is currently developing a decision support system for hill farm management known as HILLPLAN (Sibbald *et al.*, 2000), which will supersede the Hill Grazing Management Model. HILLPLAN contains sub-models for plant growth, foraging behaviour (based on the HGMM), and vegetation dynamics (Sibbald *et al.*, 2000). This enables it to predict changes in the proportions of the different vegetation types and the production of both sheep and cattle under different grazing regimes and livestock management systems (Sibbald *et al.*, 2000). The data requirements of the model have been minimised so that on-site data collection can be completed within two days (Sibbald *et al.*, 2000). The authors of HILLPLAN intend it to be used by land managers, government departments and non-government organisations as a decision support tool, allowing mutually acceptable grazing management plans to be produced on an individual farm basis (Sibbald *et al.*, 2000). HILLPLAN has not yet been released and therefore it is not known how accurate or effective it will be. Evaluation of HILLPLAN (and the sub-models that it contains) can only be done through testing. Although HILLPLAN has been developed using much more data than the HGMM, and will provide many more predictions, it will still be reliant on the input of accurate data. It does not matter how well the sub-models work, if the data entered into the model is incorrect, then the predictions will not be valid. The rapid collection of accurate vegetation data (i.e. the composition, distribution and area of the vegetation types) from sites such as the Kirkton Face would be extremely difficult if not impossible. The Kirkton Face study site is not unique. Most hill pastures consist of complex mosaics of vegetation types. I believe that hill grazing models do have a role to play by increasing our understanding of the grazing system and the impacts of management. However, I am doubtful whether a truly effective decision support tool, designed to produce grazing plans for individual farms, can ever be developed for highly complex hill grazing systems.

8.7 Future research requirements

In many circumstances, the desire to increase the plant species diversity and percentage cover of dwarf shrubs within extensive, relatively stable *Nardus stricta* grasslands is neither an appropriate nor an achievable policy objective. A more effective way of increasing biodiversity is probably through the creation of a more structurally diverse sward. Research to identify the relationships between plant community structure and diversity within a range of invertebrate and vertebrate taxa is required. Equally, research to determine the perceived value of these taxa by the general public and expert conservationists is essential, as the question remains as to whether for example an increase in one species of bird outweighs a large increase in the number of plant or invertebrate species. Research is also required to determine the most appropriate management needed to create these structurally diverse swards. It is likely that a much more flexible grazing management system, with seasonal grazing and mixed livestock will be required to actively create these desired swards.

More information is required on the vegetation dynamics, physiology and genetics of *Nardus stricta* in order to improve our understanding of the role that this key species has within hill grassland communities, especially since the tussocks of *Nardus stricta* are the most important structural component of many hill grassland swards. There is considerable evidence that DM digestibility is not the only factor that determines intake, with structural form and chemical composition being important factors. Information is required to determine whether there is any genetic basis behind the size and shape of *Nardus stricta* tussocks or whether it is related to environmental conditions or is simply a function of past or present grazing management. Research is also required on the impact that tussock form has on the intake of both *Nardus stricta* and the inter-tussock vegetation. Further information is also required on the silica content of *Nardus stricta* leaves, it's variability within and between populations, it's relationship to soil silica content, and it's impact on grazing utilisation.

With this information we will have a much better understanding of the dynamics of *Nardus stricta*-dominated grasslands, which will enable us to manage them in a much more appropriate manner, whether it be for conservation purposes or for improved animal production.

As decision support tools continue to be developed there is a vital need for research to provide parameterised data and biological understanding of the processes involved, so that these models can be tested before they are used to determine policy on the ground. More fundamentally there is a need for research and evaluation of the applications of these decision support tools. Currently there is a danger that highly sophisticated and complex models are being built to potentially deliver predictions at the farm level and be used to propose management prescriptions. As these decision support tools move from being merely describers of the current state or predictors of only short-term outcomes (e.g. the HGMM), to predictors of long-term change (e.g. the vegetation change element within HILLPLAN) then there is an urgent need to test these new models and their underlying mechanisms. This may require a degree of imaginative research to test the predictions of long-term change. Data input to all models is likely to be crucial, and therefore there is a need to identify the sensitivity of the data collection process and to include this sensitivity (and confidence limits) into model outputs. Research is needed to develop accurate and rapid methods of vegetation characterisation and mapping at an appropriate scale. Classified satellite images have the potential to be used for this purpose, but this technique requires further development and testing.

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APPENDICES

Appendix 2.1 - Meteorological data from the Kirkton Farm Meteorological Station (1994 – 1998)

Rainfall (mm)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual Total
1994	419.3	112	635.7	218.1	39.4	214.7	72.1	180.9	93.5	180.2	252.6	566.2	2985
1995	410	428.6	238.1	61.2	129.4	37.1	150.2	27.2	176.7	505.9	202.9	58.5	2426
1996	168.3	194.5	52.3	144.8	112.3	97.6	86.9	78.5	127.1	347.5	295.6	115.9	1821
1997	120.2	576.6	266.4	143.7	112.3	98.6	111.6	88.9	246.6	105.7	189.0	324.9	2384
1998	299.1	445.9	153.3	111.4	56.5	115.3	168.0	159.0	93.8	353.1	306.5	387.4	2649

Mean Maximum Temperature (°C)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual Mean
1994	5.85	3.58	7.14	9.91	13.60	14.84	18.26	17.25	14.39	11.36	10.42	7.64	11.23
1995	5.61	6.38	5.65	10.17	13.52	19.02	19.07	21.55	15.40	13.17	9.12	3.35	11.86
1996	5.89	4.48	6.54	10.16	11.65	16.69	17.24	18.41	16.89	12.43	6.62	4.58	11.00
1997	5.20	7.23	9.69	11.74	14.42	16.80	18.62	19.58	16.09	11.95	9.66	7.77	12.43
1998	6.26	9.27	8.50	9.36	15.23	16.90	16.47	17.39	16.44	11.12	8.45	8.97	12.05

Mean Minimum Temperature (°C)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual Mean
1994	-0.12	-0.73	1.28	1.79	2.04	7.05	9.63	7.22	5.54	3.33	5.70	-0.09	3.57
1995	-1.45	-0.36	-0.86	1.64	3.96	6.57	10.47	9.17	6.13	6.71	2.46	-3.26	3.45
1996	2.17	-2.45	-1.18	2.76	2.62	6.46	9.05	9.37	7.17	6.36	-0.86	-1.63	3.36
1997	-2.08	0.92	2.22	3.05	4.48	6.85	8.76	10.73	4.68	4.10	4.42	0.26	4.05
1998	0.17	4.49	2.29	1.07	5.43	4.81	8.17	7.90	6.65	3.37	-1.15	0.45	3.64

Highest Maximum Temperature (°C)

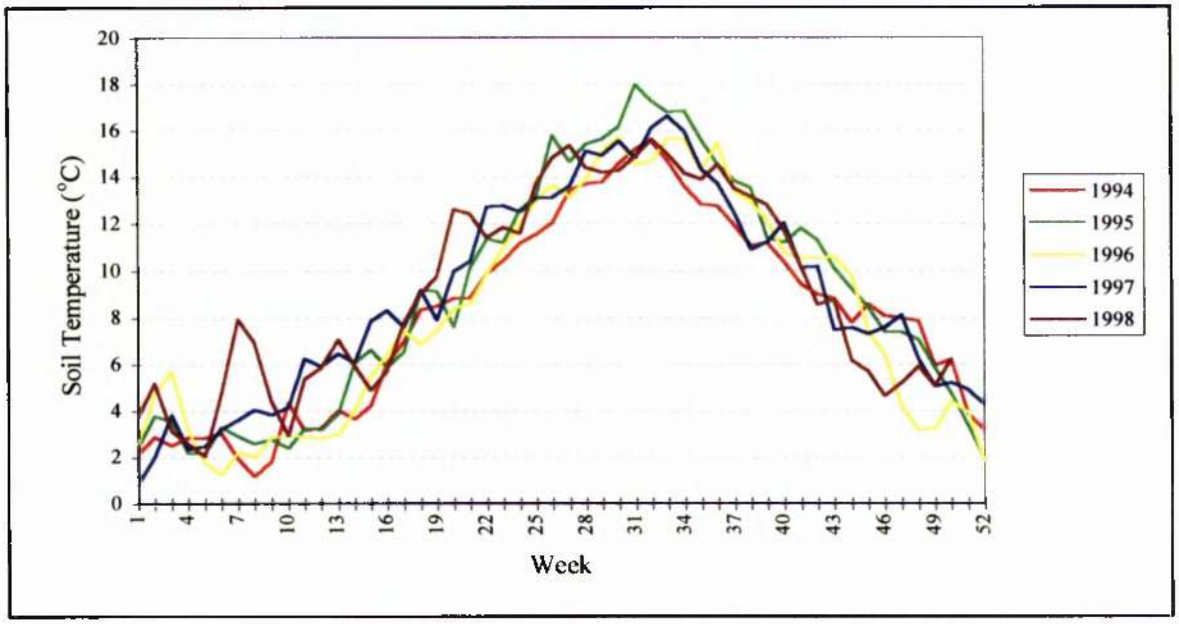
Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1994	9.9	7.1	11.0	14.8	20.5	21.3	22.1	21.1	19.8	17.2	13.7	13.4
1995	11.4	10.2	10.1	18.2	18.9	29.1	26.2	27.9	18.2	15.7	12.6	11.4
1996	9.8	9.0	11.7	14.0	16.6	23.5	23.0	21.9	22.8	16.6	14.8	9.1
1997	11.9	10.8	13.1	15.8	23.0	21.8	24	25.1	19.5	15.3	15.1	12.4
1998	11.5	13.4	12.2	13.9	24.0	23.7	21.9	21.4	23.2	14.9	13.5	13.7

Lowest Minimum Temperature (°C)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1994	-7.0	-13.4	-2.8	-3.0	-3.6	4.0	3.1	1.5	-1.3	-2.8	-1.5	-8.1
1995	-10.8	-9.1	-11	-3.9	-5.2	3.2	2.3	1.8	-3.2	-3.4	-6.4	-19.1
1996	-5	-10.2	-6.3	-6.0	-3.6	-0.5	1.5	2.9	-0.1	-1.4	-9.3	-8.7
1997	-11.0	-6.7	-4.6	-4.0	-4.8	-0.4	3.7	2.6	-3.7	-7.1	-2.8	-7.5
1998	-8.0	-5.4	-5.3	-4.8	0.2	-2.0	1.9	0.4	0.5	-6.3	-6.4	-9.0

Mean Soil Temperature (°C)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual Mean
1994	2.59	2.12	3.48	5.30	8.77	11.16	13.85	14.43	11.80	9.25	8.16	4.89	8.02
1995	2.85	2.89	3.07	6.29	9.35	12.91	15.62	16.90	13.50	11.00	7.74	4.13	8.89
1996	3.85	1.81	2.96	5.83	8.09	12.14	14.45	14.99	13.48	10.50	6.10	3.29	8.16
1997	2.29	3.36	5.37	7.42	9.68	12.82	14.71	15.76	12.25	9.79	7.69	4.89	8.87
1998	3.54	5.74	4.90	6.18	11.04	12.60	14.56	14.75	13.59	9.70	5.35	5.81	9.13



Appendix 2.2 - Mean weekly soil temperatures recorded at the Kirkton Farm Meteorological Station

Appendix 2.3 - Historical sheep numbers on the Kirkton Farm holding (Beinn Chaorach, Ben Challum and Kirkton Face).

(Counts taken in June and July at clipping)

	1869	**1897**	**1899**	**1902**	**1903**	**1904**	**1905**	**1906**	**1907**	**1908**	**1909**	**1910**	**1911**	**1912**	**1913**	**1914**	**1915**	**1916**	**1918**	**1923**	**1998**
Ewes	1001	1304	1200	1184	1228	1228	1335	1215	1208	1210	1166	1181	1183	1237	1135	1139	1152	1252	1251	1124	1254
Wethers	480	282	218	145	171	125	133	43	24	59	52	84	111	103	40	23	18	18	27	34	0
Ewe Hoggs	290	364	430	321	380	356	369	368	341	394	515	306	383	367	365	296	397	388	260	298	414
Wether Hoggs	218	205	226	176	120	114	52	70	53	54	94	112	88	60	34	10	49	79	46	82	0
Total	**1989**	**2155**	**2074**	**1835**	**1899**	**1823**	**1889**	**1696**	**1626**	**1717**	**1827**	**1683**	**1765**	**1767**	**1574**	**1468**	**1616**	**1737**	**1584**	**1538**	**1668**
Sheep ha^{-1}	**1.37**	**1.49**	**1.43**	**1.27**	**1.31**	**1.26**	**1.30**	**1.17**	**1.12**	**1.18**	**1.25**	**1.16**	**1.22**	**1.22**	**1.09**	**1.01**	**1.11**	**1.20**	**1.09**	**1.06**	**1.38**
Lambs	*ND*	*ND*	*ND*	*ND*	863	*ND*	924	805	852	907	820	867	*ND*	860	*ND*	*ND*	932	869	857	*ND*	1453
Lambs/ewe	*ND*	*ND*	*ND*	*ND*	0.70	*ND*	0.69	0.66	0.71	0.75	0.70	0.73	*ND*	0.70	*ND*	*ND*	0.81	0.69	0.69	*ND*	1.16

Notes 1) 1869 to 1923 data taken from log books and diaries of Mr John Paterson the then tenant at Kirkton Farm.

2) Totals do not include tups and tup hoggs.

3) 1998 data collected at Marking in June.

4) The area of the Kirkton Farm holding was approximately 1450 ha in 1869-1923, compared with approximately 1210 ha in 1998.

5) *ND* = No Data.

Appendix 2.4 - Estimated annual stocking rates (LU ha^{-1}) for the period 1980 - 1993 (i.e. the period prior to the erection of the enclosure fences)

	1980-1989	1990-1991	1992-1993
Estimated Annual Stocking Rate (LU ha^{-1})	0.146	0.149	0.125

Livestock Units - *Ewes & Hoggs (medium weight) = 0.08, lambs = 0.04, Cattle over 24 months = 0.8, Cattle (bullocks) 12-24 months = 0.65, Calves under 12 months = 0.34*

Appendix 2.5 - The target number of ewes from each age group present within each enclosure during the trial period (August 1994 - December 1998)

Enclosure	Hoggs (Mar-Aug)	Ewe Age			
		2	3	4	5
1	13	12	10	8	7
2	8	7	6	5	4
3	9	8	7	5	4

Appendix 2.6 - Mean ewe weights (1994 – 1998), and weaning percentages.

Enclosure	Ewe Weights (kg)	Year				
		1994	1995	1996	1997	1998
1	Mean Scanning Weight (kg)	45.20	39.69	45.74	42.77	46.73
	Mean Marking Weight (kg)	*No Data*	43.30	44.89	46.88	48.12
	Mean Weaning Weight (kg)	50.69	46.63	50.16	49.26	50.53
	Mean Pre-mating Weight (kg)	53.68	50.76	47.05	51.35	55.20
2	Mean Scanning Weight (kg)	45.43	41.53	47.15	44.20	48.68
	Mean Marking Weight (kg)	*No Data*	42.62	47.10	49.16	47.67
	Mean Weaning Weight (kg)	51.54	48.20	51.59	50.80	49.77
	Mean Pre-mating Weight (kg)	52.59	50.57	47.82	53.52	54.75
3	Mean Scanning Weight (kg)	44.80	42.79	45.83	44.23	48.35
	Mean Marking Weight (kg)	*No Data*	43.00	45.17	48.73	49.13
	Mean Weaning Weight (kg)	51.48	46.32	49.58	50.38	49.41
	Mean Pre-mating Weight (kg)	52.64	50.42	47.10	51.25	54.92

Weaning Percentage (i.e. number of weaned lambs per 100 ewes (means for 1995-1998))

	Enc. 1	Enc. 2	Enc. 3
Weaning percentage	71 %	84 %	88 %

Appendix 2.7 - Number and weight of bullocks in Enclosure 3 (1995 - 1998)

	Year			
	1995	**1996**	**1997**	**1998**
Number of bullocks	15	16	14	15
Date when introduced into Enclosure 3	19/06/95	14/06/96	16/06/97	17/06/98
Date when removed from Enclosure 3	24/09/95	17/09/96	28/09/97	15/09/98
Actual number of days present within Enclosure 3	97	87	81.8	91
Total weight at start (kg)	4451	4610	4624	4899
Mean weight per bullock at start (kg)	296.73	288.13	330.29	326.60
Total weight at end (kg)	5516	5490	5451	5680
Mean weight per bullock at end (kg)	367.73	343.13	389.36	378.67
Mean weight gain per bullock (kg)	71.00	55.00	59.07	52.07
Mean weight gain per day (kg day^{-1})	0.732	0.579	0.563	0.572

Appendix 2.8 - Dates of scanning, marking, weaning and pre-mating

	Scanning	Marking	Weaning	Pre-mating
1993	-	-	-	22/11/93
1994	23/02/94	14/06/94	18/08/94	21/11/94
1995	24/02/95	15/06/95	16/08/95	16/11/95
1996	01/03/96	20/06/96	16/08/96	03/12/96
1997	28/02/97	10/06/97	13/08/97	03/12/97
1998	26/02/98	17/06/98	18/08/98	30/11/98

Appendix 2.9 - Monthly stock numbers within the study enclosures

1994 - Year 1 (all three enclosures had similar stocking rates until 18th August, when the trial stocking rates were established)

Month	Enc. 1 (44.41 ha)	Enc. 2 (40.77 ha)	Enc. 3 (47.46 ha)
January	37 ewes (24 days)	44 ewes (24 days)	48 ewes (24 days)
February	37 ewes (25 days)	44 ewes (25 days)	48 ewes (25 days)
March	37 ewes (24 days)	44 ewes (24 days)	47 ewes (24 days)
April	37 ewes (30 days) 13 hoggs (23 days)	44 ewes (30 days) 15 hoggs (23 days)	47 ewes (30 days) 16 hoggs (23 days)
May	37 ewes (19 days) 36 ewes (12 days) 13 hoggs (31 days)	44 ewes (19 days) 42 ewes (12 days) 15 hoggs (31 days)	47 ewes (31 days) 16 hoggs (31 days)
June	36 ewes (14 days) 37 ewes (13 days) 13 hoggs (27 days) 18 lambs (13 days)	42 ewes (14 days) 44 ewes (13 days) 15 hoggs (27 days) 35 lambs (13 days)	47 ewes (14 days) 48 ewes (13 days) 16 hoggs (27 days) 41 lambs (13 days)
July	37 ewes (31 days) 13 hoggs (31 days) 18 lambs (31 days)	44 ewes (31 days) 15 hoggs (31 days) 35 lambs (31 days)	48 ewes (31 days) 16 hoggs (31 days) 41 lambs (31 days)
August	37 ewes (31 days) 13 hoggs (18 days) 18 lambs (18 days)	44 ewes (18 days) 22 ewes (13 days) 15 hoggs (18 days) 35 lambs (18 days)	48 ewes (18 days) 24 ewes (13 days) 16 hoggs (18 days) 41 lambs (18 days)
September	37 ewes (30 days)	22 ewes (30 days)	24 ewes (30 days)
October	37 ewes (31 days)	22 ewes (31 days)	24 ewes (31 days)
November	37 ewes (21 days) 83 ewes (9 days) 3 rams (9 days)	22 ewes (21 days)	24 ewes (21 days)
December	83 ewes (8 days) 3 rams (8 days)	83 ewes (10 days) 3 rams (10 days)	83 ewes (11 days) 3 rams (11 days)

1995 - Year 2

Month	Enc. 1 (44.41 ha)	Enc. 2 (40.77 ha)	Enc. 3 (47.46 ha)
January	37 ewes (19 days)	22 ewes (19 days)	24 ewes (19 days)
February	37 ewes (28 days)	22 ewes (28 days)	24 ewes (28 days)
March	37 ewes (31 days) 13 hoggs (1 day)	22 ewes (31 days) 8 hoggs (1 day)	24 ewes (31 days) 9 hoggs (1 day)
April	37 ewes (30 days) 13 hoggs (30 days)	22 ewes (30 days) 8 hoggs (30 days)	24 ewes (30 days) 9 hoggs (30 days)
May	37 ewes (31 days) 13 hoggs (31 days)	22 ewes (31 days) 8 hoggs (31 days)	24 ewes (31 days) 9 hoggs (31 days)
June	37 ewes (28 days) 13 hoggs (28 days) 26 lambs (15 days)	22 ewes (28 days) 8 hoggs (28 days) 13 lambs (15 days)	24 ewes (28 days) 9 hoggs (28 days) 21 lambs (15 days) 15 bullocks (12 days)
July	37 ewes (31 days) 13 hoggs (31 days) 26 lambs (31 days)	22 ewes (31 days) 8 hoggs (31 days) 13 lambs (31 days)	24 ewes (31 days) 9 hoggs (31 days) 21 lambs (31 days) 15 bullocks (31 days)
August	37 ewes (31 days) 13 hoggs (16 days) 26 lambs (16 days)	22 ewes (31 days) 8 hoggs (16 days) 13 lambs (16 days)	24 ewes (31 days) 9 hoggs (16 days) 21 lambs (16 days) 15 bullocks (31 days)
September	37 ewes (30 days)	22 ewes (30 days)	24 ewes (30 days) 15 bullocks (24 days)
October	37 ewes (31 days)	22 ewes (31 days)	24 ewes (31 days)
November	37 ewes (30 days)	22 ewes (30 days)	24 ewes (30 days)
December	83 ewes (5 days) 3 rams (5 days)	83 ewes (13 days) 3 rams (13 days)	83 ewes (10 days) 3 rams (10 days)
Annual Stocking Rate (LU ha^{-1})	**0.0733**	**0.0518**	**0.1029**

1996 - Year 3

Month	Enc. 1 (44.41 ha)	Enc. 2 (40.77 ha)	Enc. 3 (47.46 ha)
January	83 ewes (14 days) 3 rams (14 days)		83 ewes (3 days) 3 rams (3 days)
February	No sheep present	No sheep present	No sheep present
March	37 ewes (26 days)	22 ewes (26 days)	24 ewes (26 days)
April	37 ewes (30 days) 13 hoggs (30 days)	22 ewes (30 days) 8 hoggs (30 days)	24 ewes (30 days) 9 hoggs (30 days)
May	37 ewes (31 days) 13 hoggs (31 days)	22 ewes (31 days) 8 hoggs (31 days)	24 ewes (31 days) 9 hoggs (31 days)
June	37 ewes (30 days) 13 hoggs (30 days) 27 lambs (10 days)	22 ewes (30 days) 8 hoggs (30 days) 16 lambs (10 days)	24 ewes (30 days) 9 hoggs (30 days) 21 lambs (10 days) 16 bullocks (17 days)
July	37 ewes (31 days) 13 hoggs (31 days) 27 lambs (31 days)	22 ewes (31 days) 8 hoggs (31 days) 16 lambs (31 days)	24 ewes (31 days) 9 hoggs (31 days) 21 lambs (31 days) 16 bullocks (31 days)
August	37 ewes (31 days) 13 hoggs (16 days) 27 lambs (16 days)	22 ewes (31 days) 8 hoggs (16 days) 16 lambs (16 days)	24 ewes (31 days) 9 hoggs (16 days) 21 lambs (16 days) 16 bullocks (28 days)
September	37 ewes (30 days)	22 ewes (30 days)	24 ewes (30 days) 16 bullocks (9 days) 12 bullocks (1 day) 4 bullocks (5 days)
October	37 ewes (31 days)	22 ewes (31 days)	24 ewes (31 days)
November	37 ewes (30 days)	22 ewes (30 days)	24 ewes (30 days)
December	37 ewes (2 days)	22 ewes (2 days)	24 ewes (2 days)
Annual Stocking Rate (LU ha^{-1})	**0.0679**	**0.0403**	**0.0914**

1997 - Year 4

Month	Enc. 1 (44.41 ha)	Enc. 2 (40.77 ha)	Enc. 3 (47.46 ha)
January	37 ewes (22 days)	22 ewes (22 days)	24 ewes (22 days)
February	37 ewes (28 days)	22 ewes (28 days)	24 ewes (28 days)
March	37 ewes (31 days) 13 hoggs (14 days)	22 ewes (31 days) 8 hoggs (14 days)	24 ewes (31 days) 9 hoggs (14 days)
April	37 ewes (30 days) 13 hoggs (30 days)	22 ewes (30 days) 8 hoggs (30 days)	24 ewes (30 days) 9 hoggs (30 days)
May	37 ewes (31 days) 13 hoggs (31 days)	22 ewes (31 days) 8 hoggs (31 days)	24 ewes (31 days) 9 hoggs (31 days)
June	37 ewes (30 days) 13 hoggs (30 days) 25 lambs (21 days)	22 ewes (30 days) 8 hoggs (30 days) 20 lambs (21 days)	24 ewes (30 days) 9 hoggs (30 days) 20 lambs (21 days) 14 bullocks (1 day) 13 bullocks (16 days)
July	37 ewes (31 days) 13 hoggs (31 days) 25 lambs (31 days)	22 ewes (31 days) 8 hoggs (31 days) 20 lambs (31 days)	24 ewes (31 days) 9 hoggs (31 days) 20 lambs (31 days) 14 bullocks (6 days) 13 bullocks (9 days) 8 bullocks (1 day)
August	37 ewes (31 days) 13 hoggs (12 days) 25 lambs (12 days)	22 ewes (31 days) 8 hoggs (12 days) 20 lambs (12 days)	24 ewes (31 days) 9 hoggs (12 days) 20 lambs (12 days) 14 bullocks (24 days)
September	37 ewes (30 days)	22 ewes (30 days)	24 ewes (30 days) 14 bullocks (27 days)
October	37 ewes (31 days)	22 ewes (31 days)	24 ewes (31 days)
November	37 ewes (30 days)	22 ewes (30 days)	24 ewes (30 days)
December	37 ewes (2 days) 83 ewes (14 days) 3 rams (14 days)	22 ewes (2 days) 83 ewes (10 days) 3 rams (10 days)	24 ewes (2 days) 83 ewes (5 days) 3 rams (5 days)
Annual Stocking Rate (LU ha^{-1})	**0.0790**	**0.0584**	**0.0899**

1998 - Year 5

Month	Enc. 1 (44.41 ha)	Enc. 2 (40.77 ha)	Enc. 3 (47.46 ha)
January	37 ewes (24 days)	22 ewes (24 days)	83 ewes (7 days) 3 rams (7 days) 24 ewes (24 days)
February	37 ewes (27 days)	22 ewes (27 days)	24 ewes (27 days)
March	37 ewes (31 days)	22 ewes (31 days)	24 ewes (31 days)
April	37 ewes (30 days) 13 hoggs (22 days)	22 ewes (30 days) 8 hoggs (22 days)	24 ewes (30 days) 9 hoggs (22 days)
May	37 ewes (6 days) 36 ewes (13 days) 35 ewes (12 days) 13 hoggs (31 days)	22 ewes (31 days) 8 hoggs (31 days)	24 ewes (31 days) 9 hoggs (31 days)
June	35 ewes (17 days) 13 hoggs (17 days) 37 ewes (13 days) 10 hoggs (13 days) 27 lambs (13 days)	22 ewes (30 days) 8 hoggs (30 days) 25 lambs (13 days)	24 ewes (30 days) 9 hoggs (17 days) 8 hoggs (13 days) 22 lambs (13 days) 15 bullocks (14 days)
July	37 ewes (30 days) 10 hoggs (30 days) 27 lambs (30 days)	22 ewes (30 days) 8 hoggs (30 days) 25 lambs (30 days)	24 ewes (30 days) 8 hoggs (30 days) 22 lambs (30 days) 15 bullocks (31 days)
August	37 ewes (29 days) 10 hoggs (16 days) 27 lambs (16 days)	22 ewes (29 days) 8 hoggs (16 days) 25 lambs (16 days)	24 ewes (29 days) 9 hoggs (16 days) 22 lambs (16 days) 15 bullocks (31 days)
September	37 ewes (30 days)	22 ewes (30 days)	24 ewes (30 days) 15 bullocks (15 days)
October	37 ewes (31 days)	22 ewes (31 days)	24 ewes (31 days)
November	37 ewes (30 days)	22 ewes (30 days)	24 ewes (30 days)
December	83 ewes (17 days) 3 rams (17 days)	83 ewes (10 days) 3 rams (10 days)	83 ewes (4 days) 3 rams (4 days)
Annual Stocking Rate (LU ha^{-1})	**0.0771**	**0.0522**	**0.0991**

Appendix 3.1 - NVC community types mentioned in the text
(from: Rodwell, 1991; 1992)

NVC Code	NVC Name
U4	*Festuca ovina-Agrostis capillaris-Galium saxatile* grassland
U4b	(*Holcus lanatus-Trifolium repens* sub-community)
U4d	(*Luzula multiflora-Rhytidiadelphus loreus* sub-community)
U4e	(*Vaccinium myrtillus-Deschampsia flexuosa* sub-community)
U5	*Nardus stricta-Galium saxatile* grassland
U5b	(*Agrostis canina-Polytrichum commune* sub-community)
U5c	(*Carex panicea-Viola riviniana* sub-community)
U6	*Juncus squarrosus-Festuca ovina* grassland
U6c	(*Vaccinium myrtillus* sub-community)
U7	*Nardus stricta-Carex bigelowii* grass-heath
U7c	(*Alchemilla alpina-Festuca ovina* sub-community)
U10	*Carex bigelowii-Racomitrium lanuginosum* moss-heath
U10a	(*Galium saxatile* sub-community)
U19	*Thelypteris limbosperma-Blechnum spicant* community
U20	*Pteridium aquilinum-Galium saxatile* community
CG10	*Festuca ovina-Agrostis capillaris-Thymus praecox* grassland
CG10b	(*Carex pulicaris-Carex panicea* sub-community)
CG11	*Festuca ovina-Agrostis capillaris-Alchemilla alpina* grass heath
CG11a	(Typical sub-community)
M3	*Eriophorum angustifolium* bog pool community
M4	*Carex rostrata-Sphagnum recurvum* mire
M6	*Carex echinata-Sphagnum recurvum* mire
M6a	(*Carex echinata* sub-community)
M6b	(*Carex nigra-Nardus stricta* sub-community)
M6d	(*Juncus acutiflorus* sub-community)
M10	*Carex dioica-Pinguicula vulgaris* mire
M11	*Carex demissa-Saxifraga aizoides* mire
M11a	(*Thalictrum alpinum-Juncus triglumis* sub-community)
M15	*Scirpus cespitosus-Erica tetralix* wet heath
M17	*Scirpus cespitosus-Eriophorum vaginatum* blanket mire
M17a	(*Drosera rotundifolia-Sphagnum* sub-community)
M17b	(*Cladonia* sub-community)
M19	*Calluna vulgaris-Eriophorum vaginatum* blanket mire
M25	*Molinea caerulea-Potentilla erecta* mire
M32	*Philonotis fontana-Saxifraga stellaris* spring
H12	*Calluna vulgaris-Vaccinium myrtillus* heath
H12c	(*Galium saxatile-Festuca ovina* sub-community)
H18	*Vaccinium myrtillus-Deschampsia flexuosa* heath
H20	*Vaccinium myrtillus-Racomitrium lanuginosum* heath
H22	*Vaccinium myrtillus-Rubus chamaemorus* heath

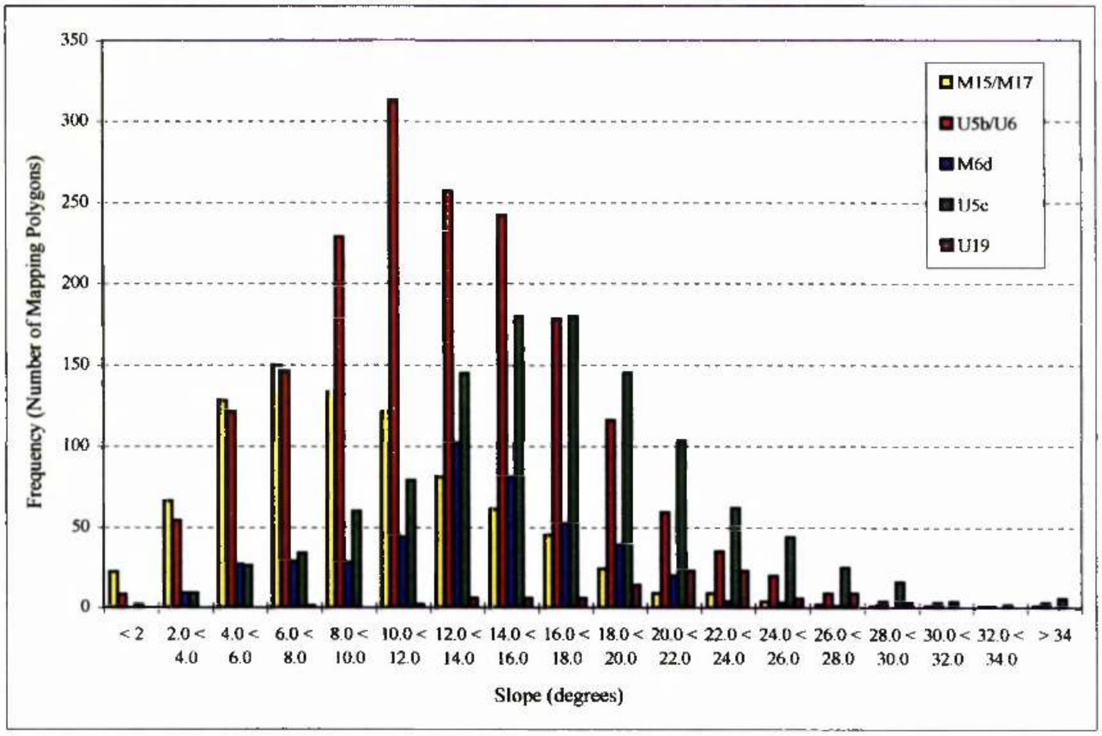
Appendix 3.2 - The number of discrete vegetation patches of each community type, and their mean, median, maximum and minimum areas

NVC Community Type	Number of Discrete Vegetation Patches	Mean Patch Area (m^2) (± 1 S.E.)	Median Patch Area (m^2)	Maximum Patch Area (m^2)	Minimum Patch Area (m^2)
U5b/U6	271	1526.7 (± 518.1)	286.3	133816.0	11.2
M6d	138	920.7 (± 189.8)	286.0	15669.9	35.7
U5c	352	785.8 (± 144.7)	260.9	43267.4	21.1
H20	12	658.0 (± 357.3)	174.6	4373.3	56.1
U19	31	649.6 (± 235.4)	258.0	7072.5	24.8
U10	56	574.3(± 131.1)	231.6	5406.3	20.4
M17	257	553.1 (± 50.5)	290.0	6472.7	0.9
M19	67	478.7 (± 84.8)	261.6	4275.1	39.3
U20	4	461.0 (± 136.7)	486.6	768.1	102.7
CG11	57	402.5 (± 52.5)	262.5	1706.5	44.8
U4	216	390.4 (± 37.6)	225.5	4753.0	15.4
H12	96	383.0 (± 54.5)	182.9	3109.4	15.6
M3	22	340.7 (± 71.9)	219.3	1498.7	62.3
CG10	5	392.9 (± 109.7)	369.8	701.4	35.3
M15	84	294.9 (± 50.6)	163.3	3861.2	16.7
M10	62	273.4 (± 35.0)	149.1	1178.5	29.2
M25	33	272.2 (± 38.9)	209.0	1092.4	16.3
M4	43	259.2 (± 36.3)	182.6	1141.8	28.1
M11	105	247.3 (± 32.8)	169.3	3223.7	41.9
M6b	114	241.2 (± 23.3)	171.0	1440.1	39.6
H22	1	204.6 (NA)	204.6	204.6	204.6
U7	21	177.2 (± 22.5)	160.7	381.0	42.9

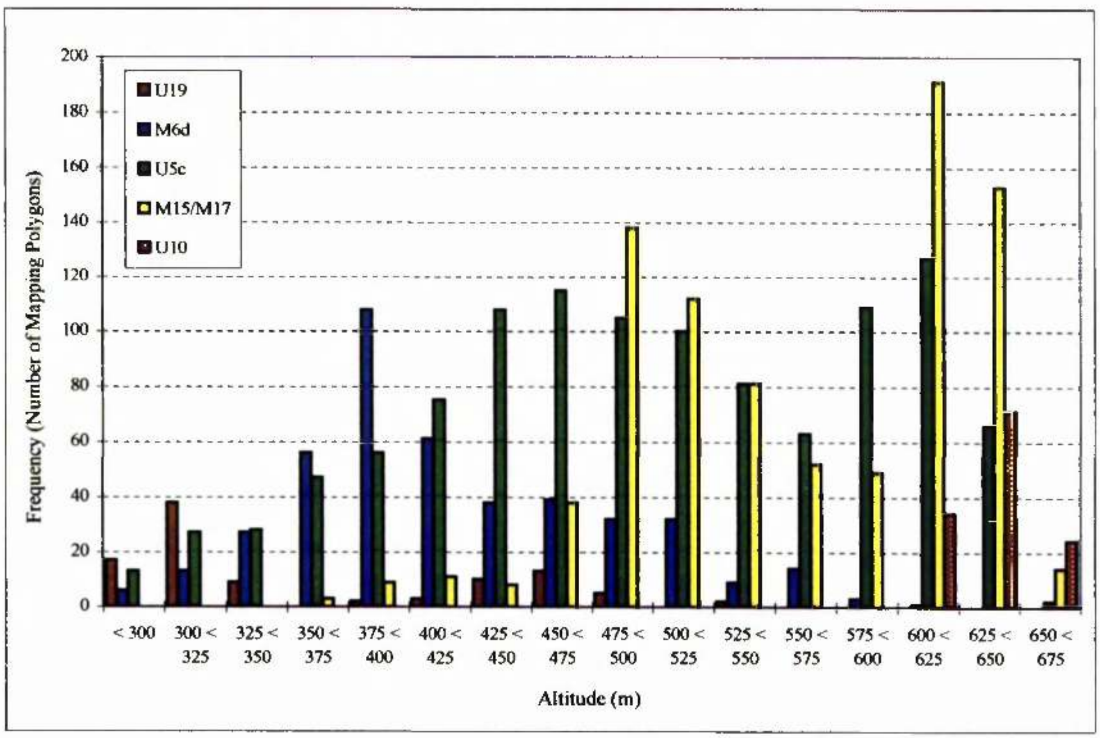
Appendix 3.3 - Mean altitude and mean slope angle of each NVC community type.

The communities are arranged in order of mean altitude (from highest to lowest) and have been colour coded according to their mean slope angle (Green = <6°, Blue = 6-12°, Red = 12-18°, Black = >18°)

NVC Community Type	Mean Altitude (metres above mean sea-level)				Mean Slope (degrees)
	Plot 1	Plot 2	Plot 3	All Plots (± 1 S.E.)	All Plots (± 1 S.E.)
H20	652.4	633.9	631.1	638.5 (± 3.07)	11.1 (± 1.69)
U10	664.1	634.3	623.9	635.0 (± 1.52)	12.2 (± 0.70)
H22		633.4		633.4 (NA)	4.1 (NA)
U7		633.8	613.4	620.5 (± 5.86)	13.6 (± 1.32)
H12	652.6	613.9	607.9	612.1 (± 2.83)	9.1 (± 0.38)
M19	627.5	622.8	602.9	610.1 (± 2.72)	7.9 (± 0.41)
M3	633.9	610.1	565.9	608.2 (± 7.52)	6.4 (± 0.88)
M4	624.9	574.0	571.0	579.2 (± 7.64)	7.3 (± 0.86)
M17	621.5	559.8	557.4	565.4 (± 2.31)	9.3 (± 0.18)
U5b/U6	585.6	569.1	546.1	562.7 (± 1.48)	12.6 (± 0.12)
M6b	542.1	560.6	514.9	545.1 (± 4.90)	10.1 (± 0.38)
M15	585.6	492.1	530.3	521.0 (± 6.03)	11.8 (± 0.48)
CG11	505.5	512.9	545.5	517.6 (± 5.54)	19.8 (± 0.69)
M10	547.1	550.0	444.1	508.5 (± 10.75)	13.8 (± 0.57)
U5c	503.2	526.9	481.4	497.9 (± 2.68)	16.47 (± 0.16)
U4	466.3	520.9	457.5	477.5 (± 4.20)	13.77 (± 0.23)
CG10	515.2	438.4	466.0	472.2 (± 19.17)	20.3 (± 1.17)
M11	535.9	519.8	427.3	463.1 (± 8.57)	14.4 (± 0.43)
M25	510.1	440.4	422.2	444.6 (± 12.77)	11.8 (± 0.64)
M6d	421.4	449.8	397.8	418.7 (± 3.01)	13.4 (± 0.21)
U19	460.6	431.5	309.2	361.9 (± 7.37)	20.8 (± 0.43)
U20			334.7	334.7 (± 2.43)	18.7 (± 0.99)



Appendix 3.4 - Histogram showing the relationship between slope angle and NVC type



Appendix 3.5 - Histogram showing the relationship between altitude and NVC type

Appendix 3.6 - The distribution of vegetation types within the study site

The study site was composed of a mosaic of grassland, mire and montane heath communities, containing a rich diversity of species. The variation in altitude, topography, soil type and hydrology within the site, and its long history of grazing management and anthropogenic influences, has led to this diversity.

The poorly-drained land within topographical Zone 2 was dominated by M6d *Carex echinata - Sphagnum recurvum* (*Juncus acutiflorus*) mire (Figure A3.1). This *Juncus acutiflorus* dominated community also formed wide flushes that extended up slope from this area into the U5c *Nardus stricta - Galium saxatile* (*Carex panicea - Viola riviniana*) grassland, which dominated the steeper more freely drained slope within topographical Zone 3 (Figure A3.2). The fern dominated U19 *Thelypteris limbosperma - Blechnum spicant* community was restricted to steep slopes along streamsides within topographical Zone 3 and on the steep banking at the base of Enclosure 3 (topographical Zone 1).

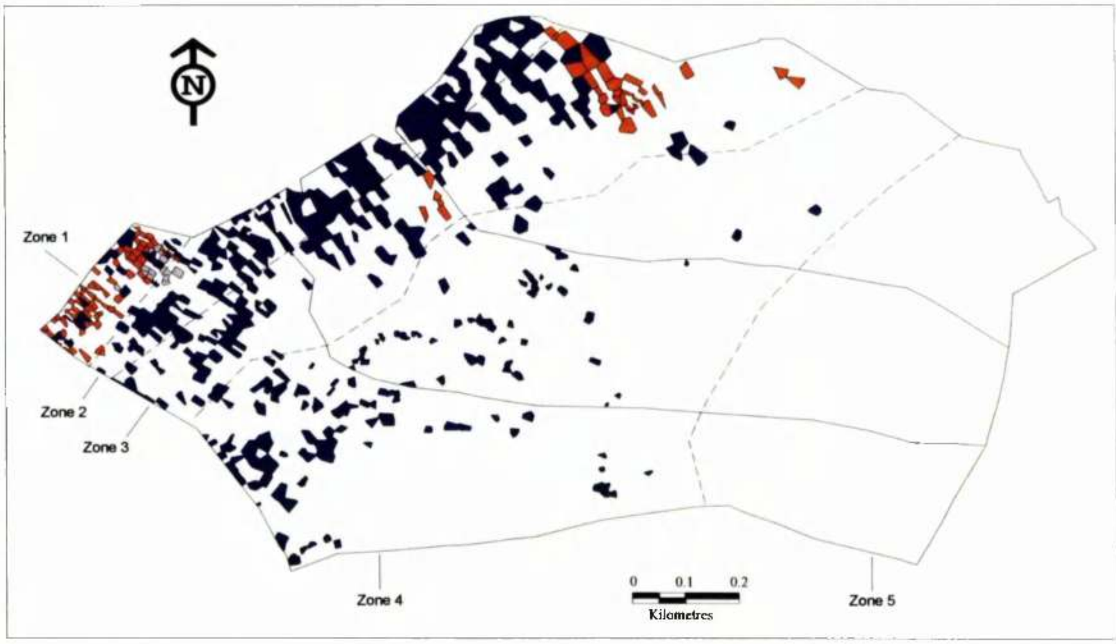


Figure A3.1 - Fern dominated communities - **U19** (fawn) and **U20** (grey), and *Juncus acutiflorus* dominated mire - **M6d** (blue)

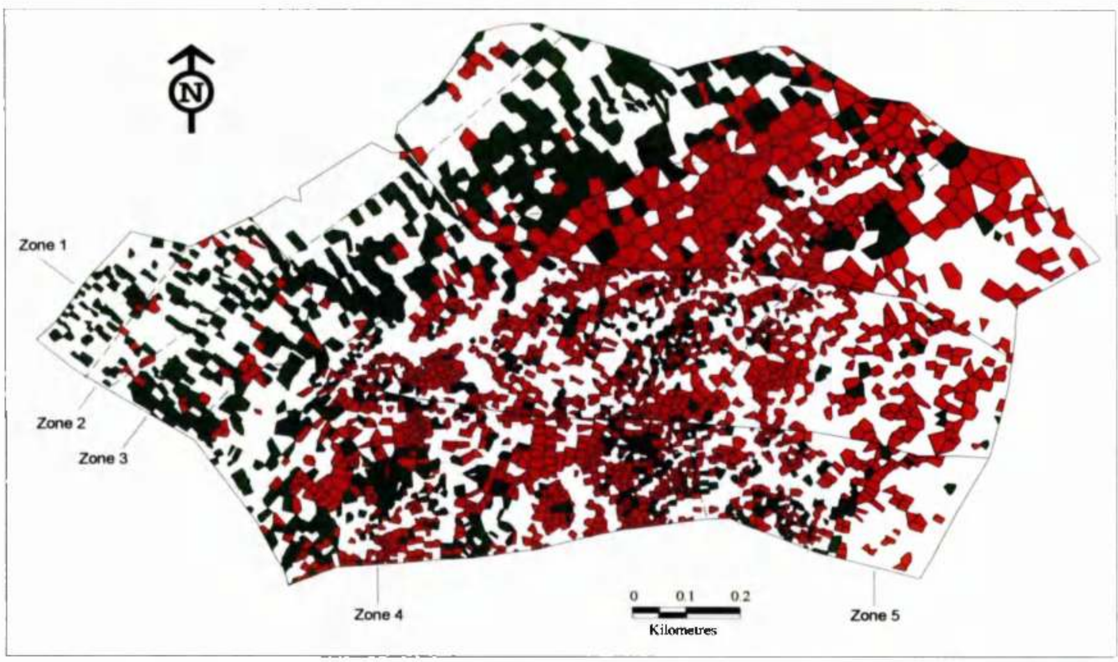


Figure A3.2 - *Nardus stricta* dominated grasslands - **U5c** (green) and **U5b/U6** (red)

The vegetation in topographical Zone 4 was a complex patchwork of mire, flush and grassland communities dominated by *Juncus squarrosus* rich U5b *Nardus stricta - Galium saxatile* (*Agrostis canina - Polytrichum commune*) grassland. There were also a few patches of U6 *Juncus squarrosus - Festuca ovina* grassland. This U6 community graded into the U5b grassland in such a way as to make it difficult to define boundaries between the two types, and therefore the two communities were mapped as a mosaic (Figure A3.2). Species such as *Thalictrum* alpinum, *Persicaria vivipara*, and *Linum catharticum*, which are more typical of montane calcareous grasslands, were present within both the U5c and U5b grasslands, where surface flushing with base rich water occurred.

On many of the free-draining knolls that occur within topographical Zones 3 and 4, patches of U4d *Festuca ovina - Agrostis capillaris - Galium saxatile* (*Luzula multiflora - Rhytidiadelphus loreus*) and U4b *Festuca ovina - Agrostis capillaris - Galium saxatile* (*Holcus lanatus - Trifolium repens*) grassland have developed. These knolls were often used as 'camp sites' by the sheep, leading to high levels of nutrient input in the form of dung and urine. On some of the knolls and within the few areas of stable boulder scree, small patches of CG11 *Festuca ovina - Agrostis capillaris - Alchemilla alpina* grass-heath were present. Scattered across the slope were a number of M11 *Carex demissa - Saxifraga aizoides* and M10 *Carex dioica - Pinguicula vulgaris* flushes. Sometimes associated with these flushed areas were small patches of moderately base-rich CG10b *Festuca ovina - Agrostis capillaris - Thymus praecox* (*Carex pulicaris - Carex panicea*) grassland or CG11 *Festuca ovina - Agrostis capillaris - Alchemilla alpina* grass-heath (Figure A3.3).

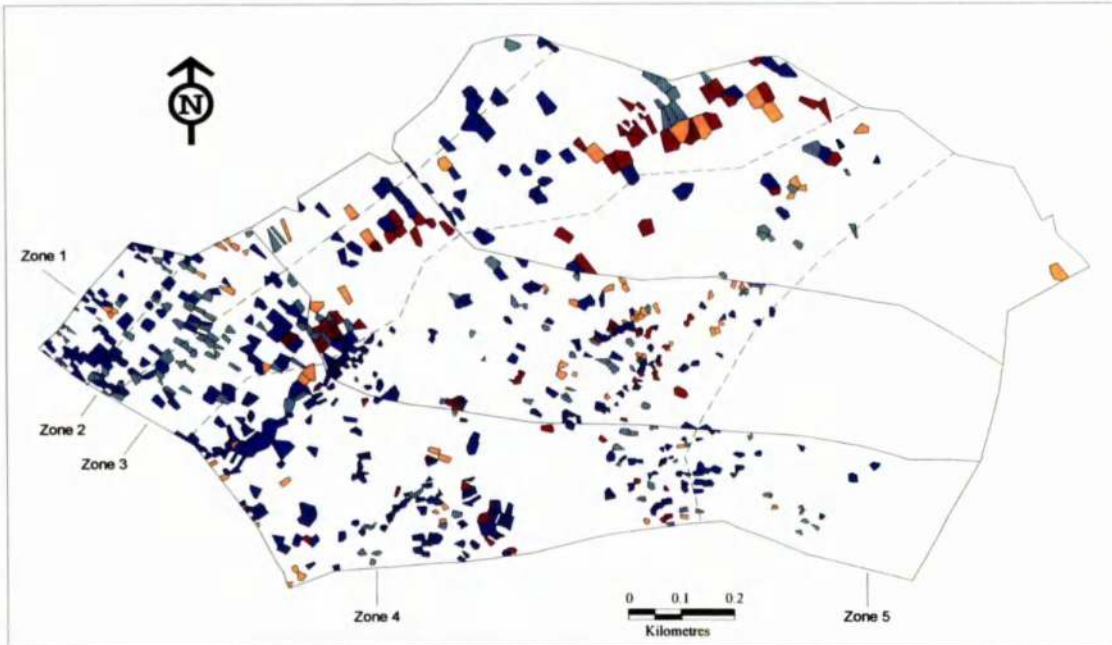


Figure A3.3 - Calcifugous and calcicolous *Festuca ovina* - *Agrostis capillaris* grasslands - **U4** (blue), **CG10** (brown) and **CG11** (mauve), and calcicolous flushes - **M10** (orange) and **M11** (blue and white hatching)

Where more acidic water flowed down the slope and in the peat filled hollows within Zone 4, patches of M17 *Scirpus cespitosus* - *Eriophorum vaginatum* blanket mire and M15 *Scirpus cespitosus* - *Erica tetralix* wet heath were present (Figure A3.4). The decision during the mapping exercise as to which of the two community types the vegetation should be allocated depended mainly upon the estimated depth of the peat substrate rather than on any major floristic differences, although *Eriophorum vaginatum* was absent from the vegetation described as M15. Two of the 'constant' species for both of the communities, *Calluna vulgaris* and *Erica tetralix*, were rather patchily distributed and were often absent from the vegetation. Even when present they tended to be heavily grazed, rarely exceeding 10 cm in height, and had low cover values. The scarcity and lack of structural importance of these two species was probably the result of past grazing management.

Within topographical Zone 5 the moist, peat filled hollows irrigated by mainly base-poor oligotrophic water contained a mosaic of mire communities (Figure A3.4). M4 *Carex rostrata - Sphagnum recurvum* mire occurred in the wettest parts of the hollows, often surrounded by M6b *Carex echinata - Sphagnum recurvum* (*Carex nigra - Nardus stricta*) mire. Large patches of M17 *Scirpus cespitosus - Eriophorum vaginatum* blanket mire were present in the better-drained areas of peat. Within the peatlands there were peat erosion features and areas of bare peat, often with pools of standing water and scattered patches of M3 *Eriophorum angustifolium* bog pool community.

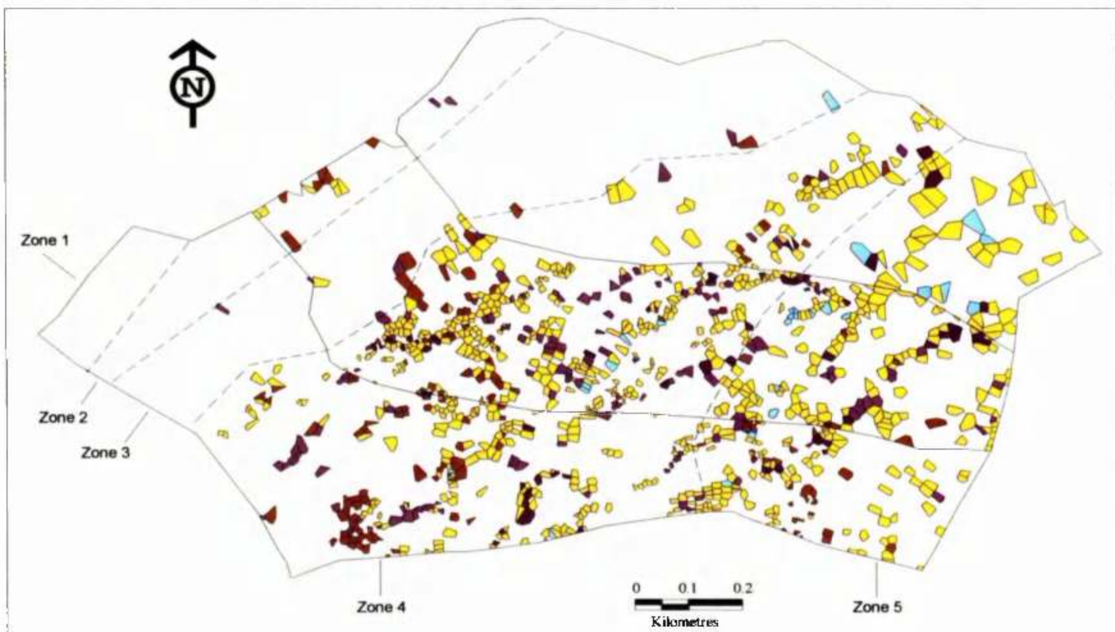


Figure A3.4 - *Trichophorum cespitosum* and *Carex* dominated mires - **M15** (yellow and brown hatching), **M17** (yellow), **M3** (pale blue), **M4** (purple) and **M6b** (purple and white hatching)

On the ridges between the peat hollows, the vegetation changed from a U6 *Juncus squarrosus - Festuca ovina* grassland at the base of the ridge, through a narrow band of U5c or U7c *Nardus stricta - Carex bigelowii* (*Alchemilla alpina - Festuca ovina*) grass-heath, to a very low growing U10a *Carex bigelowii - Racomitrium lanuginosum* (*Galium saxatile*) moss-heath community or a H20 *Vaccinium myrtillus - Racomitrium lanuginosum* heath, on the exposed summits (Figure A3.5).

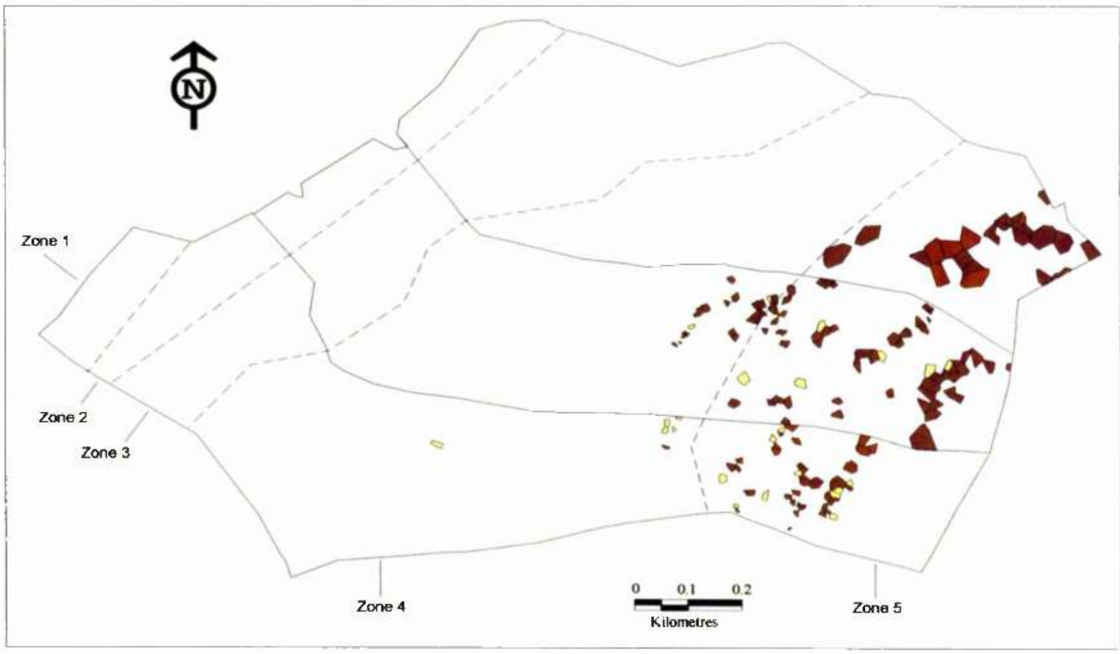


Figure A3.5 - Montane communities - **U7** (pale yellow), **U10** (brown and white hatching) and **H20** (brown)

On shallow peat mainly above 600 m, particularly within Enclosure 3, there were patches of H12c *Calluna vulgaris - Vaccinium myrtillus* (*Galium saxatile - Festuca ovina*) heath, which graded into an M19 *Calluna vulgaris - Eriophorum vaginatum* blanket mire where the peat depth and moisture content increased (Figure A3.6). *Rubus* *chamaemorus* and *Vaccinium uliginosum* were restricted to this M19 peatland community above 630 m.

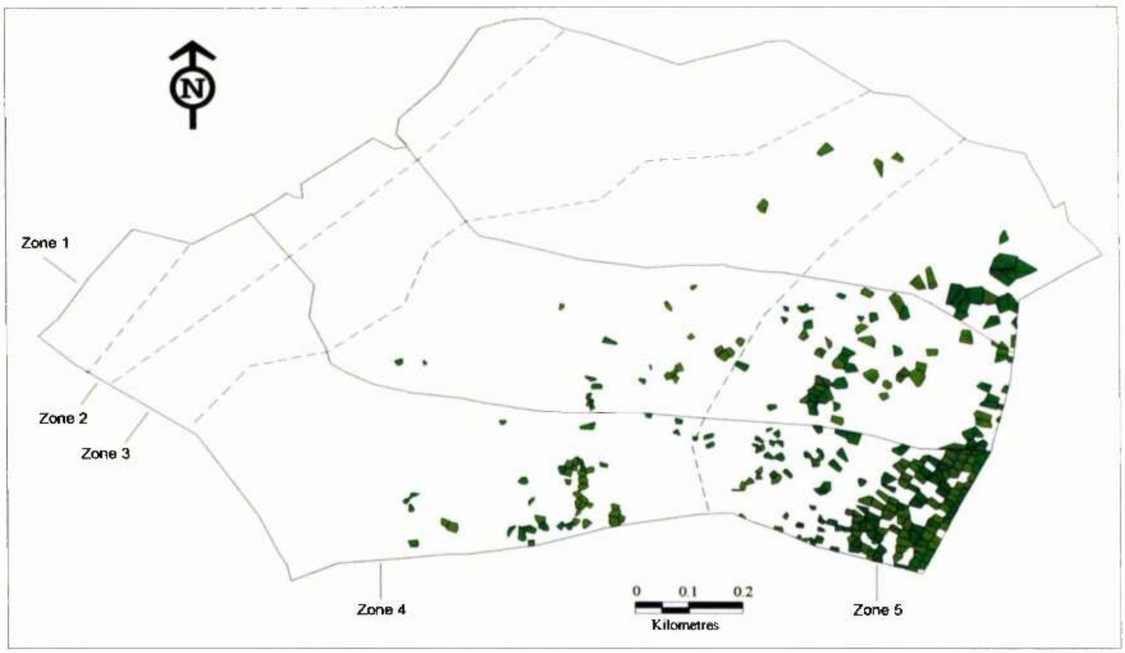


Figure A3.6 - *Calluna vulgaris* dominated heath and mire - **H12** (green) and **M19** (yellow and green hatching)

Appendix 4.1 - Nested Quadrat Data
U5c Sample stands
Baseline survey - 01/09/1994
Enclosure 1

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Agrostis capillaris	2	1	2	1	3	2	1	2	2	1	2	1	2	1	3	1	1	2	1	1	2	1	2	1	2	2	2	2	2	2	6	3
Alchemilla alpina																																
Alchemilla glabra					10													10	10											5	10	
Anemone nemorosa				9	10			9		9								9				8				2			8			
Anthoxanthum odoratum	5	2	3	5	2	1	2	3	2	3	1	2	2	2	2	7	3	2	3	5	3	4	2	3	2	2	4	4	3	3	2	2
Blechnum spicant																																
Campanula rotundifolia	9																10	5			9										3	5
Carex binervis	4	7	1	6		9	7	8	8	10	8	7	3	3	4	5	2	6	4	3	5	5			10	10	3	6	5	3	3	2
Carex echinata																																
Carex hostiana																																
Carex nigra		5					6						2	5	7	2	9	8	2	4								8	3		6	9
Carex pallescens														10					7									10	7	9		
Carex panicea	5	3	3	6	3			7	9			3	2	4	4	4	5	2	5	2	2	5					8	1	2	1	2	2
Carex pilulifera	7	7		4	7	2	3	10	1	8	2	7	10			3	6		9	9	2	2	2	5	8	10	1	9	7	10		10
Carex pulicaris	9	8	10	10	10	3	3						7	4	7	8	9	7	4	2										4	5	8
Carex viridula ssp. oedocarpa													1							7	5								9		9	6
Cerastium fontanum									9	10				6									9		10							
Crepis paludosa																																
Danthonia decumbens																																
Deschampsia cespitosa	10	9	9	2	10	9	5	5		5	10	8	10	9			8			7	10	2	9	5				7	3	7		5
Deschampsia flexuosa																								9								
Eriophorum angustifolium																																
Euphrasia officinalis agg.																		8	9												4	8
Festuca ovina/vivipara	6	3	2	6	2	2	2	6	2	2	2	5	2	2	4	2	2	1	7	3	5	2	3	2	1	2	3	2	3	2	4	1
Festuca rubra	10		6				7	9	9	8	10		8	7	10	8	6	7	6		3	7	7		5							
Galium saxatile	5	2	4	2	2	2	2	4	3	2	2	8	10	7	3	2	2	3	4	8	6	5	2	2	2	2	7	2	6	9		9
Juncus bulbosus																																
Juncus effusus																																
Juncus squarrosus																			10										8	6	8	10
Leontodon autumnalis																				10									10	8		
Luzula multiflora						9	7	5	8						10		7	9	9		8	10	2	6	3	10	10	8	6	10	10	
Molinia caerulea																																
Nardus stricta	1	3	3	3	1	3	3	1	6	5	3	3	3	4	1	4	2	3	2	2	1	2	1	7	8	5	3	4	1	2	1	5
Narthecium ossifragum																																
Oreopteris limbosperma																																
Oxalis acetosella			4																					7	7	5						
Pinguicula vulgaris																		10													5	10
Plantago lanceolata														10		10	10	8	9	6											10	5
Persicaria vivipara			10	7		6								7	10	5	10	8	3	10							6		6	9	5	10
Potentilla erecta	6	6	10	5	6	7	7	9	10	7	7	3	9	9	5	5	6	6	8	8	4	3	3		8	6	4	5	9	5	7	6
Prunella vulgaris																																9
Ranunculus acris	6	4	9	7	10				7	10		6	3	7	7	2	6	5	4	5			10	8					6	5	4	5
Rumex acetosa																							10			7						
Selaginella selaginoides																		8	10												10	
Sorbus aucuparia																																
Taraxacum agg.																																
Thymus polytrichus																																
Trichophorum cespitosum																	10	9	10	10									2	10		
Vaccinium myrtillus																											10	9				
Veronica officinalis																																
Viola palustris	10							8																								
Viola riviniana	9	6	2	4	2	2	7	9	9	5	4	2	2	2	3	6	4	3	2	6	2	2	4	2	3	9	2	3	6	7		5
Bryophytes (excluding *Sphagnum*)	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2
Sphagnum spp																																
Lichens (*Cladonia* spp.)																											10					
Bare Rock			8																								10					
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
U5c Sample stands
Second survey - 16/06/1998
Enclosure 1

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Agrostis capillaris	1	2	4	2	1	1	2	2	1	1	1	2	1	4	5	2	2	4	2	3	2	2	1	1	1	2	2	2	1	2	2	1
Alchemilla alpina																																3
Alchemilla glabra												6						10	10											7	8	
Anemone nemorosa	2	3	2	2	2	2	3	2	2	7	4	2	5	4	3	2	9	5	5	2	4	5	5	3	6	3	4	2	4	2	2	4
Anthoxanthum odoratum	6	1	4	4	5	4	2	2	2	5	2	4	7	2	2	4	1	2	8	4	4	2	2	2	2	2	2	2	2	2	3	4
Blechnum spicant																																
Campanula rotundifolia	8														10		9	7												5	3	6
Carex binervis	5	7	3	8		8	4	4	6	10	8	8	5	3	6	2	5	4	5	5	2	3			10	9	7	2	5	5	6	4
Carex echinata																																
Carex hostiana																																
Carex nigra	10	3	5	10			9	7		4			2	1	8		9	2	1	2								4	5	2	1	10
Carex pallescens																	9		8									10	7			
Carex panicea	2	5	4	5	9		10	4			10	2	2	6	4	3	5	8	3	1	6	7					9	5	6	2	4	2
Carex pilulifera	9	2	4	5	4	2	1	6	2	2	3	3	5				2			8	8	8	2	4	6	8	2	7	2			9
Carex pulicaris	9	7	5	10									5	3	4	6	8	2	7	5									10	3	8	4
Carex viridula ssp. *oedocarpa*																				6	5								8	9	9	9
Cerastium fontanum														8					7					10	2	10						
Crepis paludosa																																
Danthonia decumbens																																
Deschampsia cespitosa	8	8	8	9	8	6	7	5		5		7	9	8	5	10	6	7	10	6		6	8	6				7	6	6	9	2
Deschampsia flexuosa																																
Eriophorum angustifolium																																
Euphrasia officinalis agg.																															10	9
Festuca ovina/vivipara	5	2	6	4	2	2	2	2	2	4	2	6	4	2	4	3	2	5	7	5	5	3	3	2	2	2	4	1	2	2	2	2
Festuca rubra		9	4	9	2	4		4	9	3	10		2	10	5	10	4	2	6				7			2						
Galium saxatile	2	2	2	4	2	2	2	2	2	2	2	9	7	7	4	10	2	2	6	7	3	2	2	2	2	2	5	2	2	10		3
Juncus bulbosus																																
Juncus effusus																																
Juncus squarrosus																													8	8	8	10
Leontodon autumnalis				10								8																	10	8		
Luzula multiflora		7		6	5	6	3	2	6	8	9	8				10	3	2	9	8	7	9	2	5	2	8	8	10	5		10	
Molinia caerulea																																
Nardus stricta	3	5	5	2	3	5	5	1	6	6	5	1	4	3	1	1	5	1	6	5	1	1	2	7	8	4	1	3	7	1	2	5
Narthecium ossifragum																															2	10
Oreopteris limbosperma																																
Oxalis acetosella		7																						10	8	4						
Pinguicula vulgaris																																
Plantago lanceolata														10	6		9		9													10
Persicaria vivipara			10			6							10	8	6	8	9	10	5	10							8		3	10	7	2
Potentilla erecta	7	9	8	3	5	6	5	9		7	7	5				6	7	6	9	9	5	2	2		7	10	2	6	9	5	6	7
Prunella vulgaris																																
Ranunculus acris	6	7	6	9	9				10			2	2	5	2	6	2	6	3	5	6			8					2	7	4	3
Rumex acetosa																							9			8	8					
Selaginella selaginoides																		8													9	4
Sorbus aucuparia																																
Taraxacum agg.																																
Thymus polytrichus																																9
Trichophorum cespitosum																		9		10									2	10		
Vaccinium myrtillus																											10	9				
Veronica officinalis																																9
Viola palustris	10	6	2	1	4	3	8	9	3	4	2	7	4	3	7	8	8		7	4	6	2	2	2	3	8	4	7	4	8		2
Viola riviniana	9	7	5	4	10							2		7	5	2	5	2	2	8	3										6	8
Bryophytes (excluding *Sphagnum*)	2	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2
Sphagnum spp.																																
Lichens (*Cladonia* spp.)																																
Bare Rock																											10					
Bare Soil	7		7									9							10	2	5											

Appendix 4.1 - Nested Quadrat Data
U5c Sample stands
Baseline survey - 13/09/1994
Enclosure 2

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Agrostis capillaris	3	1	2	5	2	2	3	2	2	2	2	5	6	1	3	2	3	2	3	3	7	2	2	2	1	2	2	1	6	8	9	9
Alchemilla alpina																																
Alchemilla glabra																																
Anemone nemorosa																																
Anthoxanthum odoratum	3	2	6	1	2	6	5	10	8	8	3	7	2	4	1	4	7	2	6	5	8	6	6	7	3	3	2	3	8	7	2	2
Blechnum spicant						9																										
Campanula rotundifolia																																
Carex binervis		8	2	2	4	8	8	7	2	6	4	1	3	2	6	10	7	10	6	9	6	8	6	6	7	5	7	3	2	6	7	
Carex echinata	2		7									10	10				3	3		1	1									9	10	9
Carex hostiana																		9														
Carex nigra	9	4	5	7	3						10	5	2	5	9					7	4	9			10	9	10	2	8		10	2
Carex pallescens																																
Carex panicea	2	2	5	8				8	10			10	1	2	6	2	5	3	1	8	2		10	8	6	10		6	5	3	3	3
Carex pilulifera					2	7	7	2	1	5	6	10				5		9			7	8	3	2	4	2	7	9	7			
Carex pulicaris																	10														9	10
Carex viridula ssp. *oedocarpa*																															2	10
Cerastium fontanum																																
Crepis paludosa																																
Danthonia decumbens																																
Deschampsia cespitosa																																
Deschampsia flexuosa																																
Eriophorum angustifolium	7	10	5												9	6	2	9											9		7	2
Euphrasia officinalis agg.																		10														
Festuca ovina/vivipara	2	4	3	7	2	8	2	2	2	2	1	4	3	2	2	2	2	4	5	3	8	6	2	1	2	3	5	2	1	2	2	7
Festuca rubra																																
Galium saxatile	3	9	2	3	2	1	2	5	2	2	2	2	7	3	4	2	2	8	3	7	7	2	2	2	2	2	2	3	5	10		
Juncus bulbosus																	9															10
Juncus effusus												10	10							10	2											
Juncus squarrosus	7	6	6			7		4		8					7	6	7	10	2									8		8	3	6
Leontodon autumnalis			9											8			10	6	6										5	10	3	7
Luzula multiflora							5		10												7		10	10	10	9			10	10		
Molinia caerulea	10	10													3	8	1	8	2											2	8	
Nardus stricta	2	2	1	3	4	4	1	4	4	2	2	3	2	3	3	1	2	1	2	3	2	1	1	2	4	1	1	5	2	1	2	4
Narthecium ossifragum						6	6	4	2	7					6	10	10	2	2	8									2	2	2	2
Oreopteris limbosperma																										8						
Oxalis acetosella																																
Pinguicula vulgaris																																
Plantago lanceolata																																8
Persicaria vivipara																																
Potentilla erecta	1	2	3	3	7	7	4	5	2	2	7	7	7	4	3	4	6	4	3	2	8	8	2	3	4	3	5	8	5	6	2	1
Prunella vulgaris																															6	
Ranunculus acris												10	10							8									6	10	10	
Rumex acetosa																																
Selaginella selaginoides																	10	7	6											10	8	
Sorbus aucuparia																																
Taraxacum agg.																																
Thymus polytrichus																																
Trichophorum cespitosum	8				9	6	6	5	4	1	9				9	8	8	5	8				8						8	2	1	3
Vaccinium myrtillus					8	7	2	1	6	8	2	6										8	3	7	2	4	10					
Veronica officinalis																																
Viola palustris	5	3*	2	2	10							2	6	3	3	4	3	6	2	2	2	10					10		10	5	2	7
Viola riviniana																																
Bryophytes (excluding *Sphagnum*)	2	2	2	2	1	2	2	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Sphagnum spp.	5	4	9	4									7		9	2	10	7	2	6									6	2	10	2
Lichens (*Cladonia* spp.)							9	10	8															10	10							
Bare Rock							9	10	8															10	10	10						
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
U5c Sample stands
Second survey - 17/06/1998
Enclosure 2

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Agrostis capillaris	6	4	1	1	2	4	1	1	2	2	2	6	2	1	2	2	2	3	2	5	3	3	2	1	2	2	2	1	2	2	3	5
Alchemilla alpina																																
Alchemilla glabra																																
Anemone nemorosa																																
Anthoxanthum odoratum	2	2	7	5	6	6	6	9	5	7	6	4	3	2	5	6	9	2	5	7	2	6	3	4	2	5	4	2	7	8	6	8
Blechnum spicant						9																										
Campanula rotundifolia																																
Carex binervis		8	4	5	5	8	8	6	2	6	1	10	2	8	6	9	6	10	5		5	6	5	5	6	5	2	2	6	8	7	
Carex echinata	6	10	6															3			2											3
Carex hostiana																																
Carex nigra	8	1	3	5							6	1	4	2	10	4	4	10	2	5	1	2			10	9	2	3	10	5	10	4
Carex pallescens																																
Carex panicea	2	2	9	4					1			4	1	4	3	6	6	2	9	4	2		5	8	3			4	6	5	6	2
Carex pilulifera				2	2	6	2	2	2	7	2	10			8							7	1	2	2	4	7	10	3	10		
Carex pulicaris																	10	2											6	5	7	8
Carex viridula ssp. *oedocarpa*													10																		3	
Cerastium fontanum																																
Crepis paludosa																															7	7
Danthonia decumbens																																
Deschampsia cespitosa																																
Deschampsia flexuosa												8																				
Eriophorum angustifolium	7		10	9											10	9	8	9											10	9	10	1
Euphrasia officinalis agg.																																
Festuca ovina/vivipara	2	8	5	2	3	5	2	5	4	2	2	4	2	4	2	1	2	5	2	3	6	2	2	2	2	2	2	7	2	2	1	5
Festuca rubra																																
Galium saxatile	5	3	4	2	2	4	2	2	6	2	2	2	7	2	8	8	7		7	2	4	5	2	2	1	2	2	2	3	9	10	8
Juncus bulbosus																																
Juncus effusus													10							10	2											
Juncus squarrosus	8	2	7			6		4		8					6	3	5	10	4									8		9	4	8
Leontodon autumnalis			10										7	7			10	7	8	7								7	6	8	6	8
Luzula multiflora	9		10						7				7	10	10	8				10	6		10	8	8	9		7	7	10	10	10
Molinia caerulea	10	10													1	7	2	4	10											2	2	10
Nardus stricta	1	2	6	3	1	6	5	5	3	4	4	1	3	1	2	4	1	1	1	2	2	1	6	5	5	1	1	6	1	2	2	2
Narthecium ossifragum		10				4	10	4		4	9				2	10	8	2	2	7									2	2	2	3
Oreopteris limbosperma																							10									
Oxalis acetosella																																
Pinguicula vulgaris																			10													10
Plantago lanceolata																																8
Persicaria vivipara																																
Potentilla erecta	4	2	2	2	7	6	6	5	6	2	7	10	5	4	4	2	4	2	2	5	6	7	3	2	5	3	4	8	5	3	2	2
Prunella vulgaris																																
Ranunculus acris												10	7	10						7									6	9	10	10
Rumex acetosa																																
Selaginella selaginoides																														5		9
Sorbus aucuparia																								10								
Taraxacum agg.																																
Thymus polytrichus																																
Trichophorum cespitosum	8				9	3	6	3	3	1	8				8	2	7	8	7	10									7	1	2	2
Vaccinium myrtillus					6	7	4	6	4	8	6	9										9	6	8	6	2	9					
Veronica officinalis																																
Viola palustris	6	3	2	4								2	7	6	2	6	5	3	4	6	2	6					10	7	8	5	2	6
Viola riviniana																																
Bryophytes (excluding *Sphagnum*)	2	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	2	2
Sphagnum spp.	9	5	9										5	4	8	4	8	5	2	7									2	4	3	2
Lichens (*Cladonia* spp.)							9																									
Bare Rock						9	9	9	9															10	10	10						
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
U5c Sample stands
Baseline survey - 30/08/1994
Enclosure 3

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Agrostis capillaris	3	2	2	2	4	2	2	2	2	2	3	1	2	2	3	2	4	2	2	2	2	2	2	2	1	2	3	2	1	2	2	2
Alchemilla alpina																																
Alchemilla glabra																																
Anemone nemorosa	3			2																												
Anthoxanthum odoratum	4	8	3	7	2	2	7	2	8	8	5	5	8	6	7	4	5	8	10		10	6	5	3	8	8	2	9		10	4	8
Blechnum spicant																																10
Campanula rotundifolia																																
Carex binervis								10					10					8	8		6					8		9	10			7
Carex echinata																																
Carex hostiana																																
Carex nigra	5	2	7	2	1	4				3	6	2	7	6	6	2	8	6	2	9	3	9			6					8	2	9
Carex pallescens																																
Carex panicea	9	4	4	4	2	6	10	9	3	6	9	5	2	1	6	7	5	5	4	7	7	2	8	6	7	7	4	8	6	4	4	5
Carex pilulifera	4	2	2	2	2	2	2	1	2	2	3	2	2	9	9	1	7	2	7	2	1	4	3	4	6	1	4	6	5	5	1	4
Carex pulicaris																																
Carex viridula ssp. *oedocarpa*																																
Cerastium fontanum																																
Crepis paludosa																																
Danthonia decumbens				10			10	2		8	9		9		7	10	9	10		8	8	4	10	9	9	4	8	5	9		10	
Deschampsia cespitosa																																
Deschampsia flexuosa	10	10			9	8	10	9		9	8	9			1	10	1	10	8			8	10	6	8	7	9	6			5	10
Eriophorum angustifolium																																
Euphrasia officinalis agg.																																
Festuca ovina/vivipara	4	2	2	1	2	1	2	2	2	2	2	2	1	2	6	3	8	1	6	1	2	1	2	1	2	2	2	3	3	2	4	9
Festuca rubra																																
Galium saxatile	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	2	2	2	3	3
Juncus bulbosus																																
Juncus effusus																																
Juncus squarrosus								9	10	10	10											10	5		7	7			10			
Leontodon autumnalis																																
Luzula multiflora	6	10	8	9	8	4	2	6	6	5	4	8	2	2	10	5	10	2	6	8	6	7	8	6	7	10	7	5	5	9	4	9
Molinia caerulea																														10		
Nardus stricta	1	2	2	5	5	2	2	4	1	4	2	3	3	3	3	4	2	3	1	3	2	3	4	5	2	3	5	1	4	1	5	1
Narthecium ossifragum								10	10	8	6	10									9	2	1	10	2	3	1	10				
Oreopteris limbosperma																																
Oxalis acetosella																																
Pinguicula vulgaris																																
Plantago lanceolata																																
Persicaria vivipara																																
Potentilla erecta	6	6	4	2	3	4	1	2	3	1	4	2	2	5	7	6	2	3	4	3	2	5	2	2	7	4	7	7	4	6	2	3
Prunella vulgaris																																
Ranunculus acris																																
Rumex acetosa																																
Selaginella selaginoides																																
Sorbus aucuparia														10			9															
Taraxacum agg.																																
Thymus polytrichus																																
Trichophorum cespitosum			10		10	8	2	3	8	2	1	9	6	7	10				10	6	8	6	4	2	3	5	6	7	8	9		
Vaccinium myrtillus			4	5	10	8				9	5	3	8							8	5	3				10	2	2	10		7	10
Veronica officinalis																																
Viola palustris								10																								
Viola riviniana																																
Bryophytes (excluding *Sphagnum*)	2	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Sphagnum spp.																																
Lichens (*Cladonia* spp.)													9	10	9	9			9	7	10	8		8			9	4	7	10	9	5
Bare Rock				7		9			10				9	10	9	9	10		9	10	10	8	10	8					7	10	9	8
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
U5c Sample stands
Second survey - 09/07/1998
Enclosure 3

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Agrostis capillaris	2	2	2	2	1	2	2	2	2	2	2	2	3	1	2	5	1	3	2	2	1	2	1	1	3	2	2	3	2	2	2	2
Alchemilla alpina																																
Alchemilla glabra																																
Anemone nemorosa	2		10	5									7																			
Anthoxanthum odoratum	10	2	2	9	8	5	7	10	7	10	10	10	8	5	6	3	5	9	5			5	7	7	8	2	2				5	8
Blechnum spicant																			9													10
Campanula rotundifolia																																
Carex binervis								10	9		10	10	10					7	8		5							9	8			6
Carex echinata																																
Carex hostiana																																
Carex nigra	10		9	2	2	3						2	10	2	9	2	8	4	3	6	3	2	9		5	10	7			8	1	8
Carex pallescens																																
Carex panicea		2	5	2	4	7	4	9	6	8	9	4	2	2	8	7	5	3	4	7	4	5		2	9	5	4	8	3	6	5	5
Carex pilulifera	3	7	4	2	3	2	6	2	3	2	2	4	4	7	7	2	7	5	6	2	4	5	4	6	8	1	5	6	1	2	2	3
Carex pulicaris																																
Carex viridula ssp. *oedocarpa*																																
Cerastium fontanum																																
Crepis paludosa																																
Danthonia decumbens				10			10	2	6	9		9	9		6	7	10	10	10	10	5			9		10	8	5	9	9	10	
Deschampsia cespitosa																																
Deschampsia flexuosa	7	9				10	8			9	10			6	1	10	4		8		9	8	5	6	8	7	7			6	9	8
Eriophorum angustifolium																																
Euphrasia officinalis agg.																																
Festuca ovina/vivipara	2	2	2	2	2	1	2	2	1	2	2	2	2	1	2	2	2	1	3	3	2	2	2	1	1	2	2	2	2	2	2	3
Festuca rubra																																
Galium saxatile	2	2	2	2	2	2	2	2	2	2	2	6	2	2	5	2	4	4	2	2	2	2	2	2	2	2	2	2	2	2	2	3
Juncus bulbosus																																
Juncus effusus																																
Juncus squarrosus								9	8	10	10											10	2	9	6	9						
Leontodon autumnalis																																
Luzula multiflora	6	1	5	6	7	2	6	6	8	6	4	1	6	4	9	4	8	2	5	5	10	5		6	4	7	4	4	7	8	7	9
Molinia caerulea																																
Nardus stricta	4	2	3	6	3	5	1	1	6	1	3	5	2	3	4	3	1	2	1	2	2	4	6	4	2	6	1	2	2	1	5	1
Narthecium ossifragum						10			10	8	10	10									9	2	2	10	2	2	2	10				
Oreopteris limbosperma																																
Oxalis acetosella																																
Pinguicula vulgaris																																
Plantago lanceolata																																
Persicaria vivipara																																
Potentilla erecta	5	5	2	1	6	5	2	2	3	2	3	2	2	4	6	7	2	2	5	2	1	4	2	6	6	5	3	4	5	6	2	2
Prunella vulgaris																																
Ranunculus acris																																
Rumex acetosa																																
Selaginella selaginoides																																
Sorbus aucuparia																	10												10			
Taraxacum agg.																																
Thymus polytrichus																																
Trichophorum cespitosum	2		10		10	8	5	4	8	3	2	8	5	7	9				10	7	9	2	2	2	3	8	8	3	7	8	10	
Vaccinium myrtillus		10	2	2	9	7			10	9	2	5	8							9	6	2		2		9	2	1	9		5	9
Veronica officinalis																																
Viola palustris								10																								
Viola riviniana																																
Bryophytes (excluding *Sphagnum*)	1	2	1	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Sphagnum spp.																																
Lichens (*Cladonia* spp.)																				9									10			
Bare Rock				7										10	8	9	10			10	10	7	10	8					7	10		7
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
CG10b Sample stands
Baseline survey - 31/07/1995
Enclosure 1

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Achillea ptarmica	4	5	10	5					10	10	4	10	2	9	9	8	3	2	8	7	9	7	5		8	3	1	9	6	3	4	10
Agrostis capillaris	2	1	1	2	1	2	1	1		2	2	1	2	2	2	1	2	2	2	2	1	1			3	2	3	2	1	1	2	2
Alchemilla alpina						10	10	9	4	9	10											6	7	9	1	8	8	9				
Alchemilla glabra	2	7					10	9	3	6											10	10	9	7	8	10	9	5				
Anemone nemorosa																																
Anthoxanthum odoratum	3	6	4	4	4	3	2	2	3	2	3	2	3	4	2	3	2	1	2	2	4	4	3	2	7	8	7	3	2	3	2	2
Bellis perennis	6	10	5																		10	8	8		4	6	5	8				
Betula pubescens																																
Blechnum spicant																																
Campanula rotundifolia		10	3	5	3	7	4	7	5	9	6	2	10	8	10		10	4	6				10	9		3	9	10				10
Carex bigelowii													6																			
Carex binervis	4	2																														
Carex capillaris																							9	4								
Carex flacca																																
Carex nigra																																
Carex pallescens																																
Carex panicea	10	7						9	2	7	10				6	8	8	10	5			8	1	5	5	2	6	9	10	8	3	6
Carex pilulifera	4	7	9	2	9	9	9	3		5	2	2	9	8	7	4	1	5	7	10	2	5				7	5	6	2	4	6	2
Carex pulicaris		4	2					9	1	8	10					2					10	8	2	1	3	1	2	8	10		9	
Carex viridula ssp. *oedocarpa*								9	8													9		6		9					10	
Cerastium fontanum	10		10													7	10													9		3
Danthonia decumbens																						5	9			8	3	9				
Deschampsia cespitosa																																
Deschampsia flexuosa																																
Diphasiastrum alpinum											8	9																				
Euphrasia officinalis agg.		9	8					10	6	8	8				8		9	10				9	9	7	9			10			8	
Festuca ovina/vivipara	1	2	2	2	2	2	2	2	2	1	1	2	1	1	2	2	2	2	1	2	2	2	2	2	2	2	2	3	2	2	1	1
Festuca rubra			10	2	3				5		10			8	9	9			8				10	8	8			8	9	10		9
Galium saxatile	7	2	2	4	2	1	2	2		2	2	2	2	2	2	2	2	2	2	2	2	2	3		2	10	3	2	2	2	2	2
Helictotrichon pratense																																
Hieracium sp																																
Holcus lanatus																																
Huperzia selago																																
Juncus bulbosus									7																							
Linum catharticum								10		9													7	7	2	8	6					
Luzula multiflora	2	8	9	3	7	7	9	7		5	5	7	4	2	2	5	4	8	8	3	5							2	2	4		9
Lysimachia nemorum																																
Nardus stricta	8	4	8	9	10	2	7	4	4	7	8	4	8	8	7	4	10	4	9	10	3	4	2	8	8	3	2	8	4	2	2	7
Narthecium ossifragum																																
Oreopteris limbosperma																															10	
Oxalis acetosella																																
Parnassia palustris																																
Phegopteris connectilis																																
Pinguicula vulgaris																							9	8								
Plantago lanceolata	6	5					8	4	2	7	9				8		9				9	7	2	2	7	5	2	5	9		9	7
Polygala serpyllifolia																																
Persicaria vivipara		4	4	9	6	5	7	2	6	4	8	5	10	3	6	10	2	2	3		5	2	5	5	3	2	3	1	8	10	2	8
Potentilla erecta	3	7	2	9	6	2	3	6	2	3	2	4	6	7	5	6	9	7	4	8	2	2		8	5	5	5	2	8	6		2
Prunella vulgaris	9	4						10	8							8	9						9	5		9		8	10			8
Ranunculus acris	2	2	2	2			9	5	8	4				2	1	4	6	2			10	9	3	2	2	7	4	2	9		4	5
Ranunculus flammula																																
Ranunculus repens	7	5	10	6									3	6	4	2	10	10	10											4		5
Rumex acetosa																													5	10		
Saxifraga aizoides									10																	9	8					
Saxifraga oppositifolia																								7	6							
Selaginella selaginoides		10						10	10	10	10												7	7	5	2	7	9				
Silene acaulis									10	9													8	2								
Sorbus aucuparia																																
Taraxacum agg.								10	10																							
Thalictrum alpinum									2	9												9		10	4	7	5					
Thymus polytrichus	2	4	2	1				9		2	8			8	7	10	10	3	2	9	5	6	3	8	2	2	2	2	8	5	2	4
Trichophorum cespitosum								9																								
Trifolium repens	2	2	3	4										2	2	3	2	6			9	10			5	6	2	2	10	6	2	3
Vaccinium myrtillus																10																
Veronica officinalis				9	4		5			2	9		9	9					2	2	10							6	8	4	10	
Viola palustris			8				4	2																								
Viola riviniana	9	6	6	6	3	2	9	10		6	7	8	7	4	4	8	8	4	2	4	3	2	5	2	5	2	5	3	2	5	3	3
Bryophytes	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Lichens (*Cladonia* spp.)			3	10	8		8				10							8														
Bare Rock				10	8		8				10													10								
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
CG10b Sample stands
Second survey - 10/09/1998
Enclosure 1

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Achillea ptarmica		2			8				6	9	10	9	5	7		7		9	9	10		9	9			5	2	9			3	10
Agrostis capillaris	2	1	2	2	2	2	2	1		2	1	1	1	1	2	1	1	2	1	1	2	2		7	5	5	4	2	2	3	2	2
Alchemilla alpina						10	10	5	4	9	10	10										4	8	6	4	6	9					
Alchemilla glabra	1	8	9					9	3	6	10										10	10	8	7	6	8	9	7				
Anemone nemorosa																																
Anthoxanthum odoratum	7	2	4	5	5	2	2	4	4	3	2	2	4	4	1	3	2	2	2	3	2	2	9	3	8	7	6	6	2	3	2	2
Bellis perennis	2	10	5								10										10	8	8	10	5	4	6	7	10			
Betula pubescens																											10					
Blechnum spicant																																
Campanula rotundifolia		10	2	4	3	7	9	2	6		10	2	9	4	7		10	10	5			10	10	10		9	9				2	8
Carex bigelowii													4		5																	
Carex binervis	10	4																														
Carex capillaris									10														9	2								
Carex flacca																																
Carex nigra																																
Carex pallescens																																
Carex panicea	9	6						9	2	5					8		9	10	5			8	1	2	2	1	8	9	10	8	2	6
Carex pilulifera	9	10	8	2	9	9	7	2		6	6	7	8	8	7	2	7	3	3	10	2	8				7	7	7	2	5	7	5
Carex pulicaris		9	6				10	10	7	7											10	8	2	3	3	2	2	7	10		9	
Carex viridula ssp. *oedocarpa*	2							10	9	9												9	9	6							10	
Cerastium fontanum	8	2													3	7	6	7													8	9
Danthonia decumbens					7			5	5		9										9	10	10	9	10	7	5	9				
Deschampsia cespitosa																																
Deschampsia flexuosa																																
Diphasiastrum alpinum					9						7	7																				
Euphrasia officinalis agg.	10	7	9					10	6	8	8				5	8	6	2				10	6	5	4	8	6	9			6	7
Festuca ovina/vivipara	2	2	1	2	1	1	1	2	2	1	2	2	2	2	2	2	2	2	2	2	1	1	3	1	1	2	1	2	2	1	1	2
Festuca rubra	6		7	8	2		9	10	1	7	5	7	9	2	10					9	10	8	7		8	9	8	9	8	10	6	7
Galium saxatile	2	2	2	4	2	2	2	4		2	2	2	2	2	2	2	2	2	2	2	2	2	4		2	5	2	2	1	2	2	2
Helictotrichon pratense																																
Hieracium sp.																																
Holcus lanatus																																
Huperzia selago																																
Juncus bulbosus																																
Linum catharticum								10	7	9						7						10	5	7	9	2	8	9				
Luzula multiflora	2	7	9	9	7	7	9	3		2	4	5	8	6	9	1	5	6	6	2	5	4						5	3	5	2	7
Lysimachia nemorum																																
Nardus stricta	8	4	8	9	10	2	7	4	2	7	8	8	10	7	7	5	9	4	8	9	7	3	2	7	5	5	3	1	6	5	5	7
Narthecium ossifragum																																
Oreopteris limbosperma																															10	
Oxalis acetosella																																
Parnassia palustris																											9					
Phegopteris connectilis																																
Pinguicula vulgaris																																
Plantago lanceolata	3	6	8				10	5	3	7	10				6	10					10	6	2	4	4	2	2	6	10	10		7
Polygala serpyllifolia																																
Persicaria vivipara	9	6	4	7	9	5	7	2	3	4	8	3	9	3	4	8	8	8	3		5	3	3	4	3	5	2	5	9	10	8	10
Potentilla erecta		7	4	10	5	2	2	6	2	3	5	4	6	7	10	5	9	4	4	4	3	3	6	8	3	4	2	4	7	9	7	2
Prunella vulgaris	5	3	10				10	10	4	10						8	8				10	10	8	5	2	9		8	10		10	7
Ranunculus acris	2	5	2	1			10	5	8	4	10			3	5	6	2	3	10		8	7	3	2	10	3	3	4	7	7	4	1
Ranunculus flammula																																
Ranunculus repens	2	2	8	4									2	7	2	2	6	10												4	8	2
Rumex acetosa																													5			
Saxifraga aizoides									9															8		9	8					
Saxifraga oppositifolia									8														10	2	7							
Selaginella selaginoides			6					9	10	10	10											10	7	4	7	6	7	9			10	
Silene acaulis									10	9													7	2								
Sorbus aucuparia																																
Taraxacum agg.								10	9										5			10		10					9			
Thalictrum alpinum								10	2	10												10	10	7	9	7	5					
Thymus polytrichus	2	2	2	2		10	9	9		2	9	10		8	4	9	7	1	2	9	5	2	3	7	3	3	2	2	7	3	2	3
Trichophorum cespitosum								9																								
Trifolium repens	2	2	2	2						10				2	2	5	3	2			10	7	8	5	5	3	2	3	9	8	7	3
Vaccinium myrtillus																10																
Veronica officinalis		3		10	3	9	8			2	9		10	9	10			10	4	2	8							3	7	7	10	
Viola palustris	10	2	9	5	4	2	6	2		5	7	5	6	2	4	8	8	3	4	4	2	4			9	10	3	4	8	6	2	5
Viola riviniana		9					9	7	2	2	10			7	10	7	9	7	5	6	8	5	3	4	6	2	8	10	9	8	10	9
Bryophytes	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Lichens (*Cladonia* spp.)			3								9							5														
Bare Rock				10	9		8			9	10													10								
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
CG10b Sample stands
Baseline survey - 04/08/1995
Enclosure 2

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Achillea ptarmica																																
Agrostis capillaris	2	4	3	2	2	2	3	6	2	3	2	3	2	1	2	2	2	2	2	1	2	1	3	8	2	5	3	2	2	1	2	1
Alchemilla alpina	7	1	2	2	4	1	2	3	2	2	2	1	4	2	2	2	6	3	3	6	5	5	2	1	2	2	4	2	2	2	6	6
Alchemilla glabra								6											10													
Anemone nemorosa				5			8	10		8	9	8	8	6	4		9	4				7	8	7	6	9	5	10		10	10	10
Anthoxanthum odoratum	6	7	8	2	3	5	2	3	5	5	2	4	5	5	2	6	5	3	5	5	2	2	2	2	2	3	1	6	4	4	5	2
Bellis perennis																																
Betula pubescens																																
Blechnum spicant	6	10	9		3									5	8				9													8
Campanula rotundifolia			5	3	10	7	8	2	2	3	7	4	9	5	10	10	8	8	6	4	6	4	9	8	3	5	7	4	3	4	5	2
Carex bigelowii																																
Carex binervis							10				8			10																		
Carex capillaris																																
Carex flacca																																
Carex nigra																																
Carex pallescens											10																					
Carex panicea					10	8	2	3	5	1	3	7	10					6	8	10	10	3	4	2	6	9		4	7		8	
Carex pilulifera	10	7	5	2	6	4	4	8	3	4	3	7	4	6	9	9	8	8	7	7	8	6	3	5	5	3	2	7	10	8	9	
Carex pulicaris					10	5	7	2	1	3	3	7	6											3				8				
Carex viridula ssp. oedocarpa									10															7			10					
Cerastium fontanum																																
Danthonia decumbens		10			9									9	2	10			9			7			10	10						
Deschampsia cespitosa																													10			
Deschampsia flexuosa	9	3	8	4		10								4		9																
Diphasiastrum alpinum																																
Euphrasia officinalis agg.				10		8	5	10		5	8				9			6	9	8	5	10	8			8	8	10	3	6	9	
Festuca ovina/vivipara	2	2	1	1	2	2	1	2	2	2	1	4	2	3	2	1	2	1	1	4	1	2	1	2	1	2	2	1	3	2	1	4
Festuca rubra						10							10																			
Galium saxatile	2	2	2	4	1	2	5	3	2	3	4	3	2	2	2	3	2	2	2	2	2	2	5	7	2	6	2	2	2	2	3	2
Helictotrichon pratense																																
Hieracium sp.																																
Holcus lanatus																																
Huperzia selago																																
Juncus bulbosus																																
Linum catharticum																																
Luzula multiflora	7	7	10	6	5	8			8	9	10	9	6	9	7	2	2	6	9	8	7		10	2		8		9	3	7	7	5
Lysimachia nemorum																																
Nardus stricta	4	5	8	6	5	5	3	1	2	7	7	8	1	8	6	6	1	7	5	3	7	7	9	2	8	8	3	7	8	6	8	2
Narthecium ossifragum				10				2	7						9			10					6	10								
Oreopteris limbosperma	6	10		7	4				10					10			10					8										6
Oxalis acetosella												9	10															10	10	2		
Parnassia palustris																																
Phegopteris connectilis	10		8													6																
Pinguicula vulgaris																																
Plantago lanceolata					9	2	4	[illegible]	5	4	3	8	8	8	10				9	7	8	2	3	3		5	5	5	6	3		
Polygala serpyllifolia								10	8			10											5	9		10						
Persicaria vivipara				9		3	4	5	3	7		9	10							9		9	10	10	5	9	10		8	7		
Potentilla erecta	2	7	5	2	2	2	3	5	3	2	2	7	5	5	1	7	4	2	2	4	7	7	5	2	6	6	3	5	1	5	3	6
Prunella vulgaris								8		4																						
Ranunculus acris					10	6	4	5	3	4	7	4	10	9	10				9	6	7	7	4	2		4	6	2	8			
Ranunculus flammula																																
Ranunculus repens																																
Rumex acetosa																																
Saxifraga aizoides																																
Saxifraga oppositifolia																																
Selaginella selaginoides				10		10	8	2		5	2	10							9	8	7	8	10					4	10	10		
Silene acaulis																																
Sorbus aucuparia																																
Taraxacum agg.																																
Thalictrum alpinum																																
Thymus polytrichus				10	9	5	2	2	3	2	2	4	9	10					8	4	3	2	2	2	7	1	4	2	2	9		
Trichophorum cespitosum																																
Trifolium repens																																
Vaccinium myrtillus	2	3	2	2	2	5	10		2	5	5	5	2	2	2	8	4	2	4	5	9	4	6	8	7	3				4	2	7
Veronica officinalis																																
Viola palustris				9	9											9	8	7	9				4							9	9	10
Viola riviniana						6	5	7	10	2	2	7	6	10	10			9	10	6	5	2	10	8	5	3	6	5		2		
Bryophytes	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Lichens (*Cladonia* spp.)	8	4	5	5	7	4	2	8		2	5	2	3	2	9	5	5	2	7	2	2	3	10		8	2	9	3	4	2	7	7
Bare Rock	8	4	5	5	7	4	2	8		2	5	2	3	2	9	5	5	2	7	2	5	3	8	3	8	2	9	3	4	2	7	7
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
CG10b Sample stands
Second survey - 25/08/1998
Enclosure 2

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	21	23	24	25	26	27	28	29	30	31	32
Achillea ptarmica																																
Agrostis capillaris	2	4	1	1	2	1	2	2	2	2	5	2	2	2	2	2	2	2	2	2	1	4	2	2	2	2	2	2	3	1	1	2
Alchemilla alpina	8	2	4	2	5	2	2	3	5	2	1	2	5	1	2	3	5	3	2	5	3	4	2	7	2	1	2	4	1	3	3	3
Alchemilla glabra								7																						8		
Anemone nemorosa					5										10		2	3				7				2			10	10		9
Anthoxanthum odoratum	10	2	9	7	3	6	5	9	2	1	6	6	4	4	2	7	4	2	4	3	3	6	3	5	1	3	5	6	3	5	5	2
Bellis perennis																																
Betula pubescens																																
Blechnum spicant	6	10	9											7	8				9										10			6
Campanula rotundifolia			10	9	8	10	7	8	7	7	8	6	2	7		10	9	10	7	5	5	5	8	3	3	3	2	8	6	2	5	5
Carex bigelowii																																
Carex binervis													7	10																10		
Carex capillaris																																
Carex flacca																																
Carex nigra																																
Carex pallescens							10				9																				10	
Carex panicea					10	8	3	3	6	2	3	7	10				10	5	9	9	10	2	4	1	5	8		2	5	8	6	
Carex pilulifera	10	2	5	5	5	4	4	8	4	5	8	2	7	6	10	9	9	8	10	6	8	5	1	7	6	2	2	8		5	9	
Carex pulicaris						4	7	7	5	9	3											9	8	4				7				
Carex viridula ssp. *oedocarpa*																				9		10		7						10		
Cerastium fontanum										8																					8	
Danthonia decumbens	2	10						8						9	10	10								10								
Deschampsia cespitosa																												9	10			
Deschampsia flexuosa	10	9	4	5									1	10	4	8	10														7	
Diphasiastrum alpinum																																
Euphrasia officinalis agg.				10	9	10	5	4	8	7	9						8		10	7			4				9		9	6	10	
Festuca ovina/vivipara	4	1	2	2	2	2	1	1	2	2	2	2	2	2	2	2	2	2	1	2	4	2	2	2	2	2	1	1	2	2	2	1
Festuca rubra								10			9		8							8	9		10	9	4	8	9	7		10	10	10
Galium saxatile	2	5	2	2	2	2	7	5	7	2	2	5	2	2	2	2	3	1	2	5	5	2	2	6	2	2	2	2	2	2	2	2
Helictotrichon pratense																																
Hieracium sp.																																
Holcus lanatus																																
Huperzia selago														8																10		
Juncus bulbosus																																
Linum catharticum																																
Luzula multiflora	10		9	8		3		10				1	10	10	7	2	2	5	7	8	7	9	9	10		8	7	8	3	5	6	10
Lysimachia nemorum																																
Nardus stricta	1	6	9	7	8	9	8	7	1	5	8	2	3	9	1	1	2	7	4	4	8	6	9	7	8	5	4	5	8	4	8	7
Narthecium ossifragum				10	2			6							10								4	10		7						9
Oreopteris limbosperma	6		10	7	7				10		8																					2
Oxalis acetosella						6						8		8														9	10	2		
Parnassia palustris																																
Phegopteris connectilis	10		8	7												6																
Pinguicula vulgaris																																
Plantago lanceolata					9	3	2	2	3	3	2	6	2	8	10			10	8	6	7	6	2	2	10	8	6	7	3	5	8	
Polygala serpyllifolia										2	6												6	9								
Persicaria vivipara						9	3	3	8	9	9	8	8							8		10	8	9	6	8	7		5	5	10	10
Potentilla erecta	3	7	6	3	1	5	7	2	7	6	5	2	7	7	5	2	2	2	6	3	8	5	5	2	5	7	6	7	5	2	2	6
Prunella vulgaris							10	2	10	5														2								
Ranunculus acris				10	10	5	5	4	3	8	2	4	7	8				9	9	5	6	5	2	2		2	6	2	4	7	10	
Ranunculus flammula																																
Ranunculus repens																																
Rumex acetosa																																
Saxifraga aizoides																																
Saxifraga oppositifolia																																
Selaginella selaginoides				10	6	7	6	7	2	6	2	9	10		10			10	9	5	7	5	10				8	4	6	7		
Silene acaulis																																
Sorbus aucuparia																	8														9	
Taraxacum agg.																																
Thalictrum alpinum																																
Thymus polytrichus				10	8	2	2	2	2	2	2	2	9	10	10				6	2	2	4	2	2	5	2	2	2	2	8		
Trichophorum cespitosum																																
Trifolium repens																																
Vaccinium myrtillus	2	2	2	7	4	5	9		9	3	7	6	8	3	6	7	2	4	2		9	2	4	10	6	8	10			2	2	4
Veronica officinalis																																
Viola palustris				9	2		5									10	8	2	9	3	7			9	9	8	10		9	7	9	9
Viola riviniana					8	2	10	10	6	6	5	7	8	9	10				10	5	4	8	2	5	9	5	8	6	3	5		
Bryophytes	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	1	2	2	2	2	2	2	2	2	2	2	2	2
Lichens (*Cladonia* spp.)	7	10	2						5		2		9		10	6					3								7			10
Bare Rock	8	3	6	5	6	4	6	7			5	2	5	4	3	5	9	6	7	8	3	2	8	4	7	4	8	7	2	2	7	4
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
CG10b Sample stands
Baseline survey - 15/09/1995
Enclosure 3

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Achillea ptarmica		10	5						10				6							10			9	7	7				7	10		
Agrostis capillaris	1	2	1	2	1	1	1	2	1	2	1	2	1	2	2	1	2	3	2	2	1	2	2	2	4	2	2	1	2	2	1	1
Alchemilla alpina	8															10				9												
Alchemilla glabra							10	9	5	9											7	8	8	2	10	2	8	10	10			
Anemone nemorosa		2																														
Anthoxanthum odoratum	5	2	5	2	4	2	4	1	2	4	5	2	2	4	2	5	1	7	2	4	2	2	3	8	5		3	5	5	1	6	3
Bellis perennis			9	8	4	10		10		8	5	9	8	3	6			10	3			10	7	6	6	8	8	9	10			
Betula pubescens																																
Blechnum spicant																																
Campanula rotundifolia	9	6	6	6	10	3	2	2	2	5	5	2	2	4	8	2	10	7	4	5	10	7		3		8	9	9	8	9	3	4
Carex bigelowii																																
Carex binervis	8				7	3													10					10		10					8	5
Carex capillaris																																
Carex flacca																									10							
Carex nigra																																
Carex pallescens																																
Carex panicea	9	5	6	5		9		10	2	9	7	9	5	1	4	2	2	10	2	8	9	6	8	4	2	9	4	9	9	10	4	2
Carex pilulifera	5	7	4	5	6	7	2	4	5	5	3	5	6	7	1	2	6	10	8	6	2	5	4	5	10	2	7	4	4	2	3	5
Carex pulicaris					10	2			8	8			6	3	8		4	10			10	9		1		7		10	9	8	5	10
Carex viridula ssp. *oedocarpa*										9			10						9	10			9	5	3	10			10			
Cerastium fontanum																			7				2			8	9		7	3		10
Danthonia decumbens		10					6	9			10		3				10		10									5		8	2	
Deschampsia cespitosa																							10		3							
Deschampsia flexuosa																																
Diphasiastrum alpinum																																
Euphrasia officinalis agg.								10	9	10		8	10	10	10	9	8	9	7				10	4	10	5	9	10				9
Festuca ovina/vivipara	5	1	2	1	2	2	2	2	3	3	2	1	2	2	2	2	2	2	1	1	2	2	3	2	2	2	1	2	1	2	2	2
Festuca rubra				6		10			10			8	7					10														
Galium saxatile	2	2	2	2	7	2	2	2	2	2	5	2	2	2	2	2	5	2	2	2	2	2		10	10		2	2	4	6	2	2
Helictotrichon pratense																								10								
Hieracium sp.																														9		
Holcus lanatus																											5					
Huperzia selago																																
Juncus bulbosus																																
Linum catharticum																																
Luzula multiflora	3					8	8	6		9	10	10	5	10	4	2	10	7	8	2	10	6	2				8	6		8	8	5
Lysimachia nemorum									8																							
Nardus stricta	2	6	3	4	4	4	4	3	2	4	6	7	3	4	7	7	4	1	3	5	4	1	6	2	1	5	2	5	4	6	2	3
Narthecium ossifragum																																
Oreopteris limbosperma																																
Oxalis acetosella			9	2			2					5																	10			
Parnassia palustris																																
Phegopteris connectilis																																
Pinguicula vulgaris																																
Plantago lanceolata	10	10	4	2	2	5	8	6	3	2	2	7	8	2	2	9	5	9	2	2	8	7	1	2	5	2	7	8	3	5	5	2
Polygala serpyllifolia																	10														9	
Persicaria vivipara	9	6			8	5	8	9	6	2	2	6	7	5	2	2	4	10	4	5	4	3	2	5	4	2	2	7	2	9	10	6
Potentilla erecta	6	5	7			6			9							4	10	2	8	10	7		7	10					9		10	5
Prunella vulgaris			10		6				8	8		7	5	8	8	9	4	9	7	7	7	10	4	4	6	5	8	10	3	7	10	10
Ranunculus acris	3	9	2	3	2	2	2	2	2	1	3	2	3	2	3	8	2	9	3	2	2	3	4	2	3	2	2	2	2	2	2	2
Ranunculus flammula																																
Ranunculus repens																																
Rumex acetosa																																
Saxifraga aizoides																																
Saxifraga oppositifolia																																
Selaginella selaginoides																								6								
Silene acaulis																																
Sorbus aucuparia																																
Taraxacum agg.																																
Thalictrum alpinum																																
Thymus polytrichus		9	2	2	2	2	2	2	4	2	2	2	5	3	3	5	2	8	2	3	6	3	6	2	7	7	2	2	8	2	4	5
Trichophorum cespitosum																																
Trifolium repens		9	2	2	2	3	6	4	4	7	7	5	3	5	4	8	6	10	5	2	5	9	2	2	5	2	3	8	5	2	5	7
Vaccinium myrtillus																																
Veronica officinalis						8	7	10			5												10			1						
Viola palustris	2	2	7		7	5	6	6		8	5		10	2	6	2	5	10	4	10	2	4	10	10	8	4	3		8	10	9	6
Viola riviniana			9	3	10	4	8	4	7		9	6	5			8		8			9	7		8			9	5		2	8	
Bryophytes	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	4	2	2	2	2	2	2	2
Lichens (*Cladonia* spp.)			3	7	7		8	8	6		7	9	8		9			8			9	10					6	8	9			
Bare Rock	10		3	7	7		8	8			7	9	8		9			5			9	10					6	8	9			
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
CG10b Sample stands
Second survey - 02/09/1998
Enclosure 3

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Achillea ptarmica		10						10	9				7				4			9	10	10	8	3	6	7		6	7		7	
Agrostis capillaris	1	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2	3	2	2	2	2	2	4	1	2	1	2	2	2	2
Alchemilla alpina	8														10	10																
Alchemilla glabra							9	9	7	9	10						8			9	7	8	9	8	10	7	8		10			
Anemone nemorosa			9									6																				
Anthoxanthum odoratum	2	2	5	1	2	2	4	2	2	4	5	2	2	7	6	3	2	6	4	2	2	1	7	2	4	2	2	3	3	2	2	2
Bellis perennis		10	8	8	2	10	8	9	9	8	5	9	7	5	6			10	2		10	10	2	5	7	7	8	8	9	10		
Betula pubescens																																
Blechnum spicant																																
Campanula rotundifolia	8	4	8	5	6	3	4	6	2	6	8	2	8	3	10		10	6	5		10	8		10	10		5	9	5	9	7	
Carex bigelowii																																
Carex binervis	4				10					9									10			10	10	10		8	9				8	5
Carex capillaris																																
Carex flacca																																
Carex nigra									8																							
Carex pallescens				10	8																		10	9	10							
Carex panicea	7	3	7	2		9	10	10	5	7	7	9	7	5	2	3	2	9	2	5	8	5	6	6	3	8	4	7	9	10	6	4
Carex pilulifera	4	7	8	9	8	5	1	5	4	2	3	5	7	5	9	1	6	10	1	6	5	7	2			8	4	3	8	2	2	5
Carex pulicaris		10	6			1	10		8	2			10	2	10		5	10	9	5	10		7	8	5	6	10	10		2	4	
Carex viridula ssp. *oedocarpa*									8	9	10		10						8	10			8	5		9			9			9
Cerastium fontanum			10		8	5			8	9	3		5			10		9	10		4	9							7			4
Danthonia decumbens	10	5	10			10	8	8			8		2	10	2	10	10	8	10	10	9		7			10		9	10	7	7	
Deschampsia cespitosa				8																			9	10	1	10						
Deschampsia flexuosa																																
Diphasiastrum alpinum																																
Euphrasia officinalis agg.		8	8	10	5	2		8		5	5	5	9	6	6	7	4	8	3	3			10	2	6	5	10	8	7	2	2	9
Festuca ovina/vivipara	2	1	2	2	1	2	2	2	3	2	1	1	2	2	1	2	2	2	3	2	2	4	1	2	2	4	2	2	4	1	1	2
Festuca rubra		8	9	8	8	9	5	9	9	4	4	10	8	9		9	10	10		9	10	8		9	2		10	10	6		10	6
Galium saxatile	2	2	2	6	5	2	2	2	2	2	2	2	2	2	2	2	7	2	9	2	2	2					2	2	2	4	7	2
Helictotrichon pratense																								8								
Hieracium sp.																																
Holcus lanatus																			10	10	6	10		7			3	10	2			
Huperzia selago																																
Juncus bulbosus																																
Linum catharticum																																
Luzula multiflora	2	2	4	2	2	2	4	2	4	8	5	4	5	2	10	10	10	8	8	5	5	6		7		3	9	5	3	2	8	2
Lysimachia nemorum									8																							
Nardus stricta	7	2	5	3	4	5	6	1	5	5	8	6	2	7	7	7	2	4	2	3	3	4	8	4	4	6	1	5	2	6	2	3
Narthecium ossifragum																																
Oreopteris limbosperma																																
Oxalis acetosella			10	4			2					3																	9			
Parnassia palustris																																
Phegopteris connectilis																																
Pinguicula vulgaris	9																															
Plantago lanceolata	10	10	6	3	2	5	7	6	2	2	4	5	9	3	4	9	2	9	4	2	5	8	2	5	4	4	6	8	7	2	3	2
Polygala serpyllifolia																																
Persicaria vivipara	8	7		10	7	5	7	6	4	2	3	6	6	3	7	2	4	10	9	3	4	5	6	2	4	4	2	3	5	7	6	6
Potentilla erecta	6	3	10		10	8	10		4	7	9			7	9	2	2	2		9	4		3	6	5	10				5	4	2
Prunella vulgaris		10	10	10	5	10			7	9	10	6	7	7	4	9	7		2	7	6	9	7	6	9	3	8	9	9	6		10
Ranunculus acris		8	4	2	2	2	2	2	1	2	3	2	2	1	2	8	2	8	3	2	2	2	2	2	3	2	2	3	1	2	2	2
Ranunculus flammula																																
Ranunculus repens																																
Rumex acetosa																																
Saxifraga aizoides																																
Saxifraga oppositifolia																																
Selaginella selaginoides										10																						
Silene acaulis																																
Sorbus aucuparia																																
Taraxacum agg.																		8														
Thalictrum alpinum																																
Thymus polytrichus		9	2	2	3	5	2	2	2	2	3	2	1	5	2	6	1	7	2	3	3	2	4	2	4	6	7	2	8	2	2	4
Trichophorum cespitosum																																
Trifolium repens		10	4	4	7	8	4	2	2	2	2	8	5	3	6	9	8	9	3	1	2	6	2	3	4	2	2	4	2	3	4	5
Vaccinium myrtillus																	9															
Veronica officinalis							8	3					6		10								8			2	10					
Viola palustris	6	6	5		7	2	6	3			6	7	9		7	2	6	9	7		8	2	9	7	7		2		7	8	8	6
Viola riviniana			10	2	10	10	2	5	6	8	8	5	8	9		8		8	9	10	5	7				3	10	5		5	7	
Bryophytes	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	1	2	2	2	2	2	2	2	2
Lichens (Cladonia spp.)															10																2	
Bare Rock			1	7	7	5		8			7	9	8		9			8				10						8	8			
Bare Soil	8	8	10		6	7	10		10	7	8	5	6	10	3	10	7	9	8	8	8	10	5	7		9	7	2	8	9	6	7

Appendix 4.1 - Nested Quadrat Data
U10a Sample Stands
Basciine survey - 28/06/1995
Enclosure 1

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Agrostis capillaris & *A. vinealis*	2	2	2	1	3	5	2	2	2	3	2	2	1	2	1	2	2	2	2	1	3	1	2	4	1	2	1	3	2	3	3	2
Alchemilla alpina	10		8	10						9	8	2	9	10	7	10	6	2	1	8		9					9		5	3	5	3
Anthoxanthum odoratum	8	4	10	3	10	10	8	5	2	6	10	2	7	6	2		6	9	10	10	10	8	7	8	3	9	2	9	5	5	8	10
Blechnum spicant																																
Campanula rotundifolia																		8	2	6									7	2	2	3
Carex bigelowii								10	9								10			8			7	5	2	1		5	2	10		
Carex binervis											10								10	10	10	2	9	7	8		6					
Carex panicea																																
Carex pilulifera	8	3	2	5	6	6	2	5	2	2	5	5	2	9	2	9	3	5	5	2	2	2	6	7	5	3	2	7	4	6	2	3
Cerastium fontanum																																
Deschampsia flexuosa	10	10	2	10	2	9	10	10		9	2	8	9	4	10	3	5	3	7	7	10	5	8	7	2	4	9	3	10	10	1	10
Diphasiastrum alpinum	3	5	2	2	2							5	6	2	5	6	2	1	7	5									6	3	2	5
Empetrum nigrum	5					10	2	2		8	2						9	7	9	10								7	9		2	7
Euphrasia officinalis agg.																																
Festuca ovina/vivipara	2	2	1	2	1	1	2	1	2	1	1	1	3	1	2	5	6	4	2	2	2	2	2	2	3	5	2	5	1	7	4	2
Galium saxatile	7	2	2	2	2	4	4	8	2	2	5	2	4	5	2	1	2	2	4	4	4	2	2	3	2	3	2	3	2	3	2	2
Huperzia selago																																
Juncus squarrosus								10	8														10		5	4	9	10				
Luzula multiflora		10	5	4		8	7	10	8	6	6	10	5	10	10	9		8	10	7		9	9	10	3	7	5	10	5	2	8	10
Nardus stricta	2	3	7	7	5	6	1	6	1	3	5	9	8	6	10	3	1	4	3	5	1	5	1	6	7	2	5	5	8	1	3	7
Potentilla erecta						10	5	10	6	2	10	6					9	10	10			5			10						9	
Salix herbacea	8															8	3															
Sorbus aucuparia																																
Trichophorum cespitosum																																
Vaccinium myrtillus	1	2	2	2	2	2	2	2	2	2	3	2	2	2	2	2	2	2	2	2	2	2	2	3	2	3	2	3	2	4	2	2
Vaccinium vitis-idaea	6	6	5	4	6	3	2	4	4	8	5	3	3	7	2	5	7	2	5	5	5	8	3	7		7		6	2	3	6	7
Viola palustris																																
Viola riviniana																									10							
Bryophytes	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	3	2	2	2	2
Lichens (*Cladonia* spp.)	2	2	4	3	2	2	2	5	2	3	2	2	2	4	2	4	7	2	6	2	3	2	3	2	5	5	3	2	8	2	2	2
Lichen (*Cetraria islandica*)																																
Bare Rock	7			10	8	2		5	10	10	9	6	7	6	8		9	7	9	9	6	3	6	2			4	1	8	7		8
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
U10a Sample Stands
Second survey - 03/06/1998
Enclosure 1

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Agrostis capillaris & *A. vinealis*	2	2	2	2	2	4	2	2	2	2	2	1	2	5	1	2	2	2	2	2	2	2	2	2	4	2	1	2	2	2	2	2
Alchemilla alpina	10			10							8	6	8	10	8	9	7	2	2			9					8		2	3	5	2
Anthoxanthum odoratum	8	4	3	3		8	7	5	2	2	3	4	10	10			7	10	10	6	10	6	3	8	1	2	2	4	2	5	7	10
Blechnum spicant																																
Campanula rotundifolia																	9	8	2	7									6	3	2	4
Carex bigelowii								10	10										10	8	10	10	8	5	4	1	5	4	8	10		
Carex binervis																					10	3										
Carex panicea																																
Carex pilulifera	8	2	2	5	5	5	2	5	2	2	3	2	5	8	2	9	2	5	4	2	2	3	6	6	5	2	2	5	8	6	4	3
Cerastium fontanum																																
Deschampsia flexuosa	6	10	3	10	1	9	2	2	4	7	2	7	6	2	10	1	7	2	6		10		8	4	8	6	10	2	7	9	2	10
Diphasiastrum alpinum	2	2	2	3	2							5	2	4	1	2	6	2	2	1									7	2	2	5
Empetrum nigrum	5			10	10	7	2	2			1	10					9	8		10								6			2	7
Euphrasia officinalis agg.																																
Festuca ovina/vivipara	1	4	2	1	2	2	2	3	1	2	2	5	1	4	2	7	2	5	2	2	1	1	2	4	4	2	2	2	1	2	1	2
Galium saxatile	6	2	2	2	2	3	4	8	2	2	2	2	2	3	2	2	2	2	2	2	2	2	2	2	3	2	2	2	4	2	3	2
Huperzia selago																																
Juncus squarrosus								10	8														10		2	6	10	10				
Luzula multiflora		9	5	9		10	9	10		4	7	8	7	8	10		7	7	10	7		8	7	10	3	7	5	10	7	7	7	
Nardus stricta	2	2	7	7	5	5	6	7	4	1	4	3	7	1	10	3	3	4	1	5	2	3	1	1	5	5	6	1	7	8	2	7
Potentilla erecta						10	4		6	8	9	5						10				8			10		9	9			9	
Salix herbacea	7															8	6															
Sorbus aucuparia																																
Trichophorum cespitosum																																
Vaccinium myrtillus	2	1	1	2	2	2	1	1	2	2	2	2	2	2	2	2	1	3	2	2	2	2	2	2	5	3	2	2	2	3	2	1
Vaccinium vitis-idaea	4	4	4	4	4	6	2	7	4	4	2	2	2	3	5	2	5	4	4	5	6	4	2	7	9	8	5	5	6	3	4	4
Viola palustris																	9														10	
Viola riviniana																																
Bryophytes	2	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	2	1	2	2
Lichens (*Cladonia* spp.)	3	2	4	2	2	2	2	5	5	8	4	2	2	2	2	2	8	2	5	2	4	7	4	2	10	5	2	2	8	2	7	2
Lichen (*Cetraria islandica*)	5												10																			
Bare Rock	7			10	8	2		5	10	10	10	6	9	9	8		9	7	8	9	7	9	7	5			4		9	10		10
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
U10a Sample Stands
Baseline survey - 30/06/1995
Enclosure 2

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	29	29	30	31	32
Agrostis capillaris & A. vinealis	2	9	3	1	1	2	2	2	3	2	3	1	1	2	1	4	2	2	1	2	2	2	2	3	2	1	2	2	2	1	2	1
Alchemilla alpina	2	6	2	3	4	1	3		9	7	4	2	6	2	2	8	3	3	2	3	3	8	9	2	3	3	6	2	8	5	2	2
Anthoxanthum odoratum	8		7	2	8						8	9	5	2	8	9	9	6	2	9	2	6		8	10	10	6	5	8			2
Blechnum spicant																																
Campanula rotundifolia																	5			10	5					9						
Carex bigelowii	1	8	8	3	2	2	2	2	1	1	1	3	7	5	2	2	2	1				9	2	2	9						9	2
Carex binervis																																
Carex panicea																																
Carex pilulifera	6	4	2	6	4	7	8				9	7	8	1	6	10	8	5	7	9	4	1			7		2	6	5	3	6	9
Cerastium fontanum																																
Deschampsia flexuosa	10		8	10		10		8	8	7	3	7	2	7	5	2	1	4	8	3	6	5	6	8	2	10		8	6	3	3	7
Diphasiastrum alpinum	6	5	6	8	2	9		10	9	8	2	2	7	5	2	4	4	3	6	7	8	5	3	5	1	2	2	3	2	3	2	8
Empetrum nigrum	10	6	2				9	5	2	10		8		2	10	10	2	7					10	5	7	9		9	6	10	7	2
Euphrasia officinalis agg.																										3						
Festuca ovina/vivipara	2	3	1	2	2	2	1	4	2	2	2	3	2	2	2	5	7	3	2	2	1	2	2	3	2	3	1	5	4	3	1	2
Galium saxatile	2	2	2	2	2	3	2	2	5	2	2	2	8	2	2	2	2	2	2	2	7	2	3	5	2	5	2	2	2	2	2	2
Huperzia selago												8							10								10	8		7		
Juncus squarrosus																																
Luzula multiflora										8	8	10	10	6	9	10	10	6		9	7	7		10	2			8	10			4
Nardus stricta	7	5	10	9	9	6	8			2	8	8	10	4	9	1	5	8	9	9	10	6			10			8	6	4	8	7
Potentilla erecta													8															9				
Salix herbacea									9	10	10										10	5	5	2	2	2	4	9				
Sorbus aucuparia																																
Trichophorum cespitosum																																
Vaccinium myrtillus	2	1	3	4	2	3	2	1	2	2	2	2	2	3	3	4	2	2	3	2	2	2	1	1	3	2	3	1	2	2	2	2
Vaccinium vitis-idaea	2	3	9	7	5	6	9	7	7	8	2	2	2	7	3	7	6	8	8	3	6	7	3	5	6	8	10	5	6	7	4	8
Viola palustris																																
Viola riviniana																																
Bryophytes	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2	1	2	2	2
Lichens (*Cladonia* spp.)	5	2	4	9	4	2	5	4	2	2	2	7	2	5	6	5	3	2	5	6	9	7	3	2	2	2	5	7	2	5	5	7
Lichen (*Cetraria islandica*)																																
Bare Rock		10	4		8					10			2	8		10	10	10	10					10	10	9			5	9	7	
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
U10a Sample Stands
Second survey - 04/06/1998
Enclosure 2

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Agrostis capillaris & *A. vinealis*	1	2	3	1	1	1	2	2	2	2	1	3	x	5	2	2	2	4	3	2	2	3	2	7	6	2	2	2	4	3	2	3
Alchemilla alpina	2	6	2	4	7	2	6		9	2	2	2	6	2	2	7	6	2	2	5	3	8	9	2	1	3	1	4	8	2	3	2
Anthoxanthum odoratum	9	10	8	5	9	9				7	9	3	10	2	7	10	9	6	1	10	5	8			10		8	6	9			2
Blechnum spicant																																
Campanula rotundifolia													10		7	9	7	9		10	5	5	10		8	9			10			5
Carex bigelowii	7	8	8	4	4	2	1	1	2	2	2	6	8	3	3	2	5	5				3	1	1	9						9	3
Carex binervis																																
Carex panicea																																
Carex pilulifera	6	4	2	5	2	8	9				6	6	10	7	5	10	8	5	6	9	5	2					5	6	2	5	8	10
Cerastium fontanum																																
Deschampsia flexuosa	10	8	8	6	10	5	2	4	6	2	5	5	1	3	1	2	3	3	3	6	7	2	6	8	4	8	5	9	7	2	7	2
Diphasiastrum alpinum	2	2	2	7	2	8				9		8	6	2	2	5	7	2	6	4	5	5	2	4	2	1	6	2	2	3	3	10
Empetrum nigrum		9	1	10			9	7	2		2	8		2		10	1	6						5	7	10		9	7	10	8	3
Euphrasia officinalis agg.																																
Festuca ovina/vivipara	2	5	2	2	2	3	2	4	7	4	2	2	6	2	2	4	2	2	2	2	1	4	3	2	2	3	2	1	3	2	1	3
Galium saxatile	4	5	7	2	2	4	3	3	2	3	4	2	6	2	2	2	7	2	4	2	2	2	2	6	6	5	2	3	2	6	2	6
Huperzia selago										10								10			8	9	10			5	10	8				
Juncus squarrosus																																
Luzula multiflora											9	10	10	2	7				9	9	6	5		10	3			9				8
Nardus stricta	7	5	10	8	9	7	8			7	8	8	10	5	8	1	5	1	9	8		7			10	10		8	5	3	7	7
Potentilla erecta													9															9				
Salix herbacea									9	10											10	8	4	2	3	3	4	9				
Sorbus aucuparia																																
Trichophorum cespitosum																																
Vaccinium myrtillus	2	2	3	2	2	2	2	2	1	1	2	1	3	1	3	3	2	3	2	3	2	2	2	2	6	3	2	2	2	1	2	1
Vaccinium vitis-idaea	5	2	7	7	5	5	9	8	8	9	5	6	9	2	7	8	10	9	7	6	3	5	5	5	2	2	2	6	8	9	7	6
Viola palustris																																
Viola riviniana																																
Bryophytes	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	1	2	2	7	7	2	2	1	2	2	2
Lichens (*Cladonia* spp.)	5	9	6	9	6	2	6	3	4	9	2	6	9	6	7	9	5	4	5	5	8	2	2	2	4	3	7	6	2	8	2	8
Lichen (*Cetraria islandica*)																																
Bare Rock		10	4						8	10			2	9			10		5					10	2	9				10	9	
Bare Soil																																

Appendix 4.1 - Nested Quadrat Data
U10a Sample Stands
Baseline survey - 07/07/1995
Enclosure 3

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Agrostis capillaris & *A. vinealis*	1	3	1	1	2	1	1	2	2	2	2	2	2	1	6	2	1	1	1	1	2	2	1	3	2	2	2	9	2	1	1	1
Alchemilla alpina	4	9	2	4	8	7	7	1	2	2	9	1	10	8	7	8	10	4	5		2	5	2	8	4	1	4	8	2	9	8	8
Anthoxanthum odoratum	5	8	8	9	10		9	7	1	2	10			6	8	8	7	9	6	10		10	7	6	2	8		9	2	3	6	7
Blechnum spicant																10																
Campanula rotundifolia																																
Carex bigelowii	9	4	5	2	2	3	2	3	4	3	4	3	2	5	7			10	5	3	2	5	3	2	4	4	5	8	4	3	10	
Carex binervis																																
Carex panicea		10	4	8	7	2	7	2						9					10	9									10			
Carex pilulifera	2	3	3	3	2	2	3	2	2	4	3	9	10	2	6	2	6	2	6	8	2	10	4	5	6	4	5	9	9	7	5	5
Cerastium fontanum							10																		8	7						
Deschampsia flexuosa			10	2		8	10	9		9	10	6							10			10				8						
Diphasiastrum alpinum																																
Empetrum nigrum			6		9	7		9	8		2	5	10	7					10	7	6		9	7				9				
Euphrasia officinalis agg				10	10		10																10		2	2	10					
Festuca ovina/vivipara	2	2	4	4	3	2	3	2	4	2	3	2	2	2	5	1	4	2	4	2	1	3	2	3	1	2	1	8	1	4	2	2
Galium saxatile	2	8	2	2	7	2	8	2	2	1	2	3	8	2	5	8	6	2	2	3	3	9	2	2	2	5	7	8	2	2	3	2
Huperzia selago						6						10			10								10		10	3				9		
Juncus squarrosus	6	10	10											7		9	6	8												3	10	5
Luzula multiflora								10	6	10				9					10				8	7	8			9				
Nardus stricta	5		8	3	10		9		6	6			1	9		5		9	3	2	5		6	3					6	10		
Potentilla erecta	3	7	9		8									8	7				9	10					6	10		9	2	6	9	
Salix herbacea					9	9	3	2	2	7	9	4	10							9	7	8	2	8	2	2	5	9				
Sorbus aucuparia																						10										
Trichophorum cespitosum																																
Vaccinium myrtillus		10	3	2	8	2	2	2	3	3	2	9	2	8					8	2	4	10	3	7	2	5	5	10	3	8		
Vaccinium vitis-idaea				9	8	5	10	7	6	7	5	7	10								6	6	7	8	10	4	8					
Viola palustris																																
Viola riviniana																																
Bryophytes	2	2	2	2	1	2	2	2	2	3	1	2	2	2	5	2	2	2	2	2	2	1	2	1	2	2	5	8	2	2	2	2
Lichens (*Cladonia* spp.)	6	2	5	7	2	2	2	4	2	7	7	2	3	7	2	4	2	4	8	8	2	2	5	8	9	9	2	2	6	4	7	3
Lichen (*Cetraria islandica*)																																
Bare Rock	6	2	7	7	4	8	2	4	8	7	5	2	3	7	1	4	2	4	10	8	3	4	5	8	9	9	2	1	6	4	7	3
Bare Soil	9	2																									2					

Appendix 4.1 - Nested Quadrat Data
UI0a Sample Stands
Second survey - 09/06/1998
Enclosure 3

SPECIES	QUADRATS 1 - 32 (the values in the table represent the scale at which individual species were first located within a particular quadrat)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Agrostis capillaris & A. vinealis	1	1	1	3	2	2	2	2	2	1	2	2	2	1	6	2	1	2	1	2	2	2	1	2	2	2	5	8	2	1	1	2
Alchemilla alpina	5	9	2	3	8	9	7	1	3	2	8	2	9	6	7	5	10	8	9	10	2	1	4	7	2	2	4	8	9	8	3	6
Anthoxanthum odoratum	4	9		9	10	10	8	4	7	3	10			7	8	5	6	9	5	10		10	3	7	2	3	10	8	10	6	4	7
Blechnum spicant																10																
Campanula rotundifolia																																
Carex bigelowii	9	3	2	1	1	4	4	3	3	2	5	2	1	3	6			10	3	5	5	3	5	6	3	4	6	8	2	3	8	
Carex binervis																																
Carex panicea		8	7	10	7	2	8	3		9	1	10		9					10	9									10	9		
Carex pilulifera	3	5	2	4	4	2	7	2	8	2	6	6		[illegible]	7	3	9	2	7	10	6		5	4	5	3	8	10		3	7	8
Cerastium fontanum																																
Deschampsia flexuosa			8	2	10	10		9	2	2		5	10						10	1		10	7	5				9				
Diphasiastrum alpinum																																
Empetrum nigrum	9		5		9	6	10	8	7	8	4	10	9	10					9	8	2		8	7				8			9	
Euphrasia officinalis agg.																									4							
Festuca ovina/vivipara	2	3	2	2	2	5	2	2	2	2	2	2	9	3	6	2	2	1	2	2	4	3	2	1	1	1	4	8	3	2	2	1
Galium saxatile	2	8	2	2	4	2	8	2	2	2	2	5	2	2	7	3	4	2	2	2	6	9	2	2	4	4	4	7	2	2	2	2
Huperzia selago	8	9		8								10			10		6					8										
Juncus squarrosus	6	10	10											8	10	9	5	8	9												9	4
Luzula multiflora								10									9							7	9					8		9
Nardus stricta	4	10	8	3		10	9		8	7				8	10	5	8	8	10	2	4		3	5				10		6	8	10
Potentilla erecta	9	5	9		8									10	8	10			9						7	10		8	10	2	6	
Salix herbacea				10	9	2	3	3	5	4	6	2	9							8	6	8	5	7	7	6	6	8				
Sorbus aucuparia									10													10							10			
Trichophorum cespitosum															10						2											
Vaccinium myrtillus		10	2	2	7	1	2	3	1	2	2	5	2	8			6	9	6	4	1	6	4	2	2	2	5	8	2	5		
Vaccinium vitis-idaea				9	7	5	8	6	2	2	4	5	10							10	2	2	8	7		2	5					
Viola palustris																																
Viola riviniana																																
Bryophytes	2	4	2	2	2	2	1	2	2	2	2	2	2	2	6	1	2	2	2	2	2	2	2	2	2	2	2	7	1	2	2	2
Lichens (*Cladonia* spp.)	9	2	6	8	3	3	3	7	2	6	4	2	9	2	6	4	5	4	10	8	7	2		6	4	9	4	10	7	10	2	7
Lichen (*Cetraria islandica*)																																
Bare Rock	6	2	7	7	4	8	4	4	5	6	2	5	2	10	1	7	5	9		8	6	5	8	8	10	9	1	1	2	10	5	7
Bare Soil	9	2													6	9	10	8									7				7	

Appendix 4.2 - Quadrat data transferred into a two-dimensional matrix of species x scale
U5c Sample stands

Enclosure 1

Species	Scale 1 - 10 (the matrix components are the number of nests in which each species was recorded at each scale)																			
	1994										1998									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
Agrostis capillaris	12	28	31	31	31	32	32	32	32	32	12	27	27	30	32	32	32	32	32	32
Alchemilla alpina	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
Alchemilla glabra	0	0	0	0	1	1	1	1	1	5	0	0	0	0	0	1	2	3	3	5
Anemone nemorosa	0	1	1	1	1	1	1	3	7	8	0	13	18	24	29	30	31	31	32	32
Anthoxanthum odoratum	2	16	25	28	31	31	32	32	32	32	2	18	19	27	29	30	31	32	32	32
Blechnum spicant	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanula rotundifolia	0	0	1	1	3	3	3	3	5	6	0	0	1	1	2	3	4	5	6	7
Carex binervis	1	3	9	12	16	19	22	25	26	29	0	3	6	10	17	20	22	26	27	29
Carex echinata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex hostiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex nigra	0	3	4	5	7	9	10	12	14	14	3	7	8	10	12	12	13	14	16	19
Carex pallescens	0	0	0	0	0	0	2	2	3	5	0	0	0	0	0	0	1	2	3	4
Carex panicea	2	9	13	16	20	21	22	23	24	24	1	6	8	12	16	19	20	21	23	25
Carex pilulifera	2	7	9	10	11	12	17	19	22	27	1	9	11	14	16	18	19	23	25	25
Carex pulicaris	0	1	3	5	7	7	10	13	15	18	0	1	3	5	8	9	11	13	14	15
Carex viridula ssp. oedocarpa	1	1	1	1	2	3	4	4	6	6	0	0	0	0	1	2	2	3	6	6
Cerastium fontanum	0	0	0	0	0	1	1	1	3	5	0	1	1	1	1	1	2	3	3	5
Crepis paludosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Danthonia decumbens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deschampsia cespitosa	0	2	3	3	8	8	11	13	18	23	0	1	1	1	4	11	15	21	24	26
Deschampsia flexuosa	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Eriophorum angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphrasia officinalis agg.	0	0	0	1	1	1	1	3	4	4	0	0	0	0	0	0	0	0	1	2
Festuca ovina/vivipara	3	19	24	26	28	31	32	32	32	32	1	17	20	25	29	31	32	32	32	32
Festuca rubra	0	0	1	1	2	5	10	13	15	18	0	4	5	9	10	11	12	12	15	18
Galium saxatile	0	14	17	20	22	24	26	28	30	31	0	19	21	23	24	25	28	28	29	31
Juncus bulbosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus effusus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus squarrosus	0	0	0	0	0	1	1	3	3	5	0	0	0	0	0	0	0	3	3	4
Leontodon autumnalis	0	0	0	0	0	0	0	1	1	3	0	0	0	0	0	0	0	2	2	4
Luzula multiflora	0	1	2	2	3	5	7	10	13	19	0	4	6	6	9	12	14	19	22	25
Molinia caerulea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nardus stricta	8	13	23	26	29	30	31	32	32	32	9	12	16	18	26	29	31	32	32	32
Narthecium ossifragum	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	2
Oreopteris limbosperma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxalis acetosella	0	0	0	1	2	2	4	4	4	4	0	0	0	1	1	1	2	3	3	4
Pinguicula vulgaris	0	0	0	0	1	1	1	1	1	3	0	0	0	0	0	0	0	0	0	0
Plantago lanceolata	0	0	0	0	1	2	2	3	4	8	0	0	0	0	0	1	1	1	3	5
Persicaria vivipara	0	0	1	1	3	6	8	9	10	15	0	1	2	2	3	5	6	9	10	15
Potentilla erecta	0	0	3	5	10	17	22	25	29	31	0	3	4	4	9	14	20	21	26	27
Prunella vulgaris	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Ranunculus acris	0	1	2	5	9	13	17	18	19	22	0	5	7	8	10	15	17	18	20	21
Rumex acetosa	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	2	3	3
Selaginella selaginoides	0	0	0	0	0	0	0	1	1	3	0	0	0	1	1	1	1	2	3	3
Sorbus aucuparia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taraxacum agg.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thymus polytrichus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Trichophorum cespitosum	0	1	1	1	1	1	1	1	2	6	0	1	1	1	1	1	1	1	2	4
Vaccinium myrtillus	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	2
Veronica officinalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Viola palustris	0	0	0	0	0	0	0	1	1	2	1	7	11	17	17	19	23	28	29	30
Viola riviniana	0	11	15	19	21	25	27	27	31	31	0	4	5	6	9	10	12	14	15	16
Bryophytes (excluding *Sphagnum*)	1	31	32	32	32	32	32	32	32	32	2	32	32	32	32	32	32	32	32	32
Sphagnum spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lichens (*Cladonia* spp.)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Bare Rock	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	1
Bare Soil	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	2	4	4	5	6

Appendix 4.2 - Quadrat data transferred into a two-dimensional matrix of species x scale
U5c Sample stands

Enclosure 2

Species	Scale 1 - 10 (the matrix components are the number of nests in which each species was recorded at each scale)																			
	1994										1998									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
Agrostis capillaris	4	18	24	24	26	28	29	30	32	32	7	22	26	28	30	32	32	32	32	32
Alchemilla alpina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alchemilla glabra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anemone nemorosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthoxanthum odoratum	2	9	14	16	18	23	27	31	31	32	0	7	9	12	17	24	28	30	32	32
Blechnum spicant	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1
Campanula rotundifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex binervis	1	6	8	10	11	18	23	27	28	30	1	5	5	6	13	20	21	26	27	29
Carex echinata	2	3	5	5	5	5	6	6	8	11	0	1	3	3	3	5	5	5	5	6
Carex hostiana	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Carex nigra	0	3	4	6	9	9	11	12	16	20	3	7	8	12	16	17	17	18	19	24
Carex pallescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex panicea	2	7	11	11	14	17	17	21	21	25	2	7	9	14	16	20	20	21	23	23
Carex pilulifera	1	5	6	7	9	10	15	16	18	19	1	9	10	11	11	12	15	16	16	19
Carex pulicaris	0	0	0	0	0	0	0	0	1	3	0	1	1	1	2	3	4	5	5	6
Carex viridula ssp. *oedocarpa*	0	1	1	1	1	1	1	1	1	2	0	0	1	1	1	1	1	1	1	2
Cerastium fontanum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crepis paludosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2
Danthonia decumbens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deschampsia cespitosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deschampsia flexuosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Eriophorum angustifolium	0	2	2	2	3	4	6	6	9	10	1	1	1	1	1	1	2	3	7	11
Euphrasia officinalis agg.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Festuca ovina/vivipara	3	18	22	25	27	28	30	32	32	32	2	19	21	24	29	30	31	32	32	32
Festuca rubra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium saxatile	1	16	21	22	24	24	27	28	29	30	1	15	17	20	22	23	26	29	30	31
Juncus bulbosus	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0
Juncus effusus	0	1	1	1	1	1	1	1	1	4	0	1	1	1	1	1	1	1	1	3
Juncus squarrosus	0	1	2	3	3	7	11	14	14	15	0	1	1	4	6	8	9	13	14	15
Leontodon autumnalis	0	0	1	1	2	4	5	6	7	9	0	0	0	0	0	2	7	10	10	12
Luzula multiflora	0	0	0	0	1	1	2	2	3	9	0	0	0	0	0	1	5	8	10	18
Molinia caerulea	1	3	4	4	4	4	4	7	7	9	1	4	4	5	5	5	6	6	6	10
Nardus stricta	9	20	25	31	32	32	32	32	32	32	11	18	22	25	28	32	32	32	32	32
Narthecium ossifragum	0	7	7	8	8	11	12	13	13	15	0	6	7	10	10	10	11	12	13	16
Oreopteris limbosperma	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1
Oxalis acetosella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinguicula vulgaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Plantago lanceolata	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1
Persicaria vivipara	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla erecta	2	8	14	19	22	24	29	32	32	32	0	10	13	18	23	27	30	31	31	32
Prunella vulgaris	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Ranunculus acris	0	0	0	0	0	1	1	2	2	6	0	0	0	0	0	1	3	3	4	8
Rumex acetosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Selaginella selaginoides	0	0	0	0	0	1	2	3	3	5	0	0	0	0	1	1	1	1	2	2
Sorbus aucuparia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Taraxacum agg.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thymus polytrichus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichophorum cespitosum	2	3	4	5	7	9	9	15	18	18	2	5	8	8	8	9	12	16	17	18
Vaccinium myrtillus	1	4	5	6	6	8	10	13	13	14	0	1	1	3	3	8	9	11	14	14
Veronica officinalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola palustris	0	7	11	12	14	16	17	17	17	21	0	5	7	9	11	17	19	20	20	21
Viola riviniana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bryophytes (excluding *Sphagnum*)	1	31	32	32	32	32	32	32	32	32	2	32	32	32	32	32	32	32	32	32
Sphagnum spp.	0	4	4	6	7	9	11	11	13	15	0	3	4	7	10	10	11	13	15	15
Lichens (*Cladonia* spp.)	0	0	0	0	0	0	0	1	2	5	0	0	0	0	0	0	0	0	1	1
Bare Rock	0	0	0	0	0	0	0	1	2	6	0	0	0	0	0	0	0	0	4	7
Bare Soil	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 4.2 - Quadrat data transferred into a two-dimensional matrix of species x scale
U5c Sample stands

Enclosure 3

Species	Scale 1 - 10 (the matrix components are the number of nests in which each species was recorded at each scale)																				
	1994											1998									
	1	2	3	4	5	6	7	8	9	10		1	2	3	4	5	6	7	8	9	10
Agrostis capillaris	3	26	30	32	32	32	32	32	32	32		6	27	31	31	32	32	32	32	32	32
Alchemilla alpina	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Alchemilla glabra	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Anemone nemorosa	0	1	2	2	2	2	2	2	2	2		0	1	1	1	2	2	3	3	3	1
Anthoxanthum odoratum	0	4	6	9	13	15	18	26	27	30		0	4	5	5	11	12	16	20	22	27
Blechnum spicant	0	0	0	0	0	0	0	0	0	1		0	0	0	0	0	0	0	0	1	2
Campanula rotundifolia	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Carex binervis	0	0	0	0	0	1	2	5	6	7		0	0	0	0	1	2	3	5	7	11
Carex echinata	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Carex hostiana	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Carex nigra	1	7	9	10	11	16	18	20	23	23		1	8	10	11	12	13	14	17	20	23
Carex pallescens	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Carex panicea	1	4	5	12	16	21	26	28	31	32		0	5	6	12	19	21	24	27	30	30
Carex pilulifera	5	17	19	24	26	28	30	30	32	32		2	11	15	20	23	27	31	32	32	32
Carex pulicaris	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Carex viridula ssp. *oedocarpa*	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Cerastium fontanum	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Crepis paludosa	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Danthonia decumbens	0	1	1	3	4	4	5	9	15	21		0	1	1	1	3	5	6	7	13	21
Deschampsia cespitosa	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Deschampsia flexuosa	2	2	2	2	3	5	6	11	16	23		1	1	1	2	3	6	9	14	18	21
Eriophorum angustifolium	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Euphrasia officinalis agg.	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Festuca ovina/vivipara	7	23	26	28	28	30	30	31	32	32		6	29	32	32	32	32	32	32	32	32
Festuca rubra	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Galium saxatile	1	29	32	32	32	32	32	32	32	32		0	27	28	30	31	32	32	32	32	32
Juncus bulbosus	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Juncus effusus	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Juncus squarrosus	0	0	0	0	1	1	3	3	4	9		0	1	1	1	1	2	2	3	6	9
Leontodon autumnalis	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Luzula multiflora	0	4	4	7	11	17	20	25	28	32		2	4	4	10	14	21	25	28	30	31
Molinia caerulea	0	0	0	0	0	0	0	0	0	1		0	0	0	0	0	0	0	0	0	0
Nardus stricta	6	14	22	27	32	32	32	32	32	32		8	16	21	25	28	32	32	32	32	32
Narthecium ossifragum	2	4	5	5	5	6	6	7	8	13		0	5	5	5	5	5	5	6	7	13
Oreopteris limbosperma	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Oxalis acetosella	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Pinguicula vulgaris	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Plantago lanceolata	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Persicaria vivipara	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Potentilla erecta	2	11	15	21	24	28	32	32	32	32		2	14	17	20	26	31	32	32	32	32
Prunella vulgaris	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Ranunculus acris	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Rumex acetosa	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Selaginella selaginoides	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Sorbus aucuparia	0	0	0	0	0	0	0	0	1	2		0	0	0	0	0	0	0	0	0	2
Taraxacum agg.	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Thymus polytrichus	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Trichophorum cespitosum	1	4	6	7	8	12	14	19	20	24		0	5	8	9	11	11	14	20	22	26
Vaccinium myrtillus	0	2	4	5	8	8	9	12	13	17		1	7	7	7	9	10	11	12	18	20
Veronica officinalis	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Viola palustris	0	0	0	0	0	0	0	0	0	1		0	0	0	0	0	0	0	0	0	1
Viola riviniana	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Bryophytes (excluding *Sphagnum*	1	32	32	32	32	32	32	32	32	32		3	32	32	32	32	32	32	32	32	32
Sphagnum spp.	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Lichens (*Cladonia* spp.)	0	0	0	1	2	2	4	6	12	15		0	0	0	0	0	0	0	0	1	2
Bare Rock	0	0	0	0	0	0	2	5	11	18		0	0	0	0	0	0	4	6	7	13
Bare Soil	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0

Appendix 4.2 - Quadrat data transferred into a two-dimensional matrix of species x scale
CG10b Sample stands

Enclosure 1

Species	Scale 1 - 10 (the matrix components are the number of nests in which each species was recorded at each scale)																			
	1995										1998									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
Achillea ptarmica	1	3	6	9	12	13	15	18	22	27	0	2	3	3	5	6	8	9	16	19
Agrostis capillaris	11	27	29	29	29	29	29	29	29	29	10	25	26	27	29	29	30	30	30	30
Alchemilla alpina	1	1	1	2	2	3	4	6	10	13	0	0	0	3	4	6	6	7	9	13
Alchemilla glabra	0	1	2	2	3	4	6	7	10	14	1	1	2	2	2	4	6	9	12	15
Anemone nemorosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthoxanthum odoratum	1	13	22	28	28	29	31	32	32	32	1	14	19	24	26	28	30	31	32	32
Bellis perennis	0	0	0	1	3	5	5	8	8	10	0	1	1	2	4	5	6	8	8	13
Betula pubescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Blechnum spicant	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanula rotundifolia	0	1	4	6	8	10	12	13	16	23	0	5	6	8	9	10	12	13	16	23
Carex bigelowii	0	0	0	0	0	1	1	1	1	1	0	0	0	1	2	2	2	2	2	2
Carex binervis	0	1	1	2	2	2	2	2	2	2	0	0	0	1	1	1	1	1	1	2
Carex capillaris	0	0	0	1	1	1	1	1	2	2	0	1	1	1	1	1	1	1	2	3
Carex flacca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex nigra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex pallescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex panicea	1	3	4	4	7	10	12	16	18	22	2	6	6	6	8	10	10	14	18	20
Carex pilulifera	1	7	8	11	15	17	21	22	27	28	0	5	7	7	9	11	19	23	26	28
Carex pulicaris	3	7	8	9	9	9	9	12	14	17	0	3	5	5	5	6	9	10	12	16
Carex viridula ssp. oedocarpa	0	0	0	0	0	1	1	2	5	6	0	1	1	1	1	2	2	2	6	8
Cerastium fontanum	0	0	1	1	1	1	2	2	3	6	0	1	2	2	2	3	5	7	8	8
Danthonia decumbens	0	0	1	1	2	2	2	3	5	5	0	0	0	0	3	3	5	5	9	12
Deschampsia cespitosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deschampsia flexuosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diphasiastrum alpinum	0	0	0	0	0	0	0	1	2	2	0	0	0	0	0	0	2	2	3	3
Euphrasia officinalis agg.	0	0	0	0	0	1	2	7	12	15	0	1	1	2	4	9	11	15	17	20
Festuca ovina/vivipara	8	31	32	32	32	32	32	32	32	32	12	31	32	32	32	32	32	32	32	32
Festuca rubra	0	1	2	2	3	3	3	8	12	16	1	3	3	3	4	5	10	16	21	25
Galium saxatile	1	25	27	28	28	28	29	29	29	30	1	26	26	29	30	30	30	30	30	30
Helictotrichon pratense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hieracium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holcus lanatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Huperzia selago	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus bulbosus	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Linum catharticum	0	1	1	1	1	2	4	5	6	7	0	1	1	1	2	2	5	6	9	11
Luzula multiflora	1	6	7	10	14	14	18	21	24	24	0	5	8	10	15	18	22	23	26	26
Lysimachia nemorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nardus stricta	0	5	7	12	15	15	19	27	29	32	1	4	6	9	14	15	22	27	30	32
Narthecium ossifragum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oreopteris limbosperma	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Oxalis acetosella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parnassia palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Phegopteris connectilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinguicula vulgaris	0	0	0	0	0	0	0	1	2	2	0	0	0	0	0	0	0	0	0	0
Plantago lanceolata	0	4	4	5	8	9	13	15	20	20	0	3	5	7	8	12	14	15	15	21
Polygala serpyllifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Persicaria vivipara	1	7	11	14	19	22	23	26	27	30	0	2	9	13	17	18	20	25	29	31
Potentilla erecta	0	8	11	13	17	22	25	28	30	30	0	5	9	16	19	22	26	27	29	31
Prunella vulgaris	0	0	0	1	2	2	2	6	10	12	0	1	2	3	5	5	6	10	11	19
Ranunculus acris	1	10	11	15	17	18	19	20	23	24	2	6	11	14	17	18	21	23	23	27
Ranunculus flammula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus repens	0	1	2	4	6	8	9	9	9	13	0	6	6	8	8	9	10	12	12	13
Rumex acetosa	0	0	0	0	1	1	1	1	1	2	0	0	0	0	1	1	1	1	1	1
Saxifraga aizoides	0	0	0	0	0	0	0	1	2	3	0	0	0	0	0	0	0	2	4	4
Saxifraga oppositifolia	0	0	0	0	0	1	2	2	2	2	0	1	1	1	1	1	2	3	3	4
Selaginella selaginoides	0	1	1	1	2	2	5	5	6	11	0	0	0	1	1	3	6	6	8	13
Silene acaulis	0	1	1	1	1	1	1	2	3	4	0	1	1	1	1	1	2	2	3	4
Sorbus aucuparia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taraxacum agg.	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	1	1	1	3	6
Thalictrum alpinum	0	1	1	2	3	3	4	4	6	7	0	1	1	1	2	2	4	4	5	9
Thymus polytrichus	1	10	11	13	16	17	18	22	24	26	1	11	16	17	16	18	21	22	27	29
Trichophorum cespitosum	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1
Trifolium repens	0	8	11	12	13	16	16	16	17	19	0	8	12	12	15	15	17	19	20	22
Vaccinium myrtillus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Veronica officinalis	0	3	3	5	6	7	7	8	12	14	0	2	5	6	6	6	8	10	13	18
Viola palustris	0	1	1	2	2	2	2	3	3	3	0	6	8	14	18	21	22	25	27	29
Viola riviniana	0	6	11	15	19	23	25	28	30	31	0	3	4	5	7	9	13	16	21	25
Bryophytes	0	32	32	32	32	32	32	32	32	32	0	32	32	32	32	32	32	32	32	32
Lichens (*Cladonia* spp.)	0	0	1	1	1	1	1	4	4	6	0	0	1	1	2	2	2	2	3	3
Bare Rock	0	0	0	0	0	0	0	2	2	5	0	0	0	0	0	0	0	1	3	6
Bare Soil	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 4.2 - Quadrat data transferred into a two-dimensional matrix of species x scale
CG10b Sample stands

Enclosure 2

Species	Scale 1 - 10 (the matrix components are the number of nests in which each species was recorded at each scale)																			
	1995										1998									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
Achillea ptarmica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrostis capillaris	5	22	28	29	30	31	31	32	32	32	6	28	29	31	32	32	32	32	32	32
Alchemilla alpina	4	19	22	25	27	31	32	32	32	32	4	15	22	25	30	30	31	32	32	32
Alchemilla glabra	0	0	0	0	0	1	1	1	1	2	0	0	0	0	0	0	1	2	2	2
Anemone nemorosa	0	0	0	2	4	6	8	13	16	21	0	2	3	3	4	4	5	5	6	9
Anthoxanthum odoratum	1	11	15	18	27	30	31	32	32	32	2	7	13	17	23	27	29	29	31	32
Bellis perennis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Betula pubescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Blechnum spicant	0	0	1	1	2	3	3	5	7	8	0	0	0	0	0	2	3	4	6	8
Campanula rotundifolia	0	3	7	12	16	18	21	25	27	30	0	3	6	6	11	13	18	23	25	29
Carex bigelowii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex binervis	0	0	0	0	0	0	0	1	1	3	0	0	0	0	0	0	1	1	1	3
Carex capillaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex flacca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex nigra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex pallescens	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	3
Carex panicea	1	3	6	8	9	11	13	16	17	21	1	4	7	8	11	13	14	17	19	23
Carex pilulifera	0	2	6	10	13	16	21	26	29	31	1	5	5	8	14	17	19	24	27	30
Carex pulicaris	1	2	5	5	6	7	9	10	10	11	0	0	1	3	4	4	7	8	10	10
Carex viridula ssp. oedocarpa	0	0	0	0	0	0	1	1	1	3	0	0	0	0	0	0	1	1	2	4
Cerastium fontanum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2
Danthonia decumbens	0	1	1	1	1	1	2	2	5	9	0	1	1	1	1	1	1	2	3	7
Deschampsia cespitosa	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	2
Deschampsia flexuosa	0	0	1	3	3	3	3	4	6	7	1	1	1	3	4	4	5	6	7	10
Diphasiastrum alpinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphrasia officinalis agg.	0	0	1	1	4	6	6	12	15	19	0	0	0	2	3	4	6	8	12	16
Festuca ovina/vivipara	12	27	29	32	32	32	32	32	32	32	7	30	30	32	32	32	32	32	32	32
Festuca rubra	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	1	2	5	9	14
Galium saxatile	1	21	23	27	30	31	32	32	32	32	1	23	24	24	29	30	32	32	32	32
Helictotrichon pratense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hieracium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holcus lanatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Huperzia selago	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
Juncus bulbosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linum catharticum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Luzula multiflora	0	3	4	4	6	9	15	19	24	27	1	3	5	5	7	8	12	16	19	25
Lysimachia nemorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nardus stricta	3	6	9	10	14	18	24	31	32	32	4	6	7	11	14	16	21	28	32	32
Narthecium ossifragum	0	1	1	1	1	2	3	3	4	7	0	1	1	2	2	3	4	4	5	8
Oreopteris limbosperma	0	0	0	1	1	3	4	5	5	9	0	1	1	1	1	2	4	5	5	7
Oxalis acetosella	0	1	1	1	1	1	1	1	2	5	0	1	1	1	1	2	2	4	5	6
Parnassia palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phegopteris connectilis	0	0	0	0	0	1	1	2	2	3	0	0	0	0	0	1	2	3	3	4
Pinguicula vulgaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plantago lanceolata	0	2	6	9	13	14	15	19	21	22	0	6	10	10	11	15	17	21	22	25
Polygala serpyllifolia	0	0	0	0	1	1	1	2	3	6	0	1	1	1	1	3	3	3	4	4
Persicaria vivipara	0	0	2	3	5	5	7	8	13	17	0	0	2	2	4	5	6	12	16	19
Potentilla erecta	2	11	15	17	24	27	32	32	32	32	1	9	12	12	19	24	31	32	32	32
Prunella vulgaris	0	0	0	1	1	1	1	2	2	2	0	2	2	2	3	3	3	3	3	5
Ranunculus acris	0	2	3	8	9	12	15	16	18	21	0	5	6	9	13	15	17	19	21	24
Ranunculus flammula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus repens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex acetosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saxifraga aizoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saxifraga oppositifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Selaginella selaginoides	0	2	2	3	4	4	5	8	9	15	0	2	2	3	5	9	13	14	16	21
Silene acaulis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sorbus aucuparia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2
Taraxacum agg.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalictrum alpinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thymus polytrichus	1	10	11	14	16	16	17	18	21	23	0	15	15	16	17	18	18	20	21	24
Trichophorum cespitosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium repens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium myrtillus	0	10	12	16	21	22	24	26	27	28	0	8	10	14	15	18	21	23	26	28
Veronica officinalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola palustris	0	0	0	1	1	1	2	3	9	10	0	2	3	3	4	4	6	8	15	17
Viola riviniana	0	4	5	5	9	13	15	16	17	22	0	2	3	4	9	12	13	17	19	23
Bryophytes	1	32	32	32	32	32	32	32	32	32	2	32	32	32	32	32	32	32	32	32
Lichens (Cladonia spp.)	0	9	12	15	20	20	24	27	29	30	0	3	4	4	5	6	7	7	8	11
Bare Rock	0	8	12	15	21	21	25	29	31	31	0	4	7	12	16	20	25	29	30	30
Bare Soil	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 4.2 - Quadrat data transferred into a two-dimensional matrix of species x scale
CG10b Sample stands

Enclosure 3

Species	Scale 1 - 10 (the matrix components are the number of nests in which each species was recorded at each scale)																			
	1996										1998									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
Achillea ptarmica	0	0	0	0	1	2	5	5	6	10	0	0	1	2	2	4	8	9	11	15
Agrostis capillaris	13	30	31	32	32	32	32	32	32	32	4	30	31	32	32	32	32	32	32	32
Alchemilla alpina	0	0	0	0	0	0	0	1	2	3	0	0	0	0	0	0	0	1	1	3
Alchemilla glabra	0	2	2	2	3	3	4	7	9	13	0	0	0	0	0	0	3	7	12	15
Anemone nemorosa	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	2	2
Anthoxanthum odoratum	3	13	16	21	28	29	30	31	31	31	2	19	22	26	28	30	32	32	32	32
Bellis perennis	0	0	2	3	4	7	8	13	16	21	0	3	3	3	6	7	10	16	20	26
Betula pubescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Blechnum spicant	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanula rotundifolia	0	6	9	12	15	18	20	23	27	30	0	2	4	6	10	14	15	20	22	27
Carex bigelowii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex binervis	0	0	1	1	2	2	3	5	5	8	0	0	0	1	2	2	2	4	6	11
Carex capillaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex flacca	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Carex nigra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Carex pallescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	5
Carex panicea	1	7	7	11	14	16	17	19	27	20	0	4	7	9	13	16	22	24	28	31
Carex pilulifera	1	6	8	13	21	25	29	30	30	32	3	7	9	12	18	20	23	27	29	30
Carex pulicaris	1	2	2	3	5	6	7	11	13	18	1	4	4	5	8	10	11	13	14	22
Carex viridula ssp. *oedocarpa*	0	0	1	1	2	2	2	2	5	9	0	0	0	0	1	1	1	4	8	11
Cerastium fontanum	0	1	2	2	2	2	4	5	6	7	0	0	1	3	5	5	6	8	11	14
Danthonia decumbens	0	1	2	2	3	4	4	5	6	10	0	2	2	2	3	3	6	10	12	22
Deschampsia cespitosa	0	0	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	2	3	5
Deschampsia flexuosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diphasiastrum alpinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphrasia officinalis agg.	0	0	0	1	2	2	3	5	10	18	0	4	6	7	12	15	17	22	24	27
Festuca ovina/vivipara	7	28	31	31	32	32	32	32	32	32	8	27	29	32	32	32	32	32	32	32
Festuca rubra	0	0	0	0	0	1	2	3	3	6	0	1	1	3	4	6	6	11	19	26
Galium saxatile	0	23	23	24	26	27	28	28	28	30	0	22	22	23	24	25	27	27	28	28
Helictotrichon pratense	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1
Hieracium sp.	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Holcus lanatus	0	0	0	0	1	1	1	1	1	1	0	1	2	2	2	3	4	4	4	8
Huperzia selago	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus bulbosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linum catharticum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Luzula multiflora	0	3	4	5	7	10	11	17	18	23	0	9	11	15	20	21	22	26	27	30
Lysimachia nemorum	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1
Nardus stricta	3	8	13	22	25	28	31	32	32	32	2	8	12	17	22	26	30	32	32	32
Narthecium ossifragum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oreopteris limbosperma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxalis acetosella	0	2	2	2	3	3	3	3	4	5	0	1	2	3	3	3	3	3	4	5
Parnassia palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phegopteris connectilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinguicula vulgaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Plantago lanceolata	1	12	14	15	20	21	24	28	30	32	0	8	11	16	20	23	25	27	30	32
Polygala serpyllifolia	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0
Persicaria vivipara	0	8	9	13	17	21	23	25	28	30	0	4	8	13	16	22	27	28	29	31
Potentilla erecta	0	1	1	2	4	6	9	10	12	16	0	3	6	9	11	13	15	16	19	23
Prunella vulgaris	0	0	1	4	6	8	13	18	20	25	0	1	2	3	4	8	14	15	21	27
Ranunculus acris	1	20	28	29	29	29	29	30	32	32	3	23	26	27	28	28	28	31	31	31
Ranunculus flammula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus repens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex acetosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saxifraga aizoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saxifraga oppositifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Selaginella selaginoides	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1
Silene acaulis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sorbus aucuparia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taraxacum agg.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Thalictrum alpinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thymus polytrichus	0	15	19	21	24	26	28	30	31	31	2	16	20	23	25	27	29	30	31	31
Trichophorum cespitosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium repens	0	8	11	14	21	23	26	28	30	31	1	10	14	20	22	24	25	26	30	31
Vaccinium myrtillus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Veronica officinalis	1	1	1	1	2	2	3	4	4	6	0	1	2	2	2	3	3	5	5	7
Viola palustris	0	5	6	9	12	16	18	21	22	28	0	4	5	5	6	12	19	22	25	25
Viola riviniana	0	1	2	4	6	7	9	14	18	19	0	2	3	3	8	9	11	16	18	23
Bryophytes	0	30	31	32	32	32	32	32	32	32	2	32	32	32	32	32	32	32	32	32
Lichens (*Cladonia* spp.)	0	0	1	1	1	3	6	11	15	16	0	1	1	1	1	1	1	1	1	2
Bare Rock	0	0	1	1	1	2	5	10	14	16	1	1	1	1	2	2	5	10	12	13
Bare Soil	0	0	0	0	0	0	0	0	0	0	0	1	2	2	3	6	12	19	23	29

Appendix 4.2 - Quadrat data transferred into a two-dimensional matrix of species x scale
U10a Sample Stands

Enclosure 1

Species	Scale 1 - 10 (the matrix components are the number of nests in which each species was recorded at each scale)																				
	1995											1998									
	1	2	3	4	5	6	7	8	9	10		1	2	3	4	5	6	7	8	9	10
Agrostis capillaris & A. vinealis	7	24	29	30	32	32	32	32	32	32		3	29	29	31	32	32	32	32	32	32
Alchemilla alpina	1	3	5	5	7	8	9	12	16	20		0	4	5	5	6	7	8	12	14	17
Anthoxanthum odoratum	0	4	6	7	10	13	15	20	23	31		1	6	10	13	15	17	20	23	25	29
Blechnum spicant	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Campanula rotundifolia	0	3	4	4	4	5	6	7	7	7		0	2	3	4	4	5	6	7	8	8
Carex bigelowii	1	3	3	3	5	5	6	7	8	11		1	1	1	3	5	5	5	8	8	14
Carex binervis	0	1	1	1	1	2	3	4	5	9		0	0	1	1	1	1	1	1	1	2
Carex panicea	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Carex pilulifera	0	11	15	16	23	27	29	30	32	32		0	12	15	17	25	28	28	31	32	32
Cerastium fontanum	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Deschampsia flexuosa	1	5	8	10	12	12	15	17	21	31		2	9	10	12	12	16	20	22	24	30
Diphasiastrum alpinum	1	7	9	9	14	17	18	18	18	18		1	12	13	14	16	17	18	18	18	18
Empetrum nigrum	0	4	4	4	5	5	8	9	12	14		1	4	4	4	5	6	8	9	10	14
Euphrasia officinalis agg.	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Festuca ovina/vivipara	9	23	25	27	30	31	32	32	32	32		8	24	25	29	31	31	32	32	32	32
Galium saxatile	1	18	22	28	30	30	31	32	32	32		0	24	28	30	30	31	31	32	32	32
Huperzia selago	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Juncus squarrosus	0	0	0	1	2	2	2	3	4	7		0	1	1	1	1	2	2	3	3	7
Luzula multiflora	0	1	2	3	7	9	12	16	19	28		0	0	1	2	4	4	14	17	20	26
Nardus stricta	6	8	13	14	20	24	28	30	21	32		6	10	12	15	22	24	30	31	31	32
Potentilla erecta	0	0	0	0	2	4	4	4	7	13		0	0	0	1	2	3	3	5	9	12
Salix herbacea	0	0	1	1	1	1	1	3	3	3		0	0	0	0	0	1	2	3	3	3
Sorbus aucuparia	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Trichophorum cespitosum	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Vaccinium myrtillus	1	28	31	32	32	32	32	32	32	32		6	28	31	31	32	32	32	32	32	32
Vaccinium vitis-idaea	0	4	9	12	18	23	28	30	30	30		0	6	9	20	25	28	30	31	32	32
Viola palustris	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	1	2
Viola riviniana	0	0	0	0	0	0	0	0	0	1		0	0	0	0	0	0	0	0	0	0
Bryophytes	3	31	32	32	32	32	32	32	32	32		3	32	32	32	32	32	32	32	32	32
	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Lichens (*Cladonia* spp.)	0	18	23	26	29	30	31	32	32	32		0	17	18	22	26	26	28	31	31	32
Lichen (*Cetraria islandica*)	0	0	0	0	0	0	0	0	0	0		0	0	0	0	1	1	1	1	1	2
Bare Rock	1	3	4	5	6	10	14	18	22	25		0	1	1	2	4	5	9	12	18	24
Bare Soil	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0

Appendix 4.2 - Quadrat data transferred into a two-dimensional matrix of species x scale
U10a Sample Stands

Enclosure 2

Species	Scale 1 - 10 (the matrix components are the number of nests in which each species was recorded at each scale)																				
	1996											1990									
	1	2	3	4	5	6	7	8	9	10		1	2	3	4	5	6	7	8	9	10
Agrostis capillaris & A. vinealis	9	26	30	31	31	31	31	31	32	32		5	20	26	28	29	30	31	32	32	32
Alchemilla alpina	1	11	19	21	22	25	26	29	31	31		2	15	18	20	21	25	27	29	31	31
Anthoxanthum odoratum	0	5	5	5	7	10	11	17	21	23		1	3	4	4	6	8	10	13	19	24
Blechnum spicant	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Campanula rotundifolia	0	0	0	0	2	2	2	2	3	4		0	0	0	0	3	3	5	6	9	13
Carex bigelowii	5	15	17	17	18	18	19	21	24	24		4	9	13	15	17	18	19	22	24	24
Carex binervis	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Carex panicea	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Carex pilulifera	2	4	5	8	10	15	19	22	25	26		0	4	4	5	11	16	17	20	22	25
Cerastium fontanum	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Deschampsia flexuosa	1	4	8	9	11	11	18	24	24	28		2	8	12	14	18	22	25	29	30	32
Diphasiastrum alpinum	1	9	13	15	19	22	24	28	30	31		1	12	14	16	19	22	24	26	27	28
Empetrum nigrum	0	5	5	5	7	9	12	13	16	22		2	5	6	6	7	8	11	13	16	20
Euphrasia officinalis agg.	0	0	1	1	1	1	1	1	1	1		0	0	0	0	0	0	0	0	0	0
Festuca ovina/vivipara	5	21	27	29	31	31	32	32	32	32		3	20	25	29	30	31	32	32	32	32
Galium saxatile	0	26	28	28	31	31	31	32	32	32		0	15	19	23	25	30	32	32	32	32
Huperzia selago	0	0	0	0	0	0	1	3	3	5		0	0	0	0	1	1	1	3	4	8
Juncus squarrosus	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Luzula multiflora	0	1	1	2	2	4	6	9	11	17		0	1	2	2	3	4	5	6	10	13
Nardus stricta	1	2	2	4	6	9	11	17	22	26		2	2	4	4	7	7	13	20	22	26
Potentilla erecta	0	0	0	0	0	0	0	1	2	2		0	0	0	0	0	0	0	0	2	2
Salix herbacea	0	3	3	4	6	6	6	6	8	11		0	1	3	5	5	5	5	6	8	10
Sorbus aucuparia	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Trichophorum cespitosum	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Vaccinium myrtillus	5	23	30	32	32	32	32	32	32	32		6	24	31	32	32	32	32	32	32	32
Vaccinium vitis-idaea	0	4	7	8	12	17	24	29	31	32		0	5	6	6	13	17	22	26	31	32
Viola palustris	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Viola riviniana	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Bryophytes	2	32	32	32	32	32	32	32	32	32		4	32	32	32	32	32	32	32	32	32
	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Lichens (*Cladonia* spp.)	0	11	13	16	24	26	30	30	32	32		0	7	8	11	16	22	24	27	32	32
Lichen (*Cetraria islandica*)	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Bare Rock	0	1	1	2	3	3	4	6	8	16		0	2	2	3	4	4	4	5	8	13
Bare Soil	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0

Appendix 4.2 - Quadrat data transferred into a two-dimensional matrix of species x scale
U10a Sample Stands

Enclosure 3

Species	Scale 1 - 10 (the matrix components are the number of nests in which each species was recorded at each scale)																				
	1995											1998									
	1	2	3	4	5	6	7	8	9	10		1	2	3	4	5	6	7	8	9	10
Agrostis capillaris & A. vinealis	15	29	30	30	30	31	31	31	32	32		10	28	29	29	30	31	31	32	32	32
Alchemilla alpina	3	9	9	14	16	16	19	26	29	31		2	8	11	13	15	17	20	25	30	32
Anthoxanthum odoratum	1	4	5	5	6	10	14	19	23	27		0	1	4	7	9	11	15	18	21	28
Blechnum spicant	0	0	0	0	0	0	0	0	0	1		0	0	0	0	0	0	0	0	0	1
Campanula rotundifolia	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Carex bigelowii	0	6	13	19	24	24	25	26	27	29		3	7	15	18	22	25	25	27	28	29
Carex binervis	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Carex panicea	0	2	2	3	3	3	5	6	8	11		1	2	3	3	3	3	5	7	11	15
Carex pilulifera	0	9	14	17	21	25	26	27	30	32		0	5	10	13	16	19	23	26	27	29
Cerastium fontanum	0	0	0	0	0	0	1	2	3	3		0	0	0	0	0	0	0	0	0	0
Deschampsia flexuosa	0	1	1	1	1	2	2	4	6	11		1	4	4	4	6	6	7	8	10	15
Diphasiastrum alpinum	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Empetrum nigrum	0	1	1	1	2	4	8	9	13	15		0	1	1	2	3	4	6	11	16	19
Euphrasia officinalis agg.	0	2	2	2	2	2	2	2	2	7		0	0	0	1	1	1	1	1	1	1
Festuca ovina/vivipara	5	19	24	30	31	31	31	32	32	32		5	22	26	28	29	30	30	31	32	32
Galium saxatile	1	17	21	21	23	24	26	31	32	32		0	19	20	25	26	27	29	31	32	32
Huperzia selago	0	0	1	1	1	2	2	2	3	7		0	0	0	0	0	1	1	4	5	7
Juncus squarrosus	0	0	1	1	2	4	5	6	7	10		0	0	0	1	2	3	3	5	8	11
Luzula multiflora	0	0	0	0	0	1	2	4	6	9		0	0	0	0	0	0	1	2	5	6
Nardus stricta	1	2	5	5	8	12	12	13	16	18		0	1	3	5	7	8	9	15	16	22
Potentilla erecta	0	1	2	2	2	4	6	8	12	14		0	1	1	1	2	3	4	7	10	14
Salix herbacea	0	5	6	7	8	8	10	12	17	18		0	2	4	5	7	11	13	16	18	19
Sorbus aucuparia	0	0	0	0	0	0	0	0	0	1		0	0	0	0	0	0	0	0	0	3
Trichophorum cespitosum	0	0	0	0	0	0	0	0	0	0		0	1	1	1	1	1	1	1	1	2
Vaccinium myrtillus	0	9	14	15	17	17	17	21	22	25		3	13	14	16	19	21	22	25	26	27
Vaccinium vitis-idaea	0	0	0	1	3	6	10	13	14	17		0	5	5	6	9	10	12	14	15	17
Viola palustris	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Viola riviniana	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Bryophytes	4	29	29	29	31	31	31	32	32	32		3	29	29	30	30	31	32	32	32	32
	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Lichens (*Cladonia* spp.)	0	13	15	19	21	23	27	30	32	32		0	6	9	14	15	19	23	25	28	31
Lichen (*Cetraria islandica*)	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Bare Rock	2	7	10	16	18	20	25	29	31	32		3	7	7	10	15	18	22	26	28	31
Bare Soil	0	2	2	2	2	2	2	2	3	3		0	1	1	1	1	2	4	5	7	8

Appendix 4.3 - A comparison of the absolute change values at each individual scale, with the absolute change at the optimum scale
U5c *Nardus stricta - Galium saxatile* grassland (*Carex panicea - Viola riviniana* sub-community)

Enclosure 1 (Annual stocking rate of 0.074 LU ha^{-1})

Change in Frequency	**All Scales**										**Optimum Scale**	**Frequency at Optimum Scale**		
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**(set in 1994)**	**1994**	**1998**	**Change**
Anemone nemorosa	0	12	17	23	28	29	30	28	25	24	10	8	32	**24**
Luzula multiflora	0	3	4	4	6	7	7	9	9	6	9	13	22	**9**
Deschampsia cespitosa	0	-1	-2	-2	-4	3	4	8	6	3	9	18	24	**6**
Bare Soil	0	1	1	1	2	2	4	4	5	6	10	0	6	**6**
Carex nigra	3	4	4	5	5	3	3	2	2	5	10	14	19	**5**
Galium saxatile	0	5	4	3	2	1	2	0	-1	0	3	17	21	**4**
Anthoxanthum odoratum	0	2	-6	-1	-2	-1	-1	0	0	0	2	16	18	2
Carex binervis	-1	1	-2	-1	2	2	1	2	1	0	5	16	18	2
Carex pilulifera	-1	2	2	4	5	6	2	4	3	-2	7	17	19	2
Narthecium ossifragum	0	1	1	1	1	1	1	1	1	2	10	0	2	2
Viola spp.	1	0	1	3	3	1	0	2	1	1	3	15	16	1
Alchemilla alpina	0	0	0	0	0	0	0	0	0	1	10	0	1	1
Campanula rotundifolia	0	0	0	0	-1	0	1	2	1	1	10	6	7	1
Leontodon autumnalis	0	0	0	0	0	0	0	1	1	1	10	3	4	1
Rumex acetosa	0	0	0	0	0	0	-1	1	2	1	10	2	3	1
Thymus polytrichus	0	0	0	0	0	0	0	0	1	1	10	0	1	1
Veronica officinalis	0	0	0	0	0	0	0	0	1	1	10	0	1	1
Agrostis capillaris	0	-1	-4	-1	1	0	0	0	0	0	1	12	12	0
Nardus stricta	1	0	-6	-7	-2	-1	0	0	0	0	2	12	12	0
Ranunculus acris	0	4	5	3	1	2	0	0	1	-1	7	17	17	0
Festuca rubra	0	4	4	8	8	6	2	-1	0	0	9	15	15	0
Alchemilla glabra	0	0	0	0	-1	0	1	2	2	0	10	5	5	0
Carex viridula ssp. *oedocarpa*	-1	-1	-1	-1	-1	-1	-2	-1	0	0	10	6	6	0
Cerastium fontanum	0	1	1	1	1	0	1	2	0	0	10	5	5	0
Persicaria vivipara	0	1	1	1	0	-1	-3	-1	-1	0	10	15	15	0
Selaginella selaginoides	0	0	0	1	1	1	1	1	2	0	10	3	3	0
Vaccinium myrtillus	0	0	0	0	0	0	0	0	0	0	10	2	2	0
Carex pulicaris	0	0	0	0	1	2	1	0	-1	-2	9	15	14	-1
Carex pallescens	0	0	0	0	0	0	-1	0	0	-1	10	5	4	-1
Deschampsia flexuosa	0	0	0	0	0	0	0	0	-1	-1	10	1	0	-1
Juncus squarrosus	0	0	0	0	0	-1	-1	0	0	-1	10	5	4	-1
Prunella vulgaris	0	0	0	0	0	0	0	0	-1	-1	10	1	0	-1
Festuca ovina/vivipara	-2	-2	-4	-1	1	0	0	0	0	0	2	19	17	-2
Oxalis acetosella	0	0	0	0	-1	-1	-2	-1	-1	0	7	4	2	-2
Euphrasia officinalis agg.	0	0	0	-1	-1	-1	-1	-3	-3	-2	10	4	2	-2
Trichophorum cespitosum	0	0	0	0	0	0	0	0	0	-2	10	6	4	-2
Potentilla erecta	0	3	1	-1	-1	-3	-2	-4	-3	-4	6	17	14	**-3**
Pinguicula vulgaris	0	0	0	0	-1	-1	-1	-1	-1	-3	10	3	0	**-3**
Plantago lanceolata	0	0	0	0	-1	-1	-1	-2	-1	-3	10	8	5	**-3**
Carex panicea	-1	-3	-5	-4	-4	-2	-2	-2	-1	1	4	16	12	**-4**
Total absolute change*	11	52	76	78	88	80	79	85	79	77				95
No. of species showing no change**	31	20	18	16	11	14	12	15	11	13				9

*Total absolute change (sensitivity) is the sum of absolute change for each scale and for the optimum scale
**Number of species showing no change (blindness) is the count at each scale of species which showed no change
**Excludes *Vaccinium myrtillus* which showed no change at any scale
Note - Species which showed a change in frequency of 3 or more have been marked in bold
Note - Optimum scale showed more sensitivity and less blindness than any other scale

Appendix 4.3 - A comparison of the absolute change values at each individual scale, with the absolute change at the optimum scale
U5c *Nardus stricta - Galium saxatile* grassland (*Carex panicea - Viola riviniana* sub-community)

Enclosure 2 (Annual stocking rate of 0.051 LU ha^{-1} from August 1994)

Change in Frequency	**All Scales**											**Frequency at Optimum Scale**		
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Optimum Scale (set in 1994)**	**1994**	**1998**	**Change**
Luzula multiflora	0	0	0	0	-1	0	3	6	7	9	10	9	18	9
Agrostis capillaris	3	4	2	4	4	4	3	2	0	0	2	18	22	4
Carex nigra	3	4	4	6	7	8	6	6	3	4	9	20	24	4
Carex pulicaris	0	1	1	1	2	3	4	5	4	3	10	3	6	3
Leontodon autumnalis	0	0	-1	-1	-2	-2	2	4	3	3	10	9	12	3
Carex binervis	0	-1	-3	-4	2	2	-2	-1	-1	-1	6	18	20	2
Crepis paludosa	0	0	0	0	0	0	2	2	2	2	10	0	2	2
Pinguicula vulgaris	0	0	0	0	0	0	0	0	0	2	10	0	2	2
Ranunculus acris	0	0	0	0	0	0	2	1	2	2	10	6	8	2
Festuca ovina/vivipara	-1	1	-1	-1	2	2	1	0	0	0	2	18	19	1
Viola spp.	0	-2	-4	-3	-3	1	2	3	3	0	6	16	17	1
Trichophorum cespitosum	0	2	4	3	1	0	3	1	-1	0	8	15	16	1
Deschampsia flexuosa	0	0	0	0	0	0	0	1	1	1	10	0	1	1
Eriophorum angustifolium	1	-1	-1	-1	-2	-3	-4	-3	-2	1	10	10	11	1
Molinia caerulea	0	1	0	1	1	1	2	-1	-1	1	10	9	10	1
Narthecium ossifragum	0	-1	0	2	2	-1	-1	-1	0	1	10	15	16	1
Sorbus aucuparia	0	0	0	0	0	0	0	0	0	1	10	0	1	1
Carex pilulifera	0	4	4	4	2	2	0	0	-2	0	8	16	16	0
Blechnum spicant	0	0	0	0	0	0	0	0	0	0	10	1	1	0
Carex viridula ssp. *oedocarpa*	0	-1	0	0	0	0	0	0	0	0	10	2	2	0
Juncus squarrosus	0	0	-1	1	3	1	-2	-1	0	0	10	15	15	0
Oreopteris limbosperma	0	0	0	0	0	0	0	-1	-1	0	10	1	1	0
Plantago lanceolata	0	0	0	0	0	0	0	0	0	0	10	1	1	0
Vaccinium myrtillus	-1	-3	-4	-3	-3	0	-1	-2	1	0	10	14	14	0
Sphagnum spp.	0	-1	0	1	3	1	0	2	2	0	10	15	15	0
Galium saxatile	0	-1	-4	-2	-2	-1	-1	1	1	1	2	16	15	-1
Potentilla erecta	-2	2	-1	-1	1	3	1	-1	-1	0	3	14	13	-1
Carex hostiana	0	0	0	0	0	0	0	0	-1	-1	10	1	0	-1
Euphrasia officinalis agg.	0	0	0	0	0	0	0	0	0	-1	10	1	0	-1
Juncus effusus	0	0	0	0	0	0	0	0	0	-1	10	4	3	-1
Prunella vulgaris	0	0	0	0	0	-1	-1	-1	-1	-1	10	1	0	-1
Nardus stricta	2	-2	-3	-6	-4	0	0	0	0	0	2	20	18	-2
Juncus bulbosus	0	0	0	0	0	0	0	0	-1	-2	10	2	0	-2
Carex panicea	0	0	-2	3	2	3	3	0	2	-2	10	25	23	-2
Selaginella selaginoides	0	0	0	0	1	0	-1	-2	-1	-3	10	5	2	-3
Anthoxanthum odoratum	-2	-2	-5	-4	-1	1	1	-1	1	0	4	16	12	-4
Carex echinata	-2	-2	-2	-2	-2	0	-1	-1	-3	-5	10	11	6	-5
Total absolute change*	17	36	47	54	53	40	49	50	48	48				63
No. of species showing no change**	26	16	17	14	12	17	12	11	10	13				6

*Total absolute change (sensitivity) is the sum of absolute change for each scale and for the optimum scale

**Number of species showing no change (blindness) is the count at each scale of species which showed no change

**Excludes *Blechnum spicant* and *Plantago lanceolata* which showed no change at any scale

Note - Species which showed a change in frequency of 3 or more have been marked in **bold**

Note - Optimum scale showed more sensitivity and less blindness than any other scale

Appendix 4.3 - A comparison of the absolute change values at each individual scale, with the absolute change at the optimum scale
U5c *Nardus stricta - Galium saxatile* grassland (*Carex panicea - Viola riviniana* sub-community)

Enclosure 3 (Annual stocking rate of 0.096 LU ha^{-1} from August 1994)

Change in Frequency	All Scales											Frequency at Optimum Scale		
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Optimum Scale (set in 1994)**	**1994**	**1998**	**Change**
Festuca ovina/vivipara	-1	6	6	4	4	2	2	1	0	0	2	23	29	6
Luzula multiflora	2	0	0	3	3	4	5	3	2	-1	6	17	21	4
Carex panicea	-1	1	1	0	3	0	-2	-1	-1	-2	5	16	19	3
Vaccinium myrtillus	1	5	3	2	1	2	2	0	5	3	10	17	20	3
Nardus stricta	2	2	-1	-2	-4	0	0	0	0	0	2	14	16	2
Potentilla erecta	0	3	2	-1	2	3	0	0	0	0	3	15	17	2
Deschampsia flexuosa	-1	-1	-1	0	0	1	3	3	2	-2	9	16	18	2
Anemone nemorosa	0	0	-1	-1	0	0	1	1	1	2	10	2	4	2
Carex binervis	0	0	0	0	1	1	1	0	1	2	10	9	11	2
Agrostis capillaris	3	1	1	-1	0	0	0	0	0	0	2	26	27	1
Blechnum spicant	0	0	0	0	0	0	0	0	1	1	10	1	2	1
Sorbus aucuparia	0	0	0	0	0	0	0	0	-1	1	10	1	2	1
Trichophorum cespitosum	-1	1	2	2	3	-1	0	1	2	2	7	14	14	0
Juncus squarrosus	0	1	1	1	0	1	-1	0	2	0	10	9	9	0
Narthecium ossifragum	-2	1	0	0	0	-1	-1	-1	-1	0	10	13	13	0
Viola palustris	0	0	0	0	0	0	0	0	0	0	10	1	1	0
Molinia caerulea	0	0	0	0	0	0	0	0	0	-1	10	1	0	-1
Galium saxatile	-1	-2	-4	-2	-1	0	0	0	0	0	2	29	27	-2
Danthonia decumbens	0	0	0	-2	-1	1	1	-2	-2	0	9	15	13	-2
Anthoxanthum odoratum	0	0	-1	-4	-2	-3	-2	-6	-5	-3	6	15	12	-3
Carex nigra	0	1	1	1	1	-3	-4	-3	-3	0	6	16	13	-3
Carex pilulifera	-3	-6	-4	-4	-3	-1	1	2	0	0	2	17	11	-6
Total absolute change*	18	31	29	30	29	24	26	24	29	20				46
No. of species showing no change**	10	8	7	7	8	8	8	10	7	10				3

*Total absolute change (sensitivity) is the sum of absolute change for each scale and for the optimum scale
**Number of species showing no change (blindness) is the count at each scale of species which showed no change
**Excludes *Viola palustris* which showed no change at any scale
Note - Species which showed a change in frequency of 3 or more have been marked in **bold**
Note - Optimum scale showed more sensitivity and less blindness than any other scale

Appendix 4.3 - A comparison of the absolute change values at each individual scale, with the absolute change at the optimum scale
CG10b *Festuca ovina-Agrostis capillaris-Thymus praecox* grassland (*Carex pulicaris-Carex panicea* sub-community)
Enclosure 1 (Annual stocking rate of 0.074 LU ha^{-1})

Change in Frequency Species	All Scales 1	2	3	4	5	6	7	8	9	10	Optimum Scale (set in 1995)	Frequency at Optimum Scale 1995	1998	Change
Festuca rubra	1	2	1	1	1	2	7	8	9	9	10	16	25	9
Danthonia decumbens	0	0	-1	-1	1	1	3	2	4	7	10	5	12	7
Prunella vulgaris	0	1	2	2	3	3	4	4	1	7	10	12	19	7
***Euphrasia officinalis* agg.**	0	1	1	3	4	8	9	8	5	5	10	15	20	5
Festuca ovina/vivipara	4	0	0	0	0	0	0	0	0	0	1	8	12	4
Linum catharticum	0	0	0	0	1	0	1	1	3	4	10	7	11	4
***Taraxacum* agg.**	0	0	0	0	1	1	1	1	3	4	10	2	6	4
Veronica officinalis	0	-1	2	1	0	-1	1	2	1	4	10	14	18	4
Bellis perennis	0	1	1	1	1	0	1	0	0	3	10	10	13	3
Viola species	0	2	0	2	1	1	1	0	0	1	4	17	19	2
Potentilla erecta	0	-3	-2	3	2	0	1	-1	-1	1	5	17	19	2
Thymus polytrichus	0	1	5	4	2	1	3	0	4	3	5	16	18	2
Carex viridula ssp. *oedocarpa*	0	1	1	1	1	1	1	0	1	2	10	6	8	2
Cerastium fontanum	0	1	1	1	1	2	3	5	5	2	10	6	8	2
Parnassia palustris	0	0	0	0	0	0	0	0	1	1	10	0	2	2
Saxifraga oppositifolia	0	1	1	1	1	0	0	1	1	2	10	2	4	2
Selaginella selaginoides	0	-1	-1	0	-1	1	1	1	2	2	10	11	13	2
Thalictrum alpinum	0	0	0	-1	-1	-1	0	0	-1	2	10	7	9	2
Anthoxanthum odoratum	0	1	-3	-4	-2	-1	-1	-1	0	0	2	13	14	1
Galium saxatile	0	1	-1	1	2	2	1	1	1	0	2	25	26	1
Luzula multiflora	-1	-1	1	0	1	4	4	2	2	2	5	14	15	1
Alchemilla glabra	1	0	0	0	-1	0	0	2	2	1	10	14	15	1
Betula pubescens	0	0	0	0	0	0	0	0	0	1	10	0	1	1
Carex bigelowii	0	0	0	1	2	1	1	1	1	1	10	1	2	1
Carex capillaris	0	1	1	0	0	0	0	0	0	1	10	2	3	1
Diphasiastrum alpinum	0	0	0	0	0	0	2	1	1	1	10	2	3	1
Saxifraga aizoides	0	0	0	0	0	0	0	1	2	1	10	3	4	1
Ranunculus acris	1	-4	0	-1	0	0	2	3	0	3	5	17	17	0
Plantago lanceolata	0	-1	1	2	0	3	1	0	-5	1	8	15	15	0
Campanula rotundifolia	0	4	2	2	1	0	0	0	0	0	9	16	16	0
Alchemilla alpina	-1	-1	-1	1	2	3	2	1	-1	0	10	13	13	0
Carex binervis	0	-1	-1	-2	-1	-1	-1	-1	-1	0	10	2	2	0
Oreopteris limbosperma	0	0	0	0	0	0	0	0	0	0	10	1	1	0
Ranunculus repens	0	5	4	4	2	1	1	3	3	0	10	13	13	0
Silene acaulis	0	0	0	0	0	0	1	0	0	0	10	4	4	0
Trichophorum cespitosum	0	0	0	0	0	0	0	0	-1	0	10	1	1	0
Vaccinium myrtillus	0	0	0	0	0	0	0	0	0	0	10	1	1	0
Persicaria vivipara	-1	-5	-2	-1	-2	-4	-3	-1	2	1	4	14	13	-1
Nardus stricta	1	-1	-1	-6	-1	0	3	0	1	0	5	15	14	-1
Trifolium repens	0	0	1	0	2	-1	1	3	3	3	6	16	15	-1
Carex pulicaris	-3	-4	-3	-4	-4	-3	0	-2	-2	-1	10	17	16	-1
Juncus bulbosus	0	0	0	0	0	0	-1	-1	-1	-1	10	1	0	-1
Rumex acetosa	0	0	0	0	0	0	0	0	0	-1	10	2	1	-1
Agrostis capillaris	-1	-2	-3	-2	0	-2	1	1	1	1	2	27	25	-2
Carex panicea	1	3	2	2	1	0	-2	-2	0	-2	8	16	14	-2
Pinguicula vulgaris	0	0	0	0	0	0	0	-1	-2	-2	10	2	0	-2
Carex pilulifera	-1	-2	-1	-4	-6	-6	-2	1	-1	0	5	15	9	-6
Achillea ptarmica	-1	-1	-3	-6	-7	-9	-7	-9	-6	-8	7	15	8	-7
Total absolute change*	18	54	50	65	59	64	74	72	81	91				99
No. of species showing no change**	34	18	18	18	16	21	14	16	12	12				9

*Total absolute change (sensitivity) is the sum of absolute change for each scale and for the optimum scale
**Number of species showing no change (blindness) is the count at each scale of species which showed no change
**Excludes *Oreopteris limbosperma* which showed no change at any scale
Note - Species which showed a change in frequency of 3 or more have been marked in **bold**
Note - Optimum scale showed more sensitivity and less blindness than any other scale

Appendix 4.3 - A comparison of the absolute change values at each individual scale, with the absolute change at the optimum scale
CG10b *Festuca ovina -Agrostis capillaris -Thymus praecox* grassland (*Carex pulicaris -Carex panicea* sub-community)
Enclosure 2 (Annual stocking rate of 0.051 LU ha^{-1})

Change in Frequency	All Scales										Optimum Scale	Frequency at Optimum Scale		
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**(set in 1995)**	**1995**	**1998**	**Change**
Festuca rubra	0	0	0	1	1	1	2	5	9	12	10	2	14	12
Agrostis capillaris	1	6	1	2	2	1	1	0	0	0	2	22	28	6
Selaginella selaginoides	0	0	0	0	1	5	8	6	7	6	10	15	21	6
Ranunculus acris	0	3	3	1	4	3	2	3	3	3	8	16	19	3
Deschampsia flexuosa	1	1	0	0	1	1	2	2	1	3	10	7	10	3
Prunella vulgaris	0	2	2	1	2	2	2	1	1	3	10	2	5	3
Galium saxatile	0	2	-1	-3	-1	-1	0	0	0	0	2	21	23	2
Plantago lanceolata	0	4	4	1	-2	1	2	2	1	3	7	15	17	2
Carex pallescens	0	0	0	0	0	0	0	0	1	2	10	1	3	2
Huperzia selago	0	0	0	0	0	0	0	1	1	2	10	0	2	2
Persicaria vivipara	0	0	0	-1	-1	0	-1	4	3	2	10	17	19	2
Sorbus aucuparia	0	0	0	0	0	0	0	1	2	2	10	0	2	2
Thymus polytrichus	-1	5	4	2	1	2	1	2	0	1	5	16	17	1
Carex pilulifera	1	3	-1	-2	1	1	-2	-2	-2	-1	6	16	17	1
Carex panicea	0	1	1	0	2	2	1	1	2	2	8	16	17	1
Carex viridula ssp. *oedocarpa*	0	0	0	0	0	0	0	0	1	1	10	3	4	1
Cerastium fontanum	0	0	0	0	0	0	0	1	1	1	10	0	1	1
Deschampsia cespitosa	0	0	0	0	0	0	0	0	1	1	10	1	2	1
Narthecium ossifragum	0	0	0	1	1	1	1	1	1	1	10	7	8	1
Oxalis acetosella	0	0	0	0	0	1	1	3	3	1	10	5	6	1
Phegopteris connectilis	0	0	0	0	0	0	1	1	1	1	10	3	4	1
Nardus stricta	1	0	-2	1	0	-2	-3	-3	0	0	5	14	14	0
Alchemilla glabra	0	0	0	0	0	-1	0	1	1	0	10	2	2	0
Blechnum spicant	0	0	-1	-1	-2	-1	0	-1	-1	0	10	8	8	0
Carex binervis	0	0	0	0	0	0	1	0	0	0	10	3	3	0
Viola spp.	0	0	1	1	2	1	-1	1	2	1	7	17	16	-1
Carex pulicaris	-1	-2	-4	-2	-2	-3	-2	-2	0	-1	10	11	10	-1
Anthoxanthum odoratum	1	-4	-2	-1	-5	-3	-2	-3	-1	0	3	15	13	-2
Vaccinium myrtillus	0	-2	-2	-2	-6	-4	-3	-3	-1	0	4	16	14	-2
Euphrasia officinalis agg.	0	0	-1	1	-1	-2	0	-4	-2	-3	9	14	12	-2
Danthonia decumbens	0	0	0	0	0	0	-1	0	-2	-2	10	9	7	-2
Oreopteris limbosperma	0	1	1	0	0	-1	0	0	0	-2	10	9	7	-2
Polygala serpyllifolia	0	1	1	1	0	2	2	1	1	-2	10	6	4	-2
Luzula multiflora	1	0	1	1	1	-1	-3	-3	-5	-2	7	15	12	-3
Alchemilla alpina	0	-4	0	0	3	-1	-1	0	0	0	2	19	15	-4
Festuca ovina/vivipara	-5	3	1	0	0	0	0	0	0	0	1	12	7	-5
Potentilla erecta	-1	-2	-3	-5	-5	-3	-1	0	0	0	4	17	12	-5
Campanula rotundifolia	0	0	-1	-6	-5	-5	-3	-2	-2	-1	5	16	11	-5
Anemone nemorosa	0	2	3	1	0	-2	-3	-8	-10	-12	9	16	6	-10
Total absolute change*	14	48	41	38	52	54	53	68	69	74				100
No. of species showing no change**	29	21	17	17	16	11	12	11	10	11				4

*Total absolute change (sensitivity) is the sum of absolute change for each scale and for the optimum scale
**Number of species showing no change (blindness) is the count at each scale of species which showed no change
Note - Species which showed a change in frequency of 3 or more have been marked in **bold**
Note - Optimum scale showed more sensitivity and less blindness than any other scale

Appendix 4.3 - A comparison of the absolute change values at each individual scale, with the absolute change at the optimum scale
CG10b *Festuca ovina -Agrostis capillaris -Thymus praecox* grassland (*Carex pulicaris -Carex panicea* sub-community)
Enclosure 3 (Annual stocking rate of 0.096 LU ha^{-1})

Change in Frequency	All Scales										Optimum Scale	Frequency at Optimum Scale		
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**(set in 1995)**	**1995**	**1998**	**Change**
Bare soil	0	1	2	2	3	6	12	19	23	29	10	0	29	**29**
Festuca rubra	0	1	1	3	4	5	4	8	16	20	10	6	26	**20**
Danthonia decumbens	0	1	0	0	0	-1	2	5	6	12	10	10	22	**12**
Luzula multiflora	0	6	7	10	13	11	11	9	9	7	8	17	26	**9**
***Euphrasia officinalis* agg.**	0	4	6	6	10	13	14	17	14	9	10	18	27	**9**
Cerastium fontanum	0	-1	-1	1	3	3	2	3	5	7	10	7	14	**7**
Holcus lanatus	0	1	2	2	1	2	3	3	3	7	10	1	8	**7**
Potentilla erecta	0	2	5	7	7	7	6	6	7	7	10	16	23	**7**
Anthoxanthum odoratum	-1	6	6	5	0	1	2	1	1	1	3	16	22	**6**
Trifolium repens	1	2	3	6	1	1	-1	0	0	0	4	14	20	**6**
Achillea ptarmica	0	0	1	2	1	2	3	4	5	5	10	10	15	**5**
Carex pallescens	0	0	0	0	0	0	0	1	2	5	10	0	5	**5**
Bellis perennis	0	3	1	0	2	0	2	3	4	5	9	16	20	**4**
Carex pulicaris	0	2	2	2	3	4	4	2	1	4	10	18	22	**4**
Ranunculus acris	2	3	-2	-2	-1	-1	-1	1	-1	-1	2	20	23	**3**
Carex binervis	0	0	-1	0	0	0	-1	-1	1	3	10	8	11	**3**
Deschampsia cespitosa	1	1	0	0	0	0	0	1	2	3	10	2	5	**3**
Alchemilla glabra	0	-2	-2	-2	-3	-3	-1	0	3	2	10	13	15	2
Carex viridula ssp. *oedocarpa*	0	0	-1	-1	-1	-1	-1	2	3	2	10	9	11	2
Thymus polytrichus	2	1	1	2	1	1	1	0	0	0	2	15	16	1
Plantago lanceolata	-1	-4	-3	1	0	2	1	-1	0	0	4	15	16	1
Anemone nemorosa	0	-1	-1	-1	-1	0	0	0	1	1	10	1	2	1
Carex nigra	0	0	0	0	0	0	0	1	1	1	10	0	1	1
Pinguicula vulgaris	0	0	0	0	0	0	0	0	1	1	10	0	1	1
Taraxacum agg.	0	0	0	0	0	0	0	1	1	1	10	0	1	1
Vaccinium myrtillus	0	0	0	0	0	0	0	0	1	1	10	0	1	1
Veronica officinalis	-1	0	1	1	0	1	0	1	1	1	10	6	7	1
Carex panicea	-1	-3	0	-2	-1	0	5	5	1	1	6	16	16	0
Alchemilla alpina	0	0	0	0	0	0	0	0	-1	0	10	3	3	0
Helictotrichon pratense	0	0	0	0	0	0	0	1	1	0	10	1	1	0
Lysimachia nemorum	0	0	0	0	0	0	0	0	0	0	10	1	1	0
Oxalis acetosella	0	-1	0	1	0	0	0	0	0	0	10	5	5	0
Selaginella selaginoides	0	0	0	0	0	-1	-1	-1	-1	0	10	1	1	0
Festuca ovina/vivipara	1	-1	-2	1	0	0	0	0	0	0	2	28	27	-1
Galium saxatile	0	-1	-1	-1	-2	-2	-1	-1	0	-2	2	23	22	-1
Nardus stricta	-1	0	-1	-5	-3	-2	-1	0	0	0	3	13	12	-1
Carex pilulifera	2	1	1	-1	-3	-5	-6	-3	-1	-2	4	13	12	-1
Polygonum viviparum	0	-4	-1	0	-1	1	4	3	1	1	5	17	16	-1
Carex flacca	0	0	0	0	0	0	0	0	0	-1	10	1	0	-1
Hieracium sp.	0	0	0	0	0	0	0	0	-1	-1	10	1	0	-1
Polygala serpyllifolia	0	0	0	0	0	0	0	0	-1	-2	10	2	0	-2
Prunella vulgaris	0	1	1	-1	-2	0	1	-3	1	2	8	18	15	**-3**
Viola species	0	0	0	-5	-4	-2	2	-1	1	0	5	17	13	**-4**
Campanula rotundifolia	0	-4	-5	-6	-5	-4	-5	-3	-5	-3	5	15	10	**-5**
Agrostis capillaris	-9	0	0	0	0	0	0	0	0	0	1	13	4	**-9**
Total absolute change*	23	58	61	79	76	82	98	111	127	150				181
No. of species showing no change**	32	18	17	17	20	19	16	14	9	11				5

*Total absolute change (sensitivity) is the sum of absolute change for each scale and for the optimum scale
**Number of species showing no change (blindness) is the count at each scale of species which showed no change
Note - Species which showed a change in frequency of 3 or more have been marked in bold
Note - Optimum scale showed more sensitivity and less blindness than any other scale

Appendix 4.3 - A comparison of the absolute change values at each individual scale, with the absolute change at the optimum scale
U10a *Carex bigelowii-Racomitrium lanuginosum* moss-heath (*Galium saxatile* sub-community)
Enclosure 1 (Annual stocking rate of 0.074 LU ha^{-1})

Change in Frequency	All Scales										Optimum Scale	Frequency at Optimum Scale		
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**(set in 1995)**	**1995**	**1998**	**Change**
Vaccinium vitis-idaea	0	2	0	8	7	5	2	1	2	2	5	18	25	7
Galium saxatile	-1	6	6	2	0	1	0	0	0	0	2	18	24	6
Anthoxanthum odoratum	1	2	4	6	5	4	5	3	0	-2	7	15	20	5
Deschampsia flexuosa	1	4	2	2	0	4	5	5	3	-1	7	15	20	5
Agrostis capillaris & A. vinealis	-4	3	-1	0	-1	-1	-1	0	0	0	2	24	27	3
Carex bigelowii	0	-2	-2	0	0	0	-1	1	0	3	10	11	14	3
Viola palustris	0	0	0	0	0	0	0	0	1	2	10	0	2	2
Festuca ovina/vivipara	-1	1	0	2	1	0	0	0	0	0	2	23	24	1
Carex pilulifera	0	1	0	1	2	1	-1	1	0	0	4	16	17	1
Nardus stricta	0	2	-1	1	2	0	2	1	0	0	4	14	15	1
Luzula multiflora	0	-1	-1	-1	-3	-5	2	1	1	-2	8	16	17	1
Campanula rotundifolia	0	-1	-1	0	0	0	0	0	1	1	10	7	8	1
Vaccinium myrtillus	5	0	0	-1	0	0	0	0	0	0	2	28	28	0
Diphasiastrum alpinum	0	5	4	5	2	0	0	0	0	0	6	17	17	0
Empetrum nigrum	1	0	0	0	0	1	0	0	-2	0	10	14	14	0
Juncus squarrosus	0	1	1	0	-1	0	0	0	-1	0	10	7	7	0
Salix herbacea	0	0	-1	-1	-1	0	1	0	0	0	10	3	3	0
Lichens (Cladonia spp.)	0	-1	-5	-4	-3	-4	-3	-1	-1	0	2	18	17	-1
Potentilla erecta	0	0	0	1	0	-1	-1	1	2	-1	10	13	12	-1
Viola riviniana	0	0	0	0	0	0	0	0	0	-1	10	1	0	-1
Alchemilla alpina	-1	1	0	0	-1	-1	-1	0	-2	-3	9	16	14	-2
Carex binervis	0	-1	0	0	0	-1	-2	-3	-4	-7	10	9	2	-7
Total absolute change*	15	34	29	35	29	29	27	18	20	25				48
No. of species showing no change**	14	6	10	9	10	10	9	12	11	11				5

*Total absolute change (sensitivity) is the sum of absolute change for each scale and for the optimum scale
**Number of species showing no change (blindness) is the count at each scale of species which showed no change
Note - Species which showed a change in frequency of 3 or more have been marked in bold
Note - Optimum scale showed more sensitivity and less blindness than any other scale

Appendix 4.3 - A comparison of the absolute change values at each individual scale, with the absolute change at the optimum scale
U10a *Carex bigelowii -Racomitrium lanuginosum* moss-heath (*Galium saxatile* sub-community)
Enclosure 2 (Annual stocking rate of 0.051 LU ha^{-1})

Change in Frequency	All Scales										Optimum Scale	Frequency at Optimum Scale		
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**(set in 1995)**	**1995**	**1998**	**Change**
Campanula rotundifolia	0	0	0	0	1	1	3	4	6	9	10	4	13	9
Deschampsia flexuosa	1	4	4	5	7	8	7	5	6	4	6	14	22	8
Nardus stricta	1	0	2	0	1	-2	2	3	0	0	8	17	20	3
Huperzia selago	0	0	0	0	1	1	0	0	1	3	10	5	8	3
Vaccinium myrtillus	1	1	1	0	0	0	0	0	0	0	2	23	24	1
Diphasiastrum alpinum	0	3	1	1	0	0	0	-2	-3	-3	4	15	16	1
Carex pilulifera	-2	0	-1	-3	1	1	-2	-2	-3	-1	6	15	16	1
Vaccinium vitis-idaea	0	1	-1	-2	1	0	-2	-3	0	0	6	17	17	0
Empetrum nigrum	2	0	1	1	0	-1	-1	0	0	-2	9	16	16	0
Potentilla erecta	0	0	0	0	0	0	0	-1	0	0	10	2	2	0
Festuca ovina/vivipara	-2	-1	-2	0	-1	0	0	0	0	0	2	21	20	-1
Alchemilla alpina	1	4	-1	-1	-1	0	1	0	0	0	3	19	18	-1
Euphrasia officinalis agg.	0	0	-1	-1	-1	-1	-1	-1	-1	-1	10	1	0	-1
Salix herbacea	0	-2	0	1	-1	-1	-1	0	0	-1	10	11	10	-1
Carex bigelowii	-1	-6	-4	-2	-1	0	0	1	0	0	4	17	15	-2
Anthoxanthum odoratum	1	-2	-1	-1	-1	-2	-1	-4	-2	1	8	17	13	-4
Luzula multiflora	0	0	1	0	1	0	-1	-3	-1	-4	10	17	13	-4
Lichens (Cladonia spp.)	0	-4	-5	-5	-8	-4	-6	-3	0	0	4	16	11	-5
Agrostis capillaris & vinealis	-4	-6	-4	-3	-2	0	1	1	0	0	2	26	20	-6
Galium saxatile	0	-11	-9	-5	-6	-1	1	0	0	0	2	26	15	-11
Total absolute change*	16	45	39	31	35	23	30	33	23	29				62
No. of species showing no change**	10	8	4	7	4	9	6	7	12	10				3

*Total absolute change (sensitivity) is the sum of absolute change for each scale and for the optimum scale
**Number of species showing no change (blindness) is the count at each scale of species which showed no change
Note - Species which showed a change in frequency of 3 or more have been marked in bold
Note - Optimum scale showed more sensitivity and less blindness than any other scale

Appendix 4.3 - A comparison of the absolute change values at each individual scale, with the absolute change at the optimum scale
U10a *Carex bigelowii-Racomitrium lanuginosum* moss-heath (*Galium saxatile* sub-community)
Enclosure 3 (Annual stocking rate of 0.096 LU ha^{-1})

Change in Frequency	All Scales										Optimum Scale	Frequency at Optimum Scale		
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**(set in 1995)**	**1995**	**1998**	**Change**
Bare soil	0	-1	-1	-1	-1	0	2	3	4	5	10	3	8	5
Carex panicea	1	0	1	0	0	0	0	1	3	4	10	11	15	4
Deschampsia flexuosa	1	3	3	3	5	4	5	4	4	4	10	11	15	4
Empetrum nigrum	0	0	0	1	1	0	-2	2	3	4	10	15	19	4
Festuca ovina/vivipara	0	3	2	-2	-2	-1	-1	-1	0	0	2	19	22	3
Galium saxatile	-1	2	-1	4	3	3	3	0	0	0	2	17	19	2
Vaccinium myrtillus	3	4	0	1	2	4	5	4	4	2	5	17	19	2
Sorbus aucuparia	0	0	0	0	0	0	0	0	0	2	10	1	3	2
Trichophorum cespitosum	0	1	1	1	1	1	1	1	1	2	10	0	2	2
Anthoxanthum odoratum	-1	-3	-1	2	3	1	1	-1	-2	1	7	14	15	1
Salix herbacea	0	-3	-2	-2	-1	3	3	4	1	1	9	17	18	1
Juncus squarrosus	0	0	-1	0	0	-1	-2	-1	1	1	10	10	11	1
Nardus stricta	-1	-1	-2	0	-1	-4	-3	2	0	4	9	16	16	0
Blechnum spicant	0	0	0	0	0	0	0	0	0	0	10	1	1	0
Huperzia selago	0	0	-1	-1	-1	-1	-1	2	2	0	10	7	7	0
Potentilla erecta	0	0	-1	-1	0	-1	-2	-1	-2	0	10	14	14	0
Vaccinium vitis-idaea	0	5	5	5	6	4	2	1	1	0	10	17	17	0
Carex bigelowii	3	1	2	-1	-2	1	0	1	1	0	4	19	18	-1
Alchemilla alpina	-1	-1	2	-1	-1	1	1	-1	1	1	5	16	15	-1
Cerastium fontanum	0	0	0	0	0	0	-1	-2	-2	-3	10	3	0	-3
Luzula multiflora	0	0	0	0	0	-1	-1	-2	-1	-3	10	9	6	-3
Carex pilulifera	0	-4	-4	-4	-5	-6	-3	-1	-3	-3	4	17	13	-4
Agrostis capillaris/vinealis	-5	-1	-1	-1	0	0	0	1	0	0	1	15	10	-5
Lichens (Cladonia spp.)	0	-7	-6	-5	-6	-4	-4	-5	-4	-1	3	15	9	-6
Euphrasia officinalis agg.	0	-2	-2	-1	-1	-1	-1	-1	-1	-6	10	7	1	-6
Total absolute change*	17	42	39	37	42	42	44	42	41	47				60
No. of species showing no change**	15	8	5	6	7	6	4	2	5	7				4

*Total absolute change (sensitivity) is the sum of absolute change for each scale and for the optimum scale
**Number of species showing no change (blindness) is the count at each scale of species which showed no change
**Excludes *Blechnum spicant* which showed no change at any scale
Note - Species which showed a change in frequency of 3 or more have been marked in **bold**
Note - Optimum scale showed more sensitivity and less blindness than any other scale

Appendix 5.1 - Vascular plant species found within the herbage samples in live biomass order (highest first)

U5c *Nardus stricta - Galium saxatile* grassland (*Carex panicea - Viola riviniana* sub-community): **Enclosure 1**		
Nardus stricta	*Vaccinium myrtillus*	*Blechnum spicant*
Agrostis capillaris & A. vinealis	*Luzula multiflora*	*Oxalis acetosella*
Anthoxanthum odoratum	*Thymus polytrichus*	*Helictotrichon pratense*
Festuca ovina & F. vivipara	*Viola palustris*	*Cerastium fontanum*
Galium saxatile	*Carex echinata*	*Thalictrum alpinum*
Carex pilulifera	*Viola riviniana*	*Oreopteris limbosperma*
Deschampsia cespitosa	*Persicaria vivipara*	*Molinia caerulea*
Festuca rubra	*Carex bigelowii*	*Alchemilla filicaulis*
Carex panicea	*Danthonia decumbens*	*Geranium sylvaticum*
Carex binervis	*Juncus effusus*	*Trifolium repens*
Potentilla erecta	*Narthecium ossifragum*	*Veronica serpyllifolia*
Juncus squarrosus	*Prunella vulgaris*	*Juncus bulbosus*
Carex pulicaris	*Lysimachia nemorum*	*Euphrasia* sp.
Carex nigra	*Carex palescens*	*Polygala serpyllifolia*
Ranunculus acris	*Alchemilla alpina*	*Epilobium palustre*
Juncus acutiflorus	*Taraxacum vulgare* agg.	*Eriophorum angustifolium*
Trichophorum cespitosum	*Campanula rotundifolia*	
Anemone nemorosa	*Carex viridula* ssp. *oedocarpa*	**Number of Species = 56**
Plantago lanceolata	*Achillea ptarmica*	
Deschampsia flexuosa	*Selaginella selaginoides*	

U5c *Nardus stricta - Galium saxatile* grassland (*Carex panicea - Viola riviniana* sub-community): **Enclosure 2**		
Nardus stricta	*Narthecium ossifragum*	*Oreopteris limbosperma*
Agrostis capillaris & A. vinealis	*Luzula multiflora*	*Anemone nemorosa*
Festuca ovina & F. vivipara	*Carex pulicaris*	*Thymus polytrichus*
Galium saxatile	*Viola palustris*	*Prunella vulgaris*
Anthoxanthum odoratum	*Carex echinata Taraxacum*	*Eriophorum vaginatum*
Trichophorum cespitosum	*vulgare* agg.	*Juncus bulbosus*
Carex pilulifera	*Carex bigelowii*	*Cerastium fontanum*
Molinia caerulea	*Eriophorum angustifolium*	*Persicaria vivipara*
Juncus squarrosus	*Plantago lanceolata*	*Euphrasia* sp.
Carex panicea	*Viola riviniana*	*Helictotrichon pratense*
Potentilla erecta	*Ranunculus acris*	*Carex dioica*
Carex binervis	*Juncus effusus*	*Oxalis acetosella*
Vaccinium myrtillus	*Polygala serpyllifolia*	*Trifolium repens*
Deschampsia flexuosa	*Carex viridula* ssp. *oedocarpa*	*Danthonia decumbens*
Deschampsia cespitosa	*Juncus acutiflorus*	*Selaginella selaginoides*
Carex nigra	*Poa pratensis*	
Festuca rubra	*Blechnum spicant*	**Number of Species = 49**

Appendix 5.1 (continued) - Vascular plant species found within the herbage samples in live biomass order (highest first)

U5c *Nardus stricta - Galium saxatile* grassland (*Carex panicea - Viola riviniana* sub-community):
Enclosure 3

Nardus stricta	*Carex nigra*	*Helictotrichon pratense*
Agrostis capillaris & A. vinealis	*Carex pulicaris*	*Empetrum nigrum*
Festuca ovina & F. vivipara	*Deschampsia cespitosa*	*Viola riviniana*
Galium saxatile	*Danthonia decumbens*	*Vaccinium vitis-idaea*
Trichophorum cespitosum	*Carex caryophyllea*	*Polygala serpyllifolia*
Carex pilulifera	*Ranunculus acris*	*Oreopteris limbosperma*
Vaccinium myrtillus	*Plantago lanceolata*	*Achillea ptarmica*
Molinia caerulea	*Carex viridula* ssp. *oedocarpa*	*Carex bigelowii*
Deschampsia flexuosa	*Viola palustris*	*Ranunculus flammula*
Juncus squarrosus	*Blechnum spicant*	*Campanula rotundifolia*
Potentilla erecta	*Thymus polytrichus*	*Trifolium repens*
Anthoxanthum odoratum	*Juncus acutiflorus*	*Holcus lanatus*
Carex binervis	*Anemone nemorosa*	*Oxalis acetosella*
Carex panicea	*Prunella vulgaris*	*Bellis perennis*
Narthecium ossifragum	*Persicaria vivipara*	
Luzula multiflora	*Veronica serpyllifolia*	**Number of Species = 48**
Festuca rubra	*Euphrasia* sp.	

U5b *Nardus stricta - Galium saxatile* grassland (*Agrostis canina - Polytrichum commune* sub-community) with abundant *Juncus squarrosus*:
Enclosure 1

Juncus squarrosus	*Molinia caerulea*	*Plantago lanceolata*
Nardus stricta	*Carex pilulifera*	*Carex pulicaris*
Trichophorum cespitosum	*Deschampsia flexuosa*	*Anemone nemorosa*
Agrostis capillaris & A. vinealis	*Vaccinium myrtillus*	*Euphrasia* sp.
Carex panicea	*Eriophorum vaginatum*	*Dactylorhiza maculata*
Festuca ovina & F. vivipara	*Carex bigelowii*	*Viola riviniana*
Galium saxatile	*Carex viridula* ssp. *oedocarpa*	*Thalictrum alpinum*
Eriophorum angustifolium	*Viola palustris*	*Persicaria vivipara*
Carex binervis	*Helictotrichon pratense*	*Ranunculus acris*
Potentilla erecta	*Luzula multiflora*	*Campanula rotundifolia*
Carex echinata	*Juncus bulbosus*	*Huperzia selago*
Carex nigra	*Calluna vulgaris*	*Polygala serpyllifolia*
Deschampsia cespitosa	*Selaginella selaginoides*	
Anthoxanthum odoratum	*Taraxacum vulgare* agg.	**Number of Species = 42**
Narthecium ossifragum	*Empetrum nigrum*	

Appendix 5.1 (continued) - Vascular plant species found within the herbage samples in live biomass order (highest first)

U5b *Nardus stricta - Galium saxatile* grassland (*Agrostis canina - Polytrichum commune* sub-community) with abundant *Juncus squarrosus*: **Enclosure 2**		
Juncus squarrosus	*Molinia caerulea*	*Viola riviniana*
Nardus stricta	*Carex bigelowii*	*Persicaria vivipara*
Agrostis capillaris & A. vinealis	*Narthecium ossifragum*	*Ranunculus acris*
Festuca ovina & F. vivipara	*Carex echinata*	*Rumex acetosa*
Galium saxatile	*Juncus acutiflorus*	*Juncus bulbosus*
Deschampsia flexuosa	*Calluna vulgaris*	*Selaginella selaginoides*
Trichophorum cespitosum	*Taraxacum vulgare* agg.	*Cerastium fontanum*
Vaccinium myrtillus	*Eriophorum vaginatum*	*Carex dioica*
Anthoxanthum odoratum	*Luzula multiflora*	*Juncus effusus*
Carex panicea	*Viola palustris*	*Plantago lanceolata*
Deschampsia cespitosa	*Thalictrum alpinum*	*Euphrasia* sp.
Potentilla erecta	*Helictotrichon pratense*	*Holcus lanatus*
Eriophorum angustifolium	*Carex hostiana*	*Poa pratensis*
Carex nigra	*Carex viridula* ssp. *oedocarpa*	*Alchemilla alpina*
Carex binervis	*Anemone nemorosa*	
Carex pilulifera	*Campanula rotundifolia*	**Number of Species = 50**
Carex pulicaris	*Polygala serpyllifolia*	
Festuca rubra	*Empetrum nigrum*	

U5b *Nardus stricta - Galium saxatile* grassland (*Agrostis canina - Polytrichum commune* sub-community) with abundant *Juncus squarrosus*: **Enclosure 3**		
Juncus squarrosus	*Eriophorum vaginatum*	*Juncus bulbosus*
Nardus stricta	*Carex nigra*	*Juncus acutiflorus*
Vaccinium myrtillus	*Festuca rubra*	*Poa pratensis*
Deschampsia flexuosa	*Carex pulicaris*	*Helictotrichon pratense*
Agrostis capillaris & A. vinealis	*Deschampsia cespitosa Luzula*	*Viola palustris*
Festuca ovina & F. vivipara	*multiflora*	*Cerastium fontanum*
Molinia caerulea	*Narthecium ossifragum*	*Juncus effusus*
Trichophorum cespitosum	*Carex binervis*	*Ranunculus acris*
Galium saxatile	*Carex pilulifera*	*Campanula rotundifolia*
Potentilla erecta	*Carex hostiana*	*Ranunculus flammula*
Carex panicea	*Taraxacum vulgare* agg.	*Plantago lanceolata*
Anthoxanthum odoratum	*Polygala serpyllifolia*	*Euphrasia* sp.
Vaccinium vitis-idaea	*Carex viridula* ssp. *oedocarpa*	*Erica tetralix*
Eriophorum angustifolium	*Thalictrum alpinum*	
Calluna vulgaris	*Selaginella selaginoides*	**Number of Species = 47**
Empetrum nigrum	*Holcus lanatus*	
Carex echinata	*Rubus chamaemorus*	

Appendix 5.1 (continued) - Vascular plant species found within the herbage samples in live biomass order (highest first)

M6d *Carex echinata - Sphagnum recurvum* mire (*Juncus acutiflorus* sub-community): **Enclosure 1**		
Juncus acutiflorus	*Lysimachia nemorum*	*Trifolium repens*
Molinia caerulea	*Eriophorum vaginatum*	*Achillea ptarmica*
Agrostis capillaris & *A. vinealis*	*Deschampsia cespitosa*	*Cerastium fontanum*
Nardus stricta	*Ranunculus acris*	*Helictotrichon pratense*
Carex echinata	*Ranunculus flammula*	*Euphrasia* sp.
Carex nigra	*Viola palustris*	*Cardamine pratensis*
Festuca ovina & *F. vivipara*	*Carex pilulifera*	*Carex dioica*
Potentilla erecta	*Luzula multiflora*	*Lolium perenne*
Anthoxanthum odoratum	*Carex pulicaris*	*Veronica officinalis*
Carex panicea	*Epilobium palustre*	*Rumex acetosa*
Eriophorum angustifolium	*Taraxacum vulgare* agg.	*Persicaria vivipara*
Trichophorum cespitosum	*Prunella vulgaris*	*Equisetum palustre*
Festuca rubra	*Carex binervis*	*Viola riviniana*
Holcus lanatus	*Parnasia palustris*	*Poa pratensis*
Plantago lanceolata	*Carex viridula* ssp. *oedocarpa*	
Galium saxatile	*Polygala serpyllifolia*	**Number of Species = 50**
Narthecium ossifragum	*Saxifraga aizoides*	
Juncus squarrosus	*Juncus bulbosus*	

M6d *Carex echinata - Sphagnum recurvum* mire (*Juncus acutiflorus* sub-community): **Enclosure 2**		
Juncus acutiflorus	*Ranunculus acris*	*Pedicularis sylvatica*
Agrostis capillaris & *A. vinealis*	*Cirsium palustre*	*Lolium perenne*
Molinia caerulea	*Trichophorum cespitosum*	*Deschampsia flexuosa*
Nardus stricta	*Eriophorum vaginatum*	*Polygala serpyllifolia*
Anthoxanthum odoratum	*Viola palustris*	*Poa pratensis*
Eriophorum angustifolium	*Plantago lanceolata*	*Helictotrichon pratense*
Carex panicea	*Luzula multiflora*	*Carex pilulifera*
Carex echinata	*Carex pulicaris*	*Veronica officinalis*
Galium saxatile	*Carex binervis*	*Juncus bulbosus*
Festuca ovina & *F. vivipara*	*Carex viridula* ssp. *oedocarpa*	*Cardamine pratensis*
Narthecium ossifragum	*Ranunculus flammula*	*Danthonia decumbens*
Potentilla erecta	*Euphrasia* sp.	*Taraxacum vulgare* agg.
Festuca rubra	*Juncus effusus*	*Prunella vulgaris*
Carex nigra	*Cerastium fontanum*	*Drosera rotundifolia*
Deschampsia cespitosa	*Carex hostiana*	*Trifolium repens*
Holcus lanatus	*Persicaria vivipara*	*Achillea ptarmica*
Juncus squarrosus	*Epilobium palustre*	
Lysimachia nemorum	*Parnasia palustris*	**Number of Species = 52**

Appendix 5.1 (continued) - Vascular plant species found within the herbage samples in live biomass order (highest first)

M6d *Carex echinata - Sphagnum recurvum* mire (*Juncus acutiflorus* sub-community): **Enclosure 3**

Juncus acutiflorus	*Narthecium ossifragum*	*Cirsium palustre*
Molinia caerulea	*Ranunculus acris*	*Lysimachia nemorum*
Agrostis capillaris & A. vinealis	*Deschampsia cespitosa Luzula*	*Rumex acetosa*
Nardus stricta	*multiflora*	*Carex hostiana*
Festuca ovina & F. vivipara	*Plantago lanceolata*	*Persicaria vivipara*
Galium saxatile	*Carex pulicaris*	*Epilobium palustre*
Anthoxanthum odoratum	*Juncus effusus*	*Euphrasia* sp.
Trichophorum cespitosum	*Helictotrichon pratense*	*Cerastium fontanum*
Potentilla erecta	*Viola palustris*	*Trifolium repens*
Carex panicea	*Eriophorum vaginatum*	*Taraxacum vulgare* agg.
Eriophorum angustifolium	*Ranunculus flammula*	*Prunella vulgaris*
Juncus squarrosus	*Veronica officinalis*	*Carex pilulifera*
Festuca rubra	*Pedicularis sylvatica*	*Viola riviniana*
Carex echinata	*Carex viridula* ssp. *oedocarpa*	
Holcus lanatus	*Carex binervis*	**Number of Species = 45**
Carex nigra	*Polygala serpyllifolia*	

U4d *Festuca ovina - Agrostis capillaris - Galium saxatile* grassland (*Luzula multiflora - Rhytidiadelphus loreus* sub-community) with patches of U10a *Carex bigelowii - Racomitrium lanuginosum* moss-heath (*Galium saxatile* sub-community): **Enclosure 2**

Festuca ovina & F. vivipara**	*Nardus stricta**	*Campanula rotundifolia*
Agrostis capillaris & A. vinealis**	*Empetrum nigrum*	*Euphrasia* sp.*
*Galium saxatile**	*Cerastium fontanum**	*Carex pulicaris*
*Anthoxanthum odoratum**	*Poa pratensis**	*Helictotrichon pratense*
Alchemilla alpina	*Potentilla erecta**	*Festuca rubra**
*Carex pilulifera**	*Carex panicea**	*Danthonia decumbens*
Carex bigelowii	*Deschampsia flexuosa**	*Trifolium repens*
*Luzula multiflora**	*Viola riviniana**	
*Vaccinium myrtillus**	*Vaccinium vitis-idaea*	**Number of Species = 27**

*species found in all four communities