Grazing Management and Plant Community Composition on Bodmin Moor

by

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"Hasta la victoria siempre", Ché Guevara

Summary

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The research presented in this thesis was focused on aspects of the dynamic response of upland vegetation to grazing, to allow evaluation of the suitability of Countryside Stewardship (CS) management for the rehabilitation of dwarf-shrub cover in the upland landscape of Bodmin Moor. Initial chapters review the ecological character of Bodmin Moor, grazing management and vegetation in upland habitats, and succession in relation to grazing. Chapter Five provides the first extensive and detailed phytosociological investigation of the vegetation of Bodmin Moor—providing a baseline for further work. It also examines the spatial distribution of the plant communities in relation to environmental gradients and grazing management. Bodmin Moor was dominated by acid grassland and mire with some small heathland fragments. It lacked the cover of ericaceous dwarf-shrubs that define heathland in the rest of Britain. Chapter Six provides the first description of the soil seed banks on Bodmin Moor and determined that seed availability was not limiting the rehabilitation of dwarf-shrub cover. Chapter Seven utilised an existing monitoring scheme on Bodmin Moor North SSSI to identify vegetation changes associated with the establishment of a CS management regime. It was found that CS grazing levels were not high enough to suppress *Molinia caerulea* and dwarf-shrubs were not favoured. Chapter Eight reports on a *Molinia caerulea* defoliation experiment, which suggested that heavy summer grazing was the most suitable grazing option for the control of *Molinia caerulea* using livestock. Unfortunately, other work indicates that this is not compatible with the maintenance of dwarf-shrubs. CS protocols may not be suitable for dwarf-shrub rehabilitation on the graminoid-dominated vegetation of Bodmin Moor. Furthermore, the desirability of the objectives of CS can be questioned, and they may be impossible to achieve by the manipulation of grazing regimes alone (Chapter Nine).

1 General Introduction

1.2 Introduction

1.2.1 Project rationale

The effective conservation management of an ecosystem must be based upon a sound knowledge of the processes operating within that environment, in addition to an awareness and appreciation of its earlier development and evolution (Moss & Dickinson 1979). Despite a vast scientific literature, the ecological processes at work in the upland grazing systems of Britain are still not fully understood. The UK conservation agencies provide information and guidance on how sites can be managed to meet a variety of conservation objectives. However, detailed research to inform these management recommendations is often lacking. Further research is required, particularly in unstudied upland regions such as Bodmin Moor in Cornwall, to assess the suitability of the proposed management protocols for the effective conservation of upland grazing systems.

1.2.2 The upland resource

The British uplands cover approximately one third of Britain (Pearsall 1968, Ratcliffe 1977, Thompson & Brown 1992). The precise definition of upland varies but generally refers to land above the limits of enclosed farmland (Ratcliffe 1977). The upper limit of enclosed farmland is both an environmental and economic threshold, above which it is unprofitable to cultivate the land, primarily because of the effect of upland climate on plant growth (Fielding & Haworth 1999). Farming on this boundary is marginal and changes in agricultural funding can shift the boundary in relation to altitude (Fielding & Haworth 1999). Another ecological boundary divides the British uplands into two zones (Ratcliffe 1977, Thompson & Brown 1992). The montane zone lies above the original climax tree line and consists predominantly of montane heath and ombrogenous blanket bog. Below this is the sub-montane zone, consisting of anthropogenic dwarf-shrub heath and grassland and bog (Ratcliffe & Thompson 1988). As with the upland / lowland transition, the partitioning of the upland habitat into zones is complicated by local conditions. Factors such as slope, aspect, soil type and local climate alter the relative and absolute altitudes of the boundaries.

The uplands represent the most extensive area of semi-natural habitat in Britain. The ecological value of the uplands is variable, but their scale, naturalness, and the rare fauna and flora that upland habitats support, generally results in high nature conservation value (Ratcliffe & Thompson 1988). This is reflected in the number of upland Sites of Special Scientific Interest (SSSI), which are the most numerous by far of all the habitats in the SSSI series (Nature Conservancy Council (NCC) 1989). The vegetation of the British uplands is generally considered floristically distinctive in an international context, with Southernmost or Westernmost European occurrences of many species, and a rich and unusual combination of Atlantic, Arctic–Alpine, and Arctic and Boreal phytogeographical elements (Thompson & Horsfield 1997, Ratcliffe & Thompson 1988).

According to the current phytosociological classification of British vegetation (Rodwell 1991, 1992), the uplands contain 10 woodland, 15 heath, 30 mire, and 27 grassland/sedge-dominated communities. Of these, 29% are montane, 30% sub-montane and 32% azonal (Thompson & Sydes 1997). The montane communities are valued because they are mostly natural and they contain many endemic species (Joint Nature Conservation Committee 1995). Except for the wettest bog, the sub-montane zone consists of semi-natural vegetation (*sensu* Tansley 1939) being dominated by native plants which, although much changed in abundance, have been present since the early Holocene (Roberts 1998). Despite a strong anthropogenic influence, the communities of the sub-montane zone, particularly the blanket bog and acidophilous dwarf-shrub heaths are of international significance. For example, many of the mire communities are internationally rare and their extent is of considerable significance. Britain contains 10-15% of the total global area of blanket mire (Lindsay *et al.* 1988). Dwarf-shrub heath communities have a restricted geographical distribution and are confined to the UK, Ireland and the Western seaboard of Europe (NCC 1989). Acid grasslands are dominated by species of wide distribution, but their occurrence as widespread communities is often limited to Britain and Ireland (NCC 1989).

The value of the British uplands in a national and international context is recognised by the EC Directive on the Conservation of Natural and Semi-natural Habitats and of Wild Fauna and Flora (Thompson & Horsfield 1997). A range of montane communities, active raised bogs, blanket bogs, dry heath, *Calaminarian* grasslands, species-rich *Nardus* grasslands and semi-natural dry grasslands are among the habitats recognised as important by the habitats directive (Drewitt & Manley 1997). Most of these habitats are subject to grazing as a major influence on their natural heritage value (Milne *et al.* 1998).

The vegetation of the British uplands has been affected by human activities to some degree throughout the Holocene (Roberts 1998). The two human activities, which have had, and continue to have, most impact on the nature of the vegetation of the uplands are grazing by herbivores and burning. The ecological effects of grazing on upland vegetation and grazing / burning interactions are discussed fully in Chapters Three and Four. Thompson & Miles (1995) summarize the apparent shifts between communities under burning and heavy grazing. Further work is required to verify the nature of these relationships, the factors involved and the actual composition of the different communities in different areas of the country under different grazing regimes (Shaw *et al.* 1996).

1.3 Grazing in upland systems

The effects of grazing on the natural heritage value of the uplands are currently a cause for concern among conservationists. Since the 1940s, livestock subsidies have encouraged the keeping of greater numbers of stock throughout the uplands and there is mounting evidence that this is responsible, at least in part, for the conversion of dwarf-shrub heath to grassland. The spread of *Pteridium aquilinum* is also attributed to changes in grazing practices. Agri-environment schemes such as the Environmentally Sensitive Areas (ESA) scheme launched by the Ministry of Agriculture, Farming and Fisheries (MAFF) in 1987 and Countryside Stewardship (CS), introduced in 1991, are intended to address these concerns. The primary objectives of the ESA and CS schemes are to maintain and enhance the conservation value of the key environmental features of the designated area. This usually includes the enhancement of heather moorland in ESAs, whilst Countryside Stewardship options include recreating heathland and regenerating suppressed heather moor. The management prescriptions to achieve these objectives usually include a reduction in overall stocking level, and reduction of winter grazing especially by sheep.

However, at many sites, grazing is a characteristic part of the landscape and reduction or abandonment of grazing can lead to loss of nature conservation and amenity value (Fry 1991). The invasion of heather moorland by *Molinia caerulea* is a cause of concern in many areas of upland Britain (Chambers *et al.* 1999). The increase in *Molinia caerulea* over the last decade is assumed to be a result of changes in grazing management, particularly the reduction in stocking levels associated with agri environment schemes (Chambers *et al.* 1999); and may be an inevitable consequence of attempts to improve the condition of dwarf-shrubs (Smallshire *et al.* 1997). However, palaeoecological research suggests that vegetation dominance has alternated between *Callunetum* and *Molinietum* during the past millennium on Exmoor (South-west England). Thus management prescriptions based on a rigid adherence to present day vegetation classifications (Rodwell 1991, 1992) may exclude other equally legitimate vegetational assemblages (Chambers *et al.* 1999). Further research is required to elucidate more fully the relationships between *Calluna vulgaris*, *Molinia caerula* and grazing on short and long time scales.

1.4 Environmental heterogeneity within the British uplands

There are large regional differences in the biogeography of the British uplands related principally to increasing oceanicity from East to West and decreasing temperature from South to North. Local variations reflect the influences of topography, geology and both past and present land uses (Ratcliffe & Thompson 1988). Most research in the uplands has been undertaken in Northern England and Scotland (Shaw *et al.* 1996) possibly as a result of their extent and high natural heritage value. The uplands of South-west England differ from the uplands of Northern Britain in a number of ways. *Agrostis curtisii* and *Ulex gallii* are important components of the vegetation in plant communities that are absent from Northern Britain. The extended growing season in the South-west may allow more rapid plant growth (Smallshire *et al.* 1997). Although unquantified, this may have management implications for key species such as *Calluna vulgaris* and *Molinia caerulea.* For example, grazing to suppress *Molinia caerula* may be required earlier in the year as a result of the extended growing season. *Calluna vulgaris* may never have been a widespread component of vegetation in the South-west, as a result of the oceanic climate, in which case targets for dwarf-shrub restoration established in the North, may be inappropriate in this part of the country. Compounding these differences in plant species and environment is the presence of different species and breeds of livestock, notably ponies, which are largely absent from the British uplands outside South-west England. The foraging preferences differ between the various species and breeds and there is a lack of objective data on the effects of not only ponies, but also cattle and sheep on South-west moorland vegetation communities (Smallshire *et al.* 1997).

1.5 Bodmin Moor

Bodmin Moor is the largest area of semi-natural habitat in Cornwall and the most South-westerly upland area in Britain. Therefore it is one of the warmest upland areas in Britain (see Chapter Two). The growing season is longer than on any other upland region in Britain and conditions are ideal for *Molinia caerula* grasslands, which require annual rainfall in excess of 1000 mm per annum and more than 140 wet days per year (Rodwell 1991). The other uplands of the South-west are not only more Easterly but also higher in altitude, resulting in an upland climate that is more comparable to Northern Britain. In addition, both Exmoor and Dartmoor are ESAs, in contrast to Bodmin Moor. Bodmin Moor was not accepted as an ESA in the last review of potential areas, mainly because there was no means of effective control over graziers who used the commons in contravention of sound husbandry practice (English Nature & Environmental Consultants CTNC 1994). The management of commons is of critical importance on Bodmin Moor, as they account for 57% of the semi-natural vegetation in the natural area. In 1998, MAFF set out proposals for an experimental project to be run on Bodmin Moor to test an integrated approach to rural economy and agri-environment issues and enhancements to the upland measures in the Countryside Stewardship scheme (MAFF 1998). Under these enhancements, common land can be subject to Countryside Stewardship agreements. The opportunity to rehabilitate the unique upland landscape of Bodmin Moor now exists, as does the need for a clear objective to the process. The success of this rehabilitation and the choice of suitable objectives depend on the availability of detailed analytical data on the vegetation, its environmental and biotic controls, and the effects of different management strategies. This work reviews current knowledge and presents new information on the vegetation and environmental gradients of Bodmin Moor.

1.6 Aims

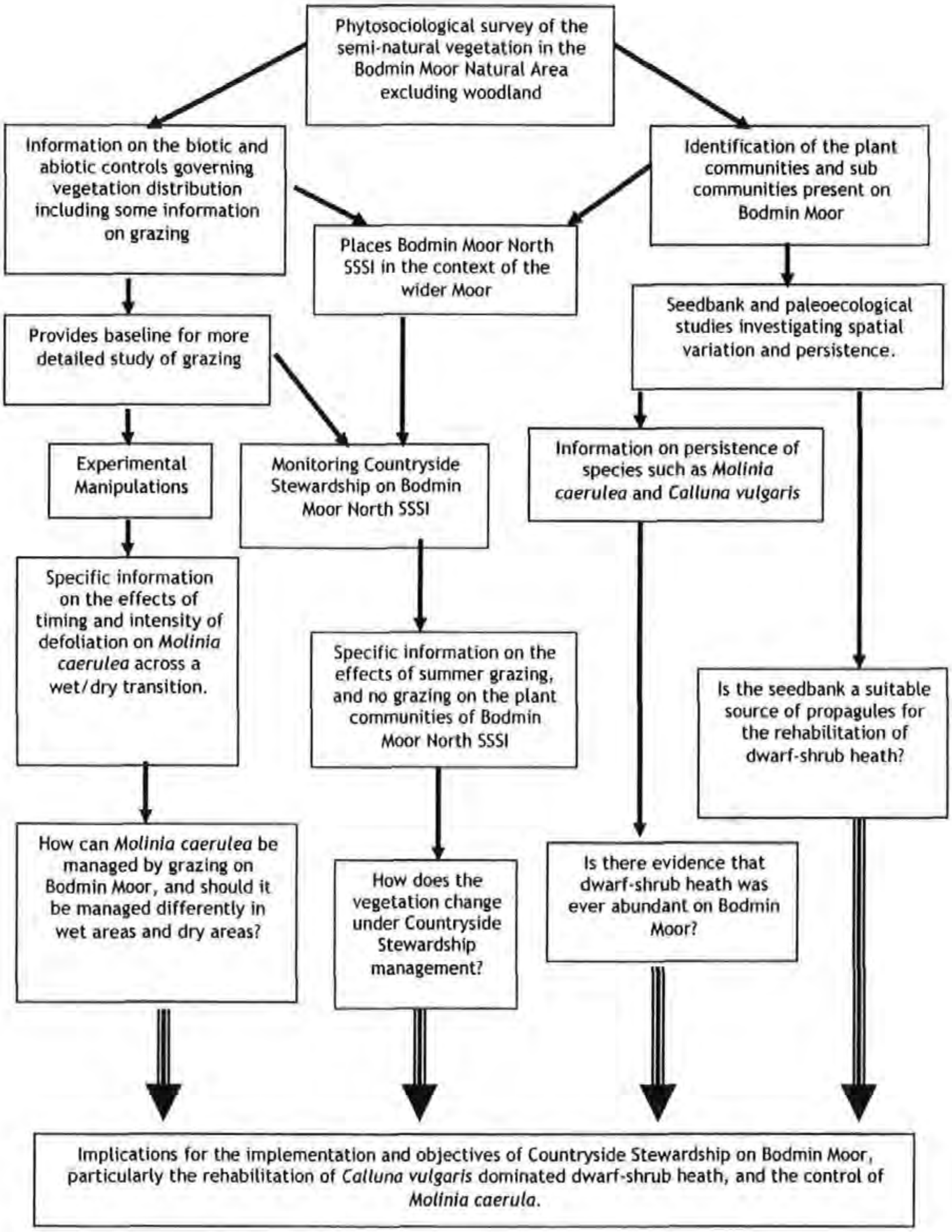
The central aim of the research is to reach an understanding of aspects of the ecology and community dynamics of the upland vegetation of Bodmin Moor in response to grazing. This primary aim will be achieved by satisfying a number of convergent objectives:

- Phytosociological classification of the upland plant communities of Bodmin Moor.
- Investigation of the spatial distribution of the plant communities in relation to environmental gradients and grazing management.
- Monitoring of vegetation in Bodmin Moor North SSSI, where winter grazing is confined to inbye under Countryside Stewardship management prescriptions. This may allow the identification of vegetation changes prompted by the reduction in summer grazing intensity and cessation of grazing during the winter. This will allow evaluation of the suitability of the Stewardship management prescription for the rehabilitation of heather cover in the upland landscape of Bodmin Moor.
- Description of the dynamics of the soil seed banks, providing:
    - Increased understanding of the ecology of *Calluna vulgaris, Ulex gallii, Molinia caerulea, Agrostis curtisii* and other species.
    - An assessment of the seedbank potential as sources of propagative materials for the rehabilitation of dwarf-shrub heath cover, and the potential for dominance of *Molinia caerulea*.
- Experimental manipulations investigating the response of *Molinia caerulea* to grazing across a wet / dry transition.

1.7 Thesis outline

Background information, essential to a full appreciation of the research presented in the thesis, is submitted in Chapters Two, Three and Four in the form of literature reviews. Chapter Two includes a review of the geology, climate, soils, past management, vegetation history and nature conservation value of Bodmin Moor. The chapter culminates by discussing the proposed future management of grazing on Bodmin Moor. Chapter Three comprises a review of the mechanisms by which grazing affect vegetation. Particular reference is made to the effects of variation in grazing practices and interactions between grazing and other environmental variables. Chapter Four provides a review of successional processes with particular reference to the effects of grazing on upland plant community succession and the limits of current knowledge of grazing management in upland habitats. Chapter Five presents the results of phytosociological classification and explores the relationships between environmental variables and vegetation. Chapter Six examines spatial variation in the seed bank of Bodmin Moor in a range of communities at different depths. Chapter Seven presents the results of a Countryside Stewardship monitoring scheme established on Bodmin Moor North SSSI. Chapter Eight investigates the effects of variation in timing, frequency and severity of defoliation, on *Molinia caerulea*, along a soil moisture gradient. Chapter Nine reviews the preceeding work focusing on the overall implications of the thesis. The structure of the thesis is presented diagrammatically in Figure 1.1.

Figure 1.1. The research context.



2 The ecological character of Bodmin Moor

2.1 Introduction

This chapter aims to define the ecological character and natural heritage value of Bodmin Moor by summarizing current knowledge concerning the key physical, ecological and land use features of the Bodmin Moor Natural Area. Much of this information has been collated in The Bodmin Moor Natural Area Profile (English Nature and Environmental Consultants Cornwall Trust for Nature Conservation 1994) and the synoptic study of Bodmin Moor (Brewster 1975). The work of Findlay *et al.* (1984) regarding soils and Gearey *et al.*(1996, 2000a, 2000b) in respect to palaeoecology provide additional knowledge. Further chapters of the thesis, particularly Chapter Five, allow the development of new perspectives on the character of Bodmin Moor. Comparison of the ecological character and natural heritage value of Bodmin Moor with other upland areas is intended to place Bodmin Moor in context, both within South-west England and in Britain as a whole.

2.2 Physical features

2.2.1 Geology and Geomorphology

The peninsula of South-west England has a geological character distinct from the rest of Britain, representing the eroded base of a Palaeozoic mountain belt formed by the Variscan orogeny (Edmonds *et al.* 1985). The mudstones, sandstones and shales of the Cornish killas were laid down during the middle and upper Devonian (415-370M.BP). Upper Devonian igneous intrusions formed bands of basalt and dolerite in this country rock. At the end of the Carboniferous (approximately 290 million years BP), the Variscan orogeny produced a series of complex major folds and metamorphism of the mudstones, basalt and dolerite resulted in the formation of slates, diabase and epidiorite, respectively (Edmonds *et al.* 1985). Towards the end of the Variscan orogeny, the granite intrusion of the Cornubian batholith subjected the killas to extreme heat and pressure, resulting in further folding and forming a metamorphic aureole that extends for up to 6.5km from the contact with the granite on Bodmin Moor. Within the metamorphic aureole, slates were metamorphosed to mica schists and calc-flinta (Kennett & Ross 1984). The cupolas of the Cornubian batholith are seen as the Dartmoor, Bodmin Moor, St Austell, Carnmenellis, Land's End and Scilly Isles granite intrusions (Figure 2.1.).

Apart from Dartmoor, there are no large upland areas of granite comparable to Bodmin Moor within England and Wales (Brown 1991), although extensive granitic uplands are common in Scotland. Bristow (1993) and Floyd *et al.* (1993) discuss the geological value of the Bodmin Moor granite. The impacts of the granite on the biota of the Moor are primarily expressed through the impact of granite bedrock on soils and the resultant effect on topography. The absence of basic material means that Bodmin Moor is dominated by acidophilous vegetation with calcicoles being largely absent and, when present, limited to extremely local areas of enrichment e.g. enriched grassland on Treslea Downs.

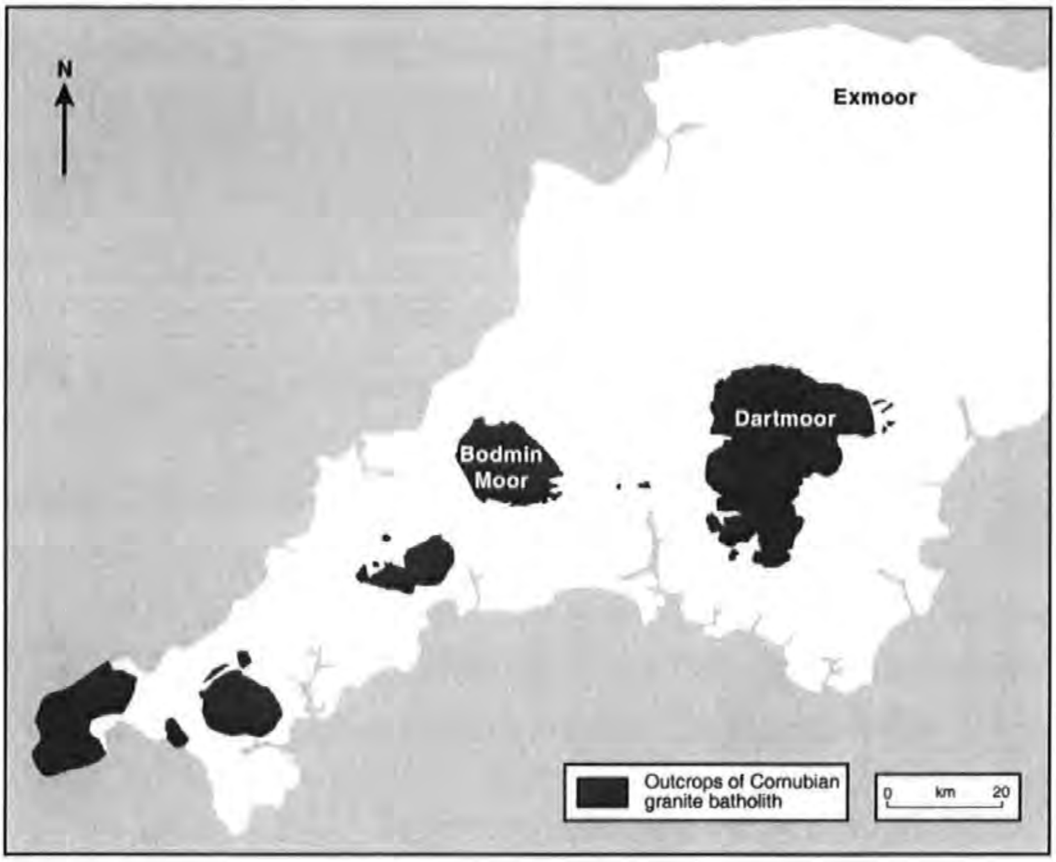
The cooling of the granite produced hypothermal and mesothermal water and volatile gases which entered fractures in the granite, leading to the development of mineral deposits. Tin, copper, wolfram, arsenic, lead, silver, cobalt, iron, zinc, nickel and uranium were deposited on Bodmin Moor (Embley & Symes 1987). Bristow (1993) and Sparrow (1994) document the mineralogical interest. The presence of minerals on the periphery of Bodmin Moor has been an important factor in the settlement and utilisation of the moorland areas throughout history and probably also prehistory. The effects of this on the biota are generally speculative, but it is known that tin streaming created disturbance in many of the valley mires on Bodmin Moor, often increasing their area and creating hummocks and pools (English Nature 1995). Peat cutting in the 19th Century is attributed to tin streaming (Gearey 1996), and an interest in tin in the less accessible areas of the Moor may have led farmers to develop areas of subsidiary farming during the Middle Ages

(Ravensdale 1974). Shaft mining created areas of metalliferous boulders, which have been colonised by rare assemblages of bryophytes (English Nature 1995). Phoenix United Mines is the most notable, being the only world site for *Ditrichum cornubicum* and *Cephaloziella nicholsonii*. It also supports the nationally rare *Pohlia andalusica*, *Cephaloziella massalongi*, *Cephaloziella integerrima* and the nationally scarce *Gymnostomum calcareum*, and *Gymnostomum viridulum* (English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994). In addition to the mineral veins, the cooling granite also gave off active solutions and gases, which caused three major structural alterations: tourmalinisation, greisening and kaolinisation. Kaolinisation involves the action of carbonic-rich gases on the feldspar to form secondary mica and kaolinite (china clay). Deposits of china clay have been worked in the Natural Area from the 19th century to the present day, with the most extensive pits occurring at Stannon, Park and Hawks Tor (English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994).

The influence of sub-aerial weathering, periglacial activity, marine erosion and fluvial processes on the geomorphology of Bodmin Moor are discussed by Coque-Delhuille (1987). Bodmin Moor and Dartmoor were the only major uplands in England which were not covered by an ice sheet during the Devensian ice age (Brown 1991), but the uplands were affected by severe periglacial activity, which is responsible in part, for the present topographical features of the moorland areas. Tors and clitter slopes are one of the most distinctive landscape features of Bodmin Moor (English Nature 1995). In Britain, they are found predominantly in South-west England, although they also occur in the Peak District and the Cairngorms. On Bodmin Moor, tors and their associated clitter are generally found above 320m, with the clitter being most abundant on the South-west slopes of tors, where there was more freeze thaw action (Coque-Delhuille 1987). The tors and clitter slopes provide habitat for diverse Atlantic lichen and bryophyte communities (English Nature and Environmental Consultants Cornwall Trust for

Nature Conservation 1994). They also support *Calluna vulgaris* at higher densities than other moorland areas, presumably because they form a refugium from grazing and are well drained. The solifluction of material under periglacial conditions resulted in the accumulation of unsorted deposits of gravel (head) in hollows on Cardinham Moor and near Siblyback reservoir (Coque-Delhuille 1987). This process has helped to form the shallow valleys and gently sloping hills of Bodmin Moor, as well as forming the parent material of the mineral soils on the moor.

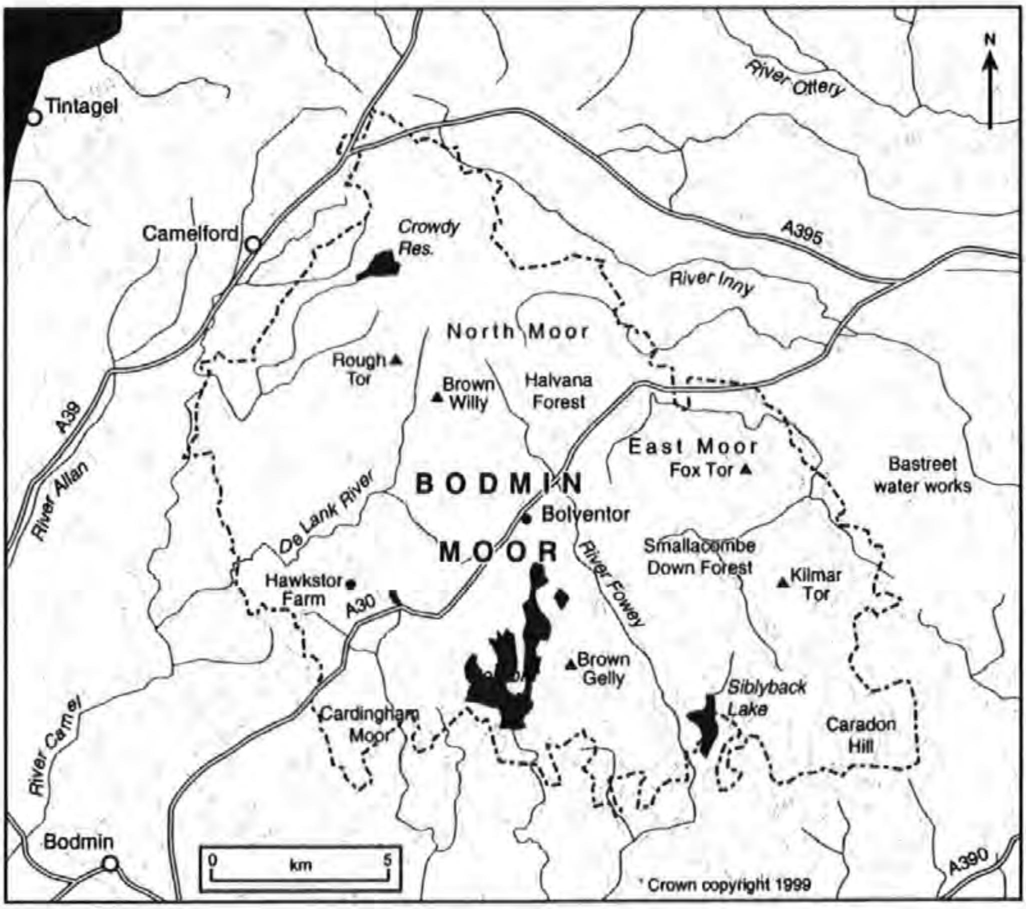
Figure 2.1. The cupolas of the Cornubian botholith and the uplands of South-west England.



2.2.2 Landform, drainage and settlement

The underlying granite determines the landform of Bodmin Moor. The granite has resisted erosion resulting in a dome about ten miles in diameter. The top of the dome comprises peneplains with gently sloping hills and shallow valleys. Numerous tors rise above this gently undulating landscape. Brown Willy is the largest of these tors, and at 420m is the highest point in Cornwall (Figure 2.2.). The moorland periphery is found on the slopes of the dome, where the ground becomes lower in altitude. These slopes give way to much flatter farmland on the slates and shales of the surrounding country rock (Brewster 1975, English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994). In this respect, Bodmin Moor is very similar to Dartmoor, albeit smaller in area and lower in altitude.

Figure 2.2. The landform and drainage of Bodmin Moor. The Less Favoured Area boundary delimits "Bodmin Moor".



The granite dome of Dartmoor provides a classic example of radial drainage, but on Bodmin Moor watercourses follow lines of weakness in the granite (Johnson and Rose 1994). These faults are generally North-South orientated hence; the De Lank and Camel run South-west into

Padstow Bay, the Warleggan, Loveny and Cardinham Water run South into the River Fowey, and the Withey Brook, Lynher and Penpont Water drain South-East into Plymouth Sound (Figure 2.2.).

Settlements on the high ground of Bodmin Moor are generally small. The moorland margins support larger villages that have arisen in response to either mining for example Minions, or agriculture for example St Breward, Blisland and Camelford. Bodmin Moor is bisected East-West by the A30 trunk road, dividing the area into the 'South Moor' and 'North Moor' (Figure 2.2.).

2.3 Climate

2.3.1 General description

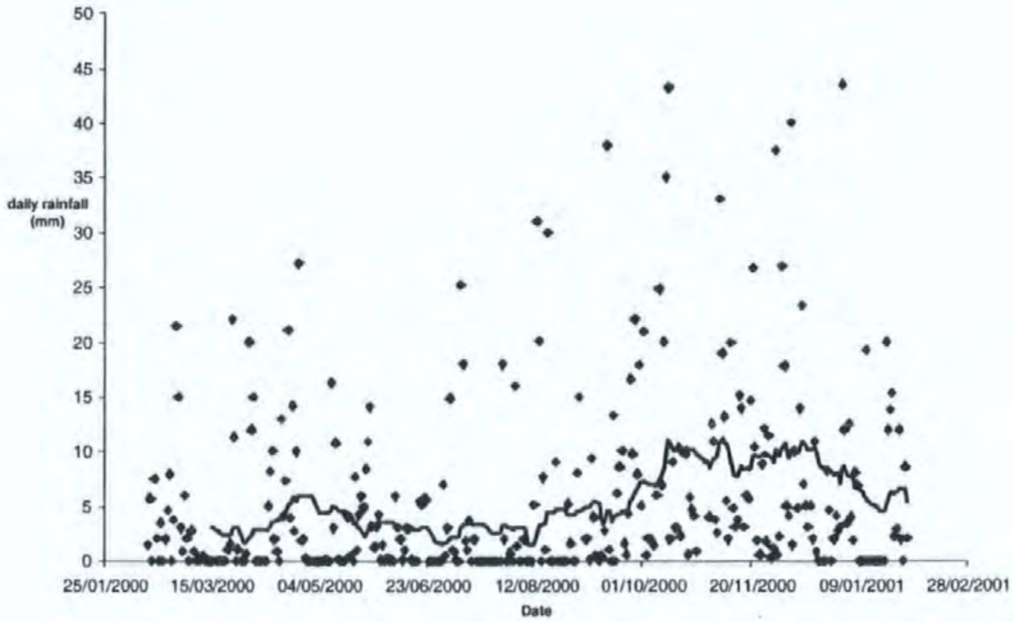
Bodmin Moor is one of the warmest upland areas in Britain as a result of its low altitude and extreme South-westerly location (Figure 2.3.). Climatological data collected at Bastreet Water Works at an altitude of 233m on the East Side of Bodmin Moor (NGR: SX244765) have been analysed by Brewster (1975). As a result of the altitudinal lapse rate, Bodmin Moor experiences lower temperatures, increased cloud cover and increased rainfall compared to lowland Cornwall. Mean annual rainfall at Bastreet Water Works from 1916 to 1950 was 1524mm with 180 wet days/year, compared to 950 mm at the coast 10km to the North (Brewster 1975). The average temperature rarely dropped to below freezing and the lowest mean winter temperature at Bastreet Water Works between 1971 and 1974 was 2-3°C. The warmest months were July and August and the highest mean summer temperature reached 19-20°C (Brewster 1975). The prevailing winds on Bodmin Moor are Westerly, but they are often replaced by Easterlies during the winter months. The Westerlies come straight off the Atlantic Ocean and contribute to the high humidity (>86%) on Bodmin Moor (Brewster 1975). The mild upland climate results in a growing season of 275 days for Bodmin Moor, compared with 175 days for Dartmoor and 325 days for lowland Cornwall (Gearey 1996).

Figure 2.3. Geographical areas of Britain above 200m.

2.3.2 Quantifying rainfall and oceanicity

The data collated by Brewster (1975) from Bastreet Water Works shows lower rainfall than that of other upland areas. Most UK uplands receive in excess of 2000mm per annum and although Rodwell (1992) cites this as the rainfall on Bodmin Moor, the data indicate lower rainfall than supposed. Brewster (1975) adjusted rainfall figures for increasing altitude and calculated that the high ground on North Moor received an annual average of 1778mm. Data collected from Hawkstor farm (Figure 2.4.) verifies that the North Moor receives higher rainfall than Bastreet Water Works, but the total rainfall in 2000 was only 1849mm compared to 2114mm recorded at Princetown (Dartmoor).

Figure 2.4. Precipitation on Hawkstor Farm (SX 134749 240 m) 15th February 2000 to 31st January 2001 (30 day moving average approximating monthly rainfall).



More rain falls in winter than summer, but high rainfall events are common during summer months (Figure 2.4.). Thus Bodmin Moor is less oceanic than previously thought, in terms of total annual rainfall, although oceanicity is exhibited in terms of rainfall distribution throughout the year, particularly in terms of the distribution of high rainfall events. More information is needed to further quantify climatic parameters in relation to oceanicity on Bodmin Moor.

The combination of high rainfall and warm temperatures is cited as the reason for development of oceanic species such as *Ulex gallii* and *Agrostis curtisii* together with their associated communities of humid heath and acid grassland (English Nature 1995, Rodwell 1992a, b). It has also encouraged the formation of rich Atlantic lichen, moss and liverwort communities (English Nature 1995), and the high rainfall has resulted in leaching, leading to iron pan creation, resulting in gleyed stagnopodzols, thus increasing soil wetness (Findlay *et al.* 1984). Although oceanicity is commonly considered ecologically benign and accounts for the presence of *Ulex gallii* and *Agrostis curtisii*, warm winters with oscillating temperatures and high rainfall can have harmful effects on species such as *Calluna vulgaris*. Warm winters with oscillating temperature reduce winter dormancy and deplete carbohydrate reserves in overwintering woody species, whilst water-saturated soils accelerate carbohydrate depletion in woody species leading to root die-back (Crawford 1997). Woody species, such as *Calluna vulgaris*, may therefore be at a disadvantage in oceanic climates, particularly as the warm spring temperatures may encourage the early growth of potential competitors such as *Molinia caerulea*.

2.4 Soils

2.4.1 Introduction

Soil is the product of several complex interacting processes. The characteristics of soil depend on the physical and chemical constitution of the parent material; past and present climate; and ecosystem processes, including the modifying effects of human activity (Brady & Weil 1999). The parent material of upland mineral soils in South-west England is an acid, gritty, sometimes bouldery, granitic head derived from deeply weathered and weakly coherent granite. The rainfall results in leaching leading to podzolization. This, in combination with the acidic bedrock, prevents decomposition of organic matter, allowing the formation of peat and stagnohumic gleys. The relief also encourages gleying and peat formation by maintaining a high water table (Findlay *et al.* 1984). Thus the uplands of Dartmoor and Bodmin Moor are dominated by a range of similar leached acidic soils, peats and waterlogged gleys, because these uplands have the same underlying bedrock and upland climates with high rainfall, although Dartmoor is wetter and colder than Bodmin Moor.

2.4.2 The Soils of Bodmin Moor

Avery (1980) describes the soil classification for England and Wales, which is hierarchical in nature and forms the basis of a system for differentiating the properties and relationships of soil. Table 2.1. shows the relationship between the main soils on Bodmin Moor and the soil series classification (modified from Hughes & Staines 1975). The occurrence of these soil associations and their relationship to precipitation and human utilization is discussed in order to compare Bodmin Moor with other areas in England and Wales, especially SouthWest England and Dartmoor. No information is available on the extent of these soil associations in Scotland.

Table 2.1. The soils of Bodmin Moor and their associations (modified from Hughes & Staines 1975).

Main Soil	Soil Association and series of main soil	Characteristics of main soil		Subsidiary soils
Podzols	Moor Gate series and Association	Dry, well drained soils ↓	Humose topsoil overlies permeable subsoil.	Hexworthy series Moretonhampstead series
Stagno-podzols	Hexworthy and Rough Tor series of the Hexworthy Association.	↓	Thin peaty surface (c.20cm) overlies thin iron pan. Considerable surface wetness	Princetown series Moorgate series
Stagno-humic Gleys	Princetown series and Association.	↓	Thin peaty surface (less than 40cm), normally 25 cm; compact subsurface overlies permeable subsoil. Extreme soil wetness.	Laployd series Hexworthy series Rough Tor series
Blanket Peat	Crowdy series and Association	↓	Peat more than 40cm deep over mineral soil; very poorly drained	Princetown series
Raw acid peats	Crowdy series and Association	↓ Very wet soils	Thick basin peats with extreme soil wetness due to depressed site and high groundwater	Laployd series

The soil associations in Table 2.1 are all restricted to acid igneous rock. The Princetown association is confined to the higher parts of the granite moors of South-west England but the other associations are found in further areas of Britain, notably Wales and to a lesser extent the Lake District. The Crowdy association occupies wide upland tracts of blanket bog and scattered peat-filled basins throughout South-west England and Wales (Findlay *et al.* 1984). The Moor Gate association is also found on uplands throughout South-west England and Wales. The Hexworthy and Moretonhampstead associations are found on the granite outcrops of South-west England from 510m on Dartmoor to sea level on the Isles of Scilly. Smaller areas of the Hexworthy association are found over granite in the Cheviots and on microgranite and rhyolite in North Wales. The Moretonhampstead association is also present in the Lake District (Findlay *et al.* 1984).

The differences between the upland soil of Bodmin Moor and the other uplands of the South-west are mostly attributable to differences in climate particularly precipitation. The climate on Dartmoor and Exmoor is severe above 400m, with an average annual rainfall in excess of 2000mm. The lower altitude of Bodmin Moor results in lower rainfall than that experienced on Dartmoor and Exmoor in spite of its more Westerly location. The Crowdy association is extensive on the blanket bogs of Dartmoor, with smaller patches on Exmoor. On Bodmin Moor, the blanket bog is very limited in extent and deep peat is restricted to basin peats in valley mires, mainly below 300 m but kept wet by high groundwater (Findlay *et al.* 1984). This also explains why the stagnohumic gleys of the Princetown association are widespread only on the highest ground of Bodmin Moor and are replaced with the Hexworthy and Rough Tor association stagnopodzols. This is in contrast to Dartmoor, where Princetown association soils occur on gentle slopes at 300m (Findlay *et al.* 1984). The main soil of the Princetown association and series is a stagnohumic gley (Harrod *et al.* 1976), but small hollows affected by groundwater contain pockets of Laployd series, humic gleys (Table 2.1). On the broad summits of Bodmin Moor, where the land is enclosed and grazed, the peaty surface horizon of the Princetown soils has wasted to a humose topsoil (Findlay *et al.* 1984). It is possible that drier climate of Bodmin Moor has contributed to the creation of a humic topsoil by allowing oxidation to occur. Humose topsoils are also found on steep slopes and where peat has been stripped for fuel (Findlay *et al.* 1984).

Although the differences in the soils associated with the upland areas of the South-west are mostly attributed to differences in precipitation related to variation in altitude, other variables such as geology and human utilization are also of some significance. In West Cornwall, the granite head is overlain by silty aeolian drift, which becomes decreasingly important Eastwards (Findlay *et al.* 1984). Thus on Bodmin Moor, in contrast to Dartmoor, the silty podzols of the Moor Gate association are more extensive than the loamy podzols of the Moretonhamstead association. On Bodmin Moor, the Moretonhampstead association is generally restricted to enclosed fields, whereas on Dartmoor, it extends onto the steep slopes and bouldery ground of the moorland (Findlay *et al.* 1984). The sandstone bedrock of Exmoor also results in a different suite of soils and topography in comparison to both Bodmin Moor and Dartmoor.

The soils of Bodmin Moor have been influenced by burning and other agricultural activities since the prehistoric (Maltby & Caseldine 1982, English Nature & Environmental Consultants 1994). Staines (1973) has argued that the Hexworthy series podzols developed from a brown earth soil as a result of enhanced acidification and leaching associated with Neolithic forest clearance on Dartmoor. On Bodmin Moor, the development of iron pan stagnopodzols post-dates the Neolithic, although brown humic podzols are found in association with Bronze Age barrows (Maltby & Caseldine 1982). However, the modifying effects of slope angle and aspect, altitude and hydrology, on the conversion of brown soils to iron pan stagnopodzols cannot be ignored and may contribute to this difference. The stagnohumic gleys of the Princetown association often have humose topsoil as a result of peat-cutting and grazing (Findlay *et al.* 1984). Peat-cutting associated with tin streaming may have occurred as early as the 14th Century on Bodmin Moor. In the 1950s, sea sand was spread on patches of open moor as a result of subsidies for land improvement. Subsoiling has allowed the reclamation of land dominated by wet stagnopodzols and stagnohumic gleys. The objective of this activity is to break up the iron pan (Hughes & Staines 1975) to allow winter rain to penetrate the lower soil horizons. Subsequent maintenance of good quality permanent pastures requires care in the timing of operations to prevent poaching, compaction of the topsoils and damage to the sward (Findlay *et al.* 1984). The retained water capacity of topsoils makes them particularly susceptible to poaching, which can encourage reversion to rushes (Findlay *et al.* 1984), especially in the case of the Princetown series stagnohumic gleys (Hughes & Staines 1975).

2.4.3 Vegetation and soils

Findlay *et al.* (1984) correlate vegetation and soil type. This primarily reflects differences in soil moisture, although regional differences are attributable more to different vegetation management than to soil type. The drier podzols of the Moor Gate and Moretonhamstead associations commonly consist of rough grazing. The Moorgate association often supports acid *Agrostis-Festuca* grassland, sometimes over-run by *Pteridium aquilinum* on rocky bouldery steep slopes. On Dartmoor, it also maintains *Agrostis curtisii* on gentle slopes, dry heath on the commons and oak wood, such as Wistman's Wood. The Moretonhamstead association is generally pasture, often infested by *Pteridium aquilinum* (Findlay *et al.* 1984). The wetter stagnopodzols and stagnohumic gleys support wet heath or *Molinia caerulea* grassland in wetter parts and acid *Festuca-Agrostis* grassland on the drier parts but grazing can mediate shifts between these communities. The intensive stocking on Bodmin Moor is believed to suppress the heather, resulting in grassland with increased cover of *Molinia caerulea* and *Agrostis curtisii* compared to Dartmoor (Findlay *et al.* 1984). The stagnohumic gleys and podzols on the drier ground of Eastern Bodmin Moor support extensive stands *of Ulex gallii.* The peats of the Crowdy association support *Molinia caerulea* bog and grassland on Dartmoor and Exmoor. *Sphagnum* and *Juncus* species tend to dominate the peats in valley mires (Findlay *et al.* 1984). The soil-site-vegetation relationships discussed above in relation to geographical variation are summarized for Bodmin Moor in Figure 2.5.

2.5 Land use on Bodmin Moor

2.5.1 Past management and vegetation history

The nature conservation interest of Bodmin Moor is a product of the physical environment and the long history of human settlement and land use (Brown 1991). The geology, climate and soils have influenced the vegetation types and the associated flora and fauna that are present on Bodmin Moor. The impact of humans on Bodmin Moor has been of considerable importance in the development of the soils and is arguably the most important factor in the development of the vegetation. In common with most of North-West Europe, Bodmin Moor has a long history of human occupation and exploitation throughout the last several hundred thousand years (Charman *et al.* 1998). The land use on Bodmin Moor as inferred from archeological and paleoecological evidence throughout the Holocene is shown in Table 2.2.

The start of the Holocene (10000 years BP) saw a rapid increase in temperature, resulting in a continental climate with warm summers and colder winters. Forest spread rapidly into South-west England, with the forest composition changing as new species migrated from the South, although in contrast to other areas in Britain, *Quercus* and *Corylus* dominated from very early on and there was no extensive spread of pine preceding this (Birks 1989). Evidence for human presence on Bodmin Moor during the Mesolithic (8000 years BP) is limited to finds of flints such as those around Dozmary Pool (Wainwright 1960). The populations were likely to have been low, with perhaps 3-4 small bands of hunter gathers using Bodmin Moor at any one time (Herring & Lewis

1992). The paleoecological evidence from Bodmin Moor suggests that there was little disturbance to the woodland cover during the Mesolithic (Gearey 1996). This provides a sharp contrast to Dartmoor, where charcoal remains suggest that fire was used to manage the tree line margin (Caseldine & Hatton 1993). There is also evidence of use of fire in other upland areas during the Mesolithic, including the North York Moors, the Pennines, the Lake District, Scotland and Wales (Charman *Pers. comm.*.). However, the fragmentary nature of the pollen profiles and lack of archeological evidence other than flints mean that care must be exercised in inferring land use on Bodmin Moor during the Mesolithic.

Figure 2.5. Soil - Site - Vegetation relationships on Bodmin Moor (modified from Hughes & Staines 1975)

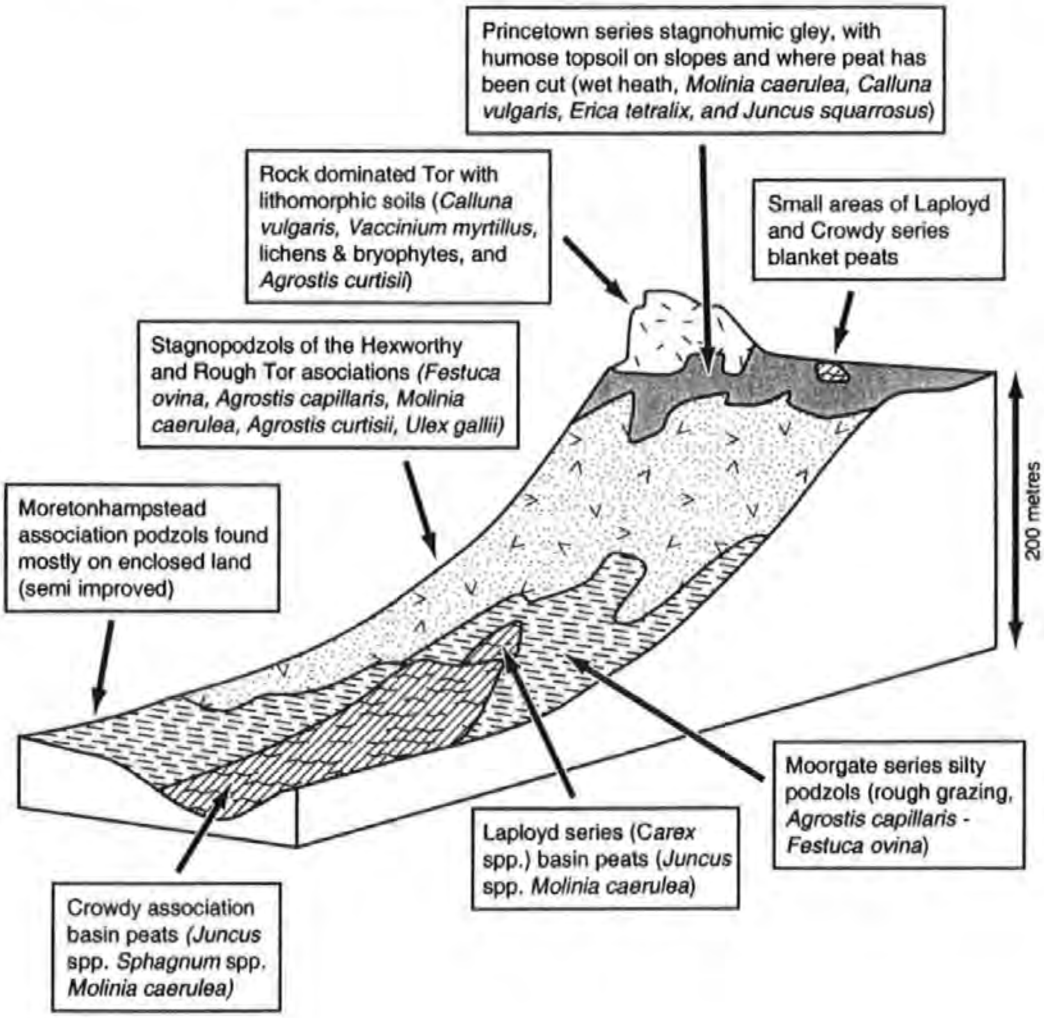


Table 2.2. The inferred landuse on Bodmin Moor throughout the Holocene (Sources: Johnson & Rose 1994, Charman et al. 1998, Gearey 1996, Gearey et al. 2000a, 2000b).

Date (BP)	Archaeological evidence	Paleoecological evidence	Inferred land use
700	Hamlets give way to single farms.		Intensive seasonal grazing.
1000	*Mediaeval* moorland hamlets.	Decrease in arboreal and herbaceous pollen interpreted as clearance of remaining local scrub and demise of meadow vegetation at the expense of acid grassland.	Increasing pastoral activity with some local cultivation.
2000	Romano-British remains.	Predominance of graminoid pollen interpreted as meadow grassland with some scattered *Alnus* and *Corylus* scrub remaining.	Low intensity pastoralism.
3000	Iron age settlement at Garrow Tor.	Reduction in *Alnus* and *Corylus*.	Seasonal grazing. High intensity transhumance with few permanent settlements?
3500?	Transhumance settlements.	Increase in *Alnus* and *Corylus* pollen interpreted as limited regeneration in wet areas.	Settlements move off uplands. Grazing continues?
4000	Bronze age settlement at Stannon & barrows at Davidstow & Colliford.	Decrease in *Corylus* pollen & increase in graminoid pollen interpreted as clearance of *Corylus* scrub and spread of grass meadows.	Intensive pastoral activity. High intensity transhumance?
6000	Neolithic flint scatters, hill top exclosures at Rough Tor & Stowes Pound. Long cairns at Louden hill.	Arboreal pollen decline interpreted as clearance of *Corylus*, *Quercus* and *Betula* woodland.	Low intensity transhumance with some huts and fields.
8000	Mesolithic flint scatters.	Woodland dominated by *Corylus*, *Quercus* and *Betula* with little open land.	Small scale seasonal use of uplands.

Clear evidence for Neolithic (6000 years BP) settlement on Bodmin Moor and Dartmoor is sparse (Quinnell 1996). The dating of hilltop enclosures on Bodmin Moor such as Rough Tor and Stowes Pound is based on morphological comparison with dated structures elsewhere (Johnson & Rose 1994). Paleoecological work is interpreted as demonstrating that large-scale alteration of the landscape was underway during the Neolithic on Bodmin Moor. *Quercus* and *Corylus* were replaced with a mosaic of grassland and woodland habitats with some *Calluna vulgaris*. The remaining tree cover was largely restricted to the wetter soils (Gearey 1996). On Dartmoor, paleoecological study suggests only minor disturbance during the Neolithic, with no large-scale removal of forest cover, although the development of heather moorland and the 'elm decline' occur during this period (West 1997). The Neolithic impacts on Bodmin Moor are therefore unusual in the context of South-west uplands. However it is possible to find <50 % arboreal pollen under a woodland canopy (Bunting *Pers. comm.*). Thus the decline in arboreal pollen on Bodmin Moor is not necessarily synonymous with Neolithic woodland clearance.

The archeological evidence for extensive settlement and use of the South-west uplands during the Bronze Age (4000 years BP) is unequivocal, as the majority of cairns, hut circles and prehistoric field boundaries found on Bodmin Moor and Dartmoor date from this period (Charman *et al.* 1998). On Bodmin Moor, the decline in arboreal pollen continues through this period, especially in the case of *Corylus*. This is interpreted as clearance of the remaining woodland on Bodmin Moor and clearance of the *Corylus* scrub that developed in response to Neolithic woodland clearance. There is a Bronze Age increase in graminoid pollen, which is interpreted as the spread of grass meadows (Gearey 1996). The Bronze Age represents a massive increase in human impact on Bodmin Moor with pastoral activity intensifying and spreading to cover the whole moor. Bronze Age human impact on Dartmoor was even more extreme as the unsettled Neolithic landscape gave way to the extensive land divisions of the reave systems which were constructed in a largely open landscape (Caseldine & Hatton 1996).

The 'high tide' of Bronze Age settlement on the uplands of the South-west receded rapidly; resulting in few Iron Age remains (Charman *et al.* 1998). There is extensive evidence of Iron Age settlement of lower lying areas, which has been interpreted as an abandonment of the uplands in the face of deteriorating climate (Todd 1987). There is little paleoecological evidence to support this for Bodmin Moor and the other

South-west uplands (Gearey 1996). There was an increase in *Alnus* and *Corylus* on Rough Tor in the late Bronze Age (3500 years BP), followed by woodland decline and a resurgence of grassland and heather (Gearey & Charman 1996). A shift in settlement patterns from upland to lowland, possibly associated with transhumance, and increase in population around 3500BP may have resulted in an intensification of upland land use which could have had a greater impact on the upland resource than that of the early Bronze Age (Gearey 1996). The absence of remains on Bodmin Moor, Dartmoor and Exmoor does not necessarily equate with an absence of anthropogenic activity. Further work is required to corroborate this interpretation of the archeological and paleoecological evidence (Charman, D. University of Plymouth. *Pers. comm.*).

The decline in arboreal and increase in graminoid pollen continued through the late Bronze Age and Romano-British period (2000 years BP) on Bodmin Moor, as it did in other areas of Britain and particularly in Wales. This suggests that pastoral activity in the moorland areas of the South-west and Wales continued throughout the first millennium with some small-scale, intermittent cultivation and continued clearance of remaining woodland and spread of meadow grasslands. It is probable that Bodmin Moor continued to be used for seasonal grazing until some time in the *Mediaeval* period (Gearey 1996).

The *Mediaeval* period (1000 years BP) marked the first large-scale settlement of Bodmin Moor since the Bronze Age. This colonisation is primarily related to an increasing population but the expansion of ship building, tin streaming, textiles and quarrying in Cornwall may also have increased the market for agricultural produce (Hatcher 1970). On Bodmin Moor, the final removal of tree and shrub cover occurred associated with the widespread occurrence of cereal pollen (probably *Avena* spp.) which testifies to the cultivation of the upland. The expansion in pasture is also apparent in increases in *Poaceae, Plantago lanceolata* and other grassland species (Gearey 1996). *Mediaeval* colonisation also occurred on Dartmoor (Beresford 1979) and there is an associated decline in arboreal pollen and increases in *Poaceae, Plantago lanceolata* and cereal pollen attributed to *Mediaeval* cultivation (Beckett 1981).

Additional information is provided by written sources. The Domesday Book records that settlements around Bodmin Moor had large areas of pasture attached to them, e.g. Fawton with 7 leagues by 4 leagues of pasture, Hamatethy with 5 leagues by 2, and Helstone, Rosecraddock and Trezance with 3 leagues by 2 (Ravenhill 1967). Ravenhill (1967) adds that only speculation is possible on the extent of this pastureland in modern units of area but Johnson & Rose (1994) believe that the five leagues by two at Hamathethy could equate to an area of 13-15 km^2. According to the Domesday Book, sheep were the most numerous of all the recorded livestock and flocks of many hundreds were frequently encountered in Cornwall (Ravenhill 1967). On Bodmin Moor, grazing was primarily by sheep, which outnumbered cattle by 13:1 (Pounds, 1947). The written sources not only provide information on land use but also give some indications of grazing pressure. Possibly the first recorded case of overgrazing occurred in 1358, when 500 bEasts were grazed illegally throughout the year on Roughtor 'to the great damage of the petitioner' (Hamatethy Manor) (Pounds, 1947).

The decline of the Mediaeval moorland hamlets and their replacement by the single farm occurs from the late 14th century onwards (Johnson & Rose 1994). Climatic deterioration and the Black Death are probably both responsible (Beresford 1979) but soil deterioration has also been defined as a possible factor (Maltby & Caseldine 1982). The end of the Mediaeval period is marked by the disappearance of cereal pollen at Rough Tor. The species-rich meadowland that had been maintained by the unintensive use of Bodmin Moor for over one millennia was replaced by acid grassland possibly as a result of intensive grazing and the decline in soil conditions due to the effects of the land use during the Mediaeval period (Gearey 1996). Thus the present day character of

Bodmin Moor (and Dartmoor) was established at the end of the Mediaeval period (Charman *et al.* 1998).

There is a scarcity of information on both land use and vegetation change after the end of the Mediaeval period but Bodmin Moor probably reverted back to its former use as an area of seasonal grazing on poor acid heath and grassland (Charman, D. University of Plymouth. *Pers. comm.*). Written sources describing vegetation on Bodmin Moor are consistent with this hypothesis and depict a landscape of limited agricultural value.

> "8 miles by morish and hilly ground and a great scarsitie of wood, in so much that the counterey thereabout brennith firres and heath" (Leland 1543).
>
> "the middle part of the shire lieth waste and open, sheweth a blackish colour, beareth heath and spiry grass, and serveth in a manner only to summer cattle" (Carew 1602).

However Bodmin Moor must have supported significant numbers of sheep, as it had became the main centre of the wool – textile industry in Cornwall by 1700 (Bowden, 1962). Mills were located around Bodmin Moor at St Breward, Blisland and Advent (Brewster 1975) and there were yarn markets at Bodmin, Liskeard and Launceston (Pounds 1947). By the late eighteenth century, a factory industry had developed at Camelford and Bodmin but this was short-lived (Brewster 1975). The wool trade in the West Country declined rapidly as a result of the Napoleonic Wars and increasing competition from other areas of the country notably, Yorkshire and Lancashire (Pounds 1947).

The 1800s saw the demise of native breeds of sheep, cattle, ponies and goats, which were replaced by hardier breeds (Brewster 1975) and there is some evidence that moorland vegetation was burnt to encourage new plant growth for grazing animals (English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994). Moorland areas were also enclosed and converted to pasture during the 19th century, particularly around Bolventor and Priddacombe (English

Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994).

The response of vegetation to post-Mediaeval land use change on Bodmin Moor has been subject to speculation with scant supporting evidence. Brewster (1975) argues that, as the basic system of pastoralism was retained with stock numbers limited by the Lords of the Manors and wintered off the commons (levancy and couchancy), the heathland and grassland communities of the moor were maintained (Brewster 1975). However Brewster (1975) and English Nature & Environmental Consultants Cornwall Trust for Nature Conservation (1994) interpret written sources as implying that ericoid shrubs, specifically *Calluna vulgaris*, were becoming increasingly sparse on the moor during the mid-1800s. They suggest that this is due to the introduction of hardy breeds (Brewster, 1975. English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994).

> 'Bodmin Moor was much more productive of grass than the heaths of Yorkshire, though every part is more or less heath' (Marshall, 1796).
>
> "The sheep on the Moor were cropping furze and heath as well as depasturing grass' (Wallis 1811)
>
> Caradon Hill is described as 'grass, short furze and a few fine heaths' (Daniell 1854).
>
> The vegetation of Brown Willy is described as 'no heather, very little furze and no other cover sufficient to screen a mouse' (Mallan, 1888)
>
> 'The surface of the Bodmin Moors is of long coarse grass with both dwarf and ordinary gorse, a little heather spread about the hillsides and the usual bracken amongst the scattered granite rocks' (Malim, 1936).

Further paleoecological work is required to determine the former extent of heathland on Bodmin Moor but current evidence suggests that it was never widespread. The paleoecological work of Gearey (1996) allows reconstruction of the paleoenvironment on Bodmin Moor between the Mesolithic and the Mediaeval. *Calluna vulgaris* never accounts for more than 15% of total pollen (Gearey 1996). More work is required to verify this, as *Calluna vulgaris* pollen is local in its occurence with little pollen travelling more than a few metres from its source (Bunting, J. University of Hull. *Pers. comm.*). Further work is also required in order to document heathland decline on Bodmin Moor during both the 1800s and last century.

2.5.2 Vegetation management and land use during the 20th century

The management of Bodmin Moor changed significantly during the 20th century as a result of reduction in the control of grazing on the commons, the introduction of subsidies and grants, and the move towards modern agricultural practices. In 1925, the Law of Property Act abolished rents for commoners rights and there was no incentive for the Lords of Manors to oversee stocking rates. From 1925 onwards, there was no legal power to control grazing on the commons (English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994). A number of financial incentives were introduced in the post-World War two years to increase food production (Table 2.3.), and legislation introduced to modify the effects of farming on the environment (Table 2.4.).

The lack of legislation governing animal numbers on the common and the introduction of subsidies had important ramifications for livestock management on Bodmin Moor. At the turn of the century, the small farms on Bodmin Moor kept flocks of up to 40 sheep and 2-3 cattle. Between the wars, the requirement for national self-sufficiency encouraged higher stock numbers, particularly for cattle (English Nature & Environmental consultants Cornwall Trust for Nature Conservation 1994) but it was the introduction of subsidies that caused the most dramatic increase in stock numbers (Brewster 1975). In 1944, the Agricultural Executive Committee recorded that the commons were being overstocked. MAFF and the Cornwall Commoners Association also noted this trend on several occasions (English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994). From 1940 to 1973, sheep numbers increased from 570 to 21,679 (x38 increase).

Cattle numbers doubled between 1945 and 1975 and from 1953 to 1974 cattle numbers increased from 2669 to 9503 (x3.5 increase) (Brewster 1975). Figures from the Dartington Institute (1984) confirm the increasing numbers of animals on the open moor. In 1953, the stocking density was one cow / eight acres; in 1964, it was one cow / five acres and by 1969 it was one cow / four acres. Cattle numbers have stayed relatively constant over the last 30 years with approximately 8-10000 suckler cows in the Less Favoured Area (LFA) today. However sheep numbers have increased from 18000 to 30-40000 in the last 30 years. There are thought to be about 700 ponies on Bodmin Moor (MAFF *Pers. comm.*).

The increase in cattle numbers over the last century means there are currently about five sheep for every cow. This is a low ratio compared to other upland areas. The ratio of cattle to sheep on Dartmoor was 1:8 (Brewster 1975), while the uplands generally have a ratio of 1:10 (Holmes 1991), with cattle more common in the Western uplands of Britain than in the East. This could reflect the low altitude of Bodmin Moor in comparison to other upland areas that are stocked with hardy sheep because the environment will not support cattle. Also on Bodmin Moor, the abundance of *Molinia caerulea* may contribute to the stocking of cattle rather than sheep, as they are more effective in controlling *Molinia caerulea* growth, especially in spring (Brewster 1975).

Cattle and sheep breeds have changed over the century, with hill breeds becoming increasingly common. Hill sheep such as Scottish Blackface and Cheviots replaced flocks of Devon Longwools, and hardier cattle breeds of Scottish ancestry such as Highland, Aberdeen Angus, Galloway and their crosses replaced Red and Broad-horned Devons (Brewster 1975). These breeds range further and stay on the moor for longer periods than lowland breeds (English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994). The introduction of these hardy stock and the relaxation of grazing control on the commons resulted in a seasonal change in stocking practice.

Table 2.3. The management implications of subsidies and legislation introduced post-1940 to increase food production (sources: Brewster 1975, English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994).

Date	Subsidies & legislation	Management implications		
		Sheep	Cattle	Other
1940	Hill Sheep subsidy	Subsidy for hardy breeds of ewes wintering on upland areas during severe winters		
1943	Hill Cattle subsidy	↓	Subsidy for beef cattle >1 year old kept on the commons for >16weeks/year.	A third of the subsidy was spent on agricultural improvements
1946	Hill Farming Act	Targeted at sheep farming areas	↓	Grants for improving land and buildings.
1947	Agricultural Act	↓		A general payment to cover many activities, such as drainage and fertilizing to encourage food production so that it was affordable to the consumer
1951	Livestock rearing Act. Bodmin Moor was designated a Hill Farming Area	Farmers became eligible for hill sheep subsidies.	The main objective of the act was to pay subsidies on beef cattle.	Payments made to assist improvements on enclosed land.
1953	Hill Cow subsidy. Replaced the hill cattle subsidy.	↓	A subsidy on breeding cows to increase the number of store cattle.	40% of the grant had to be spent on agricultural improvements. Stocking rates were initially specified at 1cow/8acres but this was increased to 1cow/4 acres by 1969.
1965	Beef Cow subsidy		A subsidy to increase beef production	↓
1973	Joined the EEC. Bodmin Moor was designated a Less Favoured Area (LFA).	Within the LFA farmers could claim Hill Livestock Compensatory Allowance (HLCA) which replaced the hill cow and hill sheep subsidies. Farmers received payments if they kept stock under sound husbandry conditions and maintained good grazing and feeding practice. Headage payments are currently being replaced by area payments under the RDC (see later).		This replaced the hill farming area and initially covered 12000ha. The EEC contributed 25% to the cost of the HLCAs
1980	Sheep Annual Premium Scheme and Suckler Calf Premium Scheme	A headage payment to regularise the market return to sheep producers	A payment to encourage specialised beef producers to produce more suckler calves	

Table 2.4. The management implications of subsidies and legislation introduced post-1940 for nature conservation.

Date	Legislation	Management implications
1981	Wildlife & Countryside Act	Agencies must be notified of potentially damaging operations such as overgrazing on Sites of Special Scientific Interest.
1986	Environmentally Sensitive Areas	Payments to farmers in designated areas as compensation for potential income lost by adopting traditional less intensive farming methods (includes reduction in stocking rates)
1991/ 1992	Countryside Stewardship piloted in response to EU Habitats Directive	Habitats directive applied through Biodiversity Action Plans. Countryside Stewardship forms a key element in habitat protection outside ESAs by encouraging reduction in stocking levels
1999	Rural Development Program	Modifications to LFA and HLCA legislation. Increased funding for Countryside Stewardship and ESA schemes.
2001	Countryside and Rights of Way act	Ratification of these acts expected imminently (2002?).
2002	Rural Development Program	The possible integration of all agri-environmental legislation has potentially important impacts on the degree of flexibility available to both policy makers and land owners at regional levels

At the beginning of last century, Bodmin Moor was still used for summer grazing. When the grasses died back at the end of summer, stock were taken off the commons and brought onto the inbye land until the following spring. The subsidies encouraged farmers to keep more breeding stock on the moor. Numbers were increased beyond the capacity of the inbye land and the excess breeding stock were turned out on the commons in the autumn and winter months. At this time of year, dwarf-shrubs of heather and gorse are available to grazing stock along with supplementary feed. The hardy breeds were better able to cope with this winter diet and therefore began to be left out on the moor for the whole year rather than wintered on inbye (Brewster 1975, English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994). Table 2.5 illustrates stock movement throughout the year on Bodmin Moor today. Essentially stock remain on the moor all year round, except for breeding and weaning young. Apart from this, only young animals and sick animals requiring attention are kept on inbye, unless there is a financial incentive for removal of stock as agreed management under agri-environment schemes.

The effects of the changes in grazing practice over the previous century on the vegetation of Bodmin Moor are anecdotal. Observations of recent vegetation change by local residents point to conversion of dwarf-shrub heath to grassland where grazing is intensified and an increase in the spread *of Pteridium aquilinum* and *Ulex gallii* where grazing is relaxed (Holmes 1991, English Nature & Environmental consultants Cornwall Trust for Nature Conservation 1994). Chapter Four reviews these grazing mediated community shifts, which are far from fully understood, even in other upland areas that have been subject to more intensive research e.g. Moorhouse in the Northern Pennines (Rawes 1971, Rawes & Heal 1978, Rawes & Hobbs 1979).

In contrast to vegetation change, changes in land use on Bodmin Moor during the latter half of the 20th century are well documented. Moorland, roughland and wetland experienced a considerable loss of area of the period 1946-1992, whilst most other land use categories increased in area (Jones & Essex 1999). Moorland, roughland and wetland accounted for 74% of the LFA in 1946. This was reduced to 59% in 1976 and to 53% of the LFA in 1992. The largest gains in land were in improved land (24% of the LFA in 1946 increasing to 35% by 1992) and coniferous forest (absent in 1946; increasing to 5% of the LFA by 1992) (Jones & Essex 1999). Statutory designations and the advent of agri-environment schemes, which have been introduced to protect valued landscapes, have partially addressed the problems of loss of moorland habitat and its degradation by modern agricultural practices. The nature conservation value of Bodmin Moor and associated environmental legislation is discussed below.

Table 2.5. The movement of stock between moorland and inbye on Bodmin Moor (Sources; English Nature & Environmental consultants Cornwall Trust for Nature Conservation 1994, Mansfield *Pers. comm.*).

Month	Cattle		Sheep	
	Inbye	Moorland	Inbye	Moorland
January				
February				
March				←
April	Breeding cows taken off moorland to calve	←	Breeding sheep taken off moorland to lamb	
May			→	The 'singles' (ewes with one lamb) and the 'hoggetts' (one year old lambs) back on the moor in May
June	Breeding cows on inbye to run with bull. (Bulls prohibited from common land since 1908)	←		
July				
August	→ →	Breeding cows back on moor after running with the bull	→	The 'doubles' (ewes with two lambs) are returned to the moor in August
September		Breeding cows back on moor after weaning calves	New lambs are kept on the inbye land until they are sold at the end of summer for fattening.	
October	Calves are reared for the October suckler calf sales and sold on to lowland farms at 6-9 months old. Some calves are overwintered indoors on silage, put out on the moor during the summer and sold as stores at 15-18 months old		The ewes brought in for tupping in October and returned to the moor for the rest of the winter →	←
November				
December				

2.6 Vegetation and conservation

2.6.1 The vegetation of Bodmin Moor and its conservation value

Bodmin Moor is probably the least well known upland area in Britain (Jones & Essex 1999). To some extent it is a microcosm of other upland areas, both in terms of habitat and land use conflict. However the granite bedrock, together with the warm wet climate and the long history of human settlement and utilisation, have created a unique area with a distinctive landscape character and a special nature conservation interest (English Nature 1995). The high moor is characterised by extensive tracts of unimproved acid grassland separated by shallow valleys with mires and bogs, scattered heathlands and rocky outcrops (Drewitt & Manley 1997). Table 2.6 lists the National Vegetation Types (Rodwell 1991; 1992) found on Bodmin Moor. The table provides a summary of the distribution and nature conservation significance of the plant communities. Where the communities are representative of vegetation listed in Annex 1 of the European Community (EC) Habitats and species directive, this has been recognised, by inclusion of a CORINE biotype (EC 1992).

The presence and extent of the communities listed in Table 2.6 requires verification. Phase One habitat survey (Nature Conservancy Council 1990) undertaken by Cornwall Trust for Nature Conservation (1988-1993) provides general information on the occurrence and extent of the semi-natural habitats on Bodmin Moor. However it does not accurately reflect the current vegetation distribution of the moor, particularly for heathland. This may reflect rapid temporal change, as a result of burning and grazing, or it may be due to lack of resources for ground truthing. Drage (1981), using Birks & Ratcliffe (1980) classification, surveyed most of the South moor. The Nature Conservancy Council Upland Survey Team (Nature Conservancy Council 1986), using a hybrid classification of Birks & Ratcliffe (1980) for grasslands and Rodwell (1991) for heaths and mires surveyed much of the North moor.

Table 2.6. TheNVC communities of Bodmin Moor. Their distribution, significance and Corine biotype codes.

NVC community	NVC code	Distribution	Significance	CORINE
Eriophorum angustifolium bog pool	M3	Largely restricted to eroded blanket mire in the North and West of Britain.	International but not national	C51.12
Carex rostrata-Sphagnum recurvum mire	M4	Widespread but local throughout NorthWest Britain.	International and national	C54.531 C52.1
Scirpus cespitosus-Eriophorum vaginatum blanket mire	M17	Largely confined to Western Britain.	International and national	
Sphagnum cuspidatum/recurvum bog pool	M2	Widespread from Wales, to the Borders and SouthWest Scotland. Local elsewhere.	International and national	C51.12
Carex echinata-Sphagnum recurvum /auriculatum mire	M6	Ubiquitous throughout the sub montane zone in Britain.	International and national	C54.423
Juncus effusus/acutiflorus-Galium palustre rush pasture	M23	Widespread in the West of Britain	International and national	C37.217 C37.312 C31.11
Scirpus cespitosus-Erica tetralix wet heath	M15	Occurs widely in Scotland and Wales. Less widespread in SouthWest England and the Lake District.	International and national	
Molinia caerulea-Potentilla erecta mire	M25	Widespread in the West of Britain especially in South-west England, Wales and Southern Scotland	International and national	
Agrostis curtisii grassland	U3	Restricted to the uplands of SouthWest England in Britain.	International and national	C35.1
Ulex gallii-Agrostis curtisii heath	H4	Confined to SouthWest England and the South Wales seaboard.	International and national	C31.235 C31.235
Calluna vulgaris-Ulex gallii heath	H8	Occurs widely throughout SouthWest England and Wales	International and national	

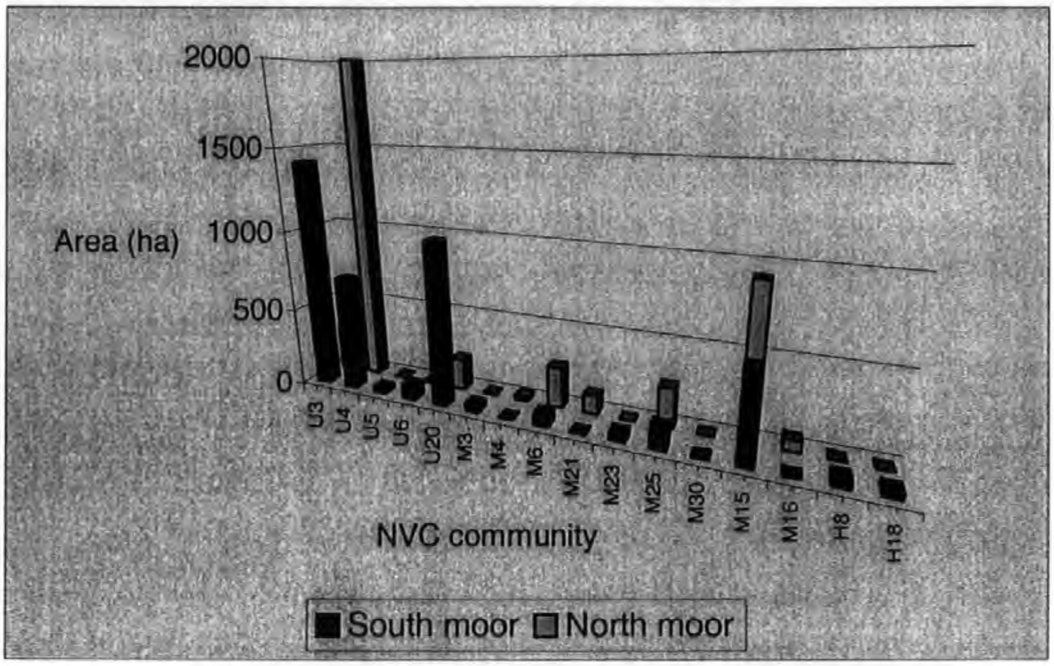
Table 2.6. Continued.

NVC community	NVC code	Distribution	Significance	CORINE
Narthecium ossifragum-Sphagnum papillosum valley mire	M21	Local community restricted to the South and found in an upland context only in SouthWest England, Wales and at its North-Eastern limit in the North York Moors.	International and national	C51.14
Hypericum elodes-potamogeton polygonifolius soakway	M29	Common in South and SouthWest England, Wales and Galloway. Probably also in the Hebrides and Eastern England	International and national	C22.313
Erica tetralix-Sphagnum compactum wet heath	M16	Largely confined to the South and East of Britain.	International and national	C31.11 C31.212
Vaccinium myrtillus-Deschampsia flexuosa heath	H18	Widespread throughout the British uplands especially Northern Scotland	International and national	
Nardus stricta-Galium saxatile grassland	U5	Widespread in the British uplands.	International significance but often of low nature conservation value in a British context.	C35.11 C37.32 C35.12
Juncus squarrosus-Festuca ovina grassland	U6	Widespread in the British uplands.		
Festuca ovina-Agrostis capillaris-Galium saxatile grassland	U4	Ubiquitous throughout the sub montane zone in Britain.		
Pteridium aquilinum-Galium saxatile community	U20	Ubiquitous throughout the sub montane zone in Britain.	Generally considered negative	C31.86

These surveys provide detailed community data and vegetation maps, but there are discrepancies between them.

Figure 2.6. illustrates the relative proportions of the communities on the North Moor and on the South Moor as surveyed by the Nature Conservancy Council Upland Survey Team (1986) and Drage (1981). The differences between the two surveys reflect both real biological differences between the North and South Moors and differences between the surveyors. There is considerably more *Pteridium aquilinum* on the South Moor than the North Moor and this is reflected in the quantity of the *Pteridium aquilinum-Galium saxatile* community. However the different quantities of *Agrostis curtisii* grassland and *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland probably represent different approaches to classification. The difference between these communities is largely dependent on value judgements about the quantity of *Agrostis curtisii* that should be present before *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland becomes *Agrostis curtisii* grassland. The widespread presence of *Molinia caerulea* also makes classification harder. Likewise, the lack of heathland in the North Moor survey probably reflects surveyor's decisions about what constitutes grassland, grass-heath, and heathland, rather than a biological difference between North and South Moors. Between-observer variation in the application of standard method habitat mapping can be very high. Cherrill & McClean (1999) found that six skilled surveyors agreed on the classification of only 8% of the study site when they surveyed it independently using the Phase One approach. In general, the discrepancies between the North and South Moors are probably due to a similar problem of between-observer variation.

Figure 2.6. The extent of plant communities on the North and South Moors. (Sources: NCC Upland Survey Team 1986, Drage 1981, English Nature & Environmental consultants Cornwall Trust for Nature Conservation 1994. For descriptions of community codes see Table 2.6.).



Chapter 5 presents the results of a phytosociological survey of the whole moor providing the first extensive and floristically detailed survey of the moor. This phytosociological work will provide a more extensive and recent description of the vegetation of Bodmin Moor than those that currently exist as well as quantifying underlying environmental gradients.

Grassland

Unimproved grassland forms the dominant habitat type on Bodmin Moor. It accounts for 7746ha or 25.6% of the Bodmin Moor Natural Area according to the Phase One survey (Cornwall Trust for Nature Conservation 1988-1993). Most of this grassland is *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland (Figure 2.6), which accounts for 32% of the semi-natural vegetation that has been surveyed at community level. *Agrostis curtisii* grassland accounts for a further

20% and the *Pteridium aquilinum-Galium saxatile* community covers 14% of the surveyed area. The other grassland communities account for little in terms of area. Unimproved acid grassland is internationally significant but common throughout the British uplands (Nature Conservancy Council 1989). In Cornwall, this habitat is confined to Bodmin Moor, which makes it important in a county context. *Agrostis curtisii* grassland is confined to South-west Britain (Table 2.6), where it develops in response to grazing and burning (Rodwell 1992a, b). It is of international and national significance because of its restricted distribution in Europe and Britain, and valued for its contribution to dry heath/grassland complexes (Nature Conservancy Council 1989, Brown 1991). *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, *Nardus stricta-Galium saxatile* grassland, and *Juncus squarrosus-Festuca ovina* grassland are all significant in an international context but widespread nationally (Nature Conservancy Council 1989). *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland is derived from sheep-grazed heathland or from woodland and is of major agricultural importance for better quality rough grazing. *Nardus stricta-Galium saxatile* grassland is derived from *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, where selective overgrazing by sheep encourages the spread of *Nardus stricta*. *Juncus squarrosus-Festuca ovina* grassland is found on redistributed peat often on the margins of mires. It may be derived from *Nardus stricta-Galium saxatile* grassland, where *Juncus squarrosus* out-competes *Nardus stricta* in the early stages of vegetation recovery after heavy grazing (Rodwell 1992b). Both *Nardus stricta-Galium saxatile* grassland and *Juncus squarrosus-Festuca ovina* grassland are rare on Bodmin Moor in contrast to other British uplands, although the constituent species of these communities are fairly widespread.

Wetland

Wetland on Bodmin Moor accounts for 1526ha or 5.1% of the Bodmin Moor Natural Area according to the Phase One survey (Cornwall Trust for Nature Conservation 1988-1993). Most of this wetland is *Scirpus* *cespitosus-Erica tetralix* wet heath, (Figure 2.6) which accounts for 17% of the semi-natural vegetation that has been surveyed at community level. *Molinia caerulea-Potentilla erecta* mire represents 9% of the surveyed area, with the other wetland communities accounting for less. The mire communities are a declining resource in Europe with *Sphagnum*-dominated acid bogs listed on Annex 1 of the EC Habitats Directive (EC 1992). *Carex echinata-Sphagnum recurvum/auriculatum* mire, *Scirpus cespitosus-Erica tetralix* wet heath, *Erica tetralix-Sphagnum compactum* wet heath, *Narthecium ossifragum-Sphagnum papillosum* valley mire, Juncus *effusus/acutiflorus-Galium palustre* rush community, *Molinia caerulea-Potentilla erecta* mire, and *Scirpus cespitosus-Eriophorum vaginatum* blanket mire all have a restricted distribution in Europe and are internationally significant (Table 2.6). Some of these communities, such as *Molinia caerulea-Potentilla erecta* mire and *Carex echinata-Sphagnum recurvum/auriculatum* mire, are ubiquitous in upland Britain but others are restricted in distribution (Table 2.6). *Erica tetralix-Sphagnum compactum* wet heath is only found in an upland context on the moors of the South-west. *Narthecium ossifragum-Sphagnum papillosum* valley mire is largely restricted to Bodmin Moor and Dartmoor. In contrast, *Scirpus cespitosus-Eriophorum vaginatum* blanket mire is widespread on the uplands of Northern Britain, but rare in the South-west, where it is best developed on Dartmoor. It is not extensive on Bodmin Moor but can be found in mosaics on Shallow Water Common and Scribble Downs (Nature Conservancy Council 1986). The relationships between these communities and grazing are less well known than the relationships between grazing and plagioclimax grasslands.

Heathland

Heathland on Bodmin Moor accounts for 263ha or 0.9% of the Bodmin Moor Natural Area, according to the Phase One survey (Cornwall Trust for Nature Conservation 1988-1993). However *Ulex gallii-Agrostis curtisii* heath is included in *Agrostis curtisii* grassland, so the figure may be slightly higher. Personal observations on the moor are not compatible with the Phase one survey as regards heathland distribution. However, they do confirm that heathland represents a very small component of the moorland vegetation as a whole. According to the survey of Drage (1981), most of the heathland is *Calluna vulgaris-Ulex gallii* heath, which accounts for 0.6% of the semi-natural vegetation that has been surveyed at community level. *Vaccinium myrtillus-Deschampsia flexuosa* heath represents a further 0.4% of the surveyed area, with the other heathland communities being of unknown area. No heathland was recorded on the North Moor by the Nature Conservancy Council Upland Survey Team (Nature Conservancy Council 1986). The current phytosociological classification of Bodmin Moor heathland therefore relies wholly on the Drage (1981) survey. An additional community, *Calluna vulgaris- Vaccinium myrtillus* heath is recorded on Bodmin Moor by English Nature and Environmental Consultants Cornwall Trust for Nature Conservation (1994) and Drewitt & Manley (1997), although it is not described by either the Nature Conservancy Council upland survey team (Nature Conservancy Council 1986) or Drage (1981). Dry and wet heaths are listed on Annex 1 of the EC habitats directive (EC 1992). All the heathland communities on Bodmin Moor are of international importance. *Ulex gallii-Agrostis curtisii* heath and *Calluna vulgaris-Ulex gallii* heath are of national importance because of their restricted distribution (Nature Conservancy Council 1989). Heathland is assumed to have declined on Bodmin Moor in the 1800s, due to the introduction of hardy breeds, and during the 20th century, as a result of increased grazing pressure including winter grazing (Brewster 1975, English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994). However there is no evidence to suggest that heathland has ever been abundant on Bodmin Moor.

Nature conservation value

The occurrence and extent of internationally and nationally important NVC communities on Bodmin Moor give the natural area 'notable mountain and moorland significance' (Drewitt & Manley 1997). The extensive areas of *Molinia caerulea-Potentilla erecta* mire and *Agrostis* *curtisii* grassland are the most important features of the natural area with additional interest provided by extensive valley mires, frequent wet heath and fragmented heathland (Drewitt & Manley 1997).

Plants of national and county significance are found across Bodmin Moor. *Physosospermum cornubiense* and *Euphrasia vigursii* occur on Bodmin Moor and are listed as RDB3 (Perring & Farrell 1983). Twenty-one nationally scarce vascular plants and nine county rarities have also been recorded from the Bodmin Moor Natural Area (English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994). The area also supports 25 bryophytes of national and county importance, including an endemic and two nationally rare species and 30 liverworts of national and county importance, including five national rarities and five species that are nationally scarce (English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994). The lichens of open habitats on Bodmin Moor are unrecorded.

The range of moorland habitats on Bodmin support a varied fauna described in detail by English Nature & Environmental Consultants Cornwall Trust for Nature Conservation (1994). In particular, Bodmin Moor is of regional and national importance for breeding birds and may be of international importance for wintering birds, specifically *Pluvialis apricaria* (golden plover), (English Nature 1991).

2.6.2 Conservation legislation and objectives. The future management of Bodmin Moor?

Grazing and its associated management (including burning) is the primary determinant of the nature conservation interest of Bodmin Moor, as it determines habitat condition, which in turn determines the associated flora and fauna. Achieving conservation objectives is therefore dependent upon the appropriate management of stock. The conservation objectives for Cornwall including Bodmin Moor are:

- To prevent further loss of, and maintain, all semi-natural habitats in the natural area and to enhance and expand the most important and characteristic types such as heathland, valley mires, rivers, tors and clitter slopes, deciduous woodland and scrub.

- To maintain and enhance the wider countryside and degraded areas to retain the essential character of the natural area.
- To maintain and expand the populations of internationally and nationally important species, and key species populations and assemblages, which are characteristic of the Natural Area.
- To ensure that the geological and geomorphological features of the Natural Area are maintained for future research and enjoyment.
- To establish a framework of adequate legislation, liason, influence, information and understanding through which objectives 1, 2, 3 and 4 can be achieved (English Nature 1999).

Achieving these objectives relies on appropriate habitat management, which is determined to some extent by legislation. Management agreements between landowners and English Nature can ensure that SSSIs, are managed primarily for nature conservation through the Wildlife Enhancement Scheme, but most of the wider moor is outside SSSI land and relies on other legislation for environmental protection. The Environmentally Sensitive Areas (ESA) scheme was launched by MAFF in 1987, with the aim of pursuing environmental objectives in designated areas of high environmental value through the encouragement of appropriate agricultural practices. There are currently 43 ESAs including Dartmoor and Exmoor (MAFF 1999a). Bodmin Moor was not accepted as an ESA in the last review because of a lack of grazing control on the common land (English Nature and Environmental Consultants Cornwall Trust for Nature Conservation 1994) which accounts for 57% of the semi-natural vegetation on Bodmin Moor. The enactment of a Bodmin Moor Commons Bill could establish a coherent management policy for the commons and thus lead to ESA status. This bill began its passage through parliament in 1993, but progress was slow and it appears to have been superceded by the rural development program and Countryside Stewardship (CS). English Nature believes that it is almost certain that Bodmin Moor will not be given ESA status but the advent of CS provides an umbrella for management that is equivalent to ESA management.

Agriculture currently relies on subsidies, which are becoming increasingly directed towards the environment. The introduction of the agri-environment regulations under EC legislation offers a range of grant-aided schemes under CS that enable farmers to enhance the wildlife value of their land. CS is a scheme piloted by the Countryside Commission in 1991 and transferred to MAFF in 1996. It offers payments to land managers to 'enhance and conserve English landscapes and their wildlife' (MAFF 1999b). CS currently operates within the framework of the England Rural Development Programme (RDP) which has a budget of £1.6 billion. Approximately two thirds of the budget will be spent on agri-environment schemes with a very large increase in financing for CS over the next few years (Table 2.7).

Table 2.7. Funding for England RDP (Source Grayson & Beech 2000)

Financial year (£ million)	99/00	00/01	01/02	02/03	03/04	04/05	05/06	06/07	Total 00/07
Agri-environment	86	95	119	136	152	167	182	197	1134
CS	29	35	51	66	81	96	111	126	566
ESAs	43	46	48	48	48	48	48	48	334

The RDP also changes Less Favoured Area payments from headage to area payments, with payments per ha set at £13.02 for moorland, £34.40 for enclosed severely Disadvantaged Land and £18.60 for all Disadvantaged Land. These initial values will all be progressively reduced by 28% during the first four years of the RDP, giving farmers a stronger incentive to enter agri-environment schemes Grayson & Beech 2000). It will be possible for farmers to increase their level of payment by adopting environmental enhancements including: decreasing stocking rates to less than 1.2 Livestock Units/ha, maintaining 1ha or 5% of the holdings LFA land under either arable or woodland cover; organic production (not including conversion), and farming cattle as well as sheep. Meeting one of these criteria gains a 10% bonus to the basic area payment, meeting two brings in a 20% bonus (Grayson & Beech 2000). There is also a decline in overall funding for the Hill Farmers Allowance. Farmers within ESAs will be able to offset falls in base payments by the adoption of environmental enhancements. Outside of ESAs CS will fulfill this function (Grayson & Beech 2000).

CS operates throughout England but is aimed at eligible areas and features and is targeted at local level to particular priorities (MAFF 1999b). Countryside Stewardship is currently operating on a number of areas on Bodmin Moor but it has been of limited value because the common land, representing 57% of the semi-natural habitat, could not be subject to stewardship agreements. In 1998, MAFF set out proposals for an experimental project to be run on Bodmin Moor, under which common land can be managed under enhancements to the upland measures of Countryside Stewardship. However, common land can now be subject to Countryside Stewardship under national Stewardship options (Countryside Stewardship Information Pack). The frameworks for moorland management under the Bodmin Moor scheme and the national scheme are summarized in Table 2.8. and Table 2.9. respectively.

There are a number of differences between the regional prescriptions and national prescriptions, either of which, may be applied on Bodmin Moor. These reflect differences in both farming practice and ecology. Firstly, stocking rates are generally higher under the Bodmin Moor options than nationally. Summer stocking levels for Bodmin Moor are 0.17 - 0.225LUs/ha compared to 0.1 - 0.15LUs/ha nationally, whilst winter stocking levels range from 0 - 0.17LUs/ha on Bodmin Moor compared to 0 - 0.1Lus/ha nationally. This reflects the heavy grazing intensity found on non-agreement land on Bodmin Moor. Secondly, the payments for Bodmin Moor options are higher than those of the national options even though the stocking rates are higher under the Bodmin Moor scheme. Presumably, this is to encourage increased uptake by farmers and land managers on Bodmin Moor.

The national scheme is concerned with sheep grazing, excepting the enhancing heather moor option, whereas the Bodmin Moor prescriptions involve sheep, cattle and ponies reflecting the use of stock other than sheep. Likewise, the Bodmin Moor options are concerned with dwarf-shrub rather than *Calluna vulgaris* reflecting the more varied heathland composition on Bodmin Moor. A degree of flexibility is built into both schemes in terms of delivery of objectives. Nationally the

Table 2.8. Moorland management options under the Bodmin Moor special agricultural area experiment. (Countryside Stewardship Scheme Information Pack).

Eligible Land	Management objectives	Management protocol	Stewardship option	Payment ha / year
All moorland with <50% dwarf-shrub heath cover.	To maintain a varied sward structure and a grass/dwarf-shrub heath mosaic (75% / 25%).	Summer stocking <0.225LUs/ha (excluding ponies). Winter stocking <0.17LUs/ha.	Moorland Management (BMM)	£80
All moorland / heathland with <50% dwarf-shrub cover with high potential for restoration.	The objective is a varied sward structure and on dry heath sites to increase dwarf-shrub cover to 50% or more.	Summer stocking <0.17LUs/ha. No winter grazing.	Moorland Restoration (BMR)	£125
All moorland / heathland with <50% dwarf-shrub cover	The objective is a varied sward structure and on dry heath sites to increase dwarf-shrub cover to 75% or more.	Summer stocking <0.17LUs/ha. Winter stocking <0.08LUs/ha. No winter grazing by cattle.	Moorland Enhancement (BME)	£92
BMM, BMR & BME supplement	Control of *Molinia caerulea*	Summer cattle grazing	Summer Purple-Moor Grass Grazing (SGX)	£30
BMM supplement	Enhance dwarf-shrub rehabilitation?	Remove cattle in Winter	Winter Cattle Removal (WCX)	£10
BME supplement	Enhance dwarf-shrub rehabilitation?	Remove all livestock in winter (including ponies)	Winter Livestock Removal (WLX)	£12
Management where grazing is not possible	Prevent a decline in the quality of moorland	Rotational cutting, scrub management, bracken clearance	Moorland Habitat Management (LH1)	£20

Table 2.9. Moorland management options under the national Countryside Stewardship options. (Countryside Stewardship Scheme Information Pack).

Eligible Land	Management objectives	Management protocol	Stewardship option	Payment ha / year
All moorland where heather comprises <25% cover but is present in >33% of the area	The objective is to increase dwarf-shrub vegetation cover to 40%, preferably 50% in years 1-5 before reintroducing winter grazing	Summer grazing at 1 sheep per ha to prevent grass growth inhibiting heather regeneration. No winter grazing in first 5 years.	Regenerating Suppressed Heather Moor (UM2, UM5, UXB)	£20 - £50
All moorland where heather comprises 25% - 50% of the sward and is in poor condition	The aim is to improve the condition and extent of heather and other moorland vegetation	Summer stocking 1.5 sheep per ha, winter stocking 0.75 sheep per ha. Light summer cattle grazing if appropriate	Enhancing Heather Moorland (UM3)	£45
Heather moorland in good condition but where there is scope to enhance heather condition	Enhance heather condition. Diversify habitat on 10% of the holding e.g. woodland, wetland.	Maintain summer stocking level of 1.5 sheep per ha. Winter stocking level, 1 sheep per ha.	Management of Heather Moorland Habitat (UM4)	£4
Supplement	Speed up regeneration or to accommodate rare or unusual species	Additional temporary stock removal	Additional Temporary Stock Removal (UA)	£3/ewe/ month
Where land not currently burnt requires burning	Maintain mosaic of heather with varied age structure?	Rotational burning over a ten year period adhering to the heather and grass burning code	Heather Burning Supplement (UB)	£5
Common land not under agreement	Supplement to bring common land into agreement	na	Commons Management Supplement (UC)	£5

Additional Temporary Stock Removal Supplement allows for stock reduction below standard Countryside Stewardship levels if desired. The Bodmin Moor options permit variation from the guidelines where site conditions are such that the environmental objective can be achieved with alternative management (Countryside Stewardship Scheme Information Pack). Thus summer stocking rates on Bodmin Moor North SSSI are set at 0.5LUs/ha under a Countryside Stewardship management agreement rather than <0.225LUs/ha as specified under the guidelines.

Research is required to determine whether these management prescriptions will achieve their primary objective of increasing dwarf-shrub heath cover. Reduction in grazing pressure may encourage *Molinia caerulea* dominance on Bodmin Moor (Smallshire *et al.* 1997), hence the Summer Purple-Moor Grass Grazing Supplement. Further research is required to establish the levels of grazing that will control *Molinia caerulea* on Bodmin Moor. Chapters Three and Four outline current knowledge regarding the effects of grazers on vegetation. Further detailed research is required in order to determine whether the proposed management objectives and protocols are appropriate for Bodmin Moor.

2.7 Conclusions

- The Cornubian batholith forms the bedrock of Bodmin Moor and Dartmoor resulting in a calcifuge flora except in extremely local areas of base enrichment.

- Bodmin Moor is very oceanic in character compared to other British Uplands. In particular mean winter temperatures are very high, rarely falling below 0 °c. resulting in perhaps the longest growing season of all British uplands. This is due to the extreme South-westerly position of Bodmin Moor and its low altitude.

- Precipitation on Bodmin Moor is higher than the surrounding lowlands although the limited altitude of the moor means that many upland areas experience much higher rainfall. However, the intensity of precipitation on Bodmin Moor is extreme although unquantified.

- As a result of geology and climate Bodmin Moor has a range of acid podzolic soils similar to those of Dartmoor and other acid upland areas. However, climatic and management differences are reflected by subtle variations in pedology.

- There is evidence of human utilization of Bodmin Moor from the Mesolithic onwards. Initially human impact on the biota seems to have been lower than in other upland regions, but Neolithic impacts may have been higher on Bodmin Moor than Dartmoor. In common with other upland areas major forest clearance occurred in the Bronze age and Mediaeval periods. The present day character of Bodmin Moor may have been established at the end of the Mediaeval period.

- Post-Mediaeval land-use and vegetation changes remain largely speculative. Sheep must have grazed on Bodmin Moor to support the textile industry in the 1700s but it is assumed that levancy and couchancy limited stock number and maintained vegetation composition until the introduction of hardy breeds in the 1800s, which may have resulted in loss of heathland.

- In common with other upland areas Bodmin Moor experienced a large increase in stock numbers post-1940 as a result of subsidies aimed at increasing food production. It has been assumed that heathland loss followed this increase in grazing pressure on Bodmin Moor as it has in other upland areas.

- Countryside Stewardship was introduced in 1991 in order to address this perceived decline in heathland. However, it is by no means certain that heather was more abundant in the past on Bodmin Moor than it is now. Additionally the long growing season on the moor favours potential competitors of heather such as *Molinia caerulea*. Hence it is by no means certain that heathland restoration on Bodmin Moor is a suitable or achievable management objective.

3 Grazing management and vegetation in upland habitats

3.1 Introduction

Grazing by domestic stock is one of the main impacts of human activity on upland habitats in Britain and has been so since the 1940s (Thompson & Horsfield 1997). Grazing is arguably the primary determinant of the nature conservation interest of Bodmin Moor. No research has been published concerning grazing on Bodmin Moor, although one site was included in an investigation of sustainable grazing practices on the South West moors of England (Smallshire *et al.* 1997). This study investigated habitat quality, stocking regimes and levels, livestock types and breeds, supplementary feeding, burning practices and other aspects of farm enterprise relevant to moorland management. The conclusions were that the factors most likely to be required for the maintenance and enhancement of high quality moorland include: low stocking levels, hardy animal breeds, limited and carefully sited supplementary feed and controlled small-scale burns of dwarf-shrubs (Smallshire *et al.* 1997). However it is difficult to separate the effects of these factors and to determine their interactions. The following literature review of upland grazing management is intended to summarise the current understanding of these effects and their interactions in the British uplands.

3.2 The direct and indirect mechanisms by which grazing affects vegetation

Grazing affects vegetation directly by reducing the competitive vigour of plants or killing them through defoliation (Shaw *et al.* 1996). Indirect effects also occur, resulting from trampling and defecation.

3.2.1 Grazing and species diversity

The direct effect of grazing operates when grazing of taller or faster growing species reduces their competitive ability or kills them, allowing smaller species, which would be shaded out in the absence of grazing, to coexist (Milne *et al.* 1998). Thus there are many instances when grazing increases species diversity (Jimaleh 1985, Marrs *et al.* 1988, Kiffe 1989, Putman *et al.* 1991). However the opposite can occur if a more aggressive, less palatable species is avoided and other species in a sward are selected. As an example, sheep grazing has promoted the spread of species-poor *Nardus stricta* grassland (Grant *et al.* 1987a). The grazing tolerance of a plant species can counter the reduction in abundance of preferred species in such situations. For example, *Festuca ovina* is preferred over species with which it coexists such as *Deschampsia flexuosa*, *Juncus squarrosus* and *Nardus stricta*, but recovers after defoliation much faster through a combination of tolerance and remobilization mechanisms (Atkinson 1986). The immediate impact of grazing on vegetation is at the level of the individual plant, but the nature and degree of the impact is determined by animal behaviour at larger scales. The choices that the animal makes within a plant community arise as a result of different feeding methods, whilst choices made between plant communities depend on foraging behaviour (Milne *et al.* 1998). Grazing also affects vegetation indirectly through trampling and defecation. These indirect effects also operate on a range of scales.

3.2.2 Trampling effects

Trampling tends to increase species diversity through the establishment of a range of new species, which are unlikely to establish in closed swards *e.g.* cattle trampling can create gaps that facilitate seed germination in a range of species (Mitchell & Kirby 1990). Gap creation is particularly important for the establishment of small-seeded species such as *Betula* (Miles 1973). However severe trampling, such as poaching by cattle, can completely destroy vegetation cover causing severe impacts at least in the short term (Milne *et al.* 1998). The amount of damage is dependent upon stocking density and the species of animal. The ratio of weight to hoof size is important in determining the degree of damage, with larger animals such as cattle being most destructive (Royal Society for the Protection of Birds 1995). Trampling, especially by cattle, causes stem breakage and bruises leaf tissue, thereby rendering them liable to winter browning (Bunce 1989). Trampling by cattle has been used to control invasive species such as *Pteridium aquilinum* (Fenton 1937, Marrs *et al.* 1995). Stocking changes from cattle to sheep and from wether sheep to ewes and lambs is said to have caused bracken expansion in upland Britain as a result of a reduction in trampling pressure which damages the fronds (Marrs & Pakeman 1995). Cattle have also been used to control *Nardus stricta* through the detrimental effects of physical damage (Fenton 1937). *Calluna vulgaris* is particularly vulnerable to trampling because stem breakage leads to loss of the aboveground growing parts of the plant. This effect becomes more severe as the plant ages, due to increased woody material and reduced growing points for recovery after damage (Gimingham 1972). Wet areas are more susceptible than dry areas to poaching damage (Royal Society for the Protection of Birds 1995). Thus trampling by sheep and deer can severely disrupt moss and lichen cover in wet heaths and mires, especially *Sphagnum* and the larger lichens (Rodwell 1991). Trampling can also cause changes in microtopography leading to a reduction in species such as *Sphagnum papillosum*. However *Sphagnum tenellum* may benefit, as it commonly colonises wet bare peat and is often associated with poached areas and animal tracks (Royal Society for the Protection of Birds 1995).

3.2.3 Effects of defecation

Like trampling, dung deposition exerts an indirect affect of grazing on vegetation. Defecation and urination can raise the soil nutrient status giving competitive advantage to faster growing graminoids (Bunce 1989). It may also cause a shift from ombrotrophic mires to mesotrophic mires (*e.g.* dominance by *Juncus* spp., *Sphagnum recurvum*, or *Narthecium ossifragum*), although the effect is likely to be localised (Royal Society for the Protection of Birds 1995). Dung can contain seeds, depending on the food consumed, which sometimes act as a means of introduction of species into a community (Welch 1984b). Dung supports coprophilous mosses such as *Splachnum* spp. and

Tetraplodon mnioides (Lindsay *et al.* 1988). Additionally, dung deposition can also physically smother plants (Milne *et al.* 1998) and affect herbivore foraging due to avoidance of dung by many herbivores (Putman *et al.* 1991). Dung deposition by many species is highly aggregated (Bakker *et al.* 1983, Putman *et al.* 1991), making the above effects localised and patchy within the vegetation.

3.3 The effect of different species and breeds of grazer within and between plant communities

3.3.1 Introduction

Animal species have varying impacts on vegetation within plant communities as a result of differences in feeding methods associated with the size and shape of their mouths (Table 3.1.).

Table 3.1. Grazing functional attributes of upland herbivores (modified from Armstrong & Milne 1995, Milne *et al.* 1998).

Species	Feeding method	selectivity	Minimum sward height grazed
Rabbits	Biting / shearing	Very high	1cm
Goats		high	>6cm
Sheep			3cm
Mountain hares			
Red deer		intermediate	
Cattle	Tear with tongue	low	>6cm
Ponies	Shearing	high	2cm

Differences in feeding methods of the various grazers (Table 3.1.) cause variation in diet selection within a plant community. Cattle tend to be less selective than sheep and graze most components of a community, although this difference is more pronounced in grasslands than on heaths or mires (Grant *et al.* 1987b). Cattle diets are slightly less variable than sheep diets and contain more dead components of the vegetation. *Calluna vulgaris*, *Erica* spp. and *Empetrum nigrum* are eaten in autumn and winter by both sheep and cattle, when the preferred species (*Molinia caerulea*, other grass species, *Carex* spp. and *Scirpus* *cespitosus*) are less available (Grant *et al.* 1987b, Gordon 1989). Cattle remove more of the shoot length of *Calluna vulgaris* than sheep, so that risks of shoot death and of broken or uprooted shoots are increased (Shaw *et al.* 1996). The use of cattle rather than sheep also gives a higher risk of trampling damage (Gimingham 1972). Finally the greater poaching damage by cattle compared to sheep provides ideal conditions for the invasion of *Juncus* spp. (Rawes 1971).

The utilization of cattle in the management of dwarf-shrub communities is therefore problematic. Gimingham (1995) considered that cattle could be used in some circumstances to manage heather moor. In contrast, Grant *et al.* (1987b) believe cattle use should be restricted to mixed communities where the aim of the management is to control the species associated with the dwarf-shrub, *e.g.* where large areas of *Molinia caerulea* and *Calluna vulgaris* occur together. In grass-dominated communities, there may be some scope for complementary grazing using sheep and cattle but the cattle may be excluded from communities grazed to a short sward height by sheep (Hodgson *et al.* 1991).

Sheep have more selective feeding preferences than cattle, preferring more palatable grasses and young *Calluna vulgaris*, where available (Grant *et al.* 1987b, Grant & Armstrong 1993). In grassland communities, sheep, in contrast to cattle, will avoid tussock species such as *Nardus stricta* and *Juncus* spp. (Grant *et al.* 1985). When restricted to blanket bog, *Calluna vulgaris* and *Eriophorum vaginatum* form the main part of the diet of sheep in winter, while *Scirpus cespitosus* and *Molinia caerula* are preferred in early summer (Grant *et al.* 1987b).

There are nine major breeds of hardy pony in Britain many of which graze in the uplands of South-west (Oates 1994). Little is known about pony grazing, which has not been studied in an upland situation. Ponies are selective feeders, preferring grass to *Calluna vulgaris* and can graze closely to the ground (Rawes 1971, Putman *et al.* 1987, Mowforth

& Sydes 1989, Gordon 1989). Consequently ponies are able to feed from *Agrostis-Festuca* grassland on Rhum even in winter and consume little heather there throughout the year (Gordon *et al.* 1987). However they will eat *Calluna vulgaris* and may damage it by trampling (Shaw *et al.* 1996). *Calluna vulgaris* may constitute up to 10% of the diet of ponies in winter (Nature Conservancy Council 1983).

Goats graze the margins of Bodmin Moor but they are insignificant both in terms of number and impact compared to the other domestic stock. Goats eat a more varied diet than sheep (Merchant 1993) and will browse woody vegetation (Cadbury 1993). Given the choice, they prefer heathland species to grassland (Gordon 1989, Grant & Armstrong 1993).

Cattle, sheep and ponies exert the greatest influence on the upland vegetation of the South-west. Wild herbivores such as rabbits, voles, red deer (on Exmoor) and hares have far less impact on the vegetation overall, although they can be locally significant. Rabbits graze grasses in preference to woody plants but eat *Calluna vulgaris* and tree seedlings (Homolka 1985, Ranwell 1960). Grazing pressure on vegetation is inversely related to distance from burrows and burrowing activity creates niches for plant regeneration (Tansley 1939). Sheep grazing facilitates rabbit grazing, as the sheep maintain the vegetation at a suitable sward height for further utilization by rabbits (Hester *Pers. comm.*). Rabbits are present on the drier soils in all the upland regions of South-west Britain (English Nature & Environmental Consultants CTNC 1994).

Short-tailed field voles (*Microtus agrestis*) are widespread in the uplands up to 1300m. They show a preference for *Molinia caerulea* and *Juncus*-dominated communities (Hill *et al.* 1992). When sheep were excluded from hill pastures in North Wales, *Microtus agrestis* became the dominant herbivore and exerted a considerable effect on the vegetation (Hill *et al.* 1992). Voles are present in large numbers in the taller vegetation on Bodmin Moor but the population sizes are unquantified.

Red deer prefer a similar habitat to sheep, selecting grass swards where available, leading to competition for preferred plant species and exacerbating damaging impacts due to sheep grazing (Royal Society for the Protection of Birds 1995). However they favour a more varied diet than sheep (Cadbury 1993) and eat proportionally less grass (Osborne 1984) and more mature *Calluna vulgaris* (Grant *et al.* 1987b). In the Scottish uplands, deer are to some extent responsible for the loss of native woodland, dwarf-shrub heath, tall herb communities and rare plant species (Staines *et al.* 1995). In the South-west, they do not have such pervasive effects, being restricted to small populations on Exmoor and Dartmoor (Smallshire *et al.*1997).

Mountain hares can have a significant impact on vegetation. Their diet is markedly seasonal, as they consume a high proportion of grass in summer and a high proportion (<100%) of *Calluna vulgaris* in winter (Hewson 1976; 1989). The distribution of mountain hares is imprecisely known (Milne *et al.* 1998) but they are present on Bodmin Moor (English Nature & Environmental Consultants CTNC 1994).

Red grouse are present on Dartmoor (English Nature & Dartmoor National Park Authority 1997) but not Bodmin Moor. Red grouse, like mountain hares, are strongly dependent upon heather (Hobbs & Gimingham 1987). The effects of other herbivores including birds, small mammals and invertebrates are largely unknown but they are insignificant in comparison to the herbivores discussed above, at least in relation to Bodmin Moor and the other uplands of South-west Britain. The specific grazing behaviour of cattle, sheep and ponies is summarized in Table 3.2.

Table 3.2. Grazing differences between sheep, cattle, and ponies/horses.

Species	*Behaviour*	Reference
Sheep	Avoid *Juncus* species.	Merchant (1993)
	More selective than cattle and graze grasses and young heather preferentially.	Grant *et al.* (1987b) Grant & Armstrong (1993)
	On blanket bog, *Calluna vulgaris* and *Eriophorum vaginatum* are eaten in winter and *Scirpus cespitosus* and *Molinia caerulea* are eaten in summer	Grant *et al.* (1987b)
	Graze selectively from the bottom of the sward and avoid *Nardus stricta* and *Juncus* spp.	Grant *et al.* (1985) Armstrong & Milne (1995)
Cattle	Cattle remove more of the shoot length of *Calluna vulgaris* than sheep	Shaw *et al.* (1996)
	Cattle tend to be less selective than sheep and graze most components of a community, although this difference is more pronounced in grasslands than on heaths or mires	Grant *et al.* (1987b)
	Cattle prefer *Molinia caerulea*, other grass species, *Carex* spp. and *Scirpus cespitosus* eating dwarf-shrubs in winter when preferred species are unavailable	Grant *et al.* (1987b) Gordon (1989)
	Cattle will graze tussock species *e.g. Nardus stricta* and *Molinia caerulea*.	Grant *et al.* (1985)
	Cattle create more trampling damage than sheep	Rawes (1971) Gimingham (1972)
Ponies/ Horses	Horses are selective feeders, preferring grass to *Calluna vulgaris* and can graze closely to the ground	Rawes (1971) Putman *et al.* (1987) Mowforth & Sydes (1989) Gordon (1989).
	Horses eat *Calluna vulgaris* and may damage it by trampling	Shaw *et al.* (1996)

There is little literature on the different grazing impacts that might be expected from different breeds of the same animal species. What little evidence there is, suggests that different breeds of the same species can differ fundamentally in their diet selection. For example, Welsh Mountain and Cheviot sheep require grass whereas Scottish Blackface will thrive on a diet of *Calluna vulgaris* (Ratcliffe 1959). This obviously has important ramifications for management. The Grazing Animal Project (GAP) recognises that knowledge of the grazing differences between breeds is currently inadequate and is attempting to collate what is known from land managers (GAP 1999).

The diet selected by one animal species can change if it grazes with another species through competition for food, social interaction and different diet selection strategies (Milne *et al.* 1998). Red deer have been observed to graze less on grass communities, when in the presence of sheep. This could be due to competition for food; social interaction or the presence of people (Osborne 1984). Alternatively, the diet selected by one species could affect the diet selected by the other, as red deer tend to select from the upper layers of vegetation and sheep from the lower layers of grass pastures (Loudon *et al.* 1984). Likewise rabbits can graze shorter grass pasture than sheep (Table 3.1), although sheep facilitate rabbit grazing (Hester, A. Macaulay Land Use Research Institute. *Pers. comm.*). However there is little published work available on the effects of these interactions, which nevertheless need to be understood if mixed species management is to be undertaken on upland vegetation.

The different sizes of herbivore species account for different impacts on vegetation, as well as the different feeding methods associated with the size and shape of their mouths. The size of the animal has a major influence on the amount of vegetation ingested. Sheep breeds have been divided into three size classes, small (*e.g.* Welsh Mountain), medium (*e.g.* Scottish Blackface, Swaledale) and large (*e.g.* Greyface, Mules), which have been shown to require increasing annual intakes of vegetation (Grant & Armstrong 1993). Larger animals have higher maximum potential intake, although this is modified by physiology *e.g.* lactating animals have higher intakes and fatter animals lower intakes. The size and body condition of the animal is reflected in the grazing livestock unit allocated in relation to stock type (Table 3.3.). These units are used in agri-environment schemes, where a maximum number of livestock units per unit area are specified in a management agreement. Thus unless stock type is defined, the land manager has a degree of flexibility about choice of grazer and the impact of these animals in terms of intake is deemed equivalent.

Table 3.3. Grazing Livestock Units in relation to stock type (Chadwick 1991, Countryside Stewardship scheme, MAFF 2001).

Stock type	Livestock Units	
	Chadwick (1991)	Countryside Stewardship
Dairy cows	1.00	1.00
Dairy bulls	0.65	
Beef cows	0.75	1.00
Beef bulls	0.65	
Other cattle 0-12 months	0.34	
Other cattle 12-24 months	0.65	0.6
Other cattle >24 months	0.8	1.00
Ponies/Horses	0.8	
Ewes light weight	0.06	
Ewes medium weight	0.08	
Ewes heavy weight	0.11	
Lowland Ewe & Lamb		0.15
Hill Ewe		0.1
Rams	0.08	0.15
Lambs	0.04	

The amount of vegetation consumed by a herbivore is not only dependent upon its size and body condition. The intake of all stock increases asymptotically, as the amount of available biomass increases and linearly, as the digestibility of the diet increases (Hodgson 1985, Gordon & Lascano 1993). Consequently, current predictions of intake by animals are usually based on the amount of available biomass and diet digestibility, as well as the size and body condition of the animal (Hodgson 1985).

The availability of biomass and its digestibility vary within and between plant communities. Within a plant community, there will be a number of plant species with different biomasses and ratios of live to dead tissue. The physical differences between herbivores mean they consume different quantities of vegetation of different digestibility. For example, cattle consume more than sheep because they are larger than sheep, and cattle eat more dead tissue than sheep because they are less selective as a result of their large tongues (Tables 3.2. and 3.3.). Thus the impact of one livestock unit of dairy cows (one dairy cow) is not the same as the impact of one livestock unit of light weight ewes (16.6 light weight ewes). The differences in herbivore impacts are magnified at larger scales, as a result of their foraging behaviour between plant communities with different biomasses and ratios of live to dead tissue.

Herbivores select plant communities that give them the highest intake of digestible nutrients. The allocation of values to plant communities for the potential intake of digestible nutrients allows the prediction of the proportion of total intake taken by the herbivore from each plant community (Armstrong *et al.* 1997). This process is complex, as the different plant communities exhibit seasonal changes in the composition and quality of their forage, as a result of changes in floristic composition and the nutritional status of component species.

This information, combined with knowledge of the relationship between intake and biomass, allows the prediction of which plant communities will be grazed. This approach is currently used in the Hill Grazing Management Model (Armstrong *et al.* 1997), a newer version of the model Hill Plan and in the red deer management decision support system Hill Deer (Milne *et al.* 1998). The Hill Grazing Management Model has been used to predict intake by sheep at different stocking intensities in an area containing *Festuca-Agrostis* grassland, *Molinia* grassland and *Calluna vulgaris* heath (Armstrong & Milne 1995). The predictions of the model are compatible with observations of sheep grazing behaviour (Armstrong *et al.* 1997).

Current models do not explicitly account for the sampling of a range of vegetation types that large herbivores normally make, or shelter-seeking behaviour (Welch 1968). Likewise they do not account for differential grazing within a community or for the effects of mosaics. The grazing impact on *Calluna vulgaris* is generally greatest at the boundary with preferred vegetation, such as grass, resulting in greater intake of *Calluna vulgaris* in fragmented communities (Hester *et al.* 1996). Thus the influences of vegetation pattern and scale on the impacts of different herbivores require further investigation (Hester 1997). Other problems with traditional simulation models of grazing systems centre on the paucity of data that underpin some of the relationships described by the models and the more general lack of testing of the models predictions. Nevertheless, they remain an important tool for understanding and predicting the dynamics of grazing in upland habitats. The future challenge is to make these models spatially explicit and to test them more rigorously in order to make their predictions more robust.

Both the Hill Grazing Management Model and observation suggest that foraging strategies are similar for sheep and other stock. However cattle were observed to eat a higher proportion of grass species than deer and to graze grass communities with a higher available biomass, even when the digestibility was lower than that of other communities. The foraging behaviour of red deer differs between sexes, with hinds occupying grassy areas with high digestibility but low biomass to a greater extent than stags (Gordon 1989). More information on foraging strategy is required particularly for horses and ponies.

3.3.2 The effects of different stocking intensities

There are considerable problems in determining the impact of different stocking intensities on vegetation. The assessment of herbivore impact needs to consider seasonal diet, distribution through the habitat and type of herbivore (Shaw *et al.* 1996). Hill grazing systems usually consist of a mosaic of different vegetation types over which herbivores range freely. The grazing animals have preferences for different plant communities and these are affected by seasonal changes in biomass availability and digestibility. Thus annual stocking rates do not usually represent a good measure of the grazing pressure exerted on any vegetation type (Armstrong & Milne 1995).

Additionally there may be problems in interpreting stocking data. It is not always clear what is being quoted; *e.g.* numbers of ewes may be given, without apparently taking lamb numbers into account (Shaw *et al.* 1996). Land may be understocked in summer and overstocked in winter, where there is a fixed year-round density (Lance 1983).

Predictions of vegetation change under different grazing pressures at the plant community level are discussed in Chapter Four but the landscape level conversion of dwarf-shrub heath to grassland throughout the British uplands during the 20th century is attributed to increased grazing pressure (Mowforth & Sydes 1989, Stevenson & Thompson 1993). The loss of heathland in the Peak District has been related to an increase in sheep density from 0.7 sheep per ha in the 1930s to 2.07 sheep per ha in the 1970s (Anderson & Yalden 1981). Aerial photography indicates that in Cumbria, since the 1940s, 70% (297000 ha) of *Calluna vulgaris*-dominated vegetation has been replaced by unimproved vegetation dominated by graminoids (Nature Conservancy Council 1987). On Bodmin Moor, the evidence of heather decline is anecdotal. MAFF commissioned a report into the feasibility of mapping the former extent of heathland on Bodmin Moor and Dartmoor using aerial photographs. It was concluded that the resolution of 1940s photographs was not sufficient to identify vegetation types accurately on Bodmin Moor, particularly where mosaics were encountered (Farming and Rural Conservation Agency 1999).

The direct and indirect effects of grazing will increase as stocking intensity rises. Increases in stocking rates have few known effects on herbivore behaviour. Therefore, in general, increasing stocking rate merely exacerbates the effects of the herbivores on the vegetation. However, grazing selectivity is likely to be more evident at low stocking densities (Grant *et al.* 1976). The effects of density-dependent selectivity can therefore increase the impact of one animal at higher stocking levels, as it is liable to consume more non-preferred species such as *Calluna vulgaris* than it would at a lower stocking rate.

3.3.3 The effects of timing

Stock preferentially graze different species at different times of year (Table 3.2). *Calluna vulgaris*, *Erica* spp. and *Empetrum nigrum* are eaten in autumn and winter when the preferred species (*Molinia caerulea*, other grass species, *Carex* spp. and *Scirpus cespitosus*) are less available to both sheep and cattle (Grant *et al.* 1987b, Gordon 1989). MacLeod (1955) found that *Calluna vulgaris* constituted 40% of the rumen content of sheep in winter, but only 20% during the summer, when more palatable species were available. Horses and ponies also preferentially graze grass species rather than *Calluna vulgaris* (Rawes 1971, Putman *et al.* 1987, Mowforth & Sydes 1989, Gordon 1989). *Calluna vulgaris* therefore tends to be eaten in autumn and winter, when its carbohydrate reserves and overwintering shoots will be damaged (Grant *et al.* 1985). The impact of grazing will therefore depend on timing as well as the species of herbivore, stocking intensity and the communities grazed.

The seasonal distribution of intake by sheep at different stocking intensities between *Festuca-Agrostis* grassland, *Molinia* grassland and *Calluna vulgaris* is predicted by the Hill Grazing Management Model (Armstrong & Milne 1995). The predictions of the model relate reasonably well to observations of sheep grazing behaviour (Armstrong *et al.* 1997). In May, the order of preference between communities is *Agrostis/Festuca, Festuca/Agrostis, and Molinia caerulea* grassland, followed by *Calluna vulgaris* heathland. Digestibility is the main determinant of this order, as biomass is high. As the summer progresses, the amount of *Molinia caerulea* in the diet increases until August, when it begins to decline, as the *Molinia caerulea* starts to senesce. In November, the proportion of *Agrostis/Festuca* in the diet declines as the sward is grazed short and intake becomes limited by harvestable biomass. In December, the proportion of *Festuca/Agrostis* also starts to decline as dead biomass starts to increase in the sward and digestibility declines. At the same time, intake from heather increases as it becomes relatively more attractive. These trends continue into January, but by February, the proportion of heather starts to decline and that of grass to increase again. This occurs because some of the dead material has been removed from the grass by grazing giving the sheep access to new live material. This continues at an increasing rate through to March. In April, *Festuca/Agrostis* becomes briefly the most preferred vegetation type because, although both it and the *Agrostis/Festuca* have started their spring growth, the *Agrostis/Festuca* is still short after the heavy grazing the previous year (Armstrong & Milne 1995). The seasonal foraging preferences of other stock are believed to be similar.

The introduction of hardy stock breeds in the late 18thand 19th centuries resulted in a trend towards overwintering sheep on moorland and providing supplementary feed rather than removing them to lower altitude pasture (Shaw *et al.* 1996). This is most notoriously associated with the Scottish Highlands, where the clearances occurred in the late 18th century (Mowforth & Sydes 1989). The change in seasonality almost certainly contributed to the replacement of *Calluna vulgaris* heathland with grassland, at least in some instances. The agri-environment schemes of the 1990s promote the use of summer grazing only, in order to address this heathland decline. The rehabilitation of *Calluna vulgaris* in response to summer only grazing has been observed experimentally. Continually grazed blanket bog has lower *Calluna vulgaris* cover and higher *Eriophorum vaginatum* cover than blanket bog that is summer-grazed only (Rawes & Heal 1978).

3.3.4 The effect of supplementary feed

The use of supplementary feed increases the amount of time that stock can remain in the uplands during winter. It can lead to localised overgrazing of heather (Walker & Elias 1989). A 5000ha estate lost 800ha of heather over a period of 20 years as a result of winter feeding across the moor (Bunce 1989). Damage can be avoided by feeding hay away from heather moorland to prevent damage to *Calluna vulgaris*. The use of feedblocks on many dispersed sites can help to prevent localised damage from poaching and overgrazing, especially if they are not sited on newly burned or aged heather, or if the location of the blocks is changed when they are replaced (Grant & Armstrong 1993).

3.3.5 The effect of stock control (shepherding)

Close shepherding has two main roles in grazing management. Primarily it is used to move stock around, to ensure even use of the available area, including the less preferred areas. It is also used to transfer (heft) a flock of sheep or herd of cattle to a given area (Shaw *et al.* 1996). Shepherding has become less common in recent years and has probably led to an increased grazing pressure on the most favoured swards as stock have been allowed to forage according to their preference (Coulson *et al.* 1992). Shepherding and enhanced control of stock movement to winter feeding areas can help to alleviate many of the problems that lead to loss of heather on grouse moors (Lawton 1990). On Kinder Scout, active shepherding, involving between 6 and 22 gathers a year, reduced grazing intensities from 2.5 ewes per ha to 0.18-0.43 ewes per ha by reducing clumping. This reversed succession in the grazed areas allowed change from bare and eroding peaty podzols to a *Calluna-Vaccinium myrtillus* community (Anderson & Radford 1994). However, personal observation indicates that even where stocking rates are < 0.5 ewes per ha, *Calluna vulgaris* is largely restricted to the high ground on the plateau.

3.3.6 Interactions between grazing and other environmental variables

Interactions between grazing and burning are virtually ubiquitous in the British uplands, as the main reason for burning is to improve conditions for stock by altering vegetation structure, composition and nutrient content. It is very difficult to separate out the effects of grazing and burning on vegetation, as the previous management on the site will inevitably have involved both these activities at some point in the past. The only widespread exceptions to this are grouse moors, some of which are managed solely by burning, with no grazing by domestic stock.

The interactions between burning and grazing on the vegetation of heather moor have been extensively studied by many workers and are reviewed by Hobbs & Gimingham (1987). By contrast, there is a paucity of work on burning in other British upland habitats. There are no direct studies of burning/grazing interactions on blanket bog (Shaw *et al.* 1996). The dearth of literature pertaining to grassland is also problematic, as rehabilitation of heathland is the primary objective of upland agri-environment schemes. The loss of heather moorland over the past century, other than conversion to pasture or forestry, is attributed to heavy grazing and burning particularly since the 1940s (Anderson & Yalden 1981, Hester & Sydes 1992). It has been suggested that this process is reversible. The 80% of the moorland vegetation in England and Wales that has been lost or has deteriorated since 1947 has some potential to regain cover at least of dwarf-shrubs, with a reduction in grazing intensity coupled with improved burning practices (Thompson *et al.* 1995). However, certain grassland types have not reverted to heathland under agri-environment management, particularly those dominated by *Nardus stricta* (Marrs 2001).

The interactions between burning and grazing are expressed most strongly by the effect of grazing on vegetation recovery after burning. Farmers often burn vegetation to obtain an early bite for stock, particularly cattle, which tend to concentrate strongly on recently burned areas (Shaw *et al.* 1996). Sheep also congregate on recently burnt areas. Thus burning in small patches can encourage sheep to disperse and graze more widely across their range than if large patches are burnt (Grant & Armstrong 1993). The impact of high stocking rates can be reduced if stock is dispersed across a moor. Therefore burning pattern can influence grazing intensity and could be particularly important where shepherding is limited.

Burning and post-burn grazing can accelerate and mutually reinforce each other. They increase the amount of bare ground and accelerate the disappearance of *Calluna vulgaris* in heavily grazed places through a rapid expansion of graminoids. Post-burn grazing prevents any subsequent regeneration by *Calluna vulgaris* (Pearsall 1941, Rawes & Hobbs 1979). The impacts of burning and grazing are modified by the wetness of the substratum. Hence drainage operations exert an indirect effect on grazing and burning impacts (Ratcliffe 1959). However, there is a presumption among land managers that drainage of moorland exerts a separate additional effect, which is neither nullified by burning and grazing, nor dependent on them to bring a response (Stewart & Lance 1991). Thompson *et al.* (1995) provide a schematic diagram of the changes in vegetation typically occurring as a result of grazing and burning, coupled with drainage and waterlogging for the major upland bog and heath communities. These are considered more fully in Chapter Four along with other predictions of vegetation change under different grazing pressures at the plant community level.

3.4 Conclusions

- Different domestic herbivores have varying impacts on vegetation. Cattle and ponies are widespread on Bodmin Moor yet little is known about their impact on upland vegetation. Ponies in particular remain unstudied in an upland context.

- The effects of different stocking intensities are hard to determine because of interactions between seasonal diet, animal type and distribution through the habitat.

- Livestock preferentially graze different species at different times of year. Dwarf-shrub species are eaten in winter when grass species are unavailable. Thus reduced stocking rates in winter are used to regenerate heathland.

- Burning and burning-grazing interactions are widespread in the British uplands. Both are poorly understood in most habitats with the exception of dry heath in North-East Britain.

- Drainage operations, supplementary feeding and shepherding can modify the impact of grazing animal species on vegetation.

4 Succession in relation to grazing

4.1 Introduction

4.1.1 The need for a coherent successional paradigm

Successional theory and foraging strategy underpin understanding of the functioning of grazed systems (Taylor 1993). Grazing influences succession by maintaining plagioclimax communities or controlling the direction and rate of change from one community type to another. Research is required to predict these changes in order for management protocols to be effective. However, there is currently unresolved debate about successional processes (Kent & Coker 1992). Reductionists argue that population and species level processes must be understood in order to gain the mechanistic understanding essential for prediction of change (McCook 1994). Holists study communities and ecosystems and argue that reductionist approaches are confounded by the multiple species interactions found in complex grazing systems. Hierarchical studies, combining holistic quantitative studies with the reductionist species strategist and plant population approach, may provide a way forward (Pickett *et al.* 1987; 1989, Keddy 1990, Andel 1999). In these hierarchies, the level below provides understanding and context is provided by the level above (Taylor 1993). There are other schisms in the scientific community concerning succession. Most, but not all authors now question the existence of a universal mechanism for succession. There are conflicting ideas about explanative models versus 'black box' predictive models. The development of 'grey box' models combining explanatory and predictive power may represent a direction for further research. However, there is a more urgent need for studies that predict the outcome of succession in response to changing management, if current nature conservation legislation is to meet its objectives.

4.1.2 Definitions of succession

Succession is a term used to describe many types of vegetation change on widely different scales in both space and time. Succession can be considered as any vegetation change with time (Gleason 1927) or it can be considered as directional change distinct from fluctuations and cyclical regeneration (Miles 1987). Succession involves floristic change (Miles 1987) but some authors consider that changes in community structure and ecosystem function should also be viewed as succession (Odum 1969, Austin 1981).

Successions are frequently divided into dichotomies such as primary and secondary, or autogenic and allogenic. Primary succession is vegetation development on newly formed or exposed substrate. It proceeds on a raw substrate usually low in fertility such as boulder clay or rock, rather than a developed soil (Gorham *et al.* 1979). There is no previous vegetation; no seedbank and no organic matter derived from prior vegetation (Glenn-Lewin & van der Maarel 1992). Secondary succession is the sequence of changes following a disturbance. There is often a developed soil and a biological legacy consisting of a seedbank, vegetative propagules and soil organic matter (Glenn-Lewin & van der Maarel 1992). The distinction between primary and secondary succession depends upon the severity of disturbance to the vegetation. Extreme disturbance such as glaciation removes all the biotic material and initiates primary succession. Any less severe disturbance initiates secondary succession. Thus primary and secondary succession occupy regions on a continuum of disturbance (McCook 1994), with secondary succession incorporating a much larger range of variation within the continuum. Secondary succession is also much more widespread than primary succession.

Allogenic and autogenic successions can also be understood in terms of disturbance. Autogenic succession is vegetation change due to forces of biotic interactions and biotic modification of the environment (Tansley 1935). An example of autogenic change is soil change on moorland in response to invasion by *Betula*, which allows the development of a ground flora that cannot tolerate edaphic moorland, conditions (Miles 1985). Autogenic succession occurs after a rapid disturbance (McCook

1994) and is sometimes synonymous with primary succession, as rapid disturbance is often severe, in its effects although it also occurs during secondary successions as well. Allogenic succession is vegetation change due to external environmental conditions and environmental change (Glen-Lewin & van der Maarel 1992) *e.g.* long-term climate change. Allogenic succession occurs during a slow disturbance or environmental change (McCook 1994). Drury & Nisbet (1973) discuss allogenic and autogenic successions as alternate hypotheses, although both are possible in the same succession. Indeed both are possible simultaneously, if the same succession is regarded at different scales.

4.2 Models of succession

4.2.1 Introduction

There are various interpretations of succession (Table 4.1). The different interpretations have complex interrelationships primarily because models were developed as alternatives to previous interpretations of succession. The historical development of these ideas has been well documented by Miles (1987) and McIntosh (1980). Briefly Egler (1954) developed the initial floristic composition model in response to Gleasons criticism of Clements (1916) model. Drury & Nisbet (1973) proposed a similar model to Egler (1954), again in a critique of Clements (1916). Connell & Slatyer (1977) expanded on the ideas of Drury & Nisbet (1973) and Egler (1954) to suggest three alternative models. Table 4.1 shows these various interpretations together with relay floristics which represents a traditional interpretation of succession, developed after Clements, in which one group of species establishes and is then replaced by another group until a stable state is achieved.

4.2.2 Discrepancies between the models

The different interpretations of succession have complex relationships. Some models are compatible with other models at least in part, but there are many discrepancies. The major discrepancies between the models (Table 4.1) are discussed below.

Table 4.1. The various interpretations of succession (modified from Luken 1990).

Author & Model	Time				
Clements (1916)	Disturbance that creates a bare patch (nudation)	Arrival of species at open site (Migration)	The establishment of organisms at the site. (Ecesis)	The interactions of the species at the site. (Competition)	The development of a stable climax (Stabilisation)
Egler (1954) Initial Floristic Composition. (I.F.C.)		Mixed propagule bank is present	All species establish	Early colonists assume dominance. Late successional species remain but are suppressed.	Early colonists die. Late successional species assume dominance
Drury & Nisbet (1983) Changing resource availability			Species dominance changes over time as each species responds to resource availability		
Connell & Slatyer (1977) Tolerance		Early and late successional species establish	Early successional species modify the environment to exclude other species	Late successional species tolerate competition and assume dominance	
Connell & Slatyer (1977) Facilitation		Early successional species establish	Initial colonists modify the environment so it is more conducive to late successional species	Late successional species invade and assume dominance	
(Egler 1954). Relay Floristics			Early successional species die	Late successional species establish	Late successional species persist
Connell & Slatyer (1977) Inhibition			Initial colonists modify the environment so that late successional species cannot establish	Late successional species establish only when early successional species die	

Clements (1916, 1928) and Egler (1954) disagree about changing species composition during succession. Clements (1916) believes that autogenic change results in waves of different species invading as succession proceeds, whereas Egler (1954) believes that all species are present at the start of succession. Drury & Nisbet (1973) support Clements in so far as their model allows for additional increments from outside sources e.g. seed invasion. Both models are applicable in different circumstances with Clements (1916) being more applicable to primary succession and Egler (1954) being more appropriate in secondary successions where propagule sources are scarce.

There are a set of complex relationships between the models of Egler (1954), Clements (1916) and Connell & Slatyer (1977), revolving around the idea of invasion resistance. Egler (1954) believes that early dominants may offer invasion resistance to later dominants. The inhibition model of Connell & Slatyer supports this idea, although it is expressed in terms of colonists rather than dominants implying a difference of opinion about additional increments from outside sources. Connell & Slatyers (1977) alternative facilitation model is at odds with this, as is Clements (1916) theory of autogenic change. It seems probable that Connell & Slatyer are correct as autogenic change could have positive or negative effects on incoming species or potential dominants. Egler (1954) can be interpreted as giving autogenic change a negative role or could be implying something about the internal relationships between species. Drury & Nisbet (1973) believe replacement of one group of species by another results in part from interspecific competition. Egler (1954) could be implying that the species currently occupying a niche resist invasion in this manner.

Drury & Nisbet (1973) agreed with Egler (1954) that life history traits are fundamental in understanding succession. This is at odds with Clements (1916), who believed that autogenic change is the driving force behind succession. Drury & Nisbet (1973) believed that each species has an individual niche, because of life history traits and that succession is driven in part by interspecific competition. This idea is supported by the concept that niche specialization permits the integration of communities in which species have different but complementary roles (McIntosh 1970, Fox 1977). This was refuted by Grubb (1977), who showed that groups of species may share niches and that versatile species occupying broad niches can be divided into strong and weak competitors (Grubb 1985). Whittaker (1977) reconciled these views in terms of evolutionary trends towards relatedness (interactions between species) and unrelatedness (distributional individuality). The idea of stabilization resulting in fewer species (Clements 1916) is compatible with Drury & Nisbets (1973) theory of individual niches, as autogenic change could result in fewer niches being available. Clements (1916) himself pointed out that distinguishing the effects of competition from autogenic change is difficult, but he believes reaction to be the most important in driving succession, whereas Drury & Nisbet believe that competition is more important. Resolving the relative importance of these two processes remains problematic today. Reductionist authors such as Pickett, Grime, Tilman and Miles explain succession in terms of life history attributes, whereas holists believe that autogenic change is of crucial importance in facilitating succession.

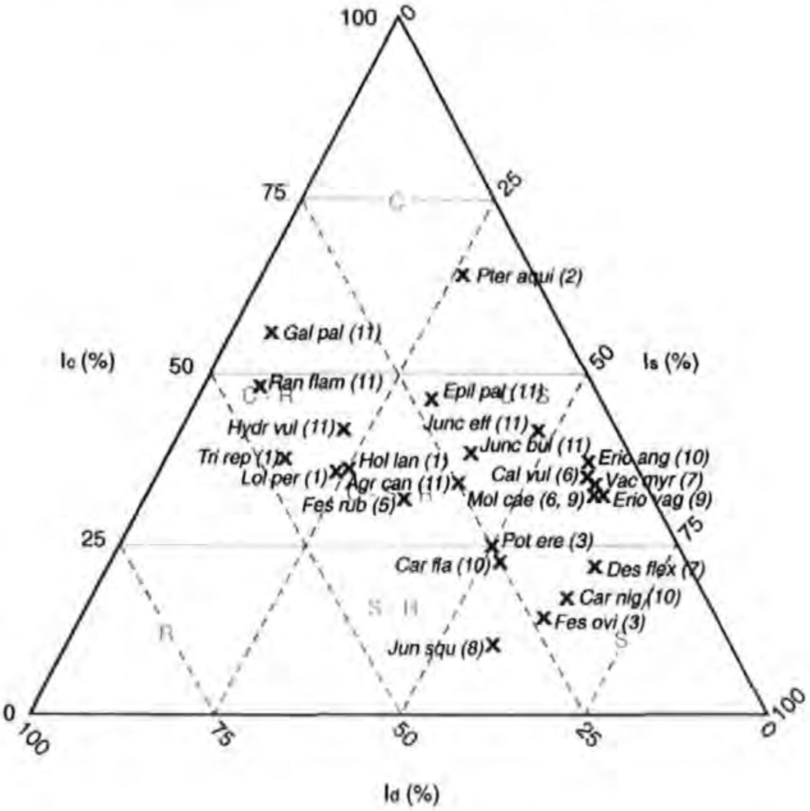
4.3 Reductionism and competition theory

Tilman (1982) developed the equilibrium theory of competition for limiting resources. This was applied to succession as the resource ratio hypothesis (Tilman 1990). The basic premise is that the successional sequence is determined by changes in the ratios of the limiting resources. Each species is specialized on a ratio of limiting resources. Thus whenever this ratio changes, succession occurs. This allows the formation of hypotheses about which limiting resources are most important. Tilman believes that some of these hypotheses are implicit in the classical models of succession *e.g.* access to a disturbance site is one constraint operating on plants (Drury & Nisbet 1973). This can be expressed as trade-off between colonization and nutrient competition, light competition, and herbivory defences. Each constraint can be overcome by allocating resources to structure or physiological function but such allocation reduces allocation to other functions causing trade-offs (Tilman 1982). Tilman (1990) suggests that field experiments should determine what the major constraints are in a given environment. Experimental studies of the relationship between plant traits and environmental variables allow quantification of the trade-offs. Alternative hypotheses about the limiting resources can be eliminated.

Keddy (1989) is critical of this approach, as the amount of information needed to construct a predictive model in this manner is excessive. As a result of the equilibrium theory of competition for limiting resources, Tilman (1982) contends that species which occupy stressful sites with limited resources, do so by excluding species that would be better competitors at more fertile and less stressful sites. In contrast, Grime (1979) argues that, in stressful sites with low productivity, competitors are not excluded by the stress-tolerators that normally occupy such sites but by an inability to tolerate the physical conditions of the environment.

The functional type approach of Grime (1979) can be used to predict a pattern of strategies and the associated life forms expected under a particular environmental regime (Shugart 1997). The C-S-R model supports the general predictability of successional pathways as 'the strategies of plants suit them to the environment of a stage' (Grime 1979). For example, Figure 4.1.illustrates that *Pteridium aquilinum* will respond to competitive stimuli more favourably than *Juncus squarrosus* as a result of its life history attributes. Thus *Pteridium aquilinum* is likely to increase in abundance in the competition phase of Clementsian succession (Table 4.1.). However, although many inferences follow from the classification of a species within the C-S-R model it does not explain the full range of plant attributes that would help in elucidating the role of individual species in vegetation change (Burrows 1990). The strategy system cannot account for the division of versatile species with broad niches into strong and weak competitors. Such species have been shown to exist by Grubb (1985).

Figure 4.1. The C-S-R model showing the positions of selected species occurring on Bodmin Moor. (The figures in brackets refer to the assemblages that the species are indicative of. See Chapter Five. Species abbreviations are listed in Appendix 2)



Another approach to life history traits is the vital attributes concept of Noble & Slatyer (1980); who identified species attributes fundamental to maintaining an active role in successional sequences after fire disturbance. The model predicted the successional sequence after fire on *Calluna vulgaris* heath (Hobbs *et al.* 1984). This model has nevertheless been criticised by Miles (1987), as the outcome is dependent upon the initial floristic composition and therefore fails to take autogenic change into account. McCook (1994) points out that statistical tests are not possible on the model.

The approaches adopted by Tilman (1990), Grime (1979), and Noble & Slatyer (1980) are not unique. There are numerous plant classification systems based on functional types (Westoby & Leishman 1997). The role of these functional type classifications is to simplify the description of vegetation to examine ecosystem dynamics. Many authors (Keddy 1990, Tilman 1990) support the use of this approach. Unfortunately they have a common failing when used to examine ecosystem dynamics in changing conditions. The aggregation of species into functional types implies a similarity in response to environmental factors, yet very little research has been reported in this area of study (Smith 1997). Some authors argue that there is 'a universal functional classification of organisms in an ecosystem' (Heal & Grime 1991). Others argue that classifications carried out for the same purpose, but with different character sets, result in different groups and therefore do not support the existence of an inherent structure in communities (Gitay & Noble 1997).

McCook (1994) argues that a reductionist synthesis of the classical models provides an explanation of autogenic sequential succession. After disturbance, species invade and autogenic change inevitably occurs. This commonly results in sequential replacement of species adapted to the varying conditions. The species adaptations are expressed as life history traits, by which a species adapts to early or late successional seres but not both. Competitive interactions result in facilitation and inhibition, which moderate or restrain the effects of the different life history traits. This hypothetical synthesis relies on evidence about correlations in life history traits. McCook argues that this is inherent in the models of Egler (1954) and Drury & Nisbet (1973) and that Huston & Smith (1987) provide evidence. Research could concentrate on extending the experimental simulation work of Huston & Smith (1987) or by field-testing the potential effects of inhibition and facilitation by decoupling the different effects of species and their interactions. McCook (1994: 117) states that field studies should be based on "current theories on succession, resource allocation, plant competition and vegetation theory". Thus work extending the population level models of Tilman (1990) should increase mechanistic understanding of succession. Other authors (Miles 1987, Usher 1987, McIntosh 1980) remain pessimistic about the achievability or desirability of general mechanistic successional models. No effective synthesis or convergence of thought has been found (McIntosh 1980) and there is no current consensus view about succession (Miles 1987). A universal, general cause for succession is unlikely because succession is site-specific. This is because of the unique nature of vegetation at any one point and because vegetation change with time is a response to many different phenomena rather than any single one (Miles 1987).

Connell & Slatyer's (1977) model is considered to represent the current understanding of empiricists (McCook 1994). Their model is sometimes misinterpreted as the complete mechanistic description of succession e.g. Begon *et al.* (1996). However, early successional species may have facilitative and inhibitory effects on later species (Walker & Chapin 1987) but Connell & Slatyer's (1977) model looks at the net effect. Additionally the model ignores the effects of stochastic events and seed availability. McCook (1994) considers Connell & Slatyer's (1977) three pathways as classifications of different outcomes of succession, which occur in different circumstances, rather than mechanistic hypotheses that explain succession. The utility of the models as a conceptual basis for thinking about succession can be increased further if they are considered as classifications of processes that may occur in combination at any one site (Walker & Chapin 1987). The relative importance of the different mechanisms varies widely between environments and they may affect the same individual successively or simultaneously. This led Finegan (1984) to believe that attempts to classify succession on the basis of a single underlying mechanism only obscure understanding and inhibit progress.

Miles (1987) is particularly critical of the classical mechanistic models, believing that they relate to the succession of particular species in particular situations and not to vegetation types. He makes the point that individuals of a species are changing in a succession and that vegetation units are made up of these species interactions not hypothetical emergent properties. He suggests that mechanisms of succession are poorly understood. Like McCook (1994), he considers vital attributes an important key to understanding but points out that these need to be linked with quantitative methods of predicting change. Examination of the mechanisms determining the structure and species composition of vegetation is of crucial importance because when these mechanisms are modified by natural events or by management, vegetation change occurs (Miles 1987). However, the current theories on resource allocation plant competition and vegetation theory are not only complex and involved, but are incomplete as explanations of succession. The once standard holistic theory of succession via autogenic change has been replaced by a reductionist neo-Darwinian theory with defects of its own. 'A less inflexible theory is much needed' (Finegan 1984: 114).

4.4 Multiple pathways

The recognition that succession can occur along multiple pathways has allowed the development of more flexible theory. Clements (1916: 11) believes 'succession is inherently and inevitably progressive, the course of development may be deflected or interrupted but movement is always towards climax'. Tansley (1935) modified this idea to account for variation in site geology and other local conditions producing the polyclimax concept but later authors went further and showed succession occurring along multiple pathways. Walker (1970) showed that succession in hydroseres followed multiple pathways. Bakker *et al.* (1983) found multiple transitions when they subjected an area of heathland to sheep grazing. Miles *et al.* (1978) developed empirical multiple pathways for upland successions from the literature (section

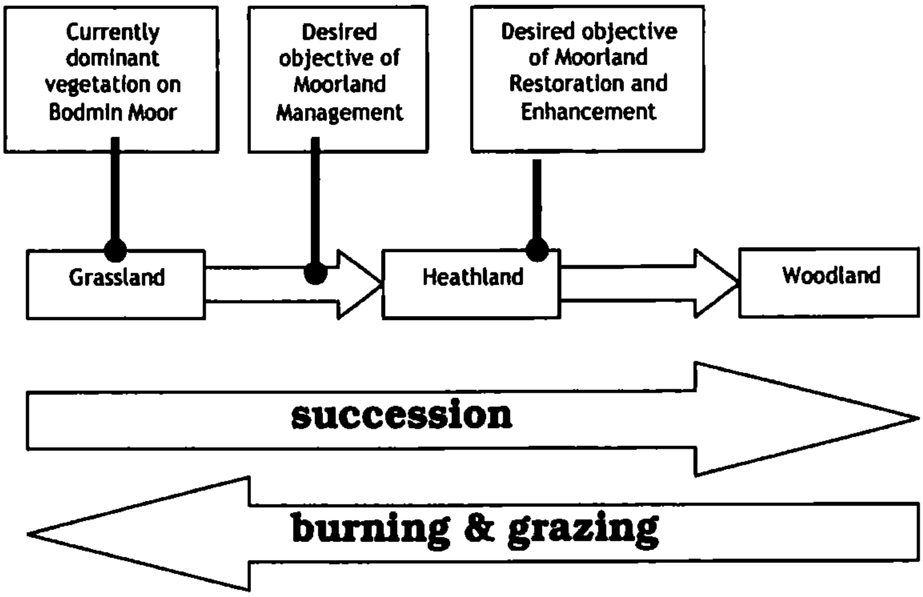
4.5.). Which pathway occurs, depends, not only on the initial conditions and mechanisms of succession, but also on community circumstances such as species diversity, landscape complexity and community isolation (Glen-Lewin & van der Maarel 1992).

4.5 The effect of burning and grazing on upland plant community succession

4.5.1 Introduction

This section considers predictions of vegetation change under different grazing pressures at the plant community level. There is a large quantity of published work on plant community shifts under different herbivore densities. In general terms, most of the observed and hypothesised changes under no grazing are towards woody species, whereas changes under grazing/burning are towards grassland with dominance by less palatable species in many situations (Figure 4.2.). Heath vegetation can be considered as a seral stage in the succession from grassland to woodland on nutrient-poor acid soils (Figure 4.2.). While successional forces tend to drive this change in one direction towards scrub and woodland, burning and grazing tend to reverse the trend (Legg 1995).

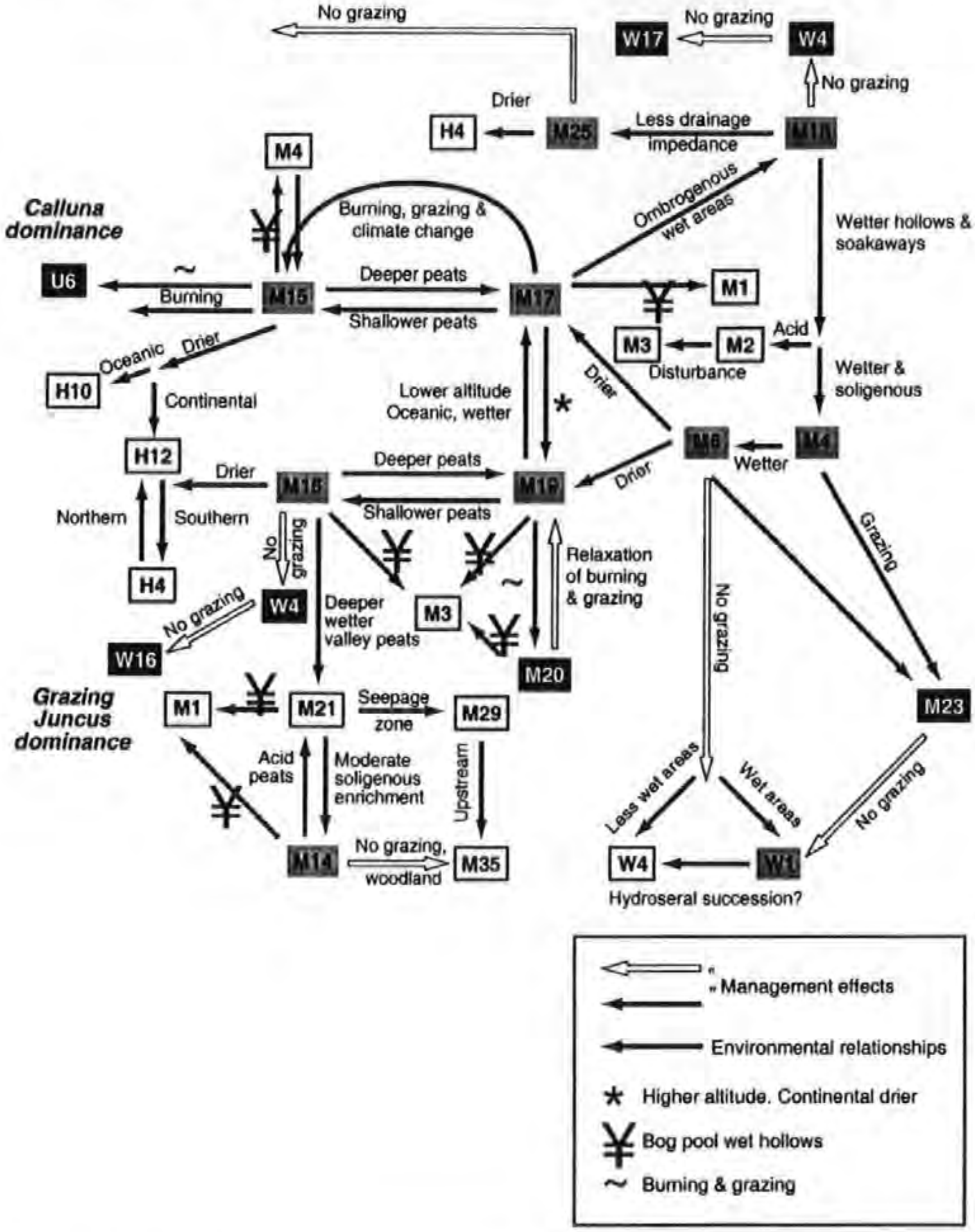
Figure 4.2. Plagioclimax vegetation and succession on Bodmin Moor.



However, predicting the outcome of successional process is not straightforward. There are many variables acting concurrently, resulting in a wide range of interactions, any one of which can potentially alter the successional pathway. The grazing impacts vary considerably between locations in relation to the vegetation type, environmental conditions and the distribution and combination of grazers present. Generalisations about the impact of grazing must therefore be treated with a degree of circumspection. However, some authors have made qualitative generalised predictions of plant community changes under different grazing intensities (Ratcliffe 1959, Institute of Terrestrial Ecology 1978, Ball *et al.* 1982, Miles 1985, 1988, Rodwell 1991, 1992, Thompson *et al.* 1995). The sources that these authors use are not always stated, so the degree to which they are based on literature, the experience of the author and general ecological understanding is unknown.

Miles (1985, 1988) and Institute of Terrestrial Ecology (1978) make predictions of changes under specified grazing densities, usually sheep per hectare but Rodwell (1991, 1992) and Thompson *et al.* (1995) use broad statements such as increased grazing or heavy grazing. Burning effects usually remain linked with grazing effects. The hypothesised directions of change under increasing or decreasing grazing and burning are comparable between all the authors who have made generalised predictions. Figures 4.3. - 4.5. summarise the changes predicted by Rodwell (1991, 1992) for the NVC-defined grassland, heathland and mire communities of the SouthWest. For each of the communities defined by Rodwell, a prediction is made about the effects of grazing, draining and fire on the vegetation concerned. There is a degree of overlap between these figures especially between the grassland and heathland. This is inevitable, as grassland is often derived from heathland but the figures cannot be combined, as the result would be too complex to interpret. The following sections try to assess the validity of these hypothesized predictions.

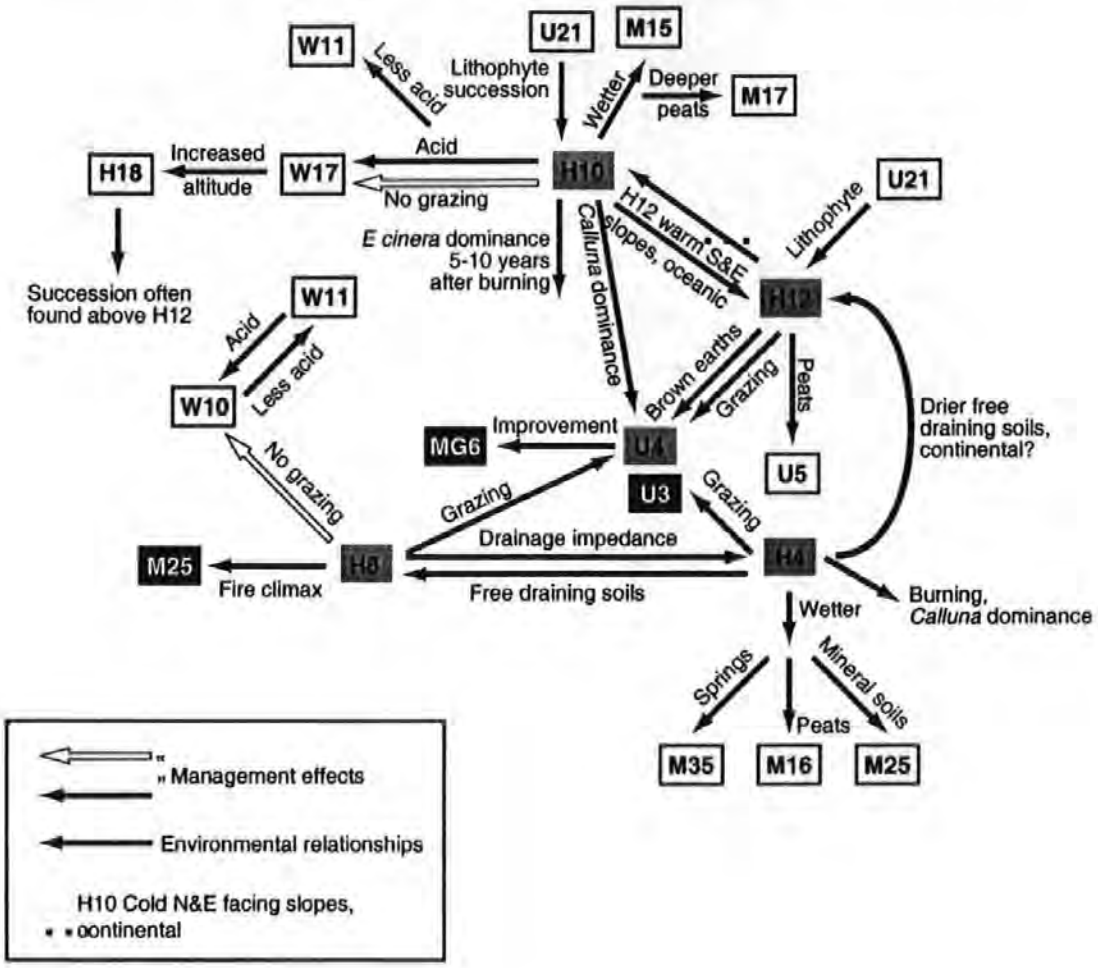
Figure 4.3. The effects of management on blanket bog, wet heaths, valley mires and associated communities in the South-west.



NVC communities & codes

Sphagnum auriculatum **bog pool**	M1	*Narthecium ossifragum -Sphagnum papillo*	M21
Sphagnum cuspidatum/recurvum	M2	*Juncus effusus/actiflorus-Galium palustr*	M23
Eriophorum angustifolium	M3	*Molonia caerulea-Potentilla erecta* **mire**	M25
Carex rostrata-Sphagnum recurvum **mire**	M4	*Hypericum elodes-Potamogeton polygonif*	M29
Carex echinata-Sphagnum recurvum	M6	*Ranunculua omiophyllus-Montia fontana*	M35
Schoenus nigricans- Narthecium ossifragum	M14	*Ulex gallii-Agrostis curtisii* **heath**	H4
Scirpus cespitosus-Erica tetralix **wet heath**	M15	*Calluna vulagris-Vaccinium myrtillus*	H12
Erica tetralix-Sphagnum compactum	M16	*Juncus squarrosus-Festuca ovina* **grassland**	U6
Scirpus cespitosus-Eriophorum vaginatum	M17	*Salix cinerea-Galium palustre* **woodland**	W1
Erica tetralix-Sphagnum papillosum	M18	*Betula pubescens-Molinia caerulea*	W4
Calluna vulgaris-Eriophorum vaginatum	M19	*Quercus-Betula-Deschampsia flexuosa*	W16
Eriophorum vaginatum **blanket mire**	M20	Quercus pet-Betula pub-Dicranum majus	W17

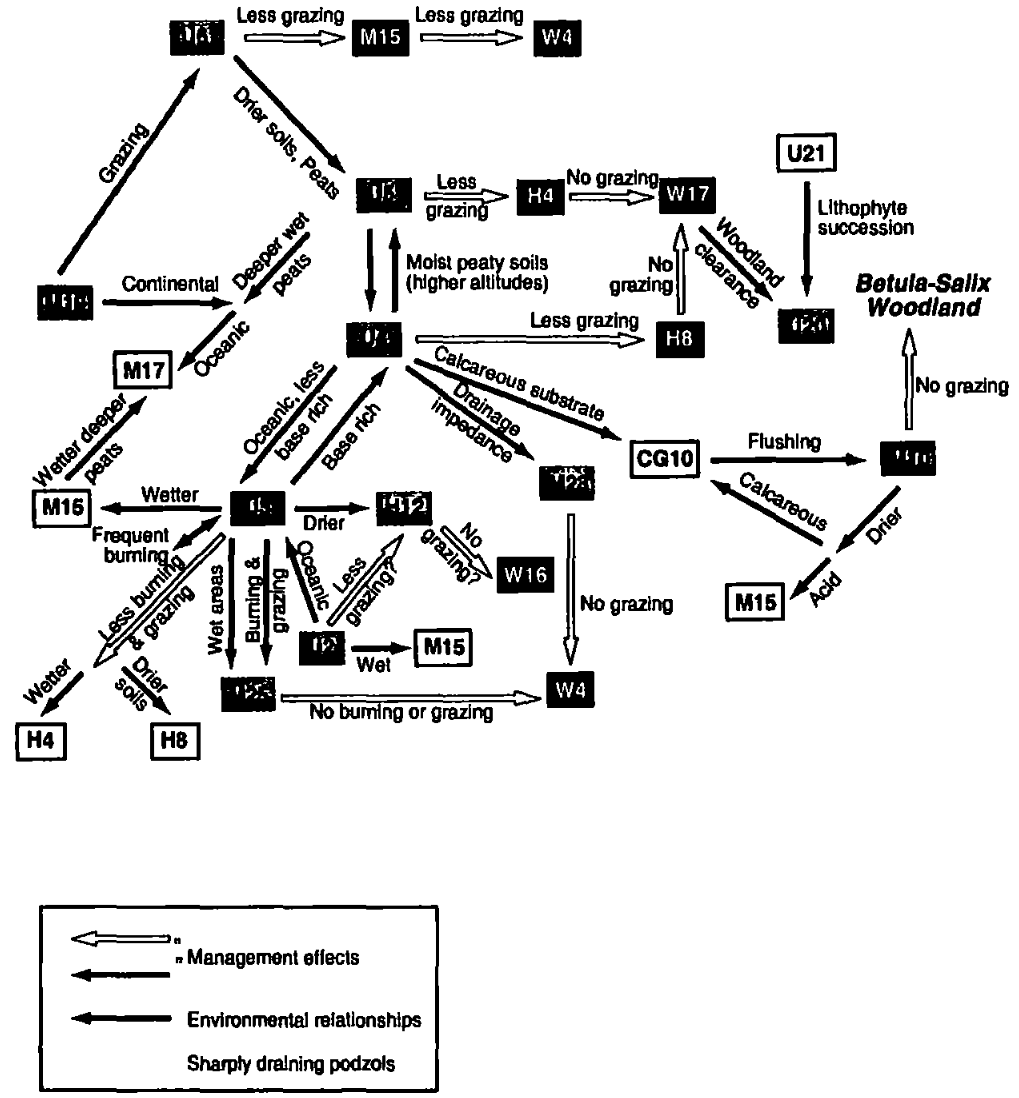
Figure 4.4. The effects of management on heathlands and associated communities in the South-west.



NVC communities & codes

Ulex gallii-Agrostis curtisii **heath**	**H4**	*Lolium perenne-Cynosurus cristatus*	**MG6**
Calluna vulgaris-Ulex gallii	**H8**	*Scirpus cespitosus-Erica tetralix* **wet heath**	**M15**
Calluna vulgaris-Erica cinerea	**H10**	*Erica tetralix-Sphagnum compactum*	**M16**
Calluna vulgaris-Vaccinium myrtilus	**H12**	*Scirpus cespitosus-Eriophorum vaginatum*	**M17**
Vaccinium myrtillus-Deschampsia flexuosa	**H18**	*Molinia caerulea-Potentilla erecta*	**M25**
Agrostis curtisii **grassland**	**U3**	*Ranunculus omiophyllus-Montia fontana*	**M35**
Festuca ovina-Agrostis capillaris-Galium sax	**U4**	*Quercus rob-Pteridum aqu-Rubus fru*	**W10**
Narduss stricta-Galium saxatlie	**U5**	*Quercus pet-Betula pub-Oxalis ace*	**W11**
Cryptogramma crispa-Deschampsia flexuosa	**U21**	*Quercus pet-Betula pub-Dicranum majus*	**W17**

Figure 4.5. The effects of management on grasslands and associated communities in the South-west.



NVC communities & codes

Deschampsia flexuosa **grassland**	U2	*Scirpus cespitosus-Eriophorum vaginatum*	M17
Agrostis curtisii	U3	*Calluna vulgaris-Eriophorum vaginatum*	M19
Festuca ovina-Agrostis capillaris-Galium sax	U4	*Juncus effusus/acutiflorus-Galium palu*	M23
Narduss stricta-Galium saxatile	U5	*Molinia caerulea-Potentilla erecta*	M25
Juncus squarrosus-Festuca ovina	U6	*Ulex gallii-Agrostis curtisii* **heath**	H4
Pteridium aquilinum-Galium saxatile	U20	*Calluna vulgaris-Ulex gallii*	H8
Cryptogramma crispa-Deschampsia flexuosa	U21	*Calluna vulagris-Vaccinium myrtillus*	H12
Festuca ovina-Agrostis capillaris-Thymus pr	CG10	*Betula pubescens-Molinia caerulea*	W4
Carex dioica-Pinguicula vulgaris **mire**	M10	*Quercus-Betula-Deschampsia flexuosa*	W16
Scirpus cespitosus-Erica tetralix **wet heath**	M15	*Quercus pet-Betula pub-Dicranum majus*	W17

The relationships between mires, dry heath, grassland and grazing can be hard to assess, as these habitats are not always clearly defined especially at the community level. One of the main conclusions of Shaw *et al.* (1996) is that there needs to be a much greater emphasis on the distinction between wet and dry upland habitats, as they are often lumped together, despite their ecological differences.

4.5.2 Mire and wet heath communities

Most knowledge of mire communities is based on a limited range of experiments and observations largely on sheep grazing on blanket bog in Northern England and Scotland. There is very little work available from Wales or the South-west (Shaw *et al.* 1996). Thus the impact of grazing on communities restricted to the South-west, such as the *Narthecium ossifragum – Sphagnum papillosum* valley mire, remains unknown.

The effect of sheep grazing on blanket bog has been researched. *Calluna vulgaris* is less productive on wet substrates than on dry (Mowforth & Sydes 1989). Thus stocking intensities that maintain *Calluna vulgaris* cover on mires are lower than those on drier substrates. Stocking densities above 1.3 ewes per ha (0.13Lus/ha) result in reduction of *Calluna vulgaris* cover or standing crop (Hewson 1977, Rawes & Hobbs 1979, Grant *et al.* 1981). Sheep grazing at 1.37 sheep/ha and 2.20 sheep/ha in both summer and all year round resulted in a decline in *Calluna vulgaris* and *Eriophorum* spp. in Argyll (Grant *et al.* 1976, Grant *et al.* 1985). At the higher density of 3.4sheep/ha, *Calluna-Eriophorum* bog resulted in total *Eriophorum* spp. dominance in NE Scotland (Hobbs & Gimingham 1980). Other documented changes on blanket bog report an increase in *Empetrum nigrum*, even in areas previously dominated by *Eriophorum* or *Molinia caerulea* on Ilkley moor (Dalby *et al.* 1971) and an increase in *Juncus* spp. at a sheep density of 0.25sheep/ha in the Pennines (Welch & Rawes 1966). Recommended maximum sheep densities for the maintenance of blanket bog communities depend on sheep breed, with large breed recommendations at 0.38sheep/ha, medium breeds at 0.47sheep/ha and small breeds at 0.6sheep/ha (Sibbald *et al.* 1987). This agrees with the previous work of Grant *et al.* (1976), that recommended a maximum density of <0.6sheep/ha for the maintenance of *Calluna-Eriophorum* bog. Wet heath remains understudied. Nolan *et al.* (1995) report that sheep grazing at 0.4, 0.8 and 1.2sheep/ha results in a positive relationship between stocking rate and utilisation of *Calluna* and a negative relationship with the cover of *Calluna* in Northumberland.

Within the mire communities, little is known about grazers other than sheep. Grant *et al* (1987b) report from work in Argyll that the seasonal preference of cattle shifts from *Molinia caerulea, Scirpus cespitosus* and *Carex* spp. (summer) to *Eriophorum vaginatum* and *Calluna vulgaris* in winter. They also found that cattle consumed more dead material and *Eriophorum vaginatum* than sheep. The only information on horse grazing in mires is in a lowland context from the New Forest (Putman *et al.* 1987, Ekins 1989).

The studies described above generally support the hypothesised changes between communities as a result of sheep grazing, although the maximum sheep densities predicted to maintain *Calluna* by Sibbald *et al.* (1987) (0.1 - 1.6sheep/ha) are lower than those of Institute of Terrestrial Ecology (1978) (2.5 - 5.0sheep/ha). However, many of the mire and wet heath communities are unstudied in relation to grazing. For those that are studied, little is known about grazers other than sheep and the manner in which grazing impact varies from place to place is also unknown.

The Bodmin Moor management prescriptions of 0.225 -0.17LUs/ha in summer (2.25 - 1.7sheep/ha) and 0.17 - 0LUs/ha in winter (1.7 - 0sheep/ha) are higher than those recommended by Sibbald *et al.* (1987), but within the guidelines of Institute of Terrestrial Ecology (1978). The more rigorous Moorland Restoration and Enhancement prescriptions of 0.17LUs/ha in summer (1.7sheep/ha) and 0.08-

0LUs/ha (0.8 – 0sheep/ha) in winter are also higher than the lower limits recommended by Sibbald *et al.* (1987). However, they are likely to be less damaging to ericoid species because the winter stocking rate is lower and winter cattle grazing is prohibited. The pony stocking for both Bodmin Moor management options is 0.04LUs/ha in summer and 0.02LUs/ha in winter. The effect of ponies on upland vegetation is largely unknown. Thus predictions about impact remain speculative.

The effects of these management prescriptions on the mire communities of Bodmin Moor cannot be ascertained from the literature. There is still debate over the optimal management for the conservation of the flora and fauna of blanket bog and wet heath and indeed, what the management requirements are particularly on the more Western examples. Further work is required to determine optimum stocking rates under different conditions by different breeds of sheep cattle and ponies (Shaw *et al.* 1996).

4.5.3 Heathland communities

The relationships between heathlands and associated communities in the South-west are better known than those of the mire communities but the South-west still remains understudied in comparison to more Northerly upland areas. The communities restricted to the South-west, such as *Ulex gallii-Agrostis curtisii* heath and *Calluna vulgaris-Ulex gallii* heath are therefore largely unstudied in relation to grazing. Nevertheless there is a great deal of literature pertaining to the more Northern dry heather moorland, particularly where it is managed primarily by burning for grouse. Bardgett, Marsden & Howard (1995) noted that, in Wales and South-west England, a large proportion of the heather was suppressed and/or showing signs of heavy grazing; here the majority of the heather moorland was stocked at more than 1.5 ewes or equivalent per hectare, with heavy autumn grazing and few areas burnt regularly. By contrast, in the North York Moors and other areas of NorthEast England, heather moorland was stocked at lower levels throughout the year, burning was more widely practiced and less heather showed signs of damage or neglect. These differences are probably largely attributable to the management of the latter areas as grouse moors.

There are numerous studies on the effects of sheep grazing on dry heath communities. Sixty years of heavy sheep grazing on Ilkley Moor converted a heather-dominated moor to a moorland, where *Calluna vulgaris* dominance was restricted to hill tops and *Empetrum nigrum* had invaded every plant community and was widely dominant (Dalby *et al.* 1971). *Calluna vulgaris* regeneration was shown to be much slower in grazed situation than ungrazed situations in SouthEast Scotland (Fenton 1937). In North-East Scotland, 5 sheep/ha caused a 9% decline in *Calluna vulgaris* cover over four years. Light grazing favoured ericoids and lichens; heavy grazing favoured grasses and forbs. *Nardus stricta* and *Vaccinium myrtillus* benefited from intermediate grazing (Welch 1984a). Another study in North-East Scotland showed a change from heath to grassland in five years when grazed by sheep at 5 sheep/ha (Miles *et al.* 1978).

Recommended maximum sheep densities for dry heath depend on the age of the *Calluna vulgaris*, rather than sheep breed, with recommended values for a medium sized sheep at 0.14 sheep/ha on old heather, 0.39 sheep/ha on intermediate heather and 1.56 sheep/ha on young heather (Sibbald *et al* 1987). This reflects the different regenerative capacity of the different life cycle stages of heather. Other workers suggest that the stocking rates of Sibbald *et al.* (1987) are conservative. Bardgett & Marsden (1992) suggest that 0.225LUs/ha (2.25 sheep/ha) is the threshold above which both heather cover and condition decline. Similarly, Lance (1987) predicted that heather cover will rapidly decline beyond a threshold stocking rate of 0.27LUs/ha and Felton & Marsden (1991) suggested that stocking rates of 0.225LUs/ha (or 0.3LUs/ha with off-wintering) are compatible with the maintenance of heather. Smallshire *et al.* (1997) found stocking rates of 0.29LUs/ha compatible with 18 areas of dwarf-shrub moorland in good condition across South-west England.

As with the mire communities, there is less literature pertaining to stock other than sheep. A figure of 1.2 cattle/ha caused a decline of 32% *Calluna vulgaris* cover in four years and a reduction in *Calluna vulgaris* cover from 80% to 5% cover in 10 years (Welch 1984a). There have been no studies looking at the effect of horses on dry heath in the British uplands. In general, the existing work on dry heath supports the hypothesised relationships of Institute of Terrestrial Ecology (1978), Ball *et al.* (1982), Miles (1985, 1988), Rodwell (1991, 1992) and Thompson *et al.* (1995). However, as with the mire communities, major gaps in knowledge still remain and there are discrepancies between authors about the effect of grazing density.

The Bodmin Moor Moorland Management prescription of 0.225LUs/ha in summer and 0.17LUs/ha in winter would result in higher sheep densities than those recommended by Sibbald *et al.* (1987) for the maintenance of dry heath. The more rigorous Moorland Restoration and Enhancement prescriptions of 0.17LUs/ha in summer and 0.08 - 0LUs/ha sheep in winter would result in no damage to young heather in winter, according to Sibbbald *et al.* (1987), but would be inappropriate for intermediate or old heather regeneration. By contrast, other workers (Lance 1987, Felton & Marsden 1991, Bardgett & Marsden 1992, Smallshire *et al.* 1997), suggest that the Countryside Stewardship stocking rates are appropriate for heathland management and restoration. Monitoring of heather biomass utilisation in the Dartmoor ESA suggests that Sibbald *et al.* (1987) are correct.

The Dartmoor ESA prescribes a summer (16th April - 31st October) stocking rate of 0.225LUs/ha (winter 0.17LUs/ha) for Tier1E and, 0.17LUs/ha (winter 0.08LUs/ha) for Tier 2B on moorland other than dry grass communities (ADAS 1998). They are therefore almost identical to the proposed management prescriptions for Bodmin Moor. The heath communities on Tier 1E land had a heather biomass utilisation of

25.1% (ADAS 1998). Smallshire (1996) found Dartmoor heath communities grazed at 0.22 LUs/ha (below Tier 1E prescribed stocking rates) had higher heather biomass utilisation (31.7%). The suppressive thresholds of biomass utilisation for heather (Table 4.2.) suggest that only young heather can withstand these stocking densities.

Table 4.2. Suppressive thresholds of biomass utilisation for *Calluna vulgaris* (after Sibbald *et al.* 1987).

Heather type	Age (years)	Utilisation (%)
Pioneer stage (young)	0 - 5	40
Building (intermediate)	5 - 15	10
Mature/senescent (old)	> 15	5
Blanket bog	All ages	15

However, further research is required to confirm this. The suppression thresholds upon which these results are based have been developed for upland grazing situations in Scotland. MAFF-commissioned research is currently investigating their applicability to the South-west (Smith *Pers. comm.*). Additionally, the biomass utililisation estimates are based on a grazing index modified by a mathematical calibration function after Poulton (1991). Measuring biomass increment using caged and uncaged plots, while time-consuming, would provide a real measure of biomass utilisation. The impact of cattle and pony grazing on dry heath communities is hard to assess using literature, due to the paucity of information.

4.5.4 Grassland communities

With the exception of *Agrostis curtisii* grassland, all the grasslands in the South-west are widespread in the British uplands and have been studied in relation to grazing. As with mire and dry heath communities, most of this work is of relevance to sheep. Excluding sheep from *Agrostis/Festuca/Nardus* grassland in the Pennines resulted in an increase in *Calluna vulgaris* and *Empetrum nigrum* (Welch 1968). On similar vegetation at Moorhouse, grazed at 3 sheep/ha, 18 years of no grazing showed an increase in *Calluna* vulgaris abundance from 0 to 15% (Marrs *et al.* 1988). Twenty-five years of no grazing on

Agrostis/Festuca grassland in Snowdonia saw an increase in *Agrostis*, *Festuca* and *Holcus lanatus*, with no invasion by new species (Hill 1982). On *Molinia caerulea*-dominated vegetation, other species were excluded after seven years of no grazing. In analogous situations with less *Molinia caerulea*, the species *Calluna vulgaris*, *Vaccinium myrtillus* and *Deschampsia flexuosa* increased as a result of no grazing over 20 years (Hill 1982). On Ilkley Moor, three years of no grazing saw a shift from *Nardus stricta* grassland to *Molinia caerulea* grassland with some heath species, and *Agrostis-Festuca* grassland shifted to *Holcus lanatus* and *Deschampsia spp.* dominance (Dalby *et al* 1971). Across Sourhope, the Cheviots and South-East Scotland, *Nardus stricta*-dominated grassland periodically mob stocked with sheep (up to 69 sheep/ha) reduced *Nardus stricta* dominance and saw an increase in *Agrostis* spp. and *Anthoxanthum odoratum* (Nicholson *et al.* 1970). Recommended maximum stocking densities to maintain plant cover are 4.67sheep/ha on 'good' grassland and 1.33 sheep/ha on 'poor' grassland for medium sized sheep (Sibbald *et al.* 1987).

Grazing by goats at 30 goats/ha, with a sward height of 4-5cm eliminated *Juncus* spp. tussocks in *Agrostis spp* swards within 3 years. At 10 goats/ha, *Juncus* spp. was reduced (Merchant 1993). In Boghall Glen on *Agrostis-Festuca* grassland, sheep were reintroduced after exclusion. There was an immediate increase in *Nardus stricta*, which declined under cattle grazing (Fenton 1937).

In general, the existing work on dry heath supports the hypothesised relationships of the Institute of Terrestrial Ecology (1978), Ball *et al.* (1982), Miles (1985, 1988), Rodwell (1991, 1992), and Thompson *et al.* (1995). The work of Nicolson *et al.* (1970) suggests that it may take stocking densities of more than 5-7 sheep/ha, as suggested by Institute of Terrestrial Ecology, (1978), to change *Molinia caerulea* or *Nardus stricta* to *Festuca* grassland. No specific grazer densities are given by Institute of Terrestrial Ecology (1978) for changes from grassland communities to heathland. Most documented changes of this type seem to have occurred under no grazing (Welch 1968, Marrs *et al.* 1988, Milne *et al.* 1998). The work of Hill (1982) demonstrated that heathland restoration on *Festuca* spp. and *Nardus stricta*-dominated sites could be modified by interactions with *Molinia caerulea.*

4.5.5 Overall implications for Countryside Stewardship prescriptions

The Bodmin Moor management prescriptions may not be suitable for the maintenance or restoration of heath, although further work is required to confirm this. Likewise, the effects of Countryside Stewardship stocking rates on the grasslands are not known and require investigation. It is possible that the reduced grazing pressure could initiate Molinia caerulea dominance. The determination of the biomass utililization and suppressive threshold of *Molinia caerulea* under different environmental conditions, by different grazers, at different stocking rates, would allow the effects of the management prescriptions on *Molinia caerulea* to be assessed.

4.6 Predictive models

In contrast to the models of universal applicability and the multiple pathway generalisations discussed above, Markovian probability projection models were developed in an attempt to produce models with high predictive power. Estimates of the probability of each species being replaced by another species are arranged in a matrix and are multiplied by a vector of the initial species composition in order to predict the future composition (see Usher, 1987 for fuller explanation).

There are two major limitations to these models. Firstly, the matrix generation requires large quantities of high quality information. Oversimplification can result from not collecting such data (Facelli & Pickett 1990). Secondly, the model treats the mechanisms and processes of succession as a black box (McCook 1994). The matrix form does allow reference to Connell & Slatyer's (1977) model (see Usher 1987) but is essentially a predictor that does not examine the mechanistics of succession. Additionally, like the general models of succession, it is untestable in the Popperian sense and concern has been expressed that, as the probabilities do not change the model is unrealistic.

4.7 The problem of scale

Different models examine succession in terms of theory and explanation or of management applications; at a range of scales from individual plant to landscape. The observed patterns will be dependent on temporal and spatial scale. For example, 'climax' vegetation exists only on a short time scale because the Quaternary climate is never stable. This means that comparison of models is further complicated because their relative merits depend on the scale on which they are viewed, both temporally and spatially.

The ergodic hypothesis states that spatial variation is equivalent to temporal variation (Miles 1979). This is true to an extent but variation in local site conditions can invalidate this hypothesis. This is a problem when studying succession, as often the only way to look at long term change is to compare sites with a known history of disturbance. This is because most successional studies have short time scales. One exception to this is the Park grass experiment, which began in 1856 (Silvertown 1980) and is still continuing today. The longest study in upland Britain, involving annual monitoring with sufficient precision to be statistically valid, recorded vegetation change over 20 years at Moorhouse (Northern Pennines) (Marrs *et al.* 1988). Keddy (1990) offers a partial solution to the problem of studies over short timescales. Instead of studying homogenous patches of vegetation, spatial variation along natural environmental gradients should be investigated. These gradients provide opportunities for comparative studies (Keddy 1989) or natural experiments (Diamond 1983), where vegetation characteristics, plant traits and species composition covary along with environmental variables. By comparing these patterns across a range of environments and vegetation types, tests can be made for general patterns and exceptions from those patterns can be detected.

McCook (1994: 132) believes "the most explanatory models of succession are those that are most explicitly reductionist, based on physiological properties of the plants, yet these models are the most integrative and useful at higher levels." This view implies that there is little information loss when scaling up from an individual to a landscape level. This is not necessarily true, especially in complex systems, subject to multiple species interactions such as grazing systems. One way to approach this problem is to use nested hierarchies of models. If large-scale general models have more specific models nested within them, then the data can be explored across a continuum of scale and across a continuum from site specific to general. Keddy (1990) and Pickett *et al.* (1987) have advocated this approach, which is illustrated in Table 4.3.

Table 4.3. Model hierarchies (modified from Keddy 1990).

Level of organisation	Increasing scale	Environmental Gradients		Plants
State variables	↓	Biomass, species richness		Traits e.g. growth rate, height, productivity
General processes and patterns		Fertility (stress)	Disturbance	Functional types e.g. ruderals, stress tolerators
Vegetation type		Soil nutrients	Grazing damage	Wetland functional types e.g. annuals, reeds
Site		Points in DCA space		Species nomenclature
Region				

Pickett *et al.* (1987) suggested a three level hierarchy. The first level examined the general universal conditions for succession by looking at availability of open sites and differential availability of species. The second level considered the contributing ecological processes and the third level examined the defining factors looking at site-specific mechanisms of succession, therefore allowing detailed prediction. The rules that determine information flow from one level of the hierarchy to the next are conjectural and therefore problematic. The construction of models of minimal structure (Pickett *et al* 1989) may help to formalise these rules but questions about their validity remain.

4.8 Models like methods are dependent upon objectives

The best model is that most appropriate to fulfilling the objectives of the study (Shugart 1984), which need to be stated beforehand. McCook (1994: 140) suggests that the goals of successional ecology are 'to describe the similarities and differences in both the pattern and process: to extract generalizations and to identify the bases for differences in process'. Miles (1987), in contrast, emphasizes the applied role of ecology suggesting that predictive models must be developed for management purposes. Explanatory models may predict but predictive models cannot explain (Loehle 1983). However acquiring the knowledge necessary to build explanatory models is a long-term process of paradigm modification and change. The need for management advice and prediction is urgent in the short term; therefore there is a more pressing need for empirical correlative studies than the mechanistic studies proposed by McCook (1994). Miles (1987) points out that both predictive and explanatory research can be carried out concurrently, but combining the two requires hierarchical studies, which will be subject to scaling problems. Any attempt at a functional aggregation for the purpose of evaluating the dynamics of plant distribution must address the environmental responses of the component species relating to dispersal, establishment, growth, reproduction and mortality (Smith 1997). Linking either species attributes at a individual or population level, or functional types to quantitative methods of predicting change and to other system variables through hierarchical classifications may be the best hope for navigating the 'difficult path between unrealistic simplicity and untestable complexity' (Watt 1975: 145).

4.9 Conclusions

- Succession has been defined as various kinds of vegetation change. It can be classified as primary or secondary and autogenic or allogenic. (Glen-Lewin & van der Maarel 1992). Care must be exercised in using these classifications as intermediate positions occur. Additionally, when viewed on different scales, the classification becomes arbitrary (McCook 1994, Glen-Lewin & van der Maarel 1992).

- Disturbance and succession are intimately linked. Grazing can be considered as a kind of disturbance variable in terms of intensity, duration and effect. The classical models of succession (Table 4.1.) are conceptual word models that attempt to explain the mechanistics of succession after disturbance. They all fail to do this, although they provide insights into some mechanisms and provide a classification of some successional processes.

- Vegetation dynamics are based on the population processes of the constituent plants (McCook 1994, Miles 1987). It is in the individual species and population processes that the mechanistic explanations of succession will be found (McCook 1994, Glen-Lewin & van der Maarel 1992, Miles 1987, Huston & Smith 1987). However, succession is a complex phenomenon, not easily understood by mechanistic explanation in isolation.

- Succession occurs via multiple pathways (Miles *et al.* 1978, Walker 1970), and is influenced by community circumstances, such as species diversity and landscape complexity (Glen-Lewin & van der Maarel 1992). The observed properties of succession change on different temporal and spatial scales.

- The classical models and Markov models are untestable in the Popperian sense (McCook 1994), although the high predictive power of Markov models make them a powerful tool potentially useful for developing management protocols (Usher 1987). Holists view the community as having complex emergent properties, whilst reductionists see stochastic events as being of critical importance. Therefore the different approaches result in different interpretations of succession. The combination of these approaches could lead to the development of grey box models with both predictive and explanatory power.

- The lack of consensus concerning succession reflects its complexity and provides a clear indication that much research is required in order to understand plant community responses to changes in grazing practice.

- Predictive diagrams of plant community change under different grazing regimes (Figures 4.3 – 4.5) provide a valuable and informative framework for assessment of the impacts of grazing on vegetation. The additions of stocking densities and of predicted speeds of change would make these diagrams much more informative.

- Many questions remain. There are little or no data on many of the hypothesised community changes. This is especially true of the less widespread communities. On Bodmin Moor, *Agrostis curtisii* and *Ulex gallii* are important components of the vegetation in plant communities that are absent from Northern Britain. There is very little information on the effects of grazing in these communities. There are also very little data on the effects of stock other than sheep, with the exception of a handful of studies on cattle grazing. . Cattle and ponies are widespread on Bodmin Moor.

- Even for communities that have been well researched, it is not possible to predict the speed of change between communities under different climatic and soil conditions. The extended growing season in the South-west allows more rapid plant growth but this increased growth rate has not been quantified (Smallshire *et al.* 1997). Thus vegetation changes in response to grazing may be different on Bodmin Moor to those reported from other areas.

- The success of upland management on Bodmin Moor depends on the availability of detailed analytical data on the vegetation, its environmental and biotic controls and the effects of different management strategies. In particular, the plant communities present on Bodmin Moor require further description. The decline of heathland on the Moor during the 20th century needs verification. The effects of the proposed management on key species such as *Calluna vulgaris* and *Molinia caerulea* must be investigated. This information is not currently available; hence the need for the research presented in this thesis.

5 The plant communities and environmental gradients of Bodmin Moor

5.1 INTRODUCTION

5.1.1 The history of vegetation description in Britain

The description and classification of vegetation has a pedigree extending back beyond the beginning of last century, as documented by many workers (Whittaker 1962, Shimwell 1971, Westhoff and van der Maarel 1978, Gimingham *et al.* 1983, Sheail 1987, Gimingham, 1997). Within Europe different schools emerged, embracing slightly different paradigms with different degrees of emphasis on floristic composition, species dominance, physiognomy and environmental factors (Shimwell 1971, Rieley & Page 1990, Kent & Coker 1992). The Zurich-Montpellier School based on the work of Braun Blanquet (1928) has been the most influential, and has generally superseded the Uppsala and Raunkaier Schools.

The first attempts at a comprehensive classification of British vegetation were those of Tansley (1939) who avoided the meticulous classification of vegetation that typifies the work of Zurich- Montpellier School. The British uplands, often the focus of phytosociological work, provided an early evolutionary step in British phytosociology. Poore (1955a, 1955b, 1955c) described the vegetation of the Breadalbane Mountains using the Braun-Blanquet approach. He was critical of the resultant hierarchical classification, but used the sampling methodology for further work (Poore & McVean 1957). This provided the methodology for a full-scale phytosociological survey of the plant communities of the Scottish Highlands (McVean & Ratcliffe 1962). Following this study, standard phytosociological descriptions were made in specific areas, for example Upper Teesdale (Bradshaw & Jones 1976), and on specific vegetation types such as heaths (Bridgewater 1970) or sea cliffs (Malloch 1971), but many ecological studies used *ad hoc* classifications, suitable for their objectives but not necessarily widely applicable. The need for a systematic treatment of all British vegetation using standard field and data analysis techniques in order to apply nature conservation objectives was recognised by Ratcliffe in 1966 during the preparation of a National Nature Conservation Review (Ratcliffe 1977). Birse (1980, 1984) extended the work of McVean & Ratcliffe to cover the Southern uplands and lowlands of Scotland, and the National Vegetation Classification (NVC) was developed culminating in the publication of the British plant communities (Rodwell 1991, 1992a, 1992b, 1994, 2000). The classic phytosociological accounts described above and other compatible work from sources such as postgraduate theses were incorporated into the NVC and new data were collected in an attempt to fill gaps.

The publication of British plant communities (Rodwell 1991, 1992a, 1992b, 1994, 2000) provides a classification covering most geographical areas and vegetation types. However there are some deficiencies of coverage and unexplained floristic variation (Rodwell 1992a, b). In general, upland vegetation is well described, with the exception of spring rills (M29), wet heath (M15, M16) and inaccessible cliff vegetation, but the uplands of South-west England have been given little detailed attention relative to other upland areas.

5.1.2 Vegetation description in the South-west uplands of Britain

Dartmoor is the largest and highest upland area in the South-west and it has received more attention from ecologists than Exmoor or Bodmin Moor. Despite this, the only comprehensive and detailed phytosociological account of Dartmoor vegetation is that of Ward *et al.* (1972). More recent phytosociological studies exist, such as an account of the vegetation of the Narrator catchment Kent & Wathern (1980) but they are restricted in geographical scope as is the little experimental work that has been undertaken (Weaver *et al.* 1998). Other recent and more widespread studies such as heather condition mapping (Wolton *et al.* 1994) and Environmentally Sensitive Area (ESA) monitoring are attempting to answer specific questions and therefore use *ad hoc* classifications inapplicable to the NVC. The Dartmoor-derived phytosociology of Ward (1972) is cited frequently by Rodwell (1992) in the context of the NVC when discussing vegetation that is restricted to South-west England and thus provides the basis of phytosociological knowledge pertaining to the South-west uplands.

Bodmin Moor is probably the least well-known upland area in Britain (Jones & Essex 1999), and although some data exist (Chapter Two), there has been no comprehensive detailed phytosociological survey of Bodmin Moor. In addition, there has been no attempt to relate vegetation composition to environmental gradients. This chapter fills these omissions providing a context for further work on vegetation dynamics, as well as providing an opportunity for hypothesis generation in relation to grazing management. It also allows critical assessment of the assumption currently prevalent in the literature, that Bodmin Moor is floristically similar to the lower altitude vegetation of Dartmoor.

5.1.3. Aims

The aim of this chapter is to produce a phytosociological classification of the plant communities present on Bodmin Moor, and to examine the relationships between species composition and a range of environmental factors including grazing management.

5.2 Methods

5.2.1 Sampling strategy

A detailed vegetation survey was undertaken on Bodmin Moor from June to September of 1999. A total of 312 samples were taken inside the boundary of the Bodmin Moor Natural Area. This was deemed a suitable sampling universe, as it contains all the semi-natural vegetation of Bodmin Moor that lies above 200m. Additionally, the Natural Area concept is used to deliver the UK Biodiversity Action Plan (BAP) and the Natural Area boundary largely conforms to the Less

Favoured Area (LFA), making it a useful boundary in terms of defining both land management objectives and change.

The sampling design employed stratification by gross vegetation type and geographical area. Attempts were made to sample heath, mire and grassland vegetation where they occurred on every area of common land, and on other large parcels of land consisting of semi-natural vegetation. This resulted in a comparatively even geographic coverage of the Natural Area. Sampling was not rigorously stratified in terms of existing Phase One habitat survey, as this was not sufficiently detailed (Chapter Two).

Within this stratification, sampling points were located in vegetation that was perceived as typical, in a standard phytosociological manner. Quadrats were also placed wherever there was an obvious change in the species composition and/or structure of the vegetation and also where obvious changes in management occurred such as fencelines or the boundaries of recent burning. The sampling method was therefore biased to record as much floristic variability as possible (Kent & Coker 1992).

5.2.2 Vegetation description

All species of higher plants, mosses and liverworts were identified in a total of 312 2 x 2 metre quadrats. Percentage cover of each species assessed by eye was deemed a suitable parameter of abundance as estimations are rapid and cause minimal damage to vegetation (Goldsmith *et al.* 1986, Kent & Coker 1992). Additionally the use of percentage cover is standard in British phytosociology. Species nomenclature follows Stace (1997) for higher plants, Smith (1978) for mosses and Watson (1981) for liverworts. The identifications of difficult taxa were confirmed using voucher material (M Newton).

5.2.3 Collection of environmental data

Rationale

Environmental data were collected on variables considered to be of relevance for plant growth in upland Britain. These variables can be classified as soil variables including nutrients, topographic modifications to climate and management variables.

Grazing together with burning and soil moisture are of primary importance in explaining the distribution of upland plant species in Britain (Ratcliffe 1977, Rodwell 1992a, b). Unfortunately it is extremely difficult to obtain accurate information on grazing and burning at an individual plant level. Thus estimates of perceived grazing intensity are used. Moisture measurements are less problematic but nethertheless only represent a "snapshot" and do not account for temporal variability.

Soil-related variables are an important group of factors affecting plant growth in upland habitats (Pearsall 1968, Fielding & Haworth 1999). The pH of a soil influences the availability of plant nutrients, *e.g.* phosphate solubility is reduced and the quantity of exchangeable calcium and magnesium cations decrease as pH increases (Rowell 1994). This has important ramifications for species composition, as different species have different requirements and tolerances for plant nutrients. Some species *e.g. Carex paniculata, Carex lepidocarpa* are restricted to sites of high pH with high nutrient availability (eutrophic), whilst others *e.g. Carex curta, Carex echinata,* inhabit acid sites with low nutrient availability (oligotrophic), but also low levels of competition from more nutrient demanding species (Jermy *et al.* 1982). Conductivity is a measure of soluble salt concentration expressed as the ability of a solution to conduct electricity (Rowell 1994). Conductivity is to some extent determined by cation concentration and is therefore related to pH. In the uplands soils with low pH tend to be low in nutrients and have low conductance but are often high in organic matter and soil moisture.

A third group of variables comprising of aspect, slope angle and altitude result in major local deviations to general climatic trends that are much more complex than previously thought (McClatchley 1996). Rainfall gradients are generally higher on West-facing slopes than on East-facing slopes because rainfall is derived primarily from Eastwards moving Atlantic depressions (Harrison 1997). This is compounded by slope angle, as West-facing slopes tend to be steeper and shorter than their Easterly counterparts (Fielding & Haworth1999). Thus, in general, the wettest upland areas are deep valleys with steep slopes that are exposed to wet Westerly air streams e.g. Dovey estuary in Wales (Taylor 1976) or the glens of Knoydart. Altitude is also of relevance as precipitation increases at altitude (Taylor 1976, McClatchley 1996). Temperature falls with height as a result of the steep adiabatic lapse rate experienced in Britain. Aspect is also important, North faces being colder than equivalent South-facing counterparts. Soil depth is of significance because shallow soils are more drought-prone than deep soils and on tors reflect lithspheric successions. Some species cannot survive until soil is of sufficient depth to support their rhizomes e.g. *Pteridium aquilinum* requires a soil depth of 0.3 metres, whilst *Vaccinium myrtillus* has rhizomes 0.15 – 0.2 metres below ground, rendering it much less vulnerable to burning than *Calluna vulgaris* (Grime 1992).

Topographic variables

At each sampling point, data were recorded on position, slope angle, altitude, soil depth, and aspect. Position was recorded as a six-figure grid reference. Slope angle was recorded using a Silva type 54 compass clinometer. Altitude was recorded with reference to the ordnance survey map (sheet SX). The nearest contour or spot height was used to provide a measure of altitude above vertical datum mean sea level at Newlyn (Transverse Mercator Projection, Airy Spheroid 1936 datum). Soil depths were determined using a two metre-long graduated metal probe marked in five cm increments. Maximum measureable soil depths were therefore two meters.

Grazing index

Data were collected in order to assist in the designation of subjective grazing pressure scores. Measurements of height were taken for *Molinia caerulea, Calluna vulgaris*, and *Ulex gallii* where present. Together with detailed information on stocking rates of common land and the accessibility of sample points to stock. A subjective five-point grazing pressure score was derived (1= heavily grazed sites, 5 = sites that are currently ungrazed or inaccessible to stock).

Orientation North

Aspect was initially recorded as degrees from North and then converted to orientation North. Orientation North, $A' = \text{cosine}\ (180° - A) + 1.1$ where A is the angle from North.This creates a scale from 0.1 (North) to 2.1 (South). Sites with no aspect *i.e.* flat sites were assigned a value of 1.1 (mean). East-West relationships were not considered, as any interaction with species composition would probably be too subtle to detect.

Soil Analysis

Soil samples were taken from a depth of 0-5 cm for subsequent laboratory analysis. During the floristic survey, soil samples were air-dried and stored prior to analysis for pH and conductivity. Supplementary fresh soil samples were collected during 2000 for further pedological analyses on soil nutrient status and soil moisture which require field fresh samples for accuracy (Rowell 1994).

Soil pH

The pH of a soil gives an indication of its overall chemical status, and provides a basis for comparison between samples Smith & Atkinson (1975). Soil pH (and conductivity) was assessed using air-dried soil collected over the course of the summer of 1999. A 1:2.5 dilution was used for the electrometric determination of pH as recommended by Allen *et al.* (1974), Smith & Atkinson (1975), Rowell (1994). Twenty five ml of de-ionized water were added to 10g of soil, along with two ml of 0.125M Calcium Chloride, stirred and allowed to stand for five minutes.

A Russell 640 pH meter with automatic temperature correction, calibrated with pH buffers 4.0 and 7.0 was used to record the pH values of the samples.

Soil conductivity

Conductivity gives a general indication of the electrolyte content of a soil. The conductivity of each sample was determined using a WTW LF96 microprocessor conductivity meter. The conductivity was recorded as micro siemans.

Soil Moisture

Soil moisture content gives an indication of the capacity of a soil to retain or lose water. Soil water content was assessed gravimetrically on field fresh samples collected in sealed double plastic bags. Approximately 10g samples of soil were passed through a 2mm sieve and dried in an oven at 105°C for 24 hours. The % soil moisture of each sample was calculated as a function of oven dried sample weight (Smith & Atkinson 1975, Rowell, 1994) so that:

$$\%\,\text{Soil moisture} = \frac{\text{Loss in soil weight (g)}}{\text{Weight of oven dried soil (g)}} \times 100$$

Soil organic matter

Soil organic matter is theoretically all the non-living organic material present in soil (Rowell 1994). However, measurement of organic matter also includes living material that passes through a 2mm sieve although this mass is small compared to the mass of dead material (Rowell 1994). Loss on ignition is generally accepted as an estimate of the amount of organic matter present in soil (Allen *et al.* 1974, Smith & Atkinson 1975, Rowell 1994), although this is really a measure of the combined content of organic matter, clay and sesquioxides (Rowell 1994). Oven-dried material from the soil moisture determination was placed in weighed porcelain crucibles. Crucibles and contents were weighed to four decimal places and fired in a muffle furnace at 500°C for eight hours. The samples were allowed to cool in a dessicator prior to reweighing. The % organic matter of each sample was calculated as a function of weight loss during ignition (Smith & Atkinson 1975, Rowell 1994) so that:

$$\%\,\text{Organic matter} = \frac{\text{weight loss (g)}}{\text{initial weight of sample (g)}} \times 100$$

Availability of plant nutrients

Determination of extract exchangeable and solution Sodium, Calcium, Magnesium and Potassium was undertaken using the routine procedure for British soils (Rowell 1994). Two grams of air-dried soil <2mm were mixed with 50ml of 1_M ammonium acetate for 30 minutes on a rotary mixer. The samples were stood for 24 hours prior to filtering through Whatman No. 1 filter paper into 50ml volumetric flasks. Each sample was made up to 50ml volume with 1_M ammonium acetate.

Sodium and potassium concentrations were determined using a CORNING 410C clinical flame photometer with separate filters. Working standards at 5mg/l and 10mg/l made up from standard solution for sodium and potassium were used to calibrate the instrument. Errors in the stability of the scale zero and 100% transmission were minimized through re-calibration of the instrument after every 20 readings.

Concentrations of exchangeable calcium and magnesium were determined using an Inductively Coupled Argon Plasma atomizer. Inductively Coupled Plasma atomizers yield significantly better quantitative analytical data than other emission sources such as flame atomizers (Skoog *et al.* 2000). For a complete discussion of their advantages and operation see Thompson & Walsh (1983) and Skoog *et al.* (2000).

5.2.4 Analysis of vegetation and environmental data

Introduction

Phytosociological classification of the plant communities present on Bodmin Moor was achieved by defining species assemblages using Two

Way Indicator Species Analysis (TWINSPAN) Hill (1979a), and Indicator species analysis Dufrene & Legendre (1997). The species assemblages were related to the plant communities of the NVC Rodwell (1992) using TABLEFIT Hill (1993), and the continuous nature of variation in community composition was described using Detrended Correspondence Analysis (DCA) (Hill 1979b). The relationships between species composition and environmental and management factors were explored using Canonical Correspondence Analysis (CCA) (Ter Braak 1986, 1988, 1994).

Classification

TWINSPAN is a polythetic divisive numerical classification method (Hill 1979a, Gauch & Whittaker 1981, Kent & Coker 1992). Various authors have criticized TWINSPAN. Like reciprocal averaging, on which it is based, TWINSPAN may perform badly when there is more than one important underlying gradient (Belbin & McDonald 1993, Dufrene & Legendre 1997, McCune & Mefford 1999). The cutting points along the dominant axis are arbitrary; instead of selecting large gaps in the data, sites that are very close in species composition may be separated (Belbin & McDonald 1993, Dufrene & Legendre 1997). It cannot effectively represent complex data sets in its one-dimensional framework (van Groenewould 1992, Belbin & McDonald 1993). Criteria for the stability of the reciprocal averaging solutions at the root of TWINSPAN can cause instability in the results depending on sample order (Oksanen & Minchin 1997). Increasing the number of iterations and applying strict criteria of tolerance in updated versions of TWINSPAN solve this problem (Oksanen & Minchin 1997); hence the use of TWINSPAN within Windows-based PC-ORD (McCune & Mefford 1999). Despite these problems TWINSPAN appears robust and is widely used (Kent & Coker 1992), especially in a British phytosociological context. This TWINSPAN analysis using the 312 quadrats was run using the standard cut levels of 0,2,5,10 and 20% to construct pseudospecies, as proposed by Hill (1979a). Eleven groups were defined subjectively using the third and subsequent divisions.

Indicator Species Analysis

Indicator species analysis (Dufrene & Legendre 1997) was used to identify indicator species for the species assemblages generated by TWINSPAN. Indicator species analysis combines information on the faithfulness of occurrence of a species in a particular group, with information on the concentration of species abundance in a particular group. The method produces indicator values for each species in each group, which are tested for statistical significance using a Monte Carlo test. As yet, there is no critique on the use of indicator species analysis in the literature, but once the technique becomes more widely disseminated this should follow.

TABLEFIT

TABLEFIT (Hill 1993) assigns samples to the vegetation types of the NVC (Rodwell 1992a, b), together with an estimate of goodness of fit (Table 5.1). The interpretation of TABLEFIT requires care. Categories of goodness of fit have subjective ratings (Hill 1993).

Table 5.1. Subjective assessment of TABLEFIT scores (Hill 1993).

Goodness of fit	Rating
80-100	Very good
70-79	Good
60-69	Fair
50-59	Poor
0-49	Very poor

However, treating even very good ratings as perfect fits to the NVC is not straightforward. The goodness of fit estimate is based on a mathematical function, which compares species presence and abundance in samples with NVC types. It takes no account of the ecology of the species. Another problem is that TABLEFIT is applied to individual samples and therefore takes no account of species fidelity. Additionally TABLEFIT ranks the top five communities, and often there is very little difference between ranks. In these cases, the sample is intermediate between two or more NVC types or has the dominant species of one community and the species composition of another (Hill 1993). The question then becomes, is the sample genuinely intermediate (and hence potentially a new community) or is it transitional between known communities? Some ecologists (Malloch, A. University of Lancaster. *Pers. comm.*, Legg 1992) express concern about squeezing vegetation into the NVC framework when it may not fit. Abstract NVC communities should not be set in concrete, when the concrete communities they purport to represent are at the very least plastic and best considered fluid (Legg 1992). The use of TABLEFIT and the NVC is therefore only valid for communication and for posing questions about the nature of the species assemblages. It is not intended to dogmatically identify samples as belonging to particular NVC communities.

Ordination

The definition and classification of species assemblages by TWINSPAN and indicator species analysis provides a framework for conceptualising communities. The current paradigm in community ecology recognises the utility of classification even when rather arbitrary dissections are imposed on essentially continuous community variation, and emphasises the complementary use of ordination and classification to explore this floristic variation (Goodall 1954, Whittaker 1962, Kent & Coker 1992, Jongman *et al.* 1995). Ordination was undertaken using Detrended Correspondence analysis (DCA) (Hill 1979b) and Canonical Correspondence analysis (CCA) (Ter Braak 1986, 1988, and 1994).

Detrended correspondence analysis (Hill 1979b, Hill and Gauch 1980) is an eigenanalysis ordination technique developed to correct the two major faults of Correspondence Analysis (CA) (Jongman *et al.* 1995). CA is a form of reciprocal averaging, where sample scores are calculated as a centroid of species scores, and *vica versa*, and iterations continue until there is no significant change. It is subject to the arch effect caused by nonlinearity of species response curves, and compression of axis ends (Palmer 2000). DCA is not subject to the arch effect or compression of the axis ends. The arch effect is nullified by dividing the first axis into segments, then setting the average score on the second axis within each segment to zero. The compression effect is negated by rescaling the axis to equalise the within-sample variance of species scores along the sample ordination axis (Hill and Gauch 1980, Kent & Coker 1992, Jongman *et al.* 1995). Although it is an improvement on CA and is widely used by ecologists, the use of DCA is critised by some. Reservations have been expressed about the desirability of detrending and rescaling all ordinations to fit a single model (Beals 1984; Ter Braak 1986, Minchin 1987). The underlying chi-square distance measure has also been been criticised (Clarke 1993). These factors account for the lack of robustness and erratic performance of DCA compared to Non Metric Multidimensional Scaling (NMS) (Minchin 1987). However, NMS is subject to other disadvantages including difficulties in detecting discontinuities and failing to find the best solution (minimum stress) because of intervening local minima (McCune & Mefford 1999). NMS can also be difficult to interpret if most of the variation is explained on the third or subsequent axes. DCA therefore remains popular, and provides an effective if approximate solution to the ordination problem for a unimodal response model in two or more dimensions (Jongman *et al.* 1995). As with TWINSPAN, earlier versions of DECORANA (Hill 1979b) were unstable because of lax criteria for stability and a problem in the rescaling algorithm (Oksanen and Minchin 1997), but these problems have been corrected in Windows-based PC-ORD.

Canonical correspondence analysis (ter Braak 1986, 1988, 1994) is an ordination technique in which the ordination of the samples and species (by reciprocal averaging) is constrained by a multiple regression on environmental variables. Thus CCA is best defined as direct gradient analysis (ter Braak 1986, Kent & Coker 1992). It is currently one of the most popular ordination techniques in community ecology (McCune & Mefford 1999), presumably because it allows direct heuristical investigation of species environment interactions. Some potential problems with CCA result from its similarity to indirect gradient analysis, while others relate to its direct nature and use of multiple regression. CCA is based on the chi-squared distance measure where samples are weighted according to their totals (Chardy *et al.* 1976; Minchin 1987), giving high weight to species whose total abundance in the data matrix is low, thus exaggerating the distinctiveness of samples containing several rare species (Faith *et al.* 1987, Minchin 1987). The use of chi-squared distance measures has also been criticised by Clarke (1993). As with TWINSPAN and DCA, early versions of CCA had problems with stability (Oksanen and Minchin 1997), but these problems have been corrected in Windows-based PC-ORD, and CANOCO. Problems specific to CCA relate, in part, to the multiple regression element of the CCA model, which in principle assumes normal distribution of individual environmental variables. Standard transformations (Kent & Coker 1992, Jongman *et al.* 1995) often fail to normalise environmental data, which are therefore left untransformed. Another potential problem with this direct ordination method is that, as the number of environmental variables increases relative to the number of samples, the results become increasingly dubious, even though an appearance of very strong relationships is inevitable (ter Braak & Prentice 1988, ter Braak & Smilauer 1998, McCune & Mefford 1999). Although CCA is subject to drawbacks, it remains a powerful ordination technique with the capacity to detect species-environment relationships, provided that it is used with care.

5.3 Results

5.3.1 Classification

A total of 135 species were found in 312 quadrats. Eleven species assemblages were defined subjectively using the third, and subsequent divisions of TWINSPAN. Mesotrophic grassland, *Pteridium aquilinum* dominated vegetation, acidic grassland and various heath and mire communities were all represented within these assemblages. The composition of the assemblages is detailed in Appendix 1 and summarized in Table 5.2. The assemblages cannot be defined with reference to single NVC communities, although some samples correspond well to the NVC (Table 5.3), whilst others are less easy to classify (Figure 5.1).

Table 5.2. Species with the highest three indicator species scores characterising the species assemblages (groups) derived by TWINSPAN, together with constancy and relative abundance (Dufrene & Legendre 1997). Monte Carlo test on observed maximum indicator species scores $p \leq 0.01$**, $0.01 < p < 0.05$ *.

Species group	Number of samples	Characterizing species	Indicator values (Dufrene & Legendre 1997)	% constancy by group	Relative abundance index (Dufrene & Legendre 1997)
1	10	*Holcus lanatus***	93	100	93
		*Lolium perenne***	60	60	100
		*Trifolium repens***	59	60	99
2	17	*Pseudoscleropodium purum***	52	71	74
		Pteridium aquilinum	50	82	61
		Agrostis capillaris	30	76	39
3	87	*Festuca ovina***	38	82	47
		*Rhytideadelphus squarrosus***	27	90	31
		*Potentilla erecta***	21	91	23
4	66	*Agrostis curtisii***	60	86	69
		*Ulex gallii***	31	77	40
		*Hypnum cupressiforme***	20	86	23
5	14	*Festuca rubra***	25	43	58
		Hypnum cupressiforme	18	79	23
		*Montia fontanum**	18	50	36
6	15	*Trichophorum cespitosus***	47	87	54
		*Dicranella heteromalla***	36	67	53
		Calluna vulgaris	18	93	19
7	32	*Vaccinium myrtillus***	65	97	68
		*Deschampsia flexuosa***	63	65	97
		*Calluna vulgaris***	33	90	37
8	26	*Juncus squarrosus***	34	69	49
		*Sphagnum capillifolium***	32	77	42
		Erica tetralix	18	81	22
9	13	*Narthecium ossifragum***	39	86	45
		*Erica tetralix***	25	93	26
		Sphagnum capillifolium	24	64	37

Table 5.2.Continued

		*Eriophorum angustifolium***	59	100	59
10	11	*Sphagnum inundatum***	39	50	77
		*Drosera rotundifolia***	39	80	48
		*Juncus acutiflorus***	63	64	99
11	21	*Juncus effusus***	48	91	53
		*Sphagnum recurvum***	40	64	62

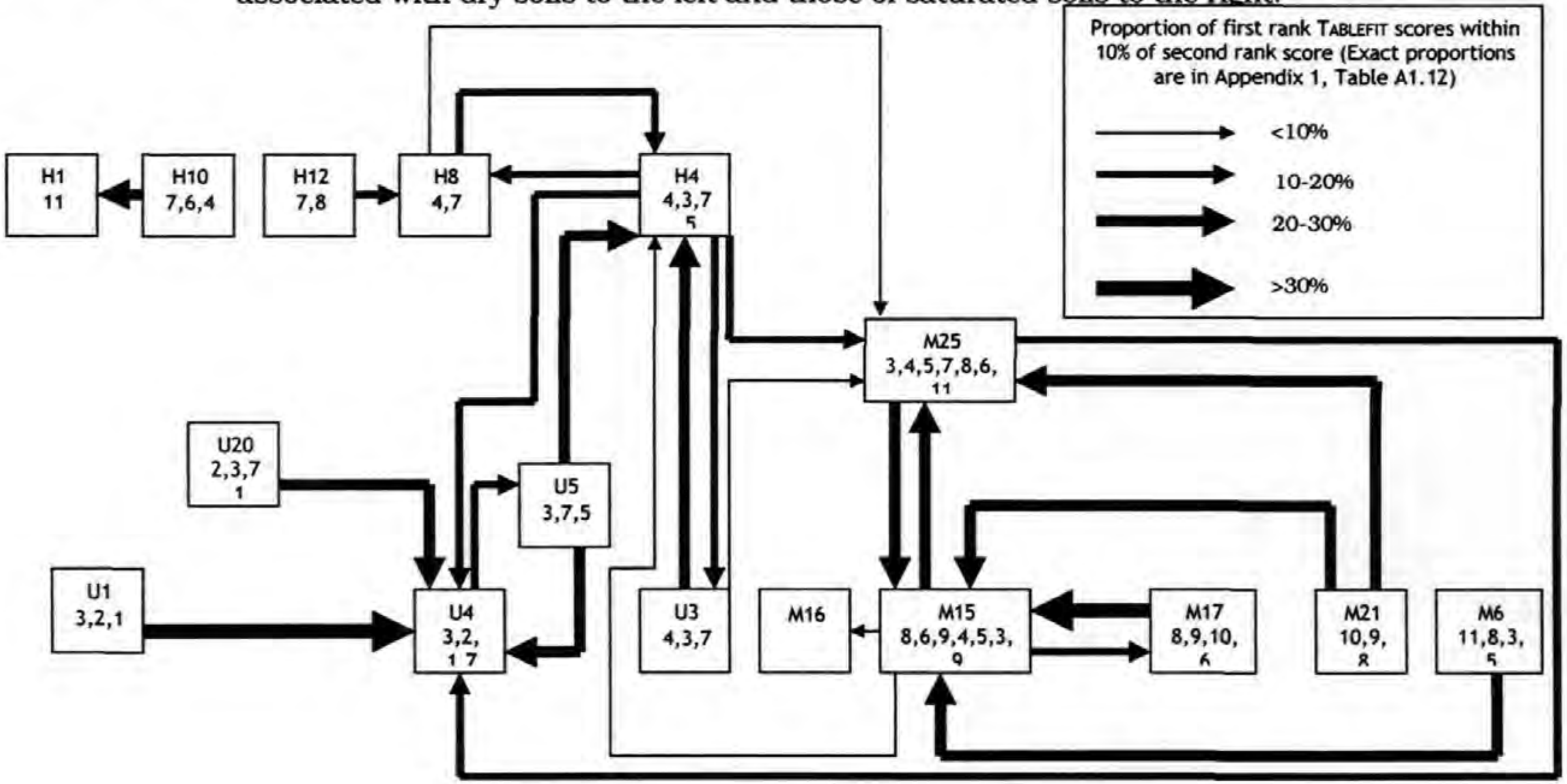
Table 5.3. Relationships between species assemblages and the National Vegetation Classification assessed by TABLEFIT.

First rank NVC community assigned by tablefit	Total number of samples	mean goodness of fit (Tablefit)	Standard deviation	Number of samples per TWINSPAN-derived species assemblage										
				1	2	3	4	5	6	7	8	9	10	11
U1 *Festuca ovina-Agrostis capillaris-Rumex acetosella* grassland	6	54.6	5.2	1	2	3								
U3 *Agrostis curtisii grassland*	34	73.7	9.2			7	26			1				
U4*Festuca ovina-Agrostis capillaris-Galium saxatile* grassland	49	69.2	10.4	4	4	40				1				
U5 *Nardus stricta-Galium saxatile* grassland	7	63.5	8.5			4		1		2				
U6 *Juncus squarrosus-Festuca ovina* grassland	3	48.6	17.5			2		1						
U16 *Luzula sylvatica-Vaccinium myrtillus* tall-herb community	1	48			1									
U20 *Pteridium aquilinum-Galium saxatile* community	12	76.5	13	1	7	2				2				
H1 *Calluna vulgaris-Festuca ovina* heath	1	31												1
H4 *Ulex gallii-Agrostis curtisii* heath	27	68.7	9.2			9	15	1		2				
H8 *Calluna vulgaris-Ulex gallii* heath	20	76	7.9				11			9				
H10 *Calluna vulgaris-Erica cinerea* heath	7	70.2	7.4				1		1	5				
H12 *Calluna vulgaris-Vaccinium myrtillus* heath	6	76.3	6							5	1			
H18 *Vaccinium myrtillus-Deschampsia flexuosa* heath	3	76.6	2.8							3				
H21 *Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* heath	1	77								1				
M1 *Sphagnum auriculatum* bog pool community	2	56.5	4.9										1	1
M2 *Sphagnum cuspidatum/recurvum* bog pool community	1	57											1	
M6 *Carex echinata-Sphagnum recurvum/auriculatum* mire	16	54.6	14			2		1			3			10

Table 5.3. Continued

M7 *Carex curta-Sphagnum russowii* mire	3	60	12.2										1	2
M15 *Scirpus cespitosus-Erica tetralix* wet heath	49	69.2	8.5			4	5	4	11		15	8	2	
M17 *Scirpus cespitosus-Eriophorum vaginatum* blanket mire	6	66.3	13						1		2	2	1	
M21 Narthecium ossifragum-Sphagnum papillosum valley mire	6	66.5	10.4								1	1	4	
M23 *Juncus effusus/acutiflorus-Galium palustre* rush pasture	2	61	19.7		1									1
M24 *Molinia caerulea-Cirsium dissectum* fen meadow	1	49												1
M25 *Molinia caerulea-Potentilla erecta* mire	37	65.5	11.9			12	8	6	2		4	3		2
M29 *Hypericum elodes-Potamogeton polygonifolius* soakway	4	45	12.1											4
W11 *Quercus petraea-Betula pubescens-Oxalis acetosella* woodland	1	14			1									
W23 *Ulex europaeus-Rubus fruticosus* scrub	1	69				1								
W25 Pteridium aquilinum-Rubus fruticosus underscrub	1	58			1									
MG6 *Lolium perenne-Cynosurus cristatus* grassland	3	70.3	1.1	3										
MG9 *Holcus lanatus-Deschampsia cespitosa* grassland	1	41		1										
CG10 *Festuca ovina-Agrostis capillaris-Thymus praecox* grassland	1	53				1								

Figure 5.1. The relationships between species assemblages, NVC communitities, physiographic features and land management on Bodmin Moor.Links indicate the occurrence of vegetation that is transitional in terms of the NVC framework. The diagram is laid out in relation to broad grazing and soil moisture reflecting the DCA axes. Assemblages found more commonly under low grazing pressure are at the top, those of high grazing pressure at the bottom, those associated with dry soils to the left and those of saturated soils to the right.



5.3.2 Ordination

The major environmental factors controlling the variation in species composition on Bodmin Moor were inferred from species ecology using DCA. Most of the variation in the data set was expressed along axis one which corresponded to a moisture gradient. Thus valley mire assemblages, mire samples, and mire species were found at the left hand end of the first axis, with drier samples and species at the right hand end (Figures 5.2, 5.3).

Other environmental variables did not directly correspond to any of the DCA axes. The ordination supported the existence of the vegetation types identified in the species assemblage tables, although there is a degree of continuity between assemblage types, particularly at the wet end of the environmental spectrum (Figure 5.2). The variation within species assemblage two was very high on the second axis as a result of outliers (Figures 5.2, 5.4). Removal of these outliers did not change the major patterns described above.

Figure 5.2. Quadrat ordination of vegetation data from Bodmin Moor using Detrended Correspondence Analysis.Coefficients of variation, axis one = 0.148, axis two =0.11.

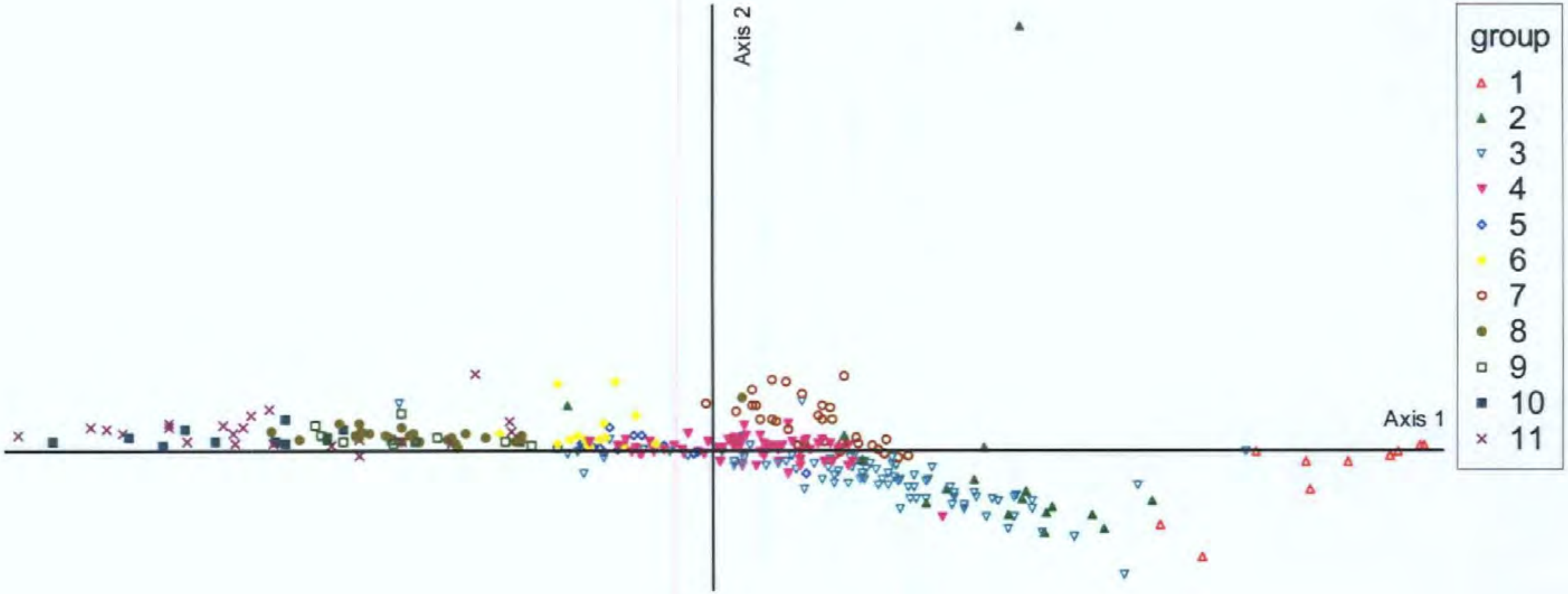


Figure 5.3. Species ordination (Detrended Correspondence Analysis) of vegetation data from Bodmin Moor. See Appendix 2 for full species names.

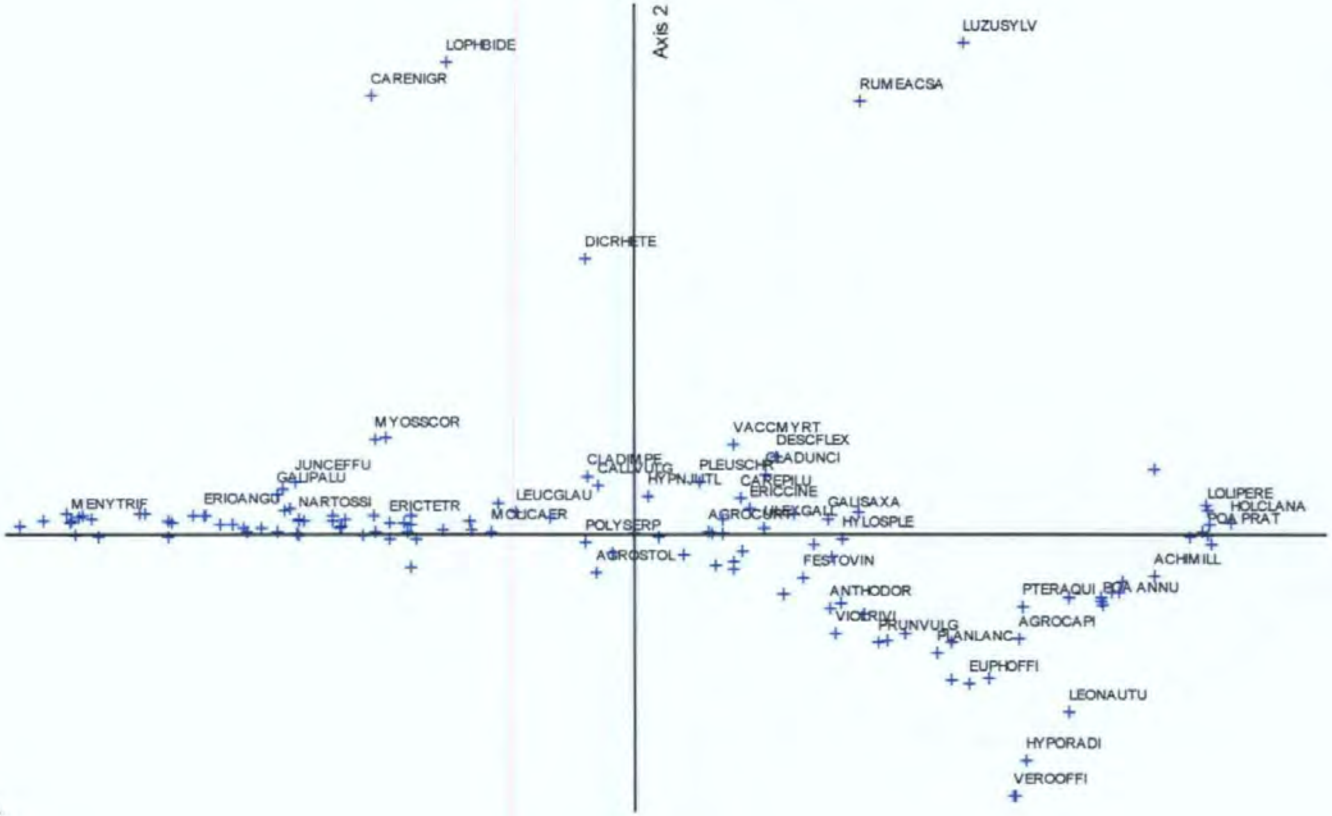
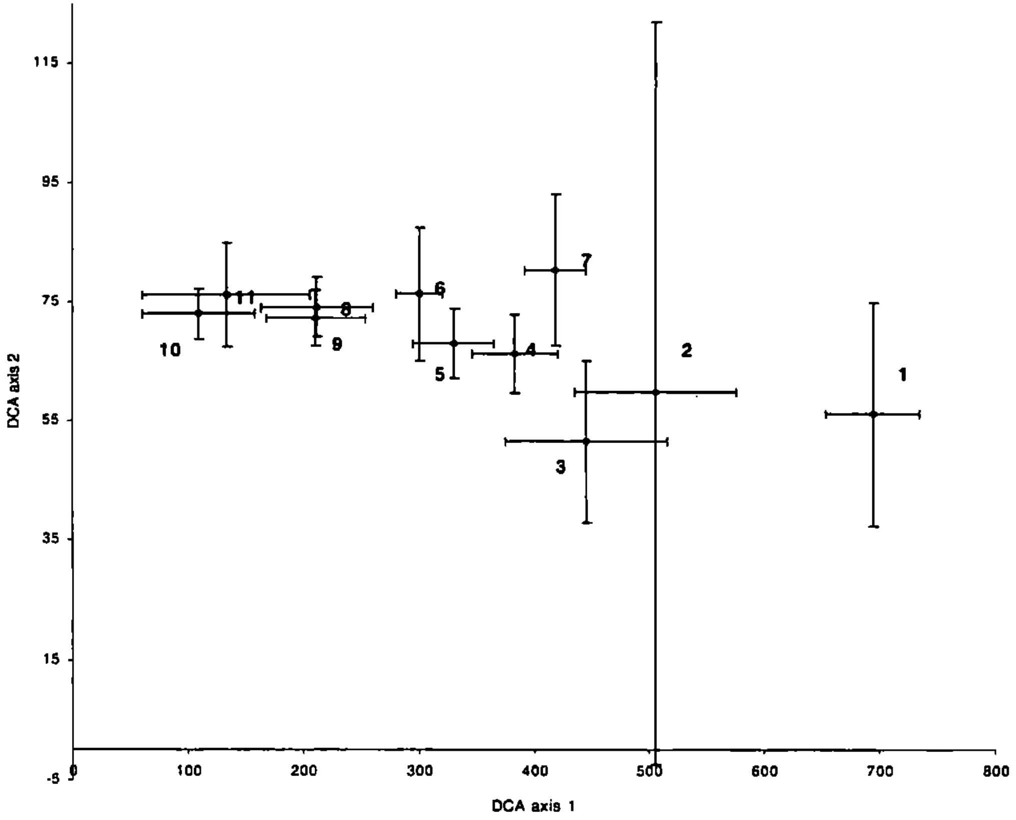


Figure 5.4. Detrended Correspondence analysis of the 11 groups derived from TWINSPAN (group centroids and standard deviations)



The quantitative relationship of the species assemblages to the environmental gradients on Bodmin Moor were approximated by CCA. The environmental variables measured in this study account for only 5.8% of the variability in floristic composition expressed on the first two CCA axes (Monte Carlo test $p < 0.01$).

The CCA diagram for samples indicated that axis one most closely corresponds to soil depth, which had the highest canonical coefficient (0.49) and inter-set correlation (0.81) for axis one (Figures 5.5, 5.6, Table 5.4). Soil moisture was also well correlated with axis one with the second highest canonical coefficient (0.4) and inter-set correlation (0.64) for axis one (Figures 5.5, 5.6, Table 5.4). Organic matter, pH, slope angle, altitude, sodium, conductivity, calcium, grazing, magnesium, potassium and orientation North had progressively lower inter-set correlations for axis one (Table 5.4). Axis two most closely corresponded to calcium and soil pH with high canonical coefficients (-0.48, -0.14 and inter-set correlations (-0.58, -0.26) respectively (Figures 5.5, 5.6, Table 5.4). However soil depth was also important on axis two with a high canonical coefficient (0.16) although this is not reflected in the inter-set correlations. Altitude, Orientation North, Grazing index, magnesium, Slope angle, Soil organic matter, potassium, sodium, soil depth, soil moisture and conductivity had progressively lower inter-set correlations with axis two (Table 5.4).

Figure 5.5. Quadrat ordination (CCA) of vegetation and environmental data from Bodmin Moor. Axis one, λ = 0.535, Axis two λ= 0.270

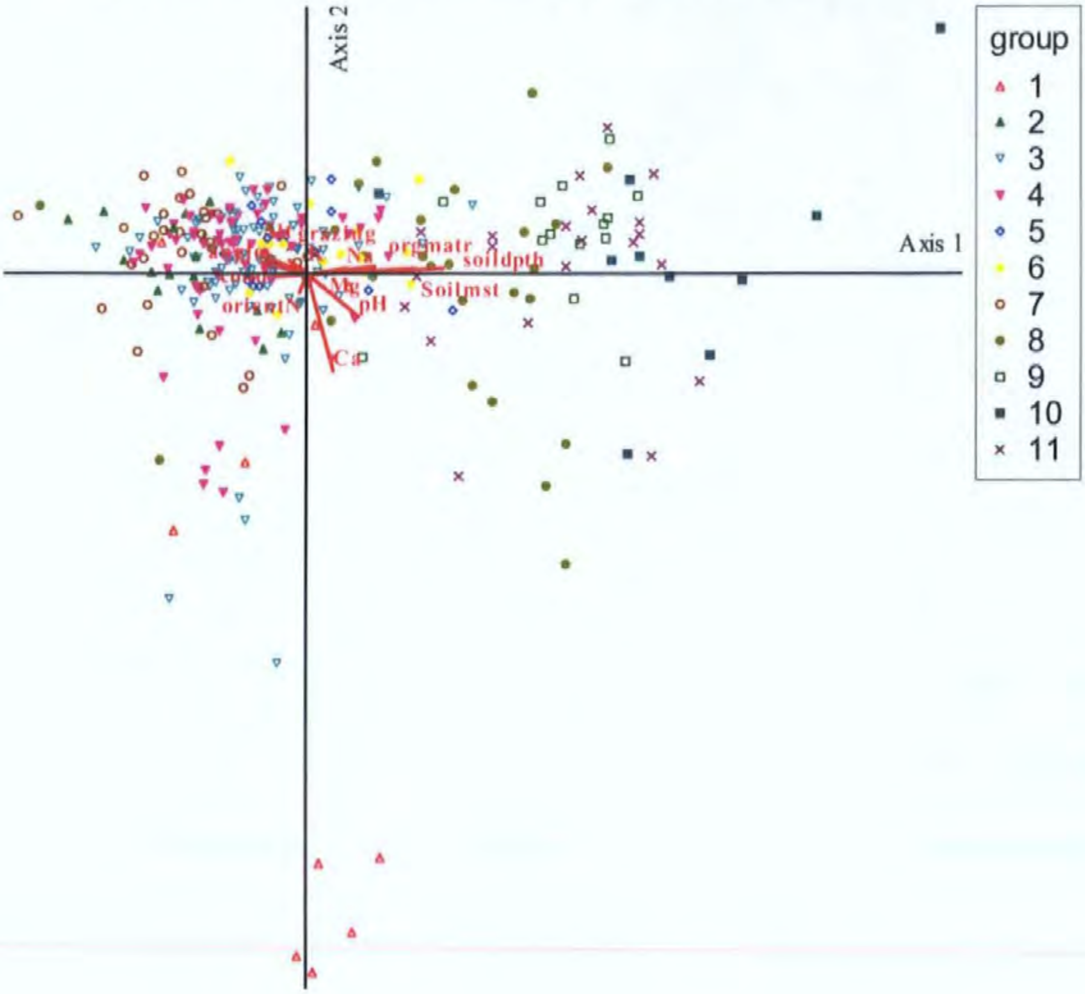


Figure 5.6. Quadrat ordination (CCA) of selected environmental variables displaying the magnitude of values. (a) Slope angle, (b) pH, (c) Grazing, (d) Soil Organic Matter, (e) Soil Moisture, (f) Soil Depth.

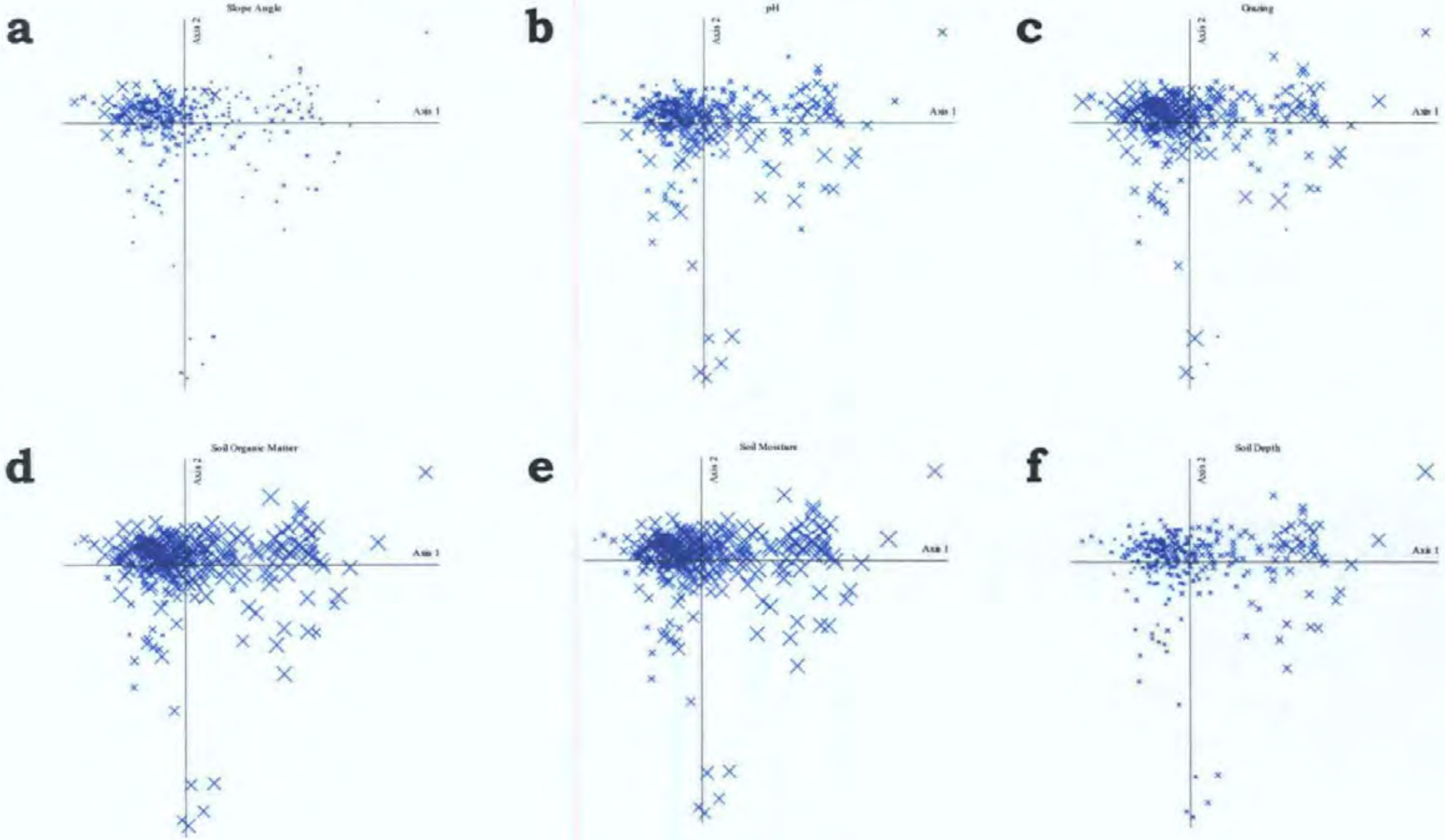


Table 5.4. Inter-set correlations of environmental variables with the first two axes of CCA.

Environmental variables	Inter-set Correlations of environmental variables with axes	
	Axis 1	Axis 2
Soil depth	0.807	0.032
Soil Moisture	0.644	0.031
Soil Organic matter	0.409	0.049
Soil pH	0.304	-0.256
Slope angle	-0.275	0.067
Altitude	-0.272	0.124
Sodium	0.236	0.033
Soil Conductivity	-0.194	-0.017
Calcium	0.157	-0.584
Grazing index	-0.110	0.089
Magnesium	0.104	-0.086
Potassium	-0.051	0.049
Orientation North	-0.050	-0.114

Every environmental variable had a variance inflation factor of <20 indicating that they all make unique contributions to the regression coefficient (ter Braak & Smilauer 1998) despite being correlated with each other (Table 5.5). Soil moisture and organic matter were strongly correlated ($r = 0.839$, $P < 0.01$), as were soil moisture and soil depth ($r = 0.543$, $p < 0.01$). Likewise there were significant correlations between pH and conductivity ($r = 0.226$, $p < 0.01$), and pH and calcium ($r = 0.27$, $p < 0.01$).

Species assemblages eight, nine, ten and eleven were characterised by deep wet soils high in organic matter (Figure 5.7). Species assemblage one was characterised by high pH and soil calcium levels. Species assemblages four, seven and ten were the least heavily grazed communities according to the grazing index.

Table 5.5. Correlation coefficients between ordination axes and environmental variables for all samples in Bodmin Moor TWINSPAN groups 1-11. Where: axis 1= Quadrat ordination axis 1, Axis 2= Quadrat ordination axis 2, Axis 3= Quadrat ordination axis 3, Alt= Altitude, OrienN= Orientation North, Angle= Slope angle, Grazing= Grazing index, Soildph= Soil depth, pH= pH, Cond= Conductivity, Soilmst= % Soil moisture, Soilorg= % Organic matter, K= Potassium, Ca= Calcium, Mg= Magnesium, Na= Sodium. N=312, r>0.021 is significant at p = 0.01(bold); 0.012 < r < 0.021 is significant at p = 0.05 (italic); r<0.012 not significant (two-tailed test).

	Axis 1	Axis 2	Axis 3	Soildph	Soilmst	Soilorg	pH	Angle	Alt	Na	Cond	Ca	Grazing	Mg	K
Soildph	**0.485**	**0.159**	**0.131**												
Soilmst	**0.392**	**-0.047**	**0.211**	**0.543**											
Soilorg	**-0.206**	**0.044**	**-0.359**	**0.365**	**0.839**										
pH	**0.080**	**-0.138**	**0.026**	**0.223**	**0.174**	**0.035**									
Angle	*-0.019*	-0.001	**0.238**	**-0.26**	**-0.153**	**-0.021**	**-0.112**								
Alt	**-0.038**	*0.017*	**0.147**	**-0.274**	**-0.118**	**-0.047**	**-0.039**	**0.309**							
Na	**0.109**	**0.055**	**0.021**	**0.076**	**0.311**	**0.327**	**0.085**	**-0.096**	*-0.02*						
Cond	**-0.053**	**0.045**	**0.03**	**-0.187**	**-0.187**	**-0.178**	**0.226**	**0.124**	**0.086**	0.000					
Ca	**-0.021**	**-0.48**	0.008	**0.151**	**0.099**	**0.098**	**0.270**	**-0.132**	**-0.236**	**0.124**	**0.025**				
Grazing	*0.012*	*0.014*	**-0.07**	**-0.104**	**-0.082**	**-0.021**	**-0.057**	**0.231**	-0.001	**-0.087**	**0.063**	**-0.125**			
Mg	**0.038**	**0.028**	**0.053**	**0.022**	**0.268**	**0.357**	**0.060**	**0.049**	0.003	**0.204**	**-0.023**	**0.248**	**-0.049**		
K	**-0.081**	**0.044**	**0.118**	**-0.089**	**0.15**	**0.221**	**-0.062**	*-0.013*	*0.02*	**0.402**	**0.037**	**0.073**	**0.05**	**0.304**	
OrienN	*0.013*	**-0.051**	**0.099**	**-0.066**	**-0.075**	**-0.052**	0.009	**-0.041**	**0.045**	**-0.047**	**-0.168**	**0.043**	**-0.06**	*-0.016*	**0.022**
	Standardized Canonical Coefficients			Raw Correlations among environmental variables											

Figure 5.7. Variation in environmental variables between species assemblages

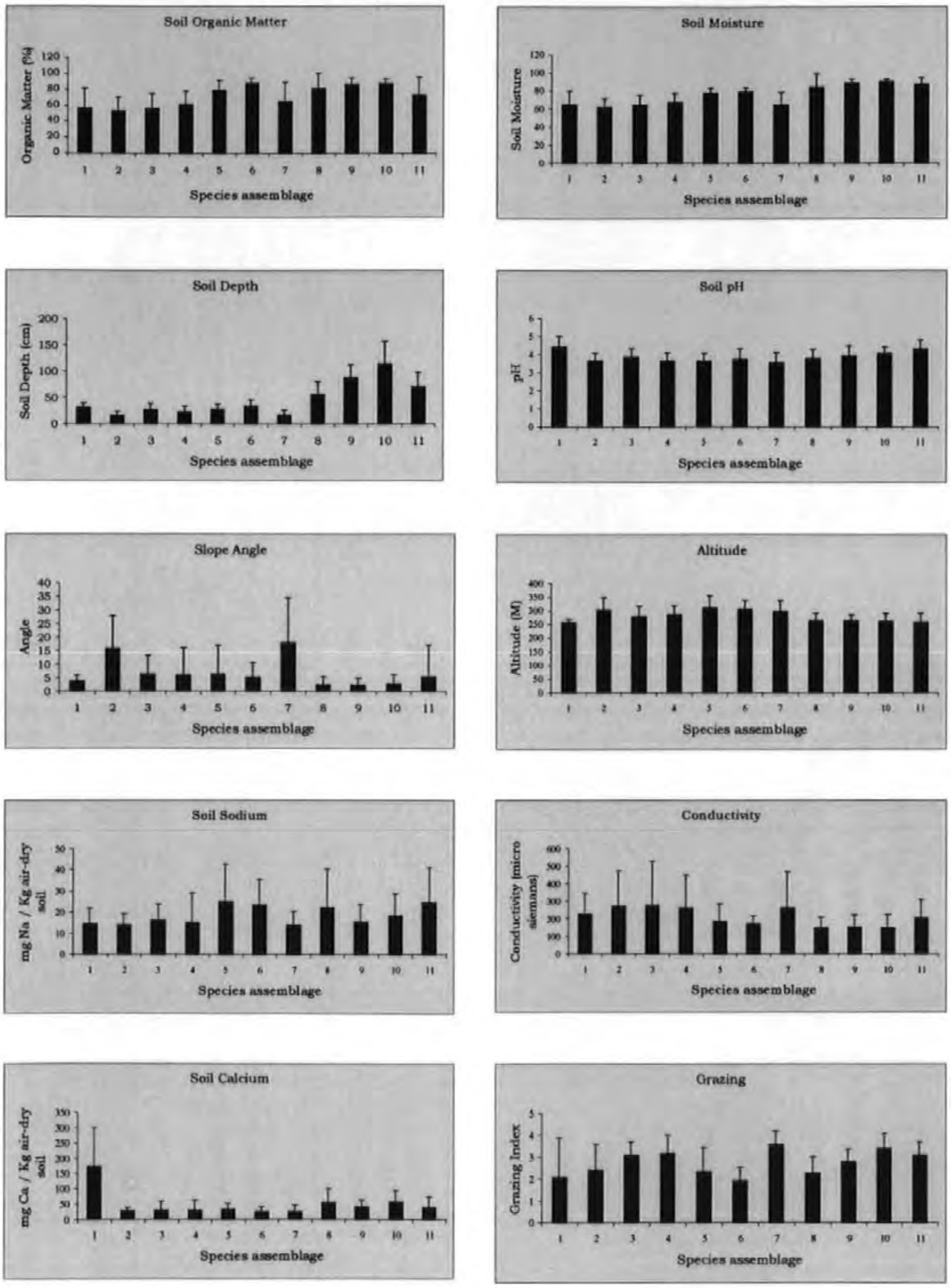
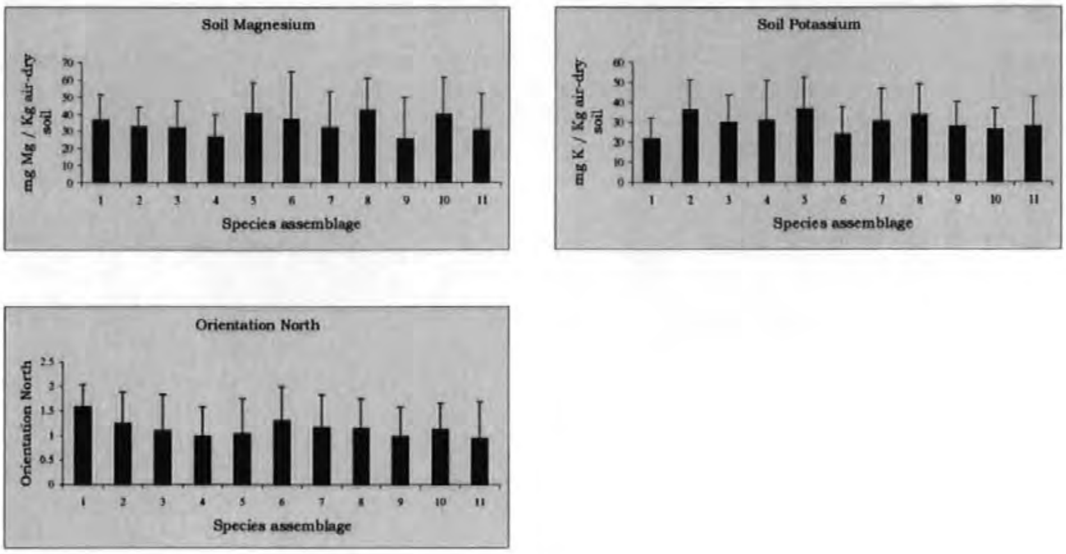


Figure 5.7. Continued.



5.4 Discussion

5.4.1 Interpretation of species assemblages

Introduction

Eleven plant community groups were defined subjectively using TWINSPAN. These groups were selected in order to facilitate ecological interpretation and to ensure that at least ten samples were present in each group. The results of the TWINSPAN analysis require careful interpretation. The endgroups produced must be checked against further information based on floristic and environmental information and experience, to reconcile apparent inconsistencies and ensure they make ecological sense (Malloch, A. University of Lancaster. *Pers. comm.*). Each endgroup is therefore considered as a species assemblage, or a number of related assemblages and interpreted in terms of the ecology of the characteristic species. TABLEFIT is used to compare samples to the NVC in order to assess the nature of the assemblage in community terms and these interpretations are linked to the available environmental data.

Assemblage one: mesotrophic grassland

Species assemblage one consisted of 10 samples characterised by the high constancy and abundance of *Holcus lanatus*, *Lolium perenne* and *Trifolium repens* (Table 5.2). These species are all C-S-R strategists (Grime *et al.* 1988, 1990), indicating that they are intermediate in terms of competitive ability, stress tolerance and disturbance resilience. Both *Lolium perenne* and *Trifolium repens* have high nutrient requirements and are very tolerant of grazing in contrast to *Holcus lanatus*, which is a later colonist during sward deterioration (Grime *et al.* 1990, Hill *et al.* 1999).

The samples can be classified as *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland or *Lolium perenne-Cynosurus cristatus grassland* in the NVC, although some samples had affinities with *Holcus lanatus-Deschampsia cespitosa* grassland, *Festuca ovina-Agrostis capillaris-Rumex acetosella* grassland or the *Pteridium aquilinum-Galium* *saxatile* community (Table 5.3). However, species assemblage one did not conform to any single National Vegetation Classification community.

Samples within *Lolium perenne-Cynosurus cristatus* grassland represent the most intensively grazed and fertilized swards, whilst the other end of the spectrum is represented by an upland, *Deschampsia cespitosa*-poor variant of *Holcus lanatus-Deschampsia cespitosa* grassland similar to a *Juncus effusus* poor *Holcus lanatus-Juncus effusus* rush pasture. The *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland samples represent mesotrophic intermediates within this continuum. The *Holcus lanatus-Trifolium repens* sub-community contained *Holcus lanatus, Achillea millefolium, Trifolium repens, Cerastium fontanum, Poa pratensis*, and *Cynosurus cristatus* (Rodwell 1992b) all of which are characterising species of species assemblage one (Table 5.2, Appendix 1). *Lolium perenne* is frequently topsown into this community in the South-west (Rodwell 1992b). Assemblage one has no equivalent in the Bodmin Moor surveys of Drage (1981) or the Nature Conservancy Council (NCC 1986), which were concerned exclusively with semi-natural vegetation. However, the assemblage has affinities with group one of Kent & Wathern (1980), which represents formerly enclosed grassland on Dartmoor. On Bodmin Moor, *Festuca ovina* is more abundant, and there is no evidence of the top sowing of *Lolium perenne* in the Dartmoor variant of this vegetation type.

Overall, the samples in assemblage one represented sown swards in varying degrees of deintensification, on the upland fringes of Bodmin Moor. This interpretation is consistent with the ecology of the characteristic species and the environmental data. The samples in assemblage one had the highest mean pH and soil calcium levels of all the assemblages (Figure 5.7). Surprisingly, the availability of other measured plant nutrients was not particularly high in assemblage one, although it was one of the more heavily grazed assemblages as expected (Figure 5.7).

Assemblage two: *Pteridium aquilinum*-dominated vegetation

Species assemblage two comprised of 17 samples characterised by the high constancy and abundance of *Pteridium aquilinum* and *Pseudoscleropodium purum* (Table 5.1). *Pteridium aquilinum* is a competitor, and in the context of the British flora, is a uniquely competitive and aggressively invasive fern (Grime *et al.* 1988, 1990). It is perceived to be spreading in the UK and is generally considered as a problem particularly in the uplands (Marrs & Pakeman 1995). *Pseudoscleropodium purum* is found in association with other bryophytes in a range of heathland and grassland communities (Watson 1981). *Pteridium aquilinum* is generally not eaten by stock, although cattle can prevent its establishment by breaking down and trampling fronds (Pearsall 1968).

Pteridium aquilinum occurs in 36 communities of the National Vegetation Classification but it is dominant only in the *Pteridium aquilinum-Galium saxatile* and *Pteridium aquilinum-Rubus fruticosus* underscrub communities (Rodwell 1992b). The samples in species assemblage two fall into these categories, although samples are also classified as *Festuca ovina-Agrostis capillaris-Rumex acetosella* grassland, *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, *Luzula sylvatica-Vaccinium myrtillus* tall herb community, *Juncus effusus-Galium palustre* rush pasture, and *Quercus petraea-Betula pubescens-Oxalis acetosella* woodland (Table 5.3). The species with significant indicator value in assemblage two (Table 5.2, Appendix 1) were all present in the *Pteridium aquilinum-Galium saxatile* community (Rodwell 1992b), except *Rubus fruticosus* and *Sedum album*. *Rubus fruticosus* has low constancy, and is found in the *Pteridium aquilinum-Rubus fruticosus* underscrub community (Rodwell 1992b). *Sedum album* colonises stony ground (Stace 1997) and is found around tors on Bodmin Moor. The tors also provide a focus for *Pteridium aquilinum*-dominated vegetation as the sloping ground allows free movement of air and water through the soil profile, which is important for the optimal growth of *Pteridium aquilinum*.

Seven of the samples that make up species assemblage two are classified as *Pteridium aquilinum-Galium saxatile* community whilst four are classified as *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland (Table 5.2). This may be a reflection of the dominance of *Pteridium aquilinum*. Where the species has high cover, it is classified as *Pteridium aquilinum-Galium saxatile* community. Conversely where the cover is low it is classified as the floristically similar *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland. This is also manifest in the second rank goodness of fit assigned by TABLEFIT (Figure 5.1). 42% of the samples classified as *Pteridium aquilinum-Galium saxatile* community were classified as *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, within ten percent goodness of fit (Figure 5.1, Appendix 1). Species assemblage two therefore represents a range of vegetation on tors where *Pteridium aquilinum* is at least present, and often dominant. The assemblage is related to the *Agrostis tenuis-Agrostis canina* with *Pteridium* community (Drage 1981) and the *Pteridium aquilinum* communities of the Nature Conservancy Council (NCC 1986), which are also centred on tors. However, *Pseudoscleropodium purum* is only occasional in the Drage (1981) community. The assemblage also bears close affinity with group D of Ward *et al.*(1972) and group two of Kent & Wathern (1980) on Dartmoor. These Dartmoor vegetation types are generally very similar in species composition to assemblage two, although *Vaccinium myrtillus* was not constant in the Bodmin Moor assemblage. Assemblage two had the lowest mean soil moisture, together with a high mean slope angle (Figure 5.7), which fit the requirement of *Pteridium aquilinum* for well-drained and aerated soils.

Assemblage three: acidic grassland

Species assemblage three contained of 87 samples. It was characterised by high constancy of *Festuca ovina, Rhytideadelphus squarrosus* and *Potentilla erecta*; and by high relative abundance of *Euphrasia officinalis* (Table 5.2, Appendix 1). *Festuca ovina* is an S strategist, *Potentilla erecta* is an S-CSR strategist, and *Euphrasia officinalis* is an S-R strategist

(Grime *et al.* 1988, 1990). Thus the characteristic species of the assemblage tend towards stress tolerance. These three species are found on infertile grazing land throughout Britain, and both *Potentilla erecta* and *Euphrasia officinalis* are unpalatable to stock, whilst *Festuca ovina* is less palatable than other graminoid species with which it is associated, although it remains an important food plant for sheep (Grime *et al.* 1990).

The samples in species assemblage three are mostly classified as *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, although some are *Molinia caerulea-Potentilla erecta* mire, *Ulex gallii-Agrostis curtisii* heath, *Agrostis curtisii* grassland or other communities (Table 5.3).

Festuca ovina, Rhytideadelphus squarrosus and *Potentilla erecta* are all found at high constancy in *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland (Rodwell 1992b), although *Rhytideadelphus squarrosus* attains higher constancy in assemblage three (Table 5.2). *Euphrasia officinalis* and *Danthonia decumbens* are also present at lower constancy, both in *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland and in assemblage three. *Hypnum cupressiforme* and *Molinia caerulea* are present in assemblage three and *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland. However, *Molinia caerulea* was at much higher constancy in species assemblage three, and shows affinity with *Molinia caerulea-Potentilla erecta* mire. The species with significant indicator values in group three (Table 5.2) are present along with *Molinia caerulea* and *Hypnum cupressiforme* in both *Ulex gallii-Agrostis curtisii* heath and *Agrostis curtisii* grassland, except *Euphrasia officinalis.*

Although Bodmin Moor has granite bedrock, there are some areas of base enrichment. Species assemblage three included some species that show an indication of base richness such as *Hieracium pilosella, Leontodon autumnalis, Plantago* sp., and *Prunella vulgaris* (Appendix 1). One sample in assemblage three is classified as *Festuca ovina-Agrostis* *capillaris-Thymus praecox* grassland (Table 5.3) representing the extreme end of this base enrichment on drier podzolic soils with some degree of surface flushing. Thus species assemblage three does not conform to any single NVC type.

Species assemblage three represents a form of *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland with *Molinia caerulea* present at low abundance but high constancy. The assemblage also includes vegetation that is either transitional to *Molinia caerulea-Potentilla erecta* mire, *Ulex gallii-Agrostis curtisii* heath, and *Agrostis curtisii* grassland or forms some type(s) of intermediate variant of these communities. This interpretation is supported by the second rank TABLEFIT communities, which show some problems of differentiation between these communities (Figure 5.1), although *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland is only directly confused with *Nardus stricta-Galium saxatile* grassland (Appendix 1).

Assemblage three is similar to species rich *Agrostis* – *Festuca* grassland (Drage 1981); particularly the base-enriched samples. It also has affinities with *Agrostis canina* – *Agrostis tenuis* grassland without *Pteridium* cover (Drage 1981), and the samples containing *Nardus stricta* are unsurprisingly related to *Nardus stricta* grassland (Drage 1981), although with lesser heathland components. The assemblage is represented by various categories of *Agrostis* – *Festuca* grassland in the Nature Conservancy Council survey (NCC 1986), which is abundant on the North Moor and often annotated with *M.C.* indicating that *Molinia caerulea* is present. The assemblage has some affinity with group C of Ward *et al.* (1972) on Dartmoor, although dwarf-shrub species are absent and *Molinia caerulea* has high constancy. This could reflect variation in management practices or climatic differences. The assemblage bears no close relationship to the vegetation of the Narrator catchment (Kent & Wathern 1980).

Assemblage four: *Agrostis curtisii* grassland / *Ulex gallii-Agrostis curtisii* grass heath / *Ulex gallii* heath

There were 66 samples in Species assemblage four with *Agrostis curtisii* at high constancy and abundance. The other species with significant indicator values (*Ulex gallii*, *Hypnum cupressiforme*) have high relative abundance but low constancy (Table 5.2, Appendix 1). *Agrostis curtisii* is confined to the South-west of Britain. It occurs on podzolic soils, kept moist by high rainfall rather than drainage impedance (Ivimey-Cook 1959); and as with *Ulex gallii*, burning and grazing can significantly affect its distribution.

A total of 40% of samples in assemblage four are classified as *Agrostis curtisii* grassland, with the remainder classified as *Ulex gallii-Agrostis curtisii* heath (23%), *Calluna vulgaris-Ulex gallii* heath (16%), *Molinia caerulea-Potentilla erecta* mire (12%) and *Scirpus cespitosus-Erica tetralix* wet heath (8%). All the characterising species of assemblage four are present in *Agrostis curtisii* grassland except *Eurhynchium praelongum*. However, both *Ulex gallii* and *Molinia caerulea* are present with higher constancy.

Other samples within assemblage four were classified as *Molinia caerulea-Potentilla erecta* mire or *Scirpus cespitosus-Erica tetralix* wet heath and represent a transition to wetter ground, recognised throughout the high ground of the South-west peninsula (Rodwell 1992a). The *Agrostis curtisii* grassland is a treatment derived replacement for *Ulex gallii-Agrostis curtisii* heath (Rodwell 1992a). The heath samples in assemblage four represent samples with a different history of burning, grazing and disturbance, with a higher relative abundance of the sub shrub component. *Ulex gallii-Agrostis curtisii* heath and *Calluna vulgaris-Ulex gallii* heath both occur in this assemblage, with *Calluna vulgaris-Ulex gallii* heath representing transition to drier ground (Rodwell 1992a).

Species assemblage four consists largely of *Agrostis curtisii* grassland, *Ulex gallii-Agrostis curtisii* heath, and *Molinia caerulea-Potentilla erecta* mire. There are problems distinguishing these communities in the South-west (Ward *et al.* 1972, Rodwell 1992a, b), as grazing can result in every graduation between dense heath and continuous grassy sward. This is reflected in the second rank NVC communities assigned by TABLEFIT (Figure 5.1), and their inclusion together in species assemblage four.

The samples in assemblage four fall within *Agrostis curtisii* -*Ulex gallii* – *Molinia* South-west heath (Drage 1981). This represents the heathland end of the assemblage four transition, whilst *Molinia caerulea* species-poor-grassland (Drage 1981) is the closest community referable to the grassier end. However, *Molinia caerulea*-species-poor grassland (Drage 1981) contains much less *Agrostis curtisii* than assemblage four. *Agrostis curtisii* is only found abundantly in association with heathland and *Molinia caerulea* – *Calluna vulgaris* mire in the Drage (1981) survey. Assemblage four vegetation is represented by *Agrostis curtisii* –*Calluna vulgaris* grassland in the Nature Conservancy Council survey (NCC 1986). It is rare relative to other grassland types and often occurs in mosaics particularly with *Agrostis* – *Festuca* grassland. Assemblage four is similar to group six of Kent & Wathern (1980) on Dartmoor, although *Ulex gallii* replaces *Vaccinium myrtillus*. It is also represents facets of groups H and I (Ward *et al.* 1972). Although assemblage four represents a continuum from heathland to grassland vegetation, this is not reflected in the measured environmental variables. Assemblage four is one of the least heavily grazed assemblages and does not have a particularly large standard deviation relative to other assemblages (Figure 5.7). This suggests that the *Agrostis curtisii* grassland within assemblage four is not grazed more heavily than *Ulex gallii* heath in contrast to the literature (Rodwell 1992a, b). It is also interesting to note that *Ulex gallii* heath / *Ulex gallii-Agrostis curtisii* grass heath / *Agrostis curtisii* grassland and unimproved acidic grassland had very similar values for all measured environmental variables including grazing (Figure 5.7). Thus neither different habitat requirements nor management, as measured by the grazing index, segregate these communities.

Assemblage five: flushed rill vegetation

Species assemblage five consisted of 14 samples. The species with significant indicator values in group five were *Festuca rubra* and *Montia fontanum* (Table 5.2, Appendix 1). *Festuca rubra* is a C-S-R strategist that is particularly common on base-rich ground (Grime *et al.* 1988, 1990), while *Montia fontanum* is a species of base and nutrient-poor rills, typically found in association with *Sphagnum* sp. and *Ranunculus omiophyllus* (Rodwell 1992a).

It is possible that this species assemblage represents areas of surface flushing over acid wet peats, explaing the presence of calcicoles and calcifuges. However, assemblage five has the lowest mean pH, suggesting that base enrichment via surface flushing is unlikely (Figure 5.7), at least when the soil samples were collected. Taxonomic confusion between *F. rubra* and *F. ovina* could explain this result as *F. ovina* is more tolerant of low pH than *F. rubra.*

The samples in assemblage five are classified as *Molinia caerulea-Potentilla erecta* mire (six samples) *Scirpus cespitosus-Erica tetralix* wet heath (four samples), *Carex echinata-Sphagnum recurvum/auriculatum* mire, *Ulex gallii-Agrostis curtisii* heath, *Juncus squarrosus-Festuca ovina* grassland, and *Nardus stricta-Galium saxatile* grassland. This is consistent with the habitat requirements of *Montia fontanum*, which can subsist in trickles of water on dry peats, where *Ulex gallii-Agrostis curtisii* heath and *Nardus stricta-Galium saxatile* grassland develop, as well as on the deeper wet peats favoured by *Molinia caerulea-Potentilla erecta* mire and *Scirpus cespitosus-Erica tetralix* wet heath (Rodwell 1992a). Assemblage five therefore represents vegetation possibly subject to flushing, in habitats that generally experience some drainage impedance, and as *Montia fontanum* has a constancy of only 50%, the assemblage probably represents samples of vegetation from the communities listed above that are only subject to flushing intermittently.

Montia fontanum is not recorded by Drage (1981) and it is therefore difficult to place assemblage five into the context of the Drage (1981) survey, except to say that it is represented by wet vegetation such as the *Carex* – moss mires (Drage 1981) in a complex mosaic of wet heath and bog pool vegetation, in extensive soligenous areas. The NVC communities assigned to assemblage five by TABLEFIT are extensive on the North Moor except for the *Juncus squarrosus-Festuca ovina* community. This is unrecorded on the North moor (NCC 1986), although it is manifest on the South moor as *Juncus squarrosus* – species poor grassland (Drage 1981). On Dartmoor, the assemblage has floristic affinities with a subset of group eight and remarkably similar mean values for slope angle, soil depth and soil moisture (Kent & Wathern 1980). This has affinities with group B of Ward *et al.* (1972), but assemblage five represents a much narrower vegetation type.

Assemblage six : *Trichophorum cespitosum-Erica tetralix* wet heath

Species assemblage six comprised of 15 samples and was characterised by high constancy and relative abundance of *Trichophorum cespitosum* and *Dicranella hetromalla. Erica tetralix, Calluna vulgaris* and *Molinia caerulea* are also present at very high constancy (Table 5.2, Appendix 1). These species are tolerant of an intermediate soil moisture regime and are able to thrive with the reduced competition from plants better adapted to the extremes (Rutter 1955, Bannister 1966, and Gimingham 1972).

The samples in assemblage six are classified primarily as *Scirpus cespitosus-Erica tetralix* wet heath although some samples are classified as *Molinia caerulea-Potentilla erecta* mire, *Scirpus cespitosus-Eriophorum vaginatum* mire, or *Calluna vulgaris-Erica cinerea* heath (Table 5.3). This probably reflects variation in soil moisture regime, although it has been suggested that *Scirpus cespitosus-Erica tetralix* wet heath may represent a seral intermediate between blanket mire and dry heath (Rodwell

1992a). This is reflected in the second rank TABLEFIT scores (Figure 5.1), which also classify assemblage six samples as *Erica tetralix-Sphagnum compactum* wet heath. However, species assemblage six bears close affinity with *Scirpus cespitosus-Erica tetralix* wet heath. The presence of *Montia fontanum* suggests that drainage runnels may be present, and *Dicranella heteromalla* replaces *Dicranum scoparium*, due its abundance in the South-west of England.

Assemblage six is intermediate between *Trichophorum caespitosum* – pure sward (Drage 1981) and *Trichophorum caespitosum* – *Calluna vulgaris* mire (Drage 1981). It has a higher abundance of *Molinia caerulea* and lower abundance of *Trichophorum caespitosum* than the *Trichophorum caespitosum* – pure sward (Drage 1981) but fewer blanket bog species than *Trichophorum caespitosum* – *Calluna vulgaris* mire (Drage 1981). On Dartmoor, the assemblage is similar to a subset of group eight (Kent & Wathern 1980) and also group B (Ward *et al.* 1972), but is best considered as a subtle variant of *Scirpus cespitosus-Erica tetralix* wet heath (Rodwell 1992a). Assemblage six had the highest mean soil organic matter and lowest mean grazing index score (Figure 5.7), indicating that it is the most heavily grazed community. This was unexpected, as some of the drier communities, such as assemblages three and four are more productive. It is possible that this reflects confusion between burning and grazing, as burning of wet heath on Bodmin Moor is not uncommon.

Assemblage seven: *Vaccinium myrtillus- Calluna vulgaris* heath

Species assemblage seven consisted of 32 samples. It was characterised by high constancy and relative abundance of *Vaccinium myrtillus* and *Deschampsia flexuosa* (Table 5.2). Both species are S-C strategists, long-lived, slow growing and shade-tolerant (Grime *et al.* 1988, 1990). Other species with significant indicator scores are *Calluna vulgaris*, *Erica cinerea*, *Pleurozium shreberi* and *Cladonia* sp. (Table 5.2, Appendix 1).

The samples in assemblage seven are classified primarily as heathland types with some samples representing grassland. The heathland samples are classified as *Calluna vulgaris-Ulex gallii* heath (28%), *Calluna vulgaris-Vaccinium myrtillus* heath (16%), *Calluna vulgaris-Erica cinerea* heath (16%), *Vaccinium myrtillus-Deschampsia flexuosa* heath (9%), *Ulex gallii-Agrostis curtisii* heath (6%) and *Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* heath (3%).

Whilst there are clear affinities between assemblage seven and *Calluna vulgaris-Ulex gallii* heath, particularly the *Vaccinium myrtillus* sub-community, the two are by no means synonymous. *Ulex gallii* is not an indicator species of assemblage seven (Table 5.2), despite having very high constancy in *Calluna vulgaris-Ulex gallii* heath (Rodwell 1992a). The constancy of *Pleurozium shreberi* and *Cladonia impexa* is far higher in assemblage seven (Table 5.2), whilst *Erica cinerea* is far lower, than in *Calluna vulgaris-Ulex gallii* heath (Rodwell 1992a). The constant species of *Calluna vulgaris-Vaccinium myrtillus* heath are all characterising species of assemblage seven, except *Dicranum scoparium*, although *Hypnum jutlandicum* is present at lower constancy.

The other heathland types have species represented in assemblage seven, but mostly they are at low constancy, suggesting that some samples may be transitional in the direction of these communities, although the high TABLEFIT values (Table 5.3) indicate good fit to the NVC where these samples do occur. The second rank TABLEFIT scores (Figure 5.1, Appendix 1) indicate a degree of similarity between these communities, although *Vaccinium myrtillus-Deschampsia flexuosa* heath and *Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* heath are excluded, as they are replicated in less than six samples.

Assemblage seven is similar to *Vaccinium myrtillus* heath (Drage 1981), sharing high abundance and constancy of *Vaccinium myrtillus*, *Calluna vulgaris* and *Deschampsia flexuosa*, and the presence of *Pleurozium schreberi* and *Cladonia* sp. However, *Erica cinerea* is restricted to *Calluna* dry heath (Drage 1981). These communities can be separated by the presence of *Erica cinerea* and *Pleurozium shreberi*, and by the relative abundance and constancy of *Calluna vulgaris*, *Vaccinium myrtillus* and *Deschampsia flexuosa* but they are doubtfully distinct in ecological terms. On Dartmoor, the assemblage has affinities with group five (Kent & Wathern 1980), although Kent & Wathern (1980) do not report the high constancy of *Deschampsia flexuosa* from the Dartmoor vegetation. Group E (Ward *et al.* 1972) includes *Deschampsia flexuosa* and intergrades with group G. Thus assemblage seven on Bodmin Moor most closely resembles vegetation transitional between groups E and G on Dartmoor.

Assemblage seven represents heathland vegetation on tors. In general, the samples represent a hybrid between *Calluna vulgaris-Ulex gallii* heath and the more Northern boreal *Calluna vulgaris-Vaccinium myrtillus* heath. This is suprising in view of the oceanic influence on Bodmin Moor, as is the presence of samples with good fits to Northern montane communities such as *Vaccinium myrtillus-Deschampsia flexuosa* heath and *Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* heath. However, these samples represent the most exposed vegetation at the highest altitudes on Bodmin Moor. The clitter and boulder fields associated with this vegetation often make it inaccessible to grazing stock and result in high environmental heterogeneity with respect to shade, aspect, slope angle and drainage. This might account for the diverse range of heathland communities assigned by TABLEFIT to assemblage seven. The assemblage has the highest mean grazing index (Figure 5.7), indicating the lowest levels of grazing partly due to the inaccessible nature of some of the samples. The inaccessible nature of these samples is alluded to by the high mean slope angle (Figure 5.7). This assemblage appears to be restricted to shallow soils (Figure 5.7).

Assemblage eight: *Sphagnum-rich* wet heath

A total of 26 samples were found in species assemblage eight. The assemblage was characterised by the high constancy of *Juncus squarrosus* and *Sphagnum capillifolium*. *Aulocomnium palustre* is also a significant indicator species of group eight characterised by high relative abundance (Table 5.2, Appendix 1). *Juncus squarrosus* is an S strategist, confined to damp, infertile and acidic soils. It is occasionally eaten by cattle and horses, and in winter, when preferred species are unavailable, by sheep. Thus it is increasing in areas grazed only by sheep in summer (Grime *et al.* 1988, 1990). *Sphagnum capillifolium* and *Aulocomnium palustre* are indicative of wet acid habitats.

The samples in assemblage eight are classified as *Scirpus cespitosus-Erica tetralix* wet heath (58%), *Molinia caerulea-Potentilla erecta* mire (15%), and *Carex echinata-Sphagnum recurvum* mire (12%). The few remaining samples are wet mires types and heathland (Table 5.2). There is some problem differentiating these communities using TABLEFIT (Figure 5.1). Clearly there is a degree of affinity between assemblage six and assemblage eight. Both assemblages have many species in common and are largely classified as *Scirpus cespitosus-Erica tetralix* wet heath. However, the inclusion of *Sphagnum* sp. and *Eriophorum angustifolium* amongst the characterising species of assemblage eight, points to a wetter environment. This is borne out by the mean soil moisture values for the assemblages (Figure 5.7). Assemblage eight represents the more *Sphagnum*-rich stands of the typical sub-community of *Scirpus cespitosus-Erica tetralix* wet heath, which form a gradual transition to blanket mire. Some blanket mire samples are also included in assemblage eight. The assemblage therefore has affinities with the blanket mire communities of Drage (1981), particularly the *Juncus squarrosus* – *Sphagnum*-rich grassland (Drage 1981), and the Dartmoor blanket bogs groups nine (Kent & Wathern 1980) and A (Ward *et al.* 1972).

Assemblage nine: *Narthecium ossifragum-Eriophorum vaginatum* blanket bog

Assemblage nine includes 13 samples, characterised by the high constancy of *Narthecium ossifragum*, *Erica tetralix*, *Molinia caerulea*, and the high relative abundance of *Eriophorum vaginatum* and *Lophocolea* *bidentata* (Table 5.2, Appendix 1). *Eriophorum vaginatum* is an S to S-C strategist, characteristic of wet, acidic, peaty sites that are waterlogged in spring but drier in summer. The species is tolerant of light grazing by sheep or cattle (Grime *et al.* 1988, 1990). *Molinia caerulea* is also an S-C strategist associated with wet grassland or soligenous mire with well oxygenated soil profiles. It is tolerant of both grazing and burning (Grime *et al.* 1988, 1990).

The samples in assemblage nine are classified as *Scirpus cespitosus-Erica tetralix* wet heath (62%), *Molinia caerulea-Potentilla erecta* mire, *Scirpus cespitosus-Eriophorum vaginatum* blanket mire and *Narthecium ossifragum-Sphagnum papillosum* valley mire. In this respect, assemblage nine is very similar to assemblage eight. However the sites are wetter, as indicated by a reduction in the constancy and abundance of hummock-forming *Sphagnum capillifolium* and the absence of *Sphagnum compactum*, which is restricted to the *Ericetum tetralicis* communities (Rodwell 1992a). Species assemblage nine represents the transition from very wet heath to mire vegetation. The increase in mean soil moisture between assemblages eight and nine is associated with other changes in abiotic conditions and management. Assemblage nine is less heavily grazed according to the grazing index, and has the lowest mean slope angle of all assemblages (Figure 5.7).

The assemblage had similar mean slope angle and floristic affinities to the blanket bog vegetation of Dartmoor. However, unlike group nine (Kent & Wathern 1980), *Hydrocotyle vulgaris* is confined to assemblage eleven, whilst *Juncus squarrosus* and *Juncus effusus* are restricted to assemblage eight. Thus assemblage nine represents a subset of group nine (Kent & Wathern 1980) and the even broader group A (Ward *et al.* 1972). The assemblage is virtually synonymous with the previously reported *Eriophorum vaginatum – Eriophorum angustifolium* mire (Drage 1981). *Scirpus cespitosus-Erica tetralix* wet heath and *Molinia caerulea-Potentilla erecta* mire are extensive on the North moor, often occurring in mosaics with *Narthecium ossifragum – Sphagnum papillosum* mire and *Carex*-*Sphagnum* mires (NCC 1986). However, *Scirpus cespitosus-Eriophorum vaginatum* blanket mire is rare on Bodmin Moor according to the Nature Conservancy Council survey (NCC 1986).

Assemblage ten: *Eriophorum angustifolium* valley bog

Species assemblage ten included 11 samples characterised by the high constancy and abundance of *Eriophorum angustifolium* and *Sphagnum inundatum*, the high constancy of *Drosera rotundifolia* and *Sphagnum papillosum* and the high relative abundance of *Rhynchospora alba*, *Carex nigra* and *Carex flacca* (Table 5.2, Appendix 1). *Eriophorum angustifolium*, *Carex nigra* and *Carex flacca* are all S strategists. They are typical of soligenous mires in sites where the growth of potential dominants is suppressed by low fertility and in the case of *Carex nigra* by grazing (Grime *et al.* 1988, 1990).

The samples in assemblage ten are classified as *Narthecium ossifragum-Sphagnum papillosum* valley mire (36%), *Scirpus cespitosus-Erica tetralix* wet heath (18%), blanket mire, bog pools and drainage channel communities (Table 5.3). All the characterising species of assemblage ten are found in *Narthecium ossifragum-Sphagnum papillosum* valley mire at similar abundance and constancy, except for *Carex nigra*, *Carex flacca*, *Lotus uliginosum* and *Potamogeton natans*, which was replaced by *Potamogeton polygonifolius*.

Lotus uliginosum, like the *Carex* species is found where low fertility suppresses the growth of potential dominants (Grime *et al.* 1988, 1990). Thus assemblage ten represents a particularly nutrient-poor variant of *Narthecium ossifragum-Sphagnum papillosum* valley mire. The environmental variables provide contradictory evidence concerning nutrient levels. On the one hand, assemblage ten has the lowest mean soil conductivity supporting the low fertility theory, but the mean pH (4.06) is higher than many other assemblages (Figure 5.7). Other samples in the assemblage reflect the transition to *Ericetum tetralicis* over periodically waterlogged shallow peats marked by the replacement of *Drosera rotundifolia*, *Sphagnum papillosum*, *Narthecium ossifragum* and *Eriophorum angustifolium* with *Sphagnum compactum* (Rodwell 1992a). In the opposite direction, bog pool communities represent wetter areas within this assemblage, which could account for the high mean soil moisture value.

The assemblage is similar to the *Narthecium ossifragum* – *Sphagnum* flush (Drage 1981) and has some affinity with the *Eleocharis* sp. – *Rhynchospora alba* flush community (Drage 1981), although both these communities contain *Trichophorum cespitosus*. On Dartmoor, the assemblage is similar to group ten (Kent & Wathern 1980) both in terms of a relatively high pH and floristically, although mesotrophic indicators like *Juncus effusus* and *Viola palustris* are restricted to the standing water assemblage eleven together with *Hydrocotyle vulgaris*, indicating drier, less nutrient-rich conditions on Bodmin Moor. The assemblage also conforms to group F (Ward *et al.* 1972), with the exception of *Juncus effusus*. As with group F, the valley bog samples of assemblage ten are separated from blanket bog samples by the absence of *Trichophorum caespitosum*.

Assemblage eleven: soligenous soakway / open water vegetation

Species assemblage eleven consisted of 21 samples, characterised by the high constancy and abundance of *Juncus acutiflorus*, *Juncus effusus*, *Sphagnum recurvum* and *Polytrichum commune*, and the high relative abundance of *Galium palustre*, *Hypericum elodes*, *Ranunculus flammula*, *Hydrocotyle vulgaris*, *Viola palustris*, *Agrostis canina*, *Juncus bulbosus*, *Potamogeton polygonifolius*, *Menyanthes trifoliata* and *Epilobium palustris*. Most of these species are intermediate in terms of strategy, often C-S-R (Grime *et al.* 1988, 1990). They are all indicative of soligenous mire and soakways in an upland context. *Galium palustre*, *Hydrocotyle vulgaris*, *Ranunculus flammula*, *Juncus bulbosus* and *Epilobium palustre* are all restricted to sites where the vigour of potential dominants is suppressed by nutrient stress and grazing or grazing-related disturbance (Grime *et al.* 1988, 1990).

The samples in assemblage eleven are classified as *Carex echinata-Sphagnum recurvum/auriculatum* mire (48%); *Hypericum elodes-Potamogeton polygonifolius* soakway (19%), *Molinia caerulea-Potentilla erecta mire* (9%), and *Carex curta-Sphagnum russowii* mire (9%).

There are clear floristic differences between assemblage eleven and *Carex echinata-Sphagnum recurvum/auriculatum* mire. *Carex echinata, Potentilla erecta, Sphagnum auriculatum* and *Sphagnum palustre* are not characterising species of assemblage eleven, despite occurring as virtual constants in *Carex echinata-Sphagnum recurvum/auriculatum* mire. By contrast, all the significant indicator species of assemblage eleven except *Sphagnum recurvum* and *Epilobium palustre* are present in *Hypericum elodes-Potamogeton polygonifolius* soakway, and the only virtual constant of this community missing is *Sphagnum auriculatum.* Assemblage eleven therefore has an obvious affinity with *Hypericum elodes-Potamogeton polygonifolius* soakway. What is less clear is the exact relationship between this assemblage and *Carex echinata-Sphagnum recurvum/auriculatum* mire indicated by the presence of *Juncus acutiflorus / effusus* and *Sphagnum recurvum.*

The assemblage represents soakways, seepage zones and pools that are acidic with few nutrients. The mean soil pH, whilst low (4.31), is higher than for many other groups (Figure 5.7), possibly reflecting the influence of rainwater entering the system as overland flow. Some samples fall within *Hypericum elodes-Potamogeton polygonifolius* soakway. Others represent soakways in a different context bearing some undefined relationship to *Carex echinata-Sphagnum recurvum/auriculatum* mire, particularly the *Juncus effusus/acutiflorus-Sphagnum recurvum* variants.

Assemblage eleven is similar to the *Narthecium ossifragum – Sphagnum* flush (Drage 1981) and the *Eleocharis* sp. - *Rhynchospora alba* flush community (Drage 1981), which are referred to assemblage ten. However, assemblage eleven appears to contain a suite of species associated with wetter conditions. The *Juncus / Sphagnum* samples show affinity to the *Juncus effusus* –*Sphagnum recurvum* mire, and the *Juncus acutiflorus* –*Sphagnum recurvum* herb moss-rich and species-poor mires (Drage 1981). The NVC equivalents of these communities occur together in mosaics on the North moor (NCC 1986) and as the transitions between them are diffuse (Rodwell 1992a), they occur together in assemblage eleven. On Dartmoor, group eleven (Kent & Wathern 1980) is synonymous with the Bodmin Moor assemblage eleven. The assemblage represents an open water community within the Dartmoor valley bog Group F (Ward *et al.* 1972).

5.4.2 The relationships between the different surveys and their classifications

Introduction

Interpreting the differences between the various surveys (Drage 1981, NCC 1986, on Bodmin Moor and Ward *et al.* 1972, Kent & Wathern 1980, on Dartmoor) is complex because they were carried out by different people, in different locations, at different times. Between-observer variation in the application of standard method habitat mapping is very high (Cherill & McClean 1999). Furthermore, within-observer variation has been shown to be almost as high as between observer variation in assessing species abundance in the Cairngorms even when surveyors are very experienced (Legg, C. University of Edinburgh. *Pers. comm.*). Thus, different surveyors will generate different results even when assessing the same vegetation. The location of sampling sites and boundaries when mapping is highly subjective and therefore difficult when replicated in different surveys. Quadrats cannot be relocated unless permanent monitoring systems have been devised *a priori*. Finally, as vegetation is dynamic, there is a temporal element to consider. Unfortunately, it is very difficult to attribute differences between surveys to any one of these factors hence a degree of circumspection is required in interpreting the meaning of differences between the various surveys on Bodmin Moor and Dartmoor.

Comparison with previous surveys on Bodmin Moor

The Nature Conservancy Council undertook habitat mapping of the North moor (NCC 1986) using Birks & Ratcliffe (1980) classification of upland vegetation, with additions derived from McVean & Ratcliffe (1962) and the NVC (Rodwell 1992a, b). No voucher quadrats exist (Sydes *Pers. comm.*). Therefore this survey only provides information on the occurrence and extent of communities on the North Moor. In contrast, Drage (1981) undertook a phytosociological survey on the South Moor using quadrats in a similar manner to the current work. There are some interesting discrepancies between the various surveys of Bodmin Moor.

The most significant difference is the lack of heathland reported from the Nature Conservancy Council survey (NCC 1986). Three major heathland types were identified in the current work occurring primarily in assemblages four (*Ulex gallii* – *Agrostis curtisii* heath in NVC terms) and seven (*Calluna vulgaris* - *Ulex gallii* heath and *Calluna vulgaris* – *Vaccinium myrtillus* heath in NVC terms). The assemblage four heath occurs amongst grassland communities on the North and South Moors, whilst the assemblage seven heathland is found on tors across the moor including Brown Willy and Rough Tor on the North Moor. The Nature Conservancy Council survey (NCC 1986: 1) explicitly states that there is 'no vegetation dominated by dwarf-shrubs' on the North Moor. This is true at a landscape scale, although mosaics containing heath or grass heath can be identified. However, at the scale of individual quadrats (in this case two by two metres), vegetation dominated by dwarf-shrubs was present on both the North Moor and South Moor. Thus heathland communities can be said to be present, but quantifying the extent of these communities is extremely difficult. This has important ramifications for applying moorland restoration protocols and assessing the effectiveness of both moorland management and restoration.

The other major differences between the NCC survey and the current work centre on the abundance of *Carex rostrata* – *Sphagnum recurvum* mire and the *Erica tetralix – Sphagnum compactum* wet heath. Both these communities are common in mosaics with other mire communities on the North Moor according to the Nature Conservancy Council survey (NCC 1986). However, *Carex rostrata – Sphagnum recurvum* mire was not identified in the current study and the *Erica tetralix – Sphagnum compactum* wet heath was only manifest as second rank TABLEFIT scores.

Drainage of *Carex rostrata – Sphagnum recurvum* mire results in a transition to *Carex echinata – Sphagnum* mire with an increase in *Juncus* where grazing is present (Rodwell 1992a). Some samples within assemblage eleven are identified as *Carex echinata – Sphagnum* mire by TABLEFIT, despite the absence of constant species. These samples could represent vegetation transitional between *Carex echinata – Sphagnum* mire and *Carex rostrata – Sphagnum recurvum* mire. However, the wettest vegetation on Bodmin Moor was not sampled exhaustively, as lone field working made it inadvisable to cross the centres of mires. Thus it is likely that the wettest *Carex rostrata – Sphagnum recurvum* mire vegetation was not recorded in the current work. A site visit in 2001 to Crowdy Marsh confirms the presence of *Carex rostrata – Sphagnum recurvum* mire. However, it occurs in complex mosaics with *Carex echinata – Sphagnum* mire, *Narthecium ossifragum – Sphagnum papillosum* mire and *Scirpus cespitosus – Erica tetralix* wet heath. Further study is necessary to fully elucidate the relationships between these communities on Bodmin Moor.

Erica tetralix – Sphagnum compactum wet heath was only represented by second rank TABLEFIT scores in the current work although it is present on the North Moor according to the Nature Conservancy Council (NCC 1986) survey. *Sphagnum compactum* is present at low constancy in *Sphagnum-rich* wet heath, along with *Scirpus cespitosus* and *Potentilla erecta* at high constancy. Thus the assemblage has more affinity with *Scirpus cespitosus-Erica tetralix* wet heath than *Erica tetralix – Sphagnum compactum* wet heath as reflected by the TABLEFIT scores.

Although the current work indicates that *Erica tetralix – Sphagnum compactum* wet heath was not present on Bodmin Moor, it is impossible to state categorically that no areas of wet heath exist where *Sphagnum compactum* is constant and *Trichophorum cespitosus* is absent. Hence further work is required to clarify the status of wet heath on Bodmin Moor.

The differences between the current work and the Nature Conservancy Council survey (NCC 1986) probably reflect the differing perceptions of the surveyors as a result of the use of different survey techniques. The Nature Conservancy Council utilised coarse landscape scale mapping, rather than quadrats that could represent highly localised vegetation composition. In contrast, the Drage survey (Drage 1981) was undertaken at the same scale as the current survey, albeit only on the South Moor.

Many of the differences between the Drage survey (Drage 1981) and the current work can be attributed to post-survey analysis. The species and assemblages encountered are generally similar, although there are some problems referring assemblage seven and assemblage five to the communities of Drage (1981). The groups in the current work were derived using TWINSPAN and indicator species analysis, whereas the Drage (1981) groups were sorted by hand. The use of multivariate classification methods increases repeatability, but decisions about the number of end groups remain subjective, whether repeatable methods are used or not. The primary difference between the Drage survey and the current work is in the number of communities; 11 in the current work and 22 in the Drage (1981) survey. Relatively few end groups were selected for simplicity of explanation, and to reflect groupings of management concern.

The minor compositional differences between the Drage (1981) survey and the current work are most likely to reflect the differing perceptions of the surveyors, although change over time cannot be ruled out. For example, *Agrostis curtisii* is generally found with heathland or in association with *Calluna vulgaris* in the Drage survey, whereas the current survey identifies areas of *Agrostis curtisii* grassland. This could be interpreted as temporal change from heathland to grassland as a result of grazing pressure since 1981, but such an interpretation is purely speculative and given the variation between different surveyors is probably safer if discounted.

Comparison with previous surveys on Dartmoor

In contrast to the previous surveys on Bodmin Moor, differences between the Dartmoor surveys (Ward *et al.* 1972, Kent & Wathern 1980) could represent differences in vegetation between Dartmoor and Bodmin Moor rather than the different perceptions of surveyors. However, neither temporal change nor differing perceptions can be ruled out. Furthermore, there are no objective criteria for believing that the differences between these surveys represent a real difference in vegetation, while the differences between the Bodmin Moor surveys do not.

The grasslands on Bodmin Moor are generally well represented in other upland areas of Britain including Dartmoor, although *Agrostis curtisii* grassland is confined to the South-west (Rodwell 1992b). However, there was an extensive variant of *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland characterized by the presence of *Molinia caerulea* at low abundance but high constancy. *Molinia caerulea* is present in *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland but only at very low constancy. This Bodmin Moor assemblage has affinities with a vegetation type described on Dartmoor (Ward *et al.* 1972) but lacks the sub-shrub component, perhaps reflecting greater grazing pressure or warmer conditions. The lack of sub-shrubs could be significant in terms of grazing management, as any reduction in grazing intensity could release *Molinia caerulea* rather than *Calluna vulgaris* or other dwarf-shrubs from suppression.

The heathlands of Bodmin Moor are generally fragmented and frequently better classified as grass heaths. The major grass heath community on Bodmin Moor (assemblage four) is found on Dartmoor (Ward *et al.* 1972, Kent & Wathern 1980) but *Ulex gallii* replaces *Vaccinium myrtillus* in the Bodmin assemblage. The heathland vegetation on tors contains *Vaccinium myrtillus* and represents both *Calluna vulgaris-Ulex gallii* heath and *Calluna vulgaris-Vaccinium myrtillus* heath, and hybrid vegetation with a more Northern montane element than previously thought. It is represented in transitional vegetation on Dartmoor (Ward *et al.* 1972).

The wetter communities on Bodmin Moor are generally more representative of those found elsewhere. The wet heath on Bodmin Moor conforms to the NVC *Scirpus cespitosus-Erica tetralix wet heath* (Rodwell 1992a). The blanket and valley bog communities conform to the NVC (Rodwell 1992a) and are represented on Dartmoor (Ward *et al.* 1972, Kent & Wathern 1980). Pool vegetation within valley mires is particularly similar on Bodmin Moor and Dartmoor (Kent & Wathern 1980).

5.4.3 The use of vegetation classification for hypothesis generation concerning grazing mediated transitions

The species assemblages derived from the phytosociological survey have been compared with previous work and to the NVC in order to fully describe and characterize the nature of the vegetation resource of Bodmin Moor. However the relationship between the different species assemblages and the NVC can be used to generate hypotheses about the possible successional trajectories that operate on the Moor.

The vegetation on Bodmin Moor did not fit precisely within the NVC framework as expressed by first and second rank TABLEFIT scores. A sample with a specific species composition can be classified by TABLEFIT as a 70% fit to *Scirpus cespitosus-Erica tetralix* wet heath (first rank) and 65% fit to *Molinia caerulea-Potentilla erecta* mire (second rank). Thus that sample has affinities with both vegetation types. There are a number of possible reasons why the species composition of a sample can fall between two (or more) communities in this manner.

The vegetation may represent unique samples of vegetation that have not been recorded by the NVC. As all vegetation samples are unique to some extent, value judgements must be made about whether the vegetation forms a new community or sub-community or whether it is a regional variant of a nationally occurring community. Alternatively the vegetation may be transitional between the two NVC types. This could reflect spatial transition from wet to dry via intermediate moisture levels and hence intermediate vegetation or it could represent temporal change. Both temporal and spatial transitions can be mediated by grazing. Figure 5.1 relates the occurrence of transitional vegetation to grazing and soil moisture. As this is expressed in terms of the NVC, it allows comparison with grazing-mediated successions from the literature providing the opportunity to speculate upon the possible effects of grazing on Bodmin Moor.

Agrostis curtisii grassland / *Ulex gallii-Agrostis curtisii* grass heath / *Ulex gallii* heath, acidic grassland, *Vaccinium myrtillus-Calluna vulgaris* heath and flushed rill vegetation all contain samples that are transitional between *Agrostis curtisii* grassland and *Ulex gallii-Agrostis curtisii* heath. The transition between these communities is believed to be mediated by grazing (Rodwell 1992a, b, also see Figure 5.1). Smallshire *et al.* (1997) have suggested that stocking rates of 0.29 LU/ha are compatible with areas of *Ulex gallii-Agrostis curtisii* heath in good condition across South-west England. However, there is no obvious difference in management between these communities as measured by the grazing index (Figure 5.7). Further work is required to verify that this transition is grazing-mediated and to determine the types of management that control it.

Ulex gallii-Agrostis curtisii heath is also transitional to *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland and *Molinia caerulea-Potentilla erecta* mire, although in both cases this is unidirectional. The transition between *Molinia caerulea-Potentilla erecta* mire and *Ulex gallii-Agrostis curtisii* heath is related to soil moisture (Rodwell 1992a) but the

Festuca ovina-Agrostis capillaris-Galium saxatile grassland / *Ulex gallii-Agrostis curtisii* heath is grazing mediated via *Nardus stricta* grassland (Rodwell 1992b, see also figure 5.1). However, the Bodmin Moor transition implies a slightly different trajectory, as *Ulex gallii-Agrostis curtisii* heath is transitional to *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland directly, whilst the transition from *Nardus stricta* grassland to *Ulex gallii-Agrostis curtisii* heath is unidirectional (figure 5.1). This suggests that *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland can only be converted *to Ulex gallii-Agrostis curtisii* heath via *Nardus stricta* grassland. This is suprising, given that *Nardus stricta* grassland is generally considered to develop in response to heavy grazing particularly by sheep. In contrast to most upland areas in Britain, *Nardus stricta* is not particularly abundant on Bodmin Moor and the unusual relationship it has with the other species and communities may reflect poorly understood differences between Bodmin Moor and other British uplands. The role of burning may also be of significance.

Other interesting occurrences of transitional vegetation centred on *Molinia caerulea-Potentilla erecta* mire and *Scirpus cespitosus -Erica tetralix* wet heath. Both *Ulex gallii-Agrostis curtisii* heath and, to a lesser extent, *Calluna vulgaris – Ulex gallii* heath are transitional to *Molinia caerulea-Potentilla erecta* mire. Frequent burning of *Calluna vulgaris – Ulex gallii* heath can result in a fire climax of *Molinia caerulea-Potentilla erecta* mire, whilst *Ulex gallii-Agrostis curtisii* heath represent transition to drier ground (Rodwell 1992a, see also Figure 5.1). The relationship between *Molinia caerulea-Potentilla erecta* mire and *Scirpus cespitosus – Erica tetralix* wet heath could reflect the manner in which the communities can intergrade on ill-drained land in South-west Britain (Rodwell 1992a) but may equally well reflect the influence of grazing. When wet heath is subject to burning and post-burn grazing, it may develop *into Molinia caerulea-Potentilla erecta* mire, extending the cover of *Molinia caerulea* beyond its normal edaphic bounds (Rodwell 1992a). This is particularly likely where drainage operations have been undertaken (Godwin & Conway 1939, Bignal & Curtis 1981, Rodwell 1992a). As with the heathland communities, the effects of stock type and seasonality on the possible trajectories remain hypothetical on Bodmin Moor and have received little attention elsewhere. Further transition to *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland could feasibly reflect a further increase in grazing pressure particularly on drier ground. Thus the widespread occurrence of *Molinia caerulea* on Bodmin Moor could reflect a history of heavy grazing (Godwin & Conway 1939, Bignal & Curtis 1981, Rodwell 1992a, b). Whilst reducing grazing intensity generally results in increased dwarf-shrub cover, it can also result in *Molinia caerulea* dominance (Hill 1982, Rodwell 1992a, Gardner et al. 2001). Thus the manner in which *Molinia caerulea* responds to relaxation of grazing pressure requires investigation in order to assess the likely outcome of Countryside Stewardship management.

5.4.4 Interpretation of environmental gradients

Ecological information on species and communities (derived primarily by Grime *et al.* 1988, 1990, Hill *et al.* 1999 and Rodwell 1992a, b) suggests that the first DCA axis was related primarily to soil moisture. Other environmental variables did not directly correspond to any of the DCA axes, although heathland assemblages tend to be higher on the second axis possibly reflecting the importance of grazing. The ordination supports the existence of the vegetation types identified in the species assemblage tables, although there is a continuum between assemblage types particularly at the wet end of the environmental spectrum (Figures 5.2, 5.3, 5.4). *Eriophorum angustifolium* valley bog overlaps with the wetter end of soligenous soakways, whilst *Sphagnum-rich* wet heath and *Narthecium ossifragum-Eriophorum vaginatum* valley bog which are virtually synonymous on the first axis, overlap with the drier end of soligenous soakways (Figure 5.2). This is consistent with the mean soil moisture values of the assemblages and species ecology. *Narthecium ossifragum-Eriophorum vaginatum* valley bog had the highest mean soil moisture value and a smaller standard deviation than soligenous soakways (Figure 5.7). Likewise mean soil moisture values and species ecology indicate that *Narthecium ossifragum-Eriophorum vaginatum* valley bog was wetter than *Sphagnum*-rich wet heath, as *Sphagnum compactum* is absent and *Sphagnum capillifolium* is less abundant (see also Figure 5.7).

The CCA biplot (Figure 5.5) indicated that soil moisture, soil depth and soil organic matter were important in explaining floristic variation. Not suprisingly these variables were correlated with each other. This results from the fact that mire samples on Bodmin Moor were predominantly found on thick basin peats or deep blanket peats of the Laployd and Crowdy series with extreme surface wetness (Hughes & Staines 1975). In this respect, Bodmin Moor is similar to Dartmoor and Exmoor (Staines 1976, Findlay *et al.* 1984), although the blanket peats on Bodmin Moor are less extensive. Additionally, Organic matter greatly increases the matrix water storage capacity of a soil (Jeffrey 1987).

Calcium and pH explained some of the residual variation on the second CCA axis and were related as Ca^{2+} and associated exchangeable cations largely control soil pH (Brady & Weil 1999). Aluminium and hydrogen enhance soil acidity, whereas calcium encourages alkalinity (Rowell 1994). Soil calcium on Bodmin Moor is elevated in mestotrophic grasslands, which have the highest pH values of all assemblages (Figure 5.7). This probably reflects a history of soil amelioration on inbye land possibly indicating liming although the use of sea sand is said to have been widespread on Bodmin Moor post 1940. The unimproved soils of Bodmin Moor are extremely acidic as a result of the granite bedrock and leaching due to high rainfall in the natural area.

The wettest sites on the moor had higher pH than the dry ones. This probably reflects the influence of precipitation, which collects in the mires as a result of overland flow during the intense rainfall events that are common on Bodmin Moor. This relationship is not reflected in previous work on Bodmin Moor, where drier soils (Moretonhampstead series) have higher pH (pH 6.2) than wet soils (Hexworthy series pH

4.9), and have higher values at the dry end of the spectrum than those of the current study (Staines 1976). However, the wettest soils (Crowdy and Laployd series) were not subject to analysis on granite bedrock (pH 4.4 over slate), and the number of samples was small in comparison to the present study. Moreover the present study was undertaken during particularly wet seasons. The pH values in the Narrator catchment (Dartmoor) show increased pH with increased soil wetness, and have similar values to those of the present study (Kent & Wathern 1980). In general, the low soil pH values for Bodmin Moor are to be expected, and are similar to those reported from other British upland areas with podzolic soils (Miles 1988, Chambers *et al.* 2001).

The importance of soil moisture and pH in the distribution of upland plant species is long recognized (Tansley 1911, 1939, Pearsall 1968, Rodwell 1992a, b). However, grazing is also a major determinant of floristic composition in the uplands due to the significance of its impact on the dynamics and succession of upland vegetation (Grant & Maxwell 1988). The measurement of direct grazing pressure is extremely difficult hence the use of subjective grazing indices. These indices reflect perceived grazing pressure rather than real grazing pressure and are therefore hard to interpret. They do not take into account seasonality of grazing or stock type, both of which have a profound influence on the outcome of grazing interactions. Furthermore, the effects of grazing may be masked by pH as more intensive management is generally linked to increased soil pH. Thus although grazing is not directly identified as a major environmental gradient the second CCA axis may represent a management axis rather than strictly a soil nutrient axis.

It is clear that whilst soil moisture, pH and grazing are important factors controlling vegetation composition, other variables have a role to play and the interactions between species and environment have not been fully elucidated. Care is required in the interpretation of the CCA output, which provides information on the relationship among sites or species in one particular environmental space. Unlike DCA, it does not explain the relationships among sites or species in species space (McCune & Mefford 1999). Further studies into these relationships, with particular regard to grazing and dwarf-shrub heath regeneration are required to inform management decisions.

5.5 Conclusions

- The nature of the plant communities on Bodmin Moor has been described by reference to species assemblages. A phytosociological classification was produced and the relationships between species composition and a range of environmental factors were explored using multivariate techniques.

- The results generally conform to expectations and previous surveys of Bodmin Moor in terms of the range and type of communities present, although numerous subtle differences in species composition exist. However, the heathland present on tors contains a more Northern montane element than previously thought, and scale-related problems in defining the nature and extent of heathland have been highlighted. Further work is required to verify the nature of some of the wet heath and mire communities.

- The classification shows vegetation on Bodmin Moor to be very similar to that found on Dartmoor, although there are some differences between certain grassland and heathland types in the two South-west upland areas. The occurrence of a *Festuca–Agrostis-Molinia* sward without sub-shrub components is not reported from Dartmoor. The relationships between species composition and environmental variables were similar, not only to Dartmoor, but also to the British uplands in general.

- The distribution of the plant communities is primarily controlled by the interaction of soil depth, soil moisture and organic matter content. Soil pH and soil calcium levels also had an influence on vegetation composition. Grazing is of importance, although the difficulty of finding objective measures of biotic pressure is a major problem in interpretation of grazing as a controlling variable. These variables are known to be of great importance in determining the floristic composition of vegetation in the British uplands. They are consistent with the findings of Kent & Wathern (1980) on Dartmoor, although burning rather than grazing was the biotic variable correlated with the second ordination axis. The role of burning and grazing-burning interactions requires further investigation on Bodmin Moor.

- The work provides a comprehensive classification of the vegetation present on Bodmin Moor, and provides some insight into the factors controlling floristic composition. It provides a platform for further work investigating the dynamics of the vegetation and its controls.

6 The Soil Seed Banks of Bodmin Moor

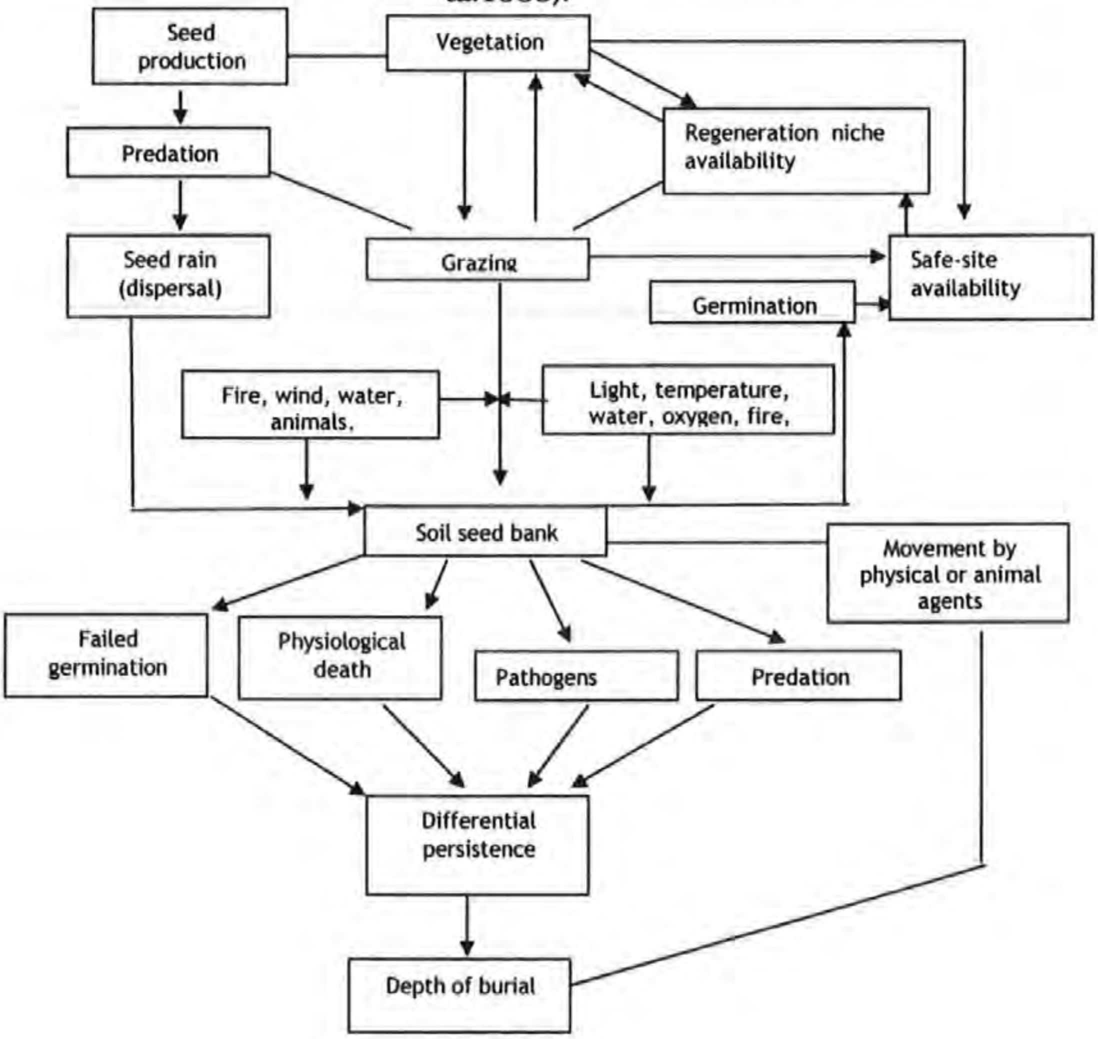
6.1 Introduction

The soils beneath plant communities generally contain large populations of buried seed (Chippendale & Milton 1934, Harper 1977, Thompson & Grime 1979, Owen *et al.* 2001). Populations of buried seed are generically termed seed banks *sensu* Harper (1977). The importance of the role of seed banks in the structure and functioning of plant communities has been increasingly recognised in the literature (Grime 1989, Simpson *et al.* 1989, Thompson *et al.* 1997, Baskin & Baskin 1998). In particular the role of seeds and the proximity of seed sources are an important determinant of the course of successional pathways (Kellman 1970, Miles 1979, Miles 1987). Knowledge of soil seed banks on Bodmin Moor is therefore a prerequisite in order to predict the manner in which the vegetation will change in response to a reduction in grazing intensity. However, a number of factors other than seed input are likely to affect regeneration dynamics and species composition following regeneration particularly climate, management practices, soil properties and nutrient availability (Britton *et al.* 2001). Knowledge of the soil seed bank alone is therefore insufficient to predict the outcome of management unless it is found that the availability of dwarf-shrub propagules is so low that heathland regeneration is not possible without the addition of seed from outside sources.

The current management objectives of increasing dwarf-shrub heath cover through a reduction in grazing intensity rely heavily on the existence of a large persistent source of propagules in the soil, as dwarf-shrub heath, particularly *Calluna vulgaris*, is scarce amongst the extant vegetation on Bodmin Moor (Chapter Five). There is currently no information on the availability of propagules for dwarf-shrub heath regeneration on Bodmin Moor. Likewise, there is no information concerning the type and abundance of propagules that could potentially compete with dwarf-shrub species for regeneration niches should they become available.

In addition to lack of information on spatial variability in the seed bank of Bodmin Moor, there is a lack of evidence concerning the recent history of vegetation on the Moor (Chapter Two). Temporal variation in the seedbank can be examined by comparing surface vegetation with the seed bank composition at different depths, and considering depth as analogous with antiquity. However, the complex feedbacks between vegetation, seed rain, seed banks, land management and the differential persistence of seeds in the seed bank (Figure 6.1.) make interpretation of such data difficult.

Figure 6.1. General model of seed bank and vegetation dynamics illustrating some grazing-related feedbacks (modified from Simpson *et al.*1989).



6.1.1 Aims

The primary objective of this chapter is to examine the spatial variability in the seed bank of Bodmin Moor to determine:

- If there are sufficient propagules of *Calluna vulgaris*, *Erica tetralix*, *Vaccinium myrtillus* and *Ulex gallii* available to allow heathland restoration on Bodmin Moor.
- How above-ground floristic composition and seed bank composition are related, primarily in order to determine if dwarf-shrub propagules are restricted to dwarf-shrub communities or if they are widespread.
- Whether propagules of other non-dwarf-shrub species are present in sufficient numbers to have the potential to inhibit heathland restoration on Bodmin Moor.
- How the propagule density of potential dwarf-shrub competitors varies amongst above-ground communities.

A further objective is to examine variability in the seed bank of Bodmin Moor in relation to depth. This will allow assessment of the degree to which the vertical distribution of seeds relates to seed persistence and may provide some insights into the ecological dynamics of the seed banks.

6.2 Methods

6.2.1 Collection of soil seed bank samples

Based on a TWINSPAN analysis of the survey data from Bodmin Moor described in Chapter 5, ten target assemblages were chosen to represent points along the transition from wet to dry communities. Ten replicates of each of these target assemblages were located near the original vegetation sampling points described in Chapter 5, and soil samples were collected from them for seed bank studies. This resulted in a total of 100 samples (ten replicate samples from each of the target assemblages). At each sampling point, a soil sample was taken from 0-

5cm depth and another from 5-10cm depth using a bulb corer. The surface vegetation was removed using a knife, although the litter layer was retained in the 0-5cm sample (Simpson *et al.* 1989). Polythene bags were used to avoid seed loss or contamination (Bullock 1996). The relationship between seed bank groups and surface vegetation is shown in Figure 6.2.

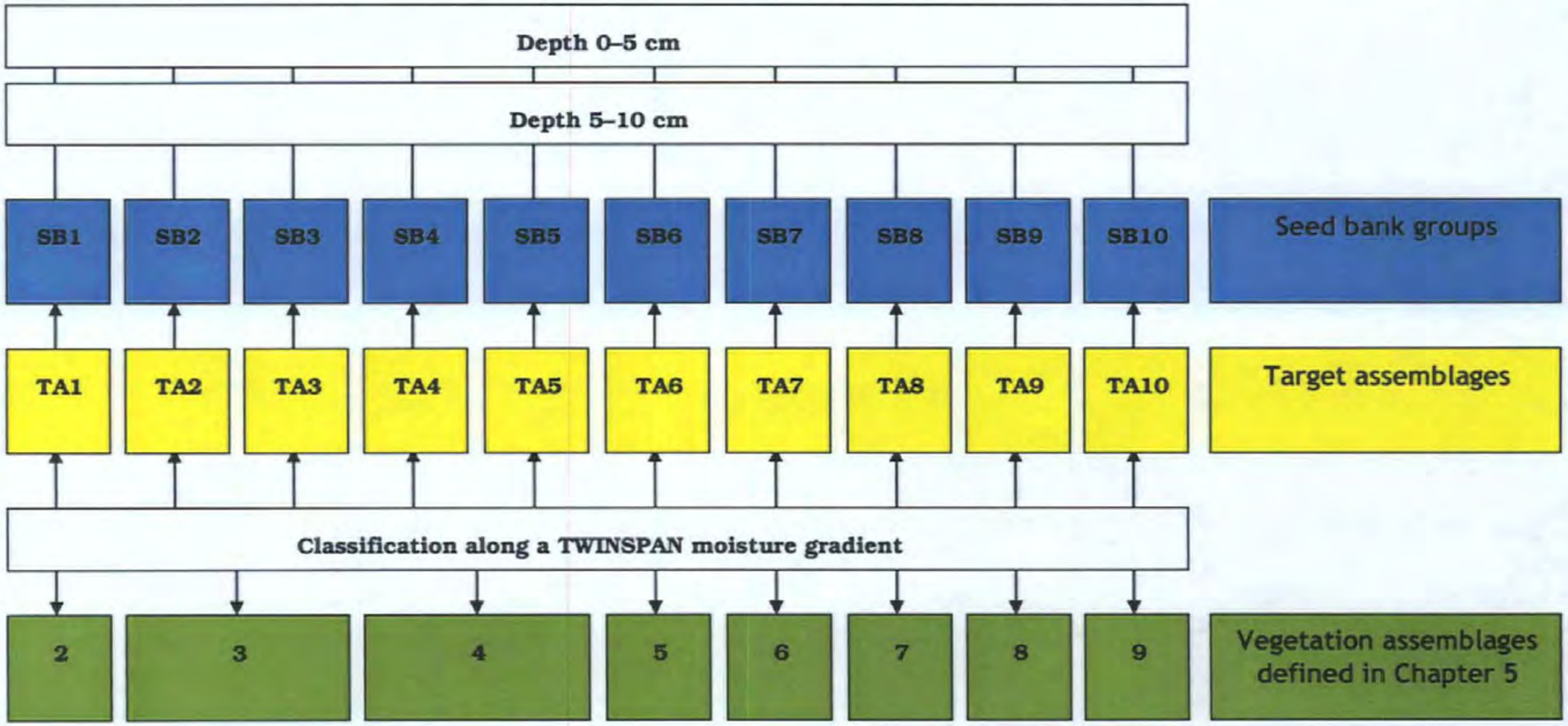
6.2.2 Treatment of seed bank samples and seedling emergence counts

Usually, seed bank samples are sieved through a 0.5 cm sieve in order to remove rhizomes, roots and other plant material that is not seed (Bullock 1996). However, the presence of rhizomes and roots could influence species composition after the creation of regeneration niches by burning, grazing, trampling or other disturbance. Therefore sieving was not undertaken because regeneration from buried rhizomes and roots could play a significant role in heathland regeneration. The soil from each core was evenly distributed over a layer of sterile sand contained within a 15 cm x 20 cm seed tray.

Seed trays were placed in an unheated glasshouse under a natural light environment and watered using a sprinkler system when required in order to maintain samples in a moist condition. Five trays of sterilized sand were also set out to detect any airborne seed contaminants. The seed trays were randomly distributed in the greenhouse and were rearranged randomly every month to allow for micro-variation in growing conditions.

There are numerous techniques for seed bank enumeration (Roberts 1981, Gross 1990, Hendry & Grime 1993, Warr *et al.* 1993, Bullock 1996, Thompson *et al.* 1997, Baskin & Baskin 1998). Seedling emergence counts were used to estimate the number of viable seeds in each sample, as this method is rapid and efficient (Owen *et al.* 2001). Emerging seedlings were identified, counted and removed at intervals (between one and three weeks) to provide a quantitative estimate of the

Figure 6.2. The relationship between seed bank groups and surface vegetation



number of viable seeds present. Identification was to the species level. Any seedlings that could not be identified initially were transplanted and grown until positive identification was possible. Each sample was stirred in August to ensure that all the seeds were exposed (Bullock 1996) and to encourage further germination (Roberts 1981). The experiment ran until October (a period of six months) as most propagules in a seedbank sample germinate during the initial two months, and little extra information is gained by continuing seed bank investigations for longer than six months (Warr *et al.* 1993).

6.2.3 Data analysis

A number of species were eliminated from the data set prior to analysis as their presence was probably due to contamination. *Buddleja davidii, Cardamine flexuosa, Epilobium montanum, Lactuca virosa, Prunella vulgaris* and *Senecio jacobaea* emerged from sterile sand controls and samples and were eliminated as contaminants. *Picris echioides, Oxalis corniculata* and *Taraxacum* agg. emerged from samples and were eliminated as contaminants, although they were not present in the control trays because they are ruderal species that are not significant elements of vegetation on Bodmin Moor.

A variety of analyses were undertaken. Initially data from both depths were combined to examine spatial variation in the seedbank in isolation. Two-Way Indicator Species Analysis (TWINSPAN) (Hill, 1979a), and Detrended Correspondence Analysis (DCA) (Hill 1979b, Hill & Gauch 1980) were used to describe both the surface vegetation and seed bank samples providing a comparison of surface vegetation floristic composition and seed bank composition in order to determine how the two are related. Mantel testing (Mantel 1967, algorithm based on Douglas & Endler 1982) provided an objective comparison between surface vegetation patterns and seed bank patterns in species composition. Analysis of variance (ANOVA) and analysis of means (ANOM) allowed examination of variation in the number of propagules present beneath the different plant communities for specific species of interest to provide information on the likelihood of successful heathland restoration occurring in specific plant communities on Bodmin Moor. Levene's tests were used to test for heterogeneity of variance (equal variance is an underlying assumption of ANOVA and ANOM).

Further analysis was undertaken by separating the seed bank samples into their component depths. DCA (Hill 1979b, Hill & Gauch 1980), Mantel testing, two-way ANOVA and ANOM were all utilized to explore variation in patterns between the two depths. This allowed examination of the degree to which the vertical distribution of seeds relates to seed persistence and to estimate the former extent of the species on Bodmin Moor.

6.3 Results

6.3.1 Surface Vegetation and seed bank composition

Target assemblages TA1, TA6 and TA9 are directly referable to *Pteridium aquilinum* vegetation (2), flushed rill vegetation (5) and *Sphagnum-rich* wet heath (8) respectively (Figure 6.2, Table 6.1). Target assemblages TA7, TA8 and TA10 largely represent *Trichophorum cespitosum-Erica tetralix* wet heath (6), *Vaccinium myrtillus-Calluna vulgaris* heath (7) and *Narthecium ossifragum-Eriophorum vaginatum* blanket bog (9) respectively. Both acidic grassland (3) and *Agrostis curtisii* grassland / *Agrostis curtisii-Ulex gallii* heath (4) are split. Acidic grassland (3) is represented by TA2 and TA3, whilst *Agrostis curtisii* grassland / *Agrostis curtisii-Ulex gallii* heath (4) is represented by TA4 and TA5. TABLEFIT and Indicator Species Analysis show little meaningful differentiation between the composition of TA2 and TA3. However, TA5 may represent grass-heath, whilst TA4 has closer affinities with heathland proper.

All the target assemblages form a continuum (Figure 6.3) although TA1 is fairly discrete. There is little distinction between TA2 and TA3, whilst TA4 and TA5 had distinct floristic compositions corroborating the interpretation of TABLEFIT and Indicator species analysis. The first two axes of the DCA ordination explain 20% of the total variance.

Table 6.1. Target assemblages (TAs) with associated indicator species and indicator species scores (ISS). Only indicator species with ISS significantly different from random expectation ($p \leq 0.05$) are shown. Affinities are summarised between TAs and the species assemblages (SAs) from Chapter 5 and the NVC (using TABLEFIT).

TA	Indicator Species	ISS	SA	NVC	No of samples	Mean TABLEFIT ± sd
1	*Pteridium aquilinum*	87	2	U20	6	79 ± 16
	Agrostis capillaris	57		U4	3	83 ± (8)
	Pseudoscleropodium purum	38		W25	1	58
2	*Polytrichum commune*	21	3	U4	6	66 ± (8)
				H4	2	57 ± (2)
				W23	1	69
				U5	1	64
3	*Hypnum jutlandicum*	39	4	U4	5	64 ± (8)
	Festuca ovina	36		H4	3	62 ± (3)
	Polygala serpyllifolia	28		U5	1	64
				M15	1	50
4	*Agrostis curtisii*	42	4 (7)	U3	4	75 ± (12)
	Ulex gallii	33		H8	3	72 ± (7)
	Hypnum cupressiforme	21		H4	2	72 ± (3)
				H10	1	63
5	*Molinia caerulea*	19	4	U3	3	72 ± (6)
				M25	3	70 ± (6)
				M15	2	72 ± (1)
				H4	1	69
				H8	1	67
6	*Festuca rubra*	48	5	M25	5	59 ± (11)
	Sphagnum auriculatum	29		M15	2	67 ± (7)
				U5	1	60
				H4	1	57
				U6	1	31
7	*Trichophorum cespitosum*	47	6 (3)	M15	6	68 ± (7)
	Dicranum heteromalla	36		M25	3	66 ± (13)
				M17	1	65
8	*Vaccinium myrtillus*	62	7 (8)	H10	4	69 ± (3)
	Deschampsia flexuosa	58		H8	1	79
	Calluna vulgaris	48		H21	1	77
				H12	1	77
				H4	1	69
				U20	1	59
				U5	1	49
9	*Juncus squarrosus*	57	8	M15	7	64 ± (6)
	Aulacomnium palustre	42		M25	2	63 ± (2)
	Agrostis canina	28		M6	1	56
10	*Eriophorum angustifolium*	58	9 (8)	M15	5	77 ± (7)
	Eriophorum vaginatum	55		M17	4	71 ± (11)
	Drosera rotundifolia	53		M25	1	82

Seed bank samples from 0-5 cm and 5-10 cm were combined for analysis of spatial variation resulting in a sample area of 785 cm^2 and volume of 7850 cm^3 for each seed bank group. DCA of the resulting 100 samples explained only 8.6% of the total variation in seed bank composition (Figure 6.4). As with the vegetation, seed bank groups overlapped. However, wet species and groups tended to appear at the upper end of the second axis. Grassland species and groups tended to appear to the right of the first axis with wet and dry heath species and groups further to the left.

The degree of overlap between seed bank groups was greater than the degree of overlap amongst target assemblages. Mantel's asymptotic approximation was used to evaluate the relationship between target assemblages and seed bank samples. There was a positive relationship between species composition and seed bank composition ($t = 2.42$, $p = 0.015$).

6.3.2 *Propagule availability*

Heterogeneity of variance means care must be exercised in interpreting the results of ANOVA because results can appear significant when in reality they are not. Levene's test indicates significant heterogeneity of variance for *Calluna vulgaris* ($t = 2.461$, $p = 0.015$), *Vaccinium myrtillus* ($t = 13.919$, $p = 0.000$), *Molinia caerulea* ($t = 6.504$, $p = 0.000$), *Agrostis capillaris* ($t = 4.437$, $p = 0.000$), *Carex pilulifera* ($t = 5.914$, $p = 0.000$) and *Juncus squarrosus* (Levene's test = 4.589, $p = 0.000$). Heterogeneity of variance can be discounted for both *Erica tetralix* ($t = 1.178$, $p = 0.319$) and *Ulex gallii* ($t = 0.956$, $p = 0.482$).

Figure 6.3. Sample (top) and species (bottom) ordinations of the 100 target assemblages using Detrended Correspondence analysis with ANOVA seed bank groups overlaid. Coefficients of variation, axis 1 = 0.16, axis 2 = 0.04.Selected species are labelled. Full names are displayed in Appendix 2.

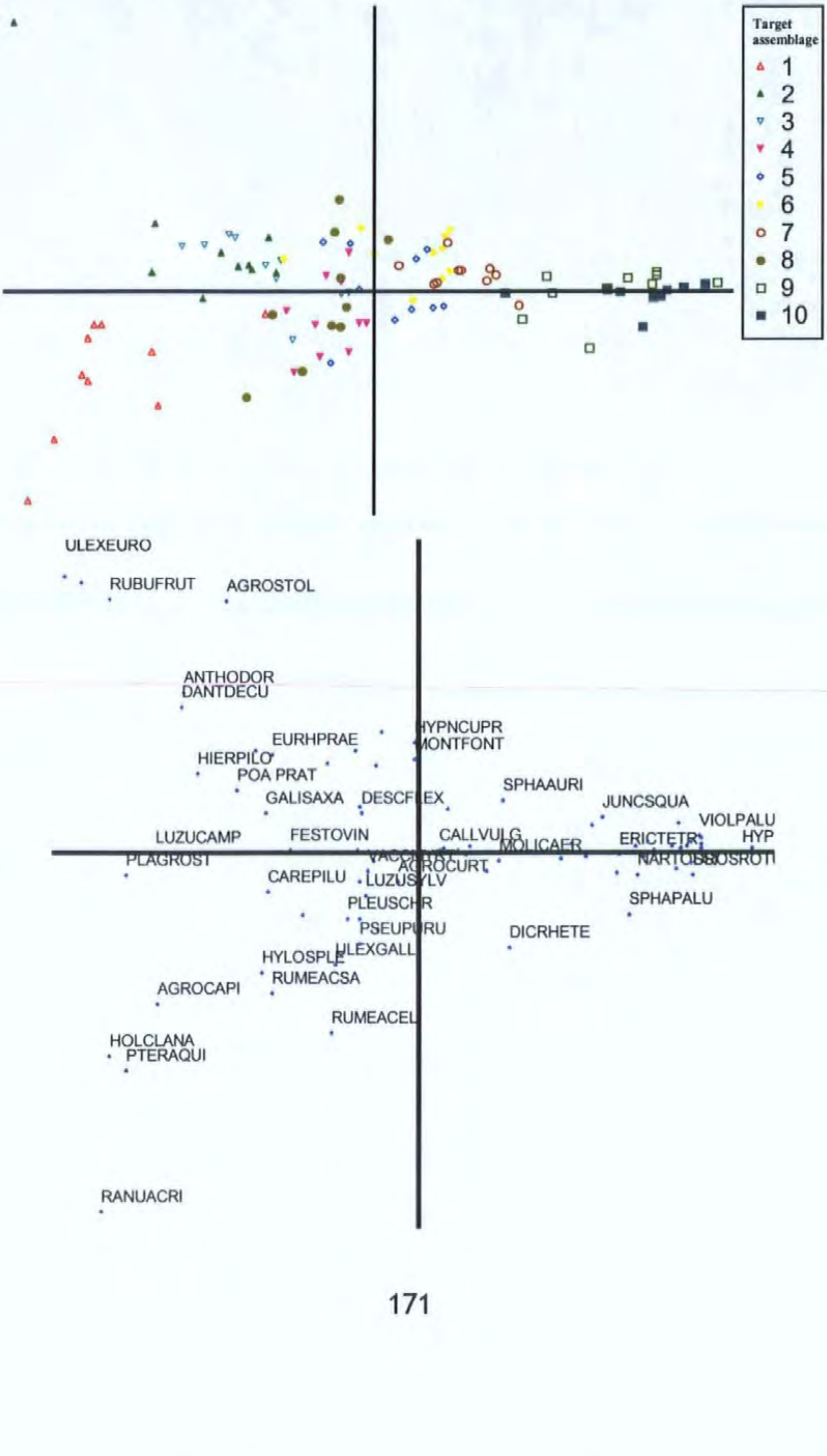
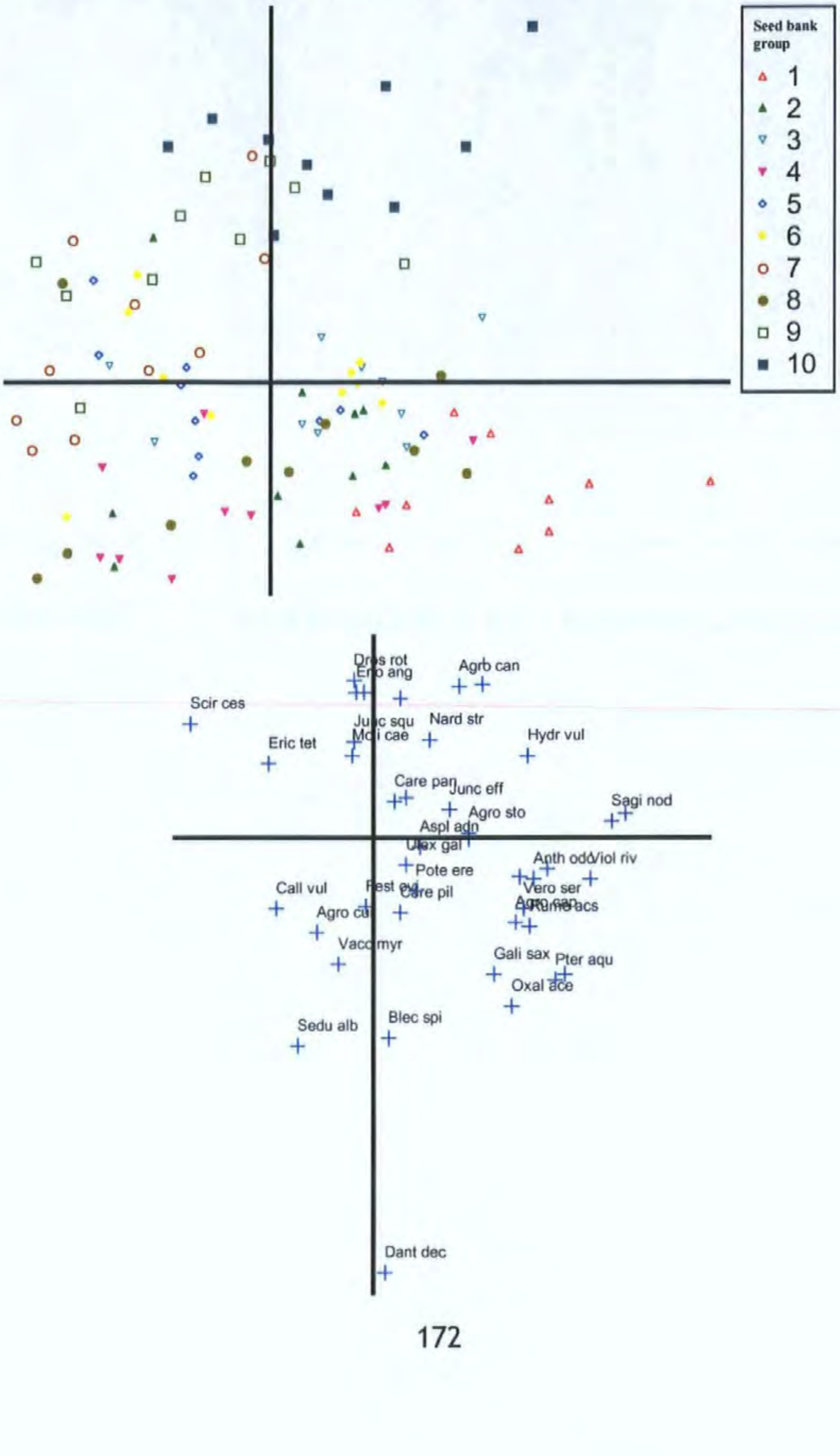


Figure 6.4. Sample (top) and species (bottom) ordination of 100 seed bank groups (depths combined) using Detrended Correspondence analysis with seed bank groups overlaid. Coefficients of variation, axis 1 = 0.047, axis 2 = 0.039. Selected species are labelled. Full names are displayed in Appendix 2.



SB4 has significantly more *Calluna vulgaris* propagules than the other communities (Table 6.2, Figure 6.5). SB8 contains significantly more *Vaccinium myrtillus* propagules than the other groups. *Calluna vulgaris* and *Vaccinium myrtillus* floristic composition and seed bank composition are related although *Calluna vulgaris* seed is found in communities where it is scarce amongst surface vegetation. The density of *Erica tetralix* and *Ulex gallii* seeds in the seed bank does not differ significantly between different seed bank groups. *Ulex gallii* is an indicator species for *Agrostis curtisii* grassland / *Agrostis curtisii-Ulex gallii* heath (4) Thus the floristic composition and seed bank composition of *Ulex gallii* are not related. *Erica tetralix* had high constancy in *Trichophorum cespitosum-Erica tetralix* wet heath (6) and *Sphagnum*-rich wet heath (8). Although not significant, *Erica tetralix* seed was found at maximum density in SB9, which is equivalent to *Sphagnum-rich* wet heath (8).

Juncus squarrosus, Agrostis capillaris, Molinia caerulea and *Carex pilulifera* were present in the seed bank at high densities and therefore have the potential to inhibit heathland restoration. SB9 had significantly more *Juncus squarrosus* seed than the other seed bank groups reflecting its abundance in *Sphagnum-rich* wet heath (8). SB1 and SB3 contain significantly more *Agrostis capillaris* seed than the other seed bank groups reflecting the abundance of *Agrostis capillaris* in *Pteridium aquilinum* dominated vegetation (2) and acidic grassland (3). SB3, SB9 and SB10 contain significantly more propagules of *Molinia caerulea* than the other seed bank groups, whilst SB4 has significantly more *Carex pilulifera* than other seed bank groups. This does not reflect the occurrence of these species in the vegetation, as both are cosmopolitan with low fidelity to any species assemblage although *Molinia caerulea* is characteristic of TA4.

6.3.3 Germination timing

Agrostis capillaris, Carex pilulifera and *Molinia caerulea* all germinate prior to dwarf-shrub species other than *Ulex gallii* in the greenhouse

(Figure 6.6). Seeds began to germinate in mid March with peaks in *Molinia caerulea* and *Carex pilulifera* abundance in June and July. *Agrostis capillaris* and *Vaccinium myrtillus* reach peak abundance at the end of July, whilst *Calluna vulgaris* and *Erica tetralix* do not reach peak abundance until August. *Juncus squarrosus* peaks prior to *Erica tetralix*. *Ulex gallii* emergence is very low but it does germinate prior to the other dwarf-shrub species.

6.3.4 Variation in seed bank composition with depth

Seed bank samples from 0-5 cm and 5-10 cm were analysed to examine variation in patterns between the two depths. Each seed bank group therefore had a sample area of 785 cm^2 and a volume of 3295 cm^3 at each depth. DCA of the resulting 200 samples explained only 7.6% of the total variation in seed bank composition (Figure 6.7). The patterns in seed bank composition at both depths are broadly similar (Mantel test, $t = 4.89$, $p = 0.000001$). Nevertheless, Two-way ANOVA and two-way ANOM, were used to assess the differences in seedling emergence from samples between groups and depths on a species by species basis (Table 6.3).

There are significant differences in emergence and hence seed density, at different depths for *Agrostis curtisii*, *Agrostis stolonifera*, *Anthoxanthum odoratum*, *Festuca ovina*, *Potentilla errecta* and *Asplenium adiantum nigrum* (Table 6.3, Figure 6.8). *Agrostis capillaris* and *Molinia caerulea* also exhibited significant differences although both had heterogeneity of variance, which can lead ANOVA to find significant differences where none exist (Levene's test, *Agrostis capillaris* $t = 3.310$, $p < 0.000$, *Molinia caerulea* $t = 9.808$, $p < 0.000$).

Two-way ANOVA did not indicate any significant differences with depth for *Vaccinium myrtillus* or *Calluna vulgaris* but Two-way ANOM does ($p<0.05$) suggesting that the mean of one group is separated from the other means (ANOVA tests for differences between treatment means, whereas ANOM tests whether treatments differ from an overall grand mean). However, ANOM is affected by heterogeneity of variance like ANOVA and both *Vaccinium myrtillus* and *Calluna vulgaris* exhibit significant heterogeneity of variance (Levene's test, *Calluna vulgaris*, t = 2.614, $p = 0.001$, *Vaccinium myrtillus* t = 5.659, $p = 0.000$). Two-way ANOM also indicates significant depth-group interactions for *Vaccinium myrtillus* and *Molinia caerulea* ($p < 0.05$).

Table 6.2. The density of seeds in the different seed bank groups on Bodmin Moor and the significance of the differences between groups.Maximum and minimum seed densities from the literature are included for comparison. Highlights indicate key results. Bold indicates one study only.

Species	Bodmin Moor seed bank groups (Mean density of seeds m^{-2})					Difference between groups. ANOVA df = 9					Densities (seeds m^{-2}) of other studies. (Thompson *et al.* 1997)				
	1	2	3	4	5	6	7	8	9	10	overall	F value	P value	Max	Min
Agrostis canina	0	0	0	0	0	0	12	12	165	546	73	2.6	0.009	5980	18
Agrostis capillaris	4318	1028	2311	635	88	152	50	825	25	0	943	10.4	0.000	1770	10
Agrostis curtisii	152	165	571	952	12	50	0	457	0	0	236	2.4	0.017	No data	
Agrostis stolonifera	1803	469	1727	787	419	368	50	1270	444	469	781	2.8	0.006	7300	8
Anthoxanthum odoratum	977	88	38	139	63	25	12	101	88	0	153	6.0	0.000	18928	3
Asplenium adiantum nigrum	3263	2743	3289	2870	4546	1714	266	1701	1193	1244	2283	1.4	0.195	*Pteridophyte*	
Blechnum spicant	0	63	0	25	0	0	0	0	0	0	8	1.7	0.098	*Pteridophyte*	
Calluna vulgaris	558	2514	1854	6654	2527	2298	2921	4381	3949	88	2774	2.3	0.020	68000	12
Carex binervis	0	101	152	25	0	76	0	25	203	50	63	2.0	0.042	423	7
Carex nigra	0	0	0	0	0	0	0	0	0	12	1	1.0	0.446	1002	9
Carex panicea	279	304	939	228	127	76	101	12	165	393	262	3.2	0.002	3090	12
Carex pilulifera	3238	2171	1524	4279	876	850	101	990	254	546	1483	5.0	0.000	5180	21
Danthonia decumbens	0	12	0	0	0	0	0	0	0	0	1	1.0	0.446	958	12
Digitalis purpurea	88	0	0	0	0	0	0	177	0	0	26	1.1	0.336	7138	7
Drosera rotundifolia	0	0	0	0	0	0	0	0	0	381	38	2.7	0.007	52	52
Erica tetralix	63	1257	977	762	1536	977	1054	508	3543	965	1164	1.2	0.270	6010	56
Eriophorum angustifolium	0	0	0	0	0	0	0	0	0	38	3	1.9	0.051	417	417

Table 6.2. Continued

Species	Bodmin Moor seed bank groups (Mean density of seeds m^{-2})					Difference between groups. ANOVA df = 9					Densities (seeds m^{-2}) of other studies. (Thompson *et al.* 1997)				
	1	2	3	4	5	6	7	8	9	10	overall	F value	P value	Max	Min
Festuca ovina	101	304	228	215	88	215	12	76	25	0	127	2.2	0.024	5236	8
Galium saxatile	533	0	76	63	0	38	0	228	0	0	93	6.4	0.000	7855	11
Holcus lanatus	698	0	0	0	0	0	0	76	0	0	77	5.5	0.000	16900	5
Hydrocotyle vulgaris	0	0	749	0	0	0	0	0	165	12	92	0.9	0.487	3933	8
Juncus bulbosus	457	152	457	139	38	101	63	101	38	3060	461	8.4	0.000	8436	31
Juncus effusus	1257	63	88	609	63	152	50	749	952	241	422	1.4	0.176	680000	13
Juncus squarrosus	0	330	25	88	228	1193	1079	1625	6985	1130	1268	8.9	0.000	12276	32
Luzula campestris	76	25	12	0	0	0	0	12	38	0	16	2.1	0.033	9600	3
Molinia caerulea	660	1193	3937	546	635	596	965	482	4737	3276	1703	11.4	0.000	8850	22
Nardus stricta	12	12	12	0	0	0	0	0	12	12	6	0.5	0.830	525	50
Narthecium ossifragum	0	0	0	0	0	0	0	0	279	355	63	2.1	0.035	227	76
Oxalis acetosella	25	12	0	0	0	0	0	0	0	0	3	1.6	0.116	2139	2
Potentilla erecta	711	635	838	1790	101	723	25	622	292	63	580	3.2	0.002	1363	1
Pteridium aquilinum	25	0	0	0	0	0	0	0	0	0	2	1.0	0.446	*Pteridophyte*	
Rubus fruticosus	25	0	0	0	0	0	0	0	0	0	2	1.0	0.446	1440	6
Rumex acetosa	177	0	12	127	0	0	0	0	0	0	31	0.8	0.549	8268	7
Rumex acetosella	0	0	0	63	0	0	0	0	0	0	6	1.0	0.446	10102	3

Table 6.2. Continued

Species	Bodmin Moor seed bank groups (Mean density of seeds m^{-2})					Difference between groups. ANOVA df = 9					Densities (seeds m^{-2}) of other studies. (Thompson *et al.* 1997)				
	1	2	3	4	5	6	7	8	9	10	overall	F value	P value	Max	Min
Sagina nodosa	457	25	12	0	0	0	0	0	0	0	49	1.0	0.411	500	500
Sedum album	0	0	0	0	0	0	0	25	0	0	2	1.0	0.446	150	150
Trichophorum cespitosum	0	0	0	0	0	0	139	0	317	0	45	0.9	0.513	1070	151
Ulex gallii	50	76	12	25	12	12	12	0	0	0	20	0.9	0.482	707	126
Vaccinium myrtillus	0	12	0	76	0	12	0	698	12	12	82	11.7	0.000	2780	11
Veronica serpyllifolia	0	0	12	139	0	0	0	0	0	0	15	0.9	0.462	2670	3
Viola riviniana	76	0	0	0	0	0	0	0	0	0	7	3.1	0.003	191	7

Figure 6.5. Density of seeds of dwarf-shrub heath species and their potential competitors in the seed bank groups (1–10) on Bodmin Moor.

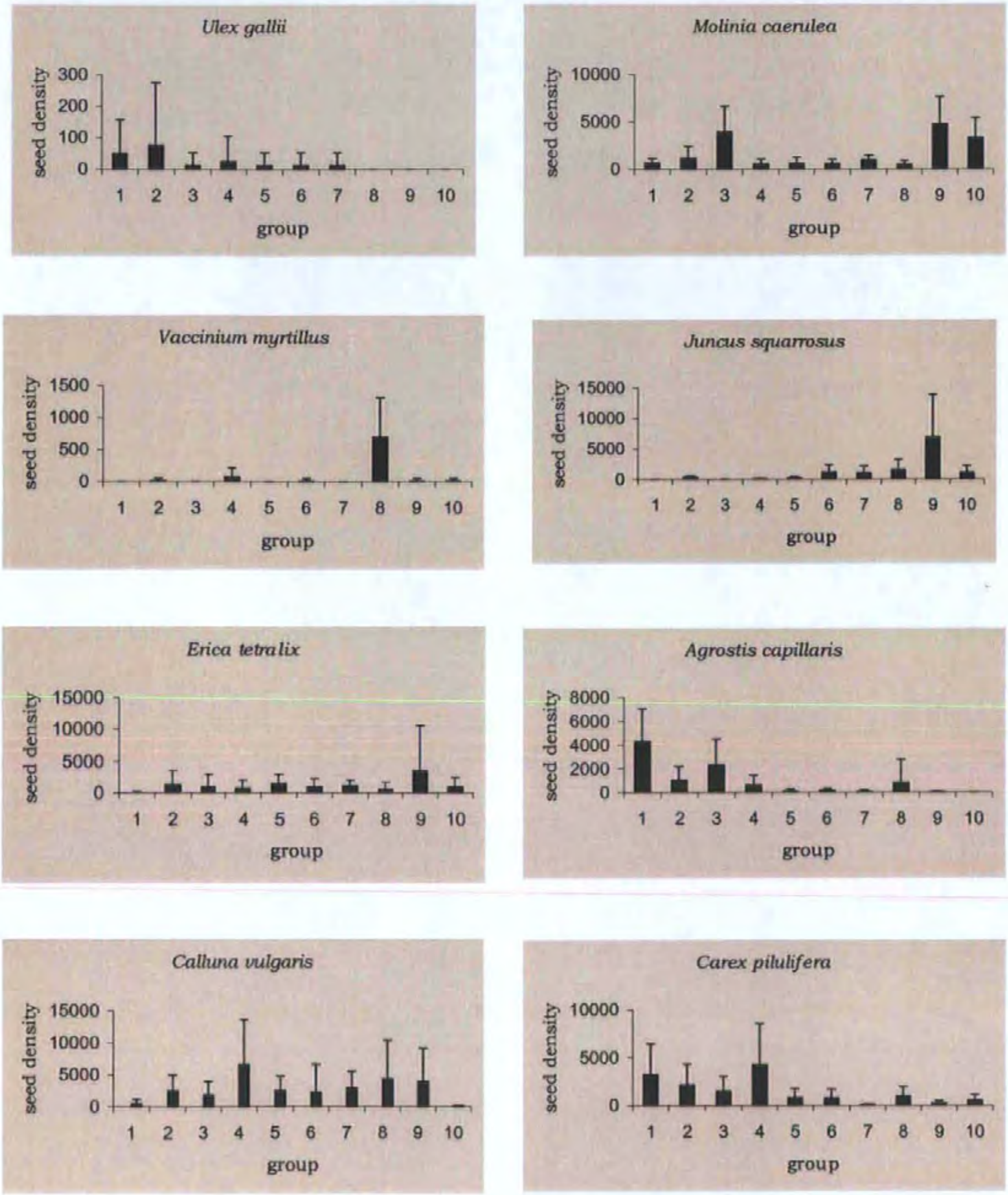


Figure 6.6. The timing of germination for dwarf-shrub heath species and some of their potential competitors.

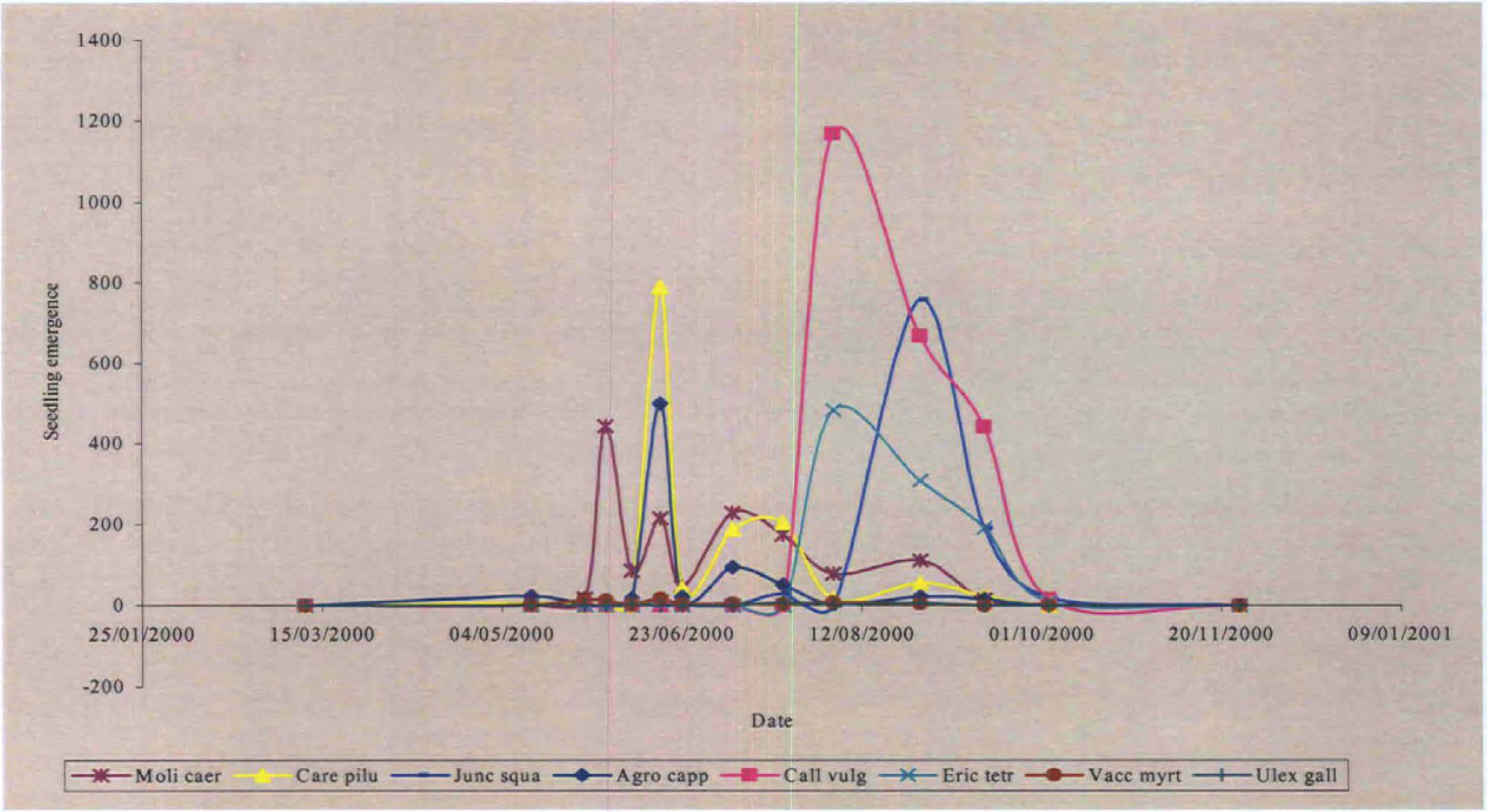


Figure 6.7. Quadrat ordination of 200 seed bank samples with depth overlaid (top) and seed bank group overlaid (bottom), using Detrended Correspondance Analysis.Samples from different depths but the same sites are linked. Coefficients of variation, axis one = 0.034, axis two = 0.042

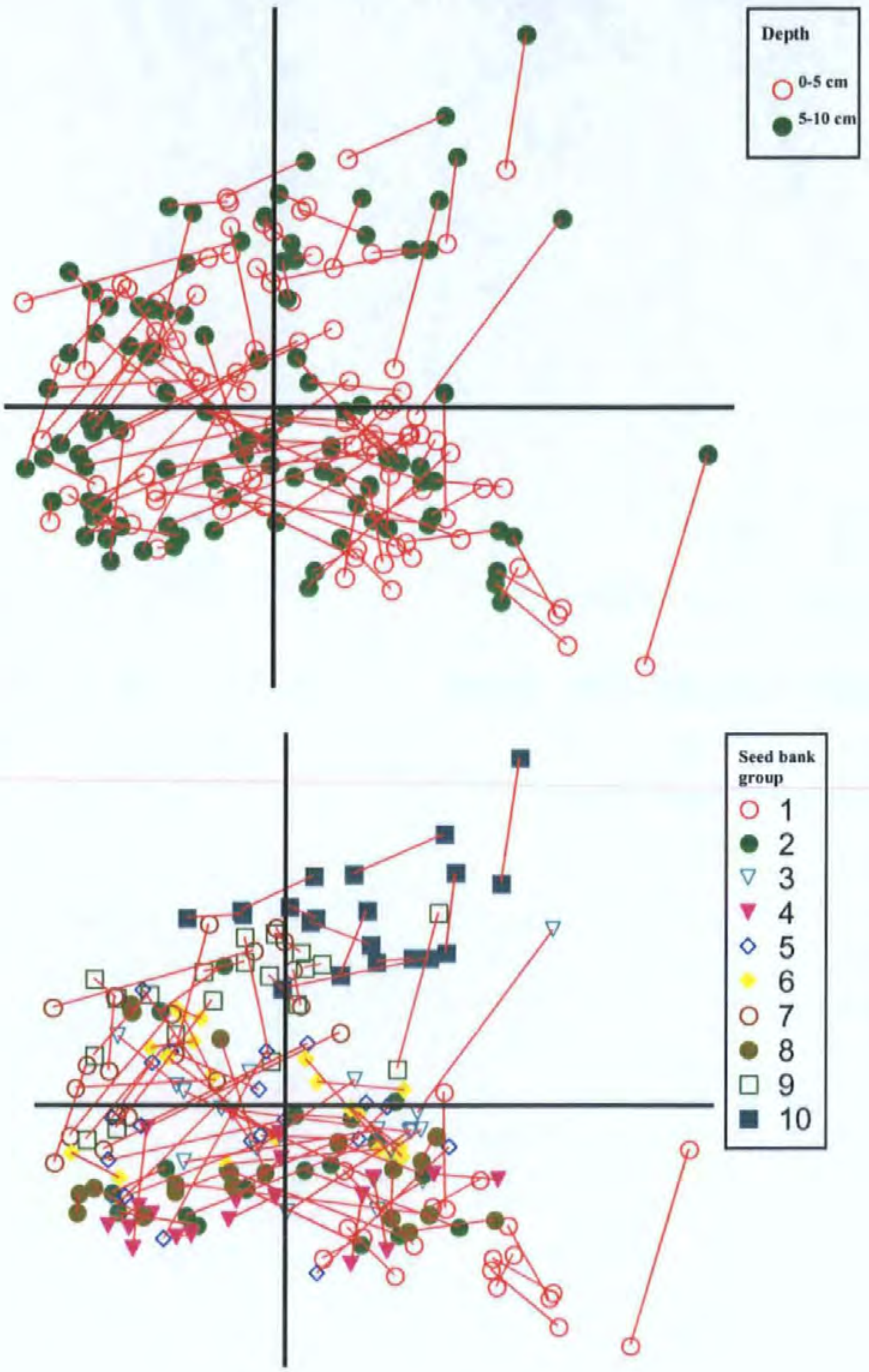


Table 6.3. The effect of depth of seed bank sample on emergence. Regenerative strategies from literature are included where available.Highlights indicate key results. Negative figures indicate greater abundance in the lower layers of the soil profile than in the upper layers.

Species	ANOVA (two-way) Factor: Depth		Differences between seedling emergence for depth (0-5 cm - 5-10 cm) by group. (based on sample means)										Seed bank type (maximum longeivity, years)	Regenerative Strategies
	F value	P value	1	2	3	4	5	6	7	8	9	10		
Agrostis canina	1.77	0.185							1	1	-0.25	1.67	I - IV	Vegetative expansion, Persistent seed bank
Agrostis capillaris	14.74	0.000	2.98	5.95	4.66	2.77	1	0.83	4	6.5	1		I-IV (> 40)	Vegetative expansion, Persistent seed bank
Agrostis curtisii	7.0	0.009	3.66	-0.33	2.76	2.90	1	1		1.46				Not previously reported
Agrostis stolonifera	12.82	0.000	3.80	0.484	2.76	-1.11	1.12	1.38	2	0.20	0.25	5.3	I - IV	Vegetative expansion, Persistent seed bank
Anthoxanthum odoratum	9.34	0.003	2.14	1.75	1.5	0.6	1.66	1	1	0.66	0.5		I - IV (> 2)	Seasonal regeneration, Persistent seed bank
Asplenium adiantum nigrum	5.47	0.02	-0.07	4.07	-0.69	-0.62	0.81	2.61	1	-0.69	2.5	1.58	Pteridophyte	
Blechnum spicant	3.03	0.084		-2.5		-2							Pteridophyte	
Calluna vulgaris	3.86	0.051	0.58	-0.10	-1.92	8.60	1.15	5.02	5.53	6.6	-0.71	-0.25	I - IV (> 68)	Persistent seed bank
Carex binervis	1.11	0.294		1.33	0.3	-1		-1		-1	1.1	1.33	I, II, IV.	
Carex nigra	1.0	0.319										1	I - IV	Vegetative expansion, Persistent seed bank
Carex panicea	0.78	0.377	-22	-3.4	1.2	7.5	-0.8	-2	-0.2	-1	0.2	-0.08	I - IV	Vegetative expansion, Persistent seed bank?
Carex pilulifera	0.46	0.498	-0.32	-1	1.67	2.45	0.05	0.90	1.33	-3	0	-0.81	I - IV (> 68)	Vegetative expansion, Persistent seed bank

Table 6.3. Continued.

Species	ANOVA (two-way) Factor: Depth		Differences between seedling emergence for depth (0-5 cm - 5-10 cm) by group. (based on sample means)										Seed bank type (maximum longeivity, years)	Regenerative Strategies
	F value	P value	1	2	3	4	5	6	7	8	9	10		
Danthonia decumbens	1.0	0.319		1									I, II, IV.(> 2)	Persistent seed bank
Digitalis purpurea	1.0	0.318	-0.5							-0.66			I - IV (> 3)	
Drosera rotundifolia	2.1	0.149										1.8	II	
Erica tetralix	2.41	0.122	5	1.87	0.27	3	0.52	2.75	1.52	4.28	-2.45	0.36	I - IV (> 30)	
Eriophorum angustifolium	1.89	0.171										1.5	I, II, IV. (2)	Vegetative expansion, numerous widely dispersed seeds
Festuca ovina	18.55	0.000	0.25	1.3	2	-0.03	1	2.2	1	-1.5	1		I -IV	Vegetative expansion, Persistent seed bank
Galium saxatile	0.02	0.902	-0.40		0	0.33		-1		0.3			I - IV (> 120)	Vegetative expansion, Persistent seed bank
Holcus lanatus	1.14	0.287	0.98							-3			I - IV (> 12)	Seasonal regeneration, Vegetative expansion, Persistent seed bank
Hydrocotyle vulgaris	1.15	0.286			-57						0.5	1	I, III, IV.	Vegetative expansion
Juncus bulbosus	0.97	0.325	-2	4	-3.66	8	0	2.66	-1	4	0	-4.36	I - IV (> 30)	Vegetative expansion, Persistent seed bank
Juncus effusus	0.14	0.706	-2.89	2	-0.25	-5.2	1.25	-2.33	0.5	2.54	-1.66	0.2	I - IV (> 50)	Vegetative expansion, Persistent seed bank
Juncus squarrosus	0	0.952		-2.37	-2	5	-0.5	0.83	-0.28	1.89	-8.53	0.07	I - IV (> 35)	Vegetative expansion, Persistent seed bank

Table 6.3. Continued.

Species	ANOVA (two-way) Factor: Depth		Differences between seedling emergence for depth (0-5 cm - 5-10 cm) by group. (based on sample means)										Seed bank type (maximum longeivity, years)	Regenerative Strategies
	F value	P value	1	2	3	4	5	6	7	8	9	10		
Luzula campestris	0.07	0.798	0.5	0	1					-1	1		I - IV (> 100)	Vegetative expansion, Persistent seed bank
Molinia caerulea	55.64	**0.000**	**1.19**	**1.69**	**2.72**	**0.70**	**0.05**	**0.31**	**0.94**	**0.73**	**3.82**	**3.18**	I - IV (> 4)	Vegetative expansion, Persistent seed bank?
Nardus stricta	0.2	0.656	-1	1	1						1	-1	I - IV	Vegetative expansion, Persistent seed bank
Narthecium ossifragum	1.71	0.192									-0.19	0.38	I, II, IV.	
Oxalis acetosella	3.14	0.078	1	1									I, II, IV.	Seasonal regeneration, Vegetative expansion, Persistent seed bank?
Potentilla erecta	4.01	**0.047**	**0.61**	**0.22**	-1.55	**1.91**	**0.16**	**2.76**	0	**0.29**	-1	**0.33**	I - IV (> 100)	Vegetative expansion, Persistent seed bank
Pteridium aquilinum	1.00	0.319	-1										Pteridophyte	Numerous widely dispersed spores, Vegetative expansion, Persistent seed bank?
Rubus fruticosus	1.00	0.319	-2										I - IV	Vegetative expansion, Persistent seed bank
Rumex acetosa	0.77	0.381	5.5		-1	-1							I - IV (> 12)	Seasonal regeneration, Persistent seed bank
Rumex acetosella	1.0	0.319				5							I - IV (> 26)	Vegetative expansion, Persistent seed bank
Sagina nodosa	1.0	**0.319**	-12	0	1								III	
Sedum album	1.0	**0.319**								2			IV	

Table 6.3. Continued.

Species	ANOVA (two-way) Factor: Depth		Differences between seedling emergence for depth (0-5 cm - 5-10 cm) by group. (based on sample means)										Seed bank type (maximum longeivity, years)	Regenerative Strategies
	F value	P value	1	2	3	4	5	6	7	8	9	10		
Trichophorum cespitosum	1.74	0.188							11		25		I,II, IV.	
Ulex gallii	0.1	0.756	-1.33	2	-1	-2	1	-1	-1				III, IV.	
Vaccinium myrtillus	3.65	0.058		-1		1.5		1		-0.05	-1	1	I - IV (> 5)	Vegetative expansion, Persistent seed bank
Veronica serpyllifolia	0.82	0.367			-1	11							I - IV (>100)	
Viola riviniana	0	1.0	-1.5										I, IV	Vegetative expansion, Persistent seed bank

Figure 6.8. Density of seeds of dwarf-shrub heath species and their potential competitors at different depths in the seed bank groups (1–10) on Bodmin Moor. A, depth 0-5cm; B, depth 5-10cm.

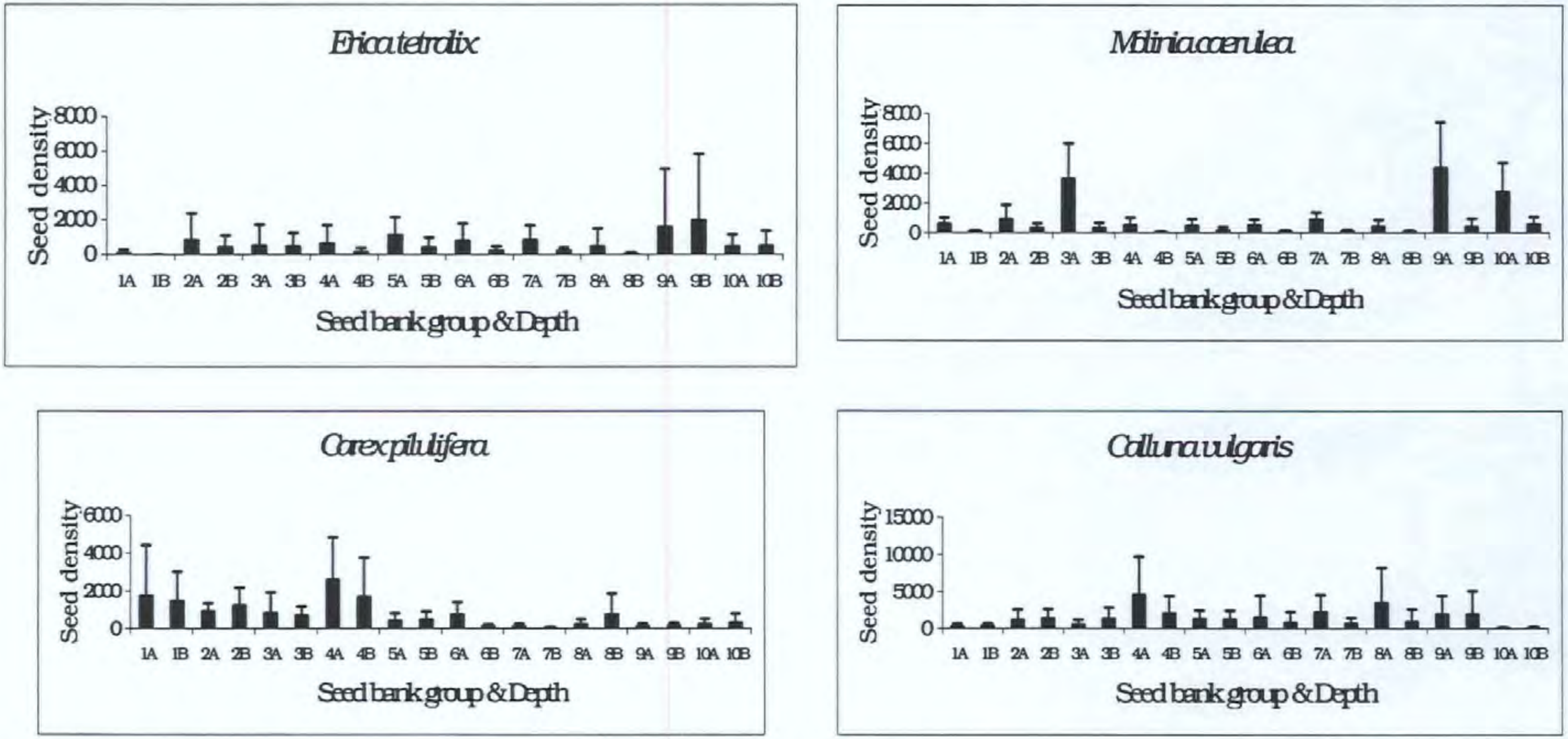
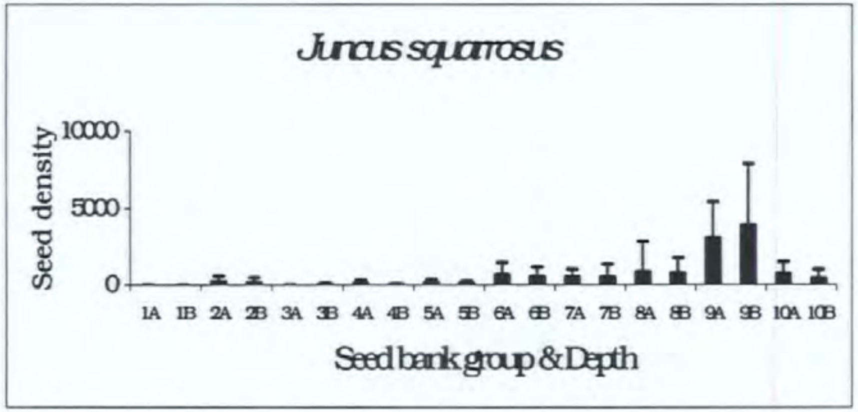
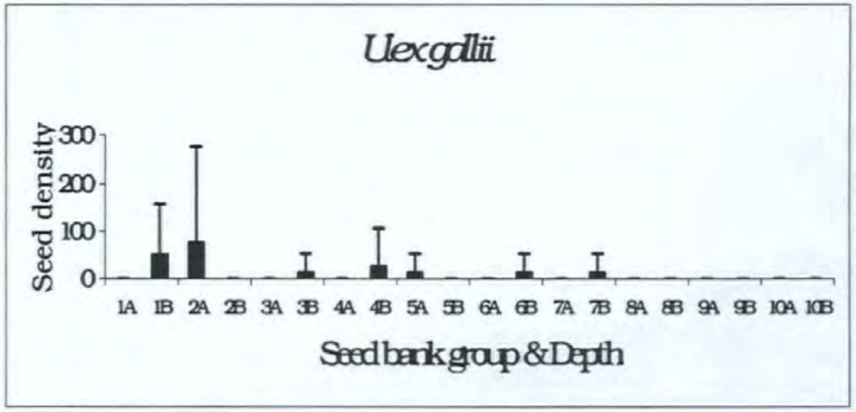
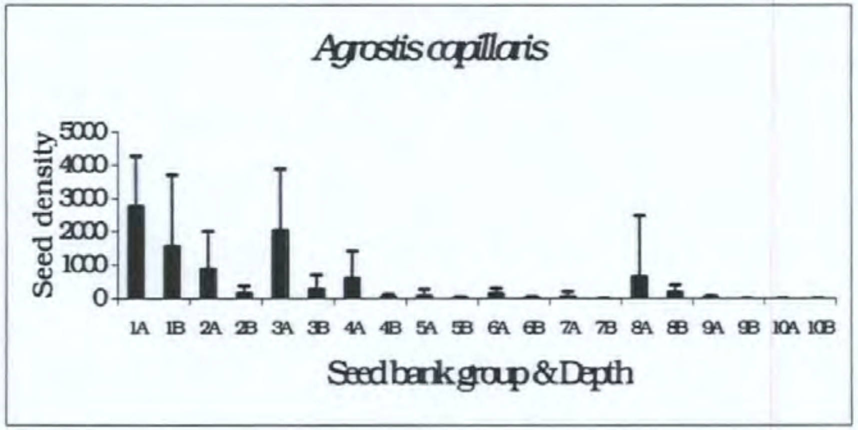
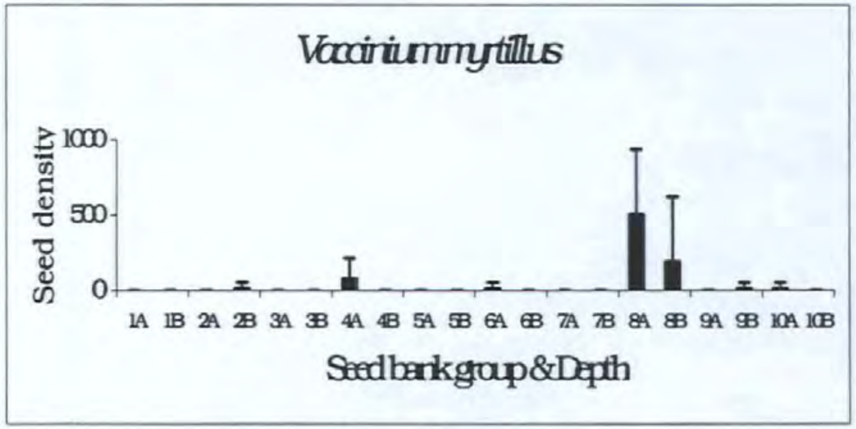


Figure 6.8. Continued.









6.4 Discussion

6.4.1 Surface vegetation

The vegetation of Bodmin Moor was described fully in Chapter Five. The vegetation samples in this chapter represent a sub-set of the full phytosociological data set. The use of 100 of the original 312 samples resulted in the removal of 46 species reflecting the removal of mesotrophic grassland (1), *Eriophorum angustifolium* valley bog (10) and soligenous soakway vegetation (11). TA1, TA2 and TA9 were directly referable to *Pteridium aquilinum*-dominated vegetation (2), flushed rill vegetation (5) and *Sphagnum*-rich wet heath (8) respectively. TA1, TA2 and TA9 contained characteristic vegetation with a limited number of difficult-to-classify intermediates. TA7, TA8 and TA10 largely represented *Trichophorum cespitosum-Erica tetralix* wet heath (6), *Vaccinium myrtillus-Calluna vulgaris* heath (7) and *Narthecium ossifragum-Eriophorum vaginatum* blanket bog (9) respectively, although some samples fell into other species assemblages. These samples probably represent transitional vegetation with affinities to more than one assemblage. Acidic grassland (3) and *Agrostis curtisii* grassland / *Agrostis curtisii-Ulex gallii* heath / grass-heath (4) were split because they are large assemblages and incorporate some difficult intermediates. Acidic grassland (3) was represented by TA2 and TA3, whilst *Agrostis curtisii* grassland / *Agrostis curtisii-Ulex gallii* heath / grass-heath (4) was represented by TA4 and TA5. TABLEFIT and Indicator Species Analysis did not allow meaningful differentiation of TA2 and TA3. They were predominantly *Agrostis-Festuca* grassland, although TA3 may represent vegetation with a slightly more dwarf-shrub heath character as indicated by *Hypnum jutlandicum*. However, TA4 and TA5 were differentiated by TABLEFIT and Indicator Species Analysis. TA4 represented *Agrostis curtisii* grassland, *Agrostis curtisii-Ulex gallii* grass-heath and *Agrostis curtisii-Ulex gallii* heath (4) with abundant *Agrostis curtisii*, *Ulex gallii* and *Hypnum cupressiforme* and good fits to the *Agrostis curtisii* grassland and *Agrostis curtisii-Ulex gallii* heath NVC communities. TA5 represented similar vegetation with a lesser dwarf-shrub component and more abundant *Molinia caerulea*. This is reflected in a reduction in the proportion of heathland samples, lower TABLEFIT scores for heathland, high TABLEFIT scores for the *Molinia caerulea-Potentilla errecta* NVC community and the occurrence of *Molinia caerulea* as an indicator species.

Ordination of the vegetation samples using DCA revealed similar patterns to those generated in Chapter Five, as the vegetation was subject to the same underlying controls. Axis one corresponded to moisture gradient. Thus mire and wet heath assemblages (6, 8, 9, 10, 11) and species were found at the right hand end of the first axis, with drier assemblages (2, 3, 4, 5, 7) and species at the left hand end. The second axis remained unexplained in terms of environmental gradients in contrast to the second axis on the full phytosociological data set. This may reflect the need for large sample sizes to detect vegetation-environment interactions in multivariate data sets. It is unlikely to indicate that the controlling factors identified in chapter Five for species assemblages do not apply to the target assemblages of this chapter.

In general, the DCA ordination supports the classification derived using target assemblages with reasonably discrete groups of samples forming a continuum. However, TA2 and TA3 were juxtaposed corroborating TABLEFIT and Indicator Species Analysis, which do not allow meaningful differentiation between these groups.

6.4.2 Spatial variation in the composition of seed bank samples

There was a positive relationship between the floristic composition of target assemblages and seed bank groups. However, the seed bank groups were more variable in composition than the target assemblages of surface vegetation they were taken from. Therefore the outcome of a particular management prescription reliant on seed bank propagules may also be variable within a target assemblage. The fact that subtle variations in target assemblage composition were not reflected in seed bank composition while major variation in target assemblages were more closely related is consistent with other work on heathlands, where vegetation composition was related to both seed rain and seed bank composition at a large scale (Miles 1973, Mallik *et al.* 1984). The smaller scale discrepancies in composition were probably due to differential production, predation, dispersal and persistence of seed. They are consistent with other work (Hester *et al.* 1991) and suggest that attempts to relate changes in vegetation, seed rain and seed bank composition to management would require very intensive sampling.

These results indicate that 'Moorland Management' and 'Moorland Restoration' will be most successful where heathland in good condition is already present. However, seed bank composition was more variable than the floristic composition within a group suggesting that the result of management within a community may not be uniform. It also suggests that the distribution of individual species in the seed bank may not reflect their above-ground distribution in every case. Further analysis is necessary to ascertain how the target species of 'Moorland Management' and 'Moorland Restoration' are distributed in the seed bank.

6.4.3 Propagule availability for dwarf-shrub regeneration

Calluna vulgaris

Calluna vulgaris had significantly different densities of seed beneath different communities. SB4 had significantly more *Calluna vulgaris* seed in the seed bank than the other communities. Heathland restoration relying on seed from the seed bank is therefore most likely to result in an increase in *Calluna vulgaris* in *Agrostis curtisii* grassland, *Agrostis curtisii-Ulex gallii* grass-heath and *Agrostis curtisii-Ulex gallii* heath. SB4 had a mean seed density of 6655 *Calluna vulgaris* seeds m^{-2}, compared with 2775 m^{-2} overall on Bodmin Moor. These are low densities compared to other figures from the literature for the UK (Table 6.4).

Table 6.4. Density of *Calluna vulgaris* seed in the UK under heathland.

Site	Density m^2	Vegetation type	Source
North York Moors	204000 - 1066000	*Callunetum*, *Calluna-Eriophorum* mire	Legg, Maltby, Proctor 1992
Cairngorms	50 - 3000	Montane heath	Bayfield 1984
Aberdeenshire	1700	*Callunetum*	Miles 1973
Various UK	< 8000	Upland & lowland heath	Putwain & Gillham 1990
Aberdeenshire	23000	Montane heath	Mallik, Hobbs & Legg 1984
Cairngorms	68,000	Montane heath	Miller & Cummins 1987
Cairngorms	69000	Montane heath	Miller & Cummins 1981

The relatively low density of *Calluna vulgaris* in the seed bank on Bodmin Moor is a consequence of the low abundance of *Calluna vulgaris* in vegetation on Bodmin Moor in comparison to other upland areas. Unsurprisingly, more seed was found under vegetation types that contain *Calluna vulgaris*, such as the *Agrostis curtisii* - *Ulex gallii* heath of assemblage Four (SB4 and SB5) and the *Calluna vulgaris-Vaccinium myrtillus* heath of assemblage Seven (SB8). This is probably due to the poor dispersal of *Calluna vulgaris* (Welch *et al.* 1990). In the North York Moors, *Calluna vulgaris* seed rain density was inversely proportional to the dispersal distance, resulting in an annual seed rain of 25 seeds m^{-2} at 10 m from source plants (Legg *et al.* 1992). Thus *Calluna vulgaris* seed is unlikely to be present in the seed bank in large quantities, unless *Calluna vulgaris* is or has been present amongst surface vegetation.

However, more seed was present on Bodmin Moor than was found by Miles (1973) under *Callunetum* in Aberdeenshire, except in mire communities and *Pteridium aquilinum*-dominated vegetation (2) and this was sufficient to allow heathland regeneration in the absence of competition from above-ground species. Gimingham, C. (University of Aberdeen. *Pers. comm.*) considers the numbers of *Calluna vulgaris* seeds on Bodmin Moor low but still sufficient as a source of propagules for upland heath regeneration, except in the wettest and driest assemblages.

Erica tetralix

In contrast to *Calluna vulgaris*, there was no significant difference in the density of *Erica tetralix* seed in the seed bank beneath different communities. Overall seed bank density for *Erica tetralix* on Bodmin Moor was 1165 seeds m^{-2} rising to a maximum of 3543 seeds m^{-2} in SB9 (*Sphagnum*-rich *Scirpus cespitosus-Erica tetralix* wet heath (8), and falling to a minimum of 64 seeds m^{-2} in SB1 (*Pteridium aquilinum-Galium saxatile* community (2). The density of *Erica tetralix* seed on Bodmin Moor was probably low relative to other UK upland areas, although there is a paucity of accessible information. Hester *et al.* (1991) report densities of 56 - 295 seeds m^{-2} in *Callunetum* under a *Betula* canopy. However, on lowland heath densities of 17760-4049 have been reported (Pywell *et al.* 1996). Seeds of *Erica tetralix* were more abundant beneath surface vegetation containing *Erica tetralix* plants indicating that its dispersal ability is poor, thus corroborating the findings of Welch *et al.* (1990). There is a paucity of information on the quantities of *Erica tetralix* seed required for heathland restoration. It is therefore not possible to determine if seed availability will restrict establishment of *Erica tetralix* on Bodmin Moor.

Vaccinium myrtillus

Vaccinium myrtillus had significant differences in seed bank density beneath differing vegetation types. SB8 (*Calluna vulgaris-Vaccinium myrtillus* heath (7) had 699 seeds m^{-2} compared to 83 seeds m^{-2} overall and was significantly different from other groups. SB4 (*Agrostis curtisii - Ulex gallii* heath (4) was also elevated relative to other groups with 76 seeds m^{-2}. This reflects the above-ground distribution of *Vaccinium myrtillus* on Bodmin Moor and is consistent with the low seed dispersal, storage and dependence on vegetative spread of *Vaccinium myrtillus* (Thompson & Grime 1979, Hill & Stevens 1981, Hester *et al.* 1991). It suggests that attempts to regenerate *Vaccinium myrtillus* will only be successful where there are appreciable quantities of *Vaccinium myrtillus* in the vegetation. In the case of Bodmin Moor, this largely restricts restoration efforts to *Calluna vulgaris-Vaccinium myrtillus* heath (7) on the tors.

Ulex gallii

The density of *Ulex gallii* seeds in the seed bank did not differ significantly between different communities. Overall on Bodmin Moor there were 20 *Ulex gallii* seeds m^{-2} rising to a maximum of 76 seeds m^{-2} in SB2 (Acidic grassland (3). The density of *Ulex gallii* seeds on Bodmin Moor was low compared to the 662 seeds m^{-2} found under moorland plantations in Wales (Hill & Stevens 1981). The distribution of *Ulex gallii* in the seed bank did not reflect the above ground distribution of *Ulex gallii*, which was characteristic of TA4 (*Agrostis curtisii* - *Ulex gallii* heath (4). However, two samples in TA2 were classified as *Agrostis curtisii* - *Ulex gallii* heath indicating that at least some *Ulex gallii* was present amongst acid grassland. *Ulex gallii* seed was present where *Ulex gallii* was not present in the vegetation, suggesting that factors other than seed availability were of importance in its establishment. It also implies that *Ulex gallii* possesses efficient dispersal mechanisms or that a seed bank has persisted, and that the former distribution of *Ulex gallii* was different from the current distribution on Bodmin Moor. There is no information on the quantities of *Ulex gallii* seed required for heathland restoration. Clearly more work is necessary to elucidate not only the number of propagules that are required for heathland restoration but what factors are necessary for successful regeneration when the seed is present.

6.4.4 Competitive interactions between germinating species within safe-sites

Heathland restoration relies on the availability of propagules in the seed bank if recolonisation by vegetative spread is not occurring or is too slow and there are no additional increments from other sources. All things being equal, the more seed there is, the more successful restoration is likely to be. However, the presence of large quantities of seed of the desired species does not of itself guarantee successful heathland restoration. The quantities of *Calluna vulgaris* seed on Bodmin Moor are sufficient for heathland restoration in the absence of competition (Gimingham, C. University of Aberdeen. *Pers. comm.*, Miles 1973). It is not clear if the other species are present in sufficient numbers to allow restoration because the focus of heathland resoration has been on *Calluna vulgaris*, therefore little data exists for the other heathland species. Following germination, the seedlings must establish and survive if restoration is to be successful.

The early growth of a seedling is the most vulnerable stage in the plant life cycle (Fenner 1985). Competition from other plants may kill any emerging seedlings. Thus safe-sites must be free from competition. The creation of bare patches eliminates competition from established species (Miles 1973, Hester *et al.* 1991, Britton *et al.* 2000), but seeds of species other than the desired species could germinate and potentially out-compete the desired species. Thus the abundance and distribution of non-dwarf-shrub species in the seed bank is also of relevance in assessing the likely outcome of restoration attempts.

On Bodmin Moor, *Asplenium adiantum nigrum, Molinia caerulea, Carex pilulifera, Juncus squarrosus* and *Agrostis capillaris* were present at higher densities than other non-dwarf-shrub species. Assuming that all seeds are equally likely to survive after germination, then these species are the most likely to compete with dwarf-shrub species for safe-sites. *Asplenium adiantum nigrum* is common in lanebanks across South-west Britain (Page1997), but was absent from the above-ground vegetation of Bodmin Moor. Its abundance in the seed bank is probably due to long distance dispersal of spores, although airborne contamination of samples cannot be discounted. In either case, it is unlikely to compete for regeneration niches with dwarf-shrub heath seedlings. The other species were abundant in the vegetation as well as the seed bank, and are therefore considered as potential competitors for safe-sites.

Molinia caerulea

The density of *Molinia caerulea* seed was significantly different beneath the different communities of Bodmin Moor. SB3 (Acidic grassland (3), SB9 (*Sphagnum*-rich *Scirpus cespitosus-Erica tetralix* wet heath (8) and SB10, (*Narthecium ossifragum-Eriophorum vaginatum* blanket mire (9) had significantly more *Molinia caerulea* seeds than the other seed bank groups. The density of *Molinia caerulea* seed in SB9, SB3 and SB10 was 4737 seeds m^{-2}, 3937 seeds m^{-2} and 3277 seeds m^{-2} respectively, compared to an overall mean of 1703 seeds m^{-2}. These figures are lower than the maximum recorded density of 8850 seeds m^{-2} (Poschlod 1990), but considerably higher than other UK figures of 87 seeds m^{-2} (Hill & Stevens 1981) or 146 seeds m^{-2} (Pywell *et al.* 1996). The low UK figures could reflect failure to provide suitable germination conditions for *Molinia caerulea.* If seed is not pre-chilled, then *Molinia caerulea* has low germination success, unless temperatures are high (Grime *et al.* 1981). The distribution of *Molinia caerulea* seed did not appear to reflect the distribution of *Molinia caerulea* in the vegetation. suggesting one or a combination of explanations:

- factors other than seed availability are of importance in the establishment of *Molinia caerulea.*
- *Molinia caerulea* posesses efficient dispersal mechanisms.
- *Molinia caerulea* has a persistent seedbank.
- The former distribution of *Molinia caerulea* was different from the current distribution on Bodmin Moor.

The first point is consistent with the existing knowledge of the ecology of *Molinia caerulea,* which is known to reproduce primarily through lateral vegetative spread (Grime *et al.* 1990, Taylor *et al.* 2001). Likewise, seed dispersal is effective. *Molinia caerulea* has compact inflorescences on long stalks, which often persist into winter, when strong winds disperse the seeds carrying them long distances (Taylor *et al.*2001). The third point is debated. Some work suggests that *Molinia caerulea* seed is short-lived (Thompson *et al* 1997), but others argue that it has a persistent seed bank (Pons 1989, Grime *et al.* 1990). There is no information concerning the inhibitory effects of germinating *Molinia caerulea* seedlings on dwarf-shrub species although competition from established *Molinia caerulea* prevents heathland establishment (Backshall *et al.* 2001).

Carex pilulifera

Carex pilulifera had significantly different densities of seed beneath different communities. SB4 (*Agrostis curtisii- Ulex gallii* heath (4) had significantly more *Carex pilulifera* seed in the seed bank than the other communities with a mean seed density of 4280 *Carex pilulifera* seeds m^{-2} compared with 1483 m^{-2} overall on Bodmin Moor. This is a high density compared to 3 seeds m^{-2} (Hill & Stevens 1981) in Wales but lower than the maximum density recorded in South-west England (Warr *et al.* 1994). The distribution of *Carex pilulifera* seed did not reflect its distribution in the vegetation, where it had low fidelity to any target assemblage. This indicates that *Carex pilulifera* possesses efficient dispersal mechanisms or that a seed bank has persisted, and that the former distribution of *Carex pilulifera* was different from the current distribution on Bodmin Moor. It also suggests that factors other than seed availability are of importance in its establishment.

Juncus squarrosus

Juncus squarrosus had significantly different densities of seed beneath different communities. SB9 (*Sphagnum*-rich *Scirpus cespitosus-Erica tetralix* wet heath (8) had significantly more *Juncus squarrosus* seed in the seed bank than the other communities with a mean seed density of 6985 m^{-2} compared with 1269 m^{-2} overall on Bodmin Moor. This is a high density compared to 63 seeds m^{-2} (Miles 1973, top 2 cm) but lower than maximum recorded density of 12276 seeds m^{-2} (Thompson 1985). The distribution of *Juncus squarrosus* seeds reflected its distribution in the vegetation, as it was a characteristic species in TA9 (*Sphagnum*-rich *Scirpus cespitosus-Erica tetralix* wet heath (8)).

Agrostis capillaris

Agrostis capillaris had significantly different densities of seed beneath different communities. SB1 (*Pteridium aquilinum* community (2) and SB3 (Acidic grassland (3) had more seed with mean seed densities of 4318 seeds m^{-2} and 2311 seeds m^{-2} respectively, compared to an overall mean for Bodmin Moor of 944 seeds m^{-2}. These densities are high compared to the 287 seeds m^{-2} of Miles (1973) but this represents seed in the initial 2 cm of the profile rather than 10 cm. The distribution of *Agrostis capillaris* seeds reflected its distribution in the vegetation as it was characteristic of TA1 and was abundant throughout assemblage Three. This contrasts with Hester *et al.* (1991) who found *Agrostis capillaris* seeds where *Agrostis capillaris* was not present in the vegetation. The reason for this discrepancy is not apparent.

6.4.5 Heathland restoration: The spatial distribution of germinating propagules within assemblages on Bodmin Moor

There is a general lack of information concerning the inhibitory effects of germinating competitors on seedlings of dwarf-shrub species. Crustose lichens reduced *Calluna vulgaris* germination by 40% following burning in the North York Moors (Legg *et al* 1992), illustrating the potential severity of competition effects. There is recognition that competition from established *Molinia caerulea* prevents heathland establishment (Backshall *et al.* 2001), but there are few data concerning the effects of competition between seed bank species for germination in a safe-site. *Molinia caerulea, Carex pilulifera, Juncus squarrosus* and *Agrostis capillaris* may be potential competitors for safe-sites on Bodmin Moor but further work is required to verify this hypothesis.

Propagule availability was not limiting the regeneration of *Calluna vulgaris* on Bodmin Moor, except in the wettest and driest conditions, although most seed was found beneath *Agrostis curtisii-Ulex gallii* type heath, suggesting that restoration relying on seed availability will be most successful in this community. However, attempts to rehabilitate or recreate this community may be problematic due to large quantities of *Molinia caerulea*, *Carex pilulifera* and *Agrostis capillaris* seed and the potential for competition. There was no significant difference in the distribution of propagules of *Ulex gallii* or *Erica tetralix* on Bodmin Moor, although *Ulex gallii* seed density was higher in dry communities and *Erica tetralix* seed density was higher in wet communities. Further work is required to determine if there is sufficient seed present for the restoration of these species. *Erica tetralix* seed was most abundant within *Sphagnum*-rich *Scirpus cespitosus*-*Erica tetralix* wet heath but here competition from *Juncus squarrosus* propagules may limit regeneration. The density of *Ulex gallii* seed was low compared to other uplands areas, and remains low even where it is locally abundant in the surface vegetation. This suggests propagule availability is not the key factor in explaining the abundance of *Ulex gallii* in present-day vegetation on Bodmin Moor. Propagules of *Vaccinium myrtillus* were largely restricted to *Calluna vulgaris*-*Vaccinium myrtillus* heath. Attempts to restore this community must therefore be limited to areas where it is already extant. The seed density of potential competitors within this assemblage was low relative to the other assemblages. However, competitive interactions between germinating seeds could still pose problems.

6.4.6 Heathland restoration: Variation in the timing of germination

The timing of germination for dwarf-shrub species and some of their potential competitors is also of some relevance to potential competitive effects. The timing of germination of *Molinia caerulea*, *Carex pilulifera*, *Agrostis capillaris* and *Ulex gallii* was approximately synchronous, although the species germinate in waves and *Ulex gallii* produced little seed. *Calluna vulgaris*, *Erica tetralix* and *Vaccinium myrtillus* germinated after these species. They will therefore experience a competitive disadvantage relative to *Molinia caerulea*, *Carex pilulifera*, *Agrostis* *capillaris* and *Ulex gallii*, all things being equal. The germination of *Juncus squarrosus* occurs after *Molinia caerulea*, *Carex pilulifera*, *Agrostis capillaris*, *Ulex gallii*, *Calluna vulgaris* and *Vaccinum myrtillus* but prior to the peak for *Erica tetralix*. Thus with the exception of *Ulex gallii*, the dwarf-shrub species germinate after the potential competitors for safe-sites in the assemblages in which they are likely to encounter them. This places dwarf-shrub heath species at a competitive disadvantage.

However, it is not clear if these patterns in emergence are responses to seasonal triggers (photo-period) or time since disturbance. Additionally, germination conditions in the greenhouse differ from field germination conditions and post-germination mortality of seedlings is higher in the field than in the glasshouse (Graham & Hutchings 1988). The differential responses of species to various ecological cues will result in different competitive outcomes. If *Ulex gallii* seed in the soil is heated by burning, it may germinate faster or have a higher germination success rate. Frosts may stimulate the germination of *Molinia caerulea* by fulfilling a chilling requirement (Grime *et al.* 1981). Seedling establishment on moorland sites is limited by nutrient deficiencies or acidity dependent toxicities, with *Agrostis capillaris* responding to higher nutrient levels where *Calluna vulgaris* does not (Miles 1973). Grazing pressure on the different species will be differential and will vary seasonally. Seedling response to grazing will also be differential. These and other potential feedbacks require investigation in order to predict the outcome of competition between seedlings.

6.4.7 Does variation in seed bank composition with depth reflect seed bank persistence and temporal variability?

There was very little difference in seed bank composition in the 0-5 cm and 5-10 cm horizons. In general, heathland species with a persistent seed bank were more numerous in the litter and top 5cm (or less) of the soil profile but were present at lower depths due to their persistence (Pywell *et al.* 1996, Miller & Cummins 1987, Mallik *et al.* 1984). Species that lack a persistent seed bank were either absent or present only in the upper layers of the soil profile.

Temporal variation in the abundance and distribution of persistent heathland species might be expected to result in variation in species composition with depth. If heathland was more abundant in the past on Bodmin Moor, then persistent heathland propagules would be found beneath communities where heathland is now absent in the lower layers of the soil profile, as these reflect the seed banks of former vegetation (Thompson *et al.* 1997).

The majority of species were more abundant in the upper layers of the soil. *Carex panicea* was more abundant in the 5-10cm cm profile than the 0-5 cm profile in seven seed bank groups but this was not significant. *Agrostis capillaris*, *Agrostis curtisii*, *Agrostis stolonifera*, *Anthoxanthum odoratum*, *Festuca ovina* and *Molinia caerulea*. *Potentilla erecta* and *Asplenium adiantum nigrum* were all significantly more abundant in the upper layers of the soil profile reflecting the production of large quantities of seed (or spores). This is generally consistent with the available literature (Thompson *et al.* 1997). However, *Agrostis curtisii* remains understudied. 41 seeds m^{-2} are reported from lowland heath (Pywell *et al.* 1996) with no upland figures available. This study suggests that *Agrostis curtisii* had a large seed bank in common with other *Agrostis* spp. in North-West Europe.

Most data from naturally buried seed suggest that *Molinia caerulea* is short-lived, implying that *Molinia caerulea* seeds rarely become buried (Thompson *et al.* 1997). However, there were large quantities of *Molinia caerulea* seed in SB3 and SB9. These groups contained significantly more *Molinia caerulea* seed in both horizons than the other groups did in the upper, with the exception of SB10. This suggests that *Molinia caerulea* seed does have a persistent seed bank when seed is produced in large quantities. It has been demonstrated that artificially buried seeds survived for at least three years (Pons 1989) and some consider it likely that *Molina caerulea* has a persistent seed bank (Grime *et al.* 1990).

Similarly, *Vaccinium myrtillus* seed was abundant in SB8 and significantly more seeds were present in the SB8 5-10 cm horizon than the 0-5 cm horizons of other groups. It is widely accepted that *Vaccinium myrtillus* does not form a persistent seed bank and is dependent on vegetative spread (Thompson & Grime 1979, Hill & Stevens 1981, Hester *et al.* 1991), although buried viable seed has been reported in boreal forest areas in North Sweden (Grime *et al.* 1990). The extensive rhizome system of *Vaccinium myrtillus* is found 150-200mm below the soil surface (Grime *et al.* 1990). Thus the presence of rhizome fragments is the most likely explanation for the existence of *Vaccinium myrtillus* in the 5-10 cm horizon on Bodmin Moor although the possibility of higher abundance in the past cannot be discounted.

There was significantly more seed of *Calluna vulgaris* in the lower soil horizons of SB2, SB3, SB9 and SB10 than in the upper horizon of these groups. This could theoretically indicate that *Calluna vulgaris* was more abundant under Acidic grassland (3), *Sphagnum*-rich *Scirpus cespitosus-Erica tetralix* wet heath (8) and *Narthecium ossifragum-Eriophorum vaginatum* blanket bog (9) in the past suggesting loss of heathland to grassland and a decline in *Calluna vulgaris* in mire vegetation. However, the considerable longevity of *Calluna vulgaris* seed (Hill & Stevens 1981, Granstrom 1987, Miller & Cummins 1987) is a more likely explanation of this result.

There were no significant differences between depths for any other species. However, it is worth noting that *Sedum album* and *Sagina nodosa* had seed banks primarily in the 0-5cm and 5-10cm horizons respectively. This suggests that *Sagina nodosa* has a persistent seed bank and that seed banks play a role in the regeneration strategy of *Sedum album* although the seed bank may not be persistent. The existence of seed banks for these species has not been previously reported.

6.4.8 Management implications

It appears that the objectives of 'Moorland Management' (maintenance of a 75% grass/ 25% dwarf-shrub heath mosaic) and 'Moorland Restoration' (increase dwarf-shrub cover to 50% or more) are not restricted by propagule availability because *Calluna vulgaris* seed was abundant everywhere. However, the composition of dwarf-shrub heath vegetation is limited by the propagule availability of other dwarf-shrub species.

Calluna vulgaris seed is present on Bodmin Moor in higher quantities than were necessary to restore *Callunetum* in North-East Scotland after the creation of gaps (Miles 1973), except in *Pteridium aquilinum-Galium saxatile* and *Eriophorum* mire communities. *Calluna vulgaris* seed was most abundant beneath *Agrostis curtisii* grassland, *Agrostis curtisii-Ulex gallii* grass-heath and *Agrostis curtisii-Ulex gallii* heath, where *Calluna vulgaris* is present amongst surface vegetation. 'Moorland Restoration' and 'Moorland Management' schemes are therefore more likely to result in an increased abundance of *Calluna vulgaris* in *Agrostis curtisii-Ulex gallii* grass-heath and *Agrostis curtisii-Ulex gallii* heath than in *Pteridium aquilinum-Galium saxatile*, *Eriophorum* mire, wet heath or grassland communities. However, the availablity of *Calluna vulgaris* seed in grassland and wet heath communities is not limiting heathland restoration. The presence of *Calluna vulgaris* seed beneath grassland reflects the persistence of its seed. It is probable that the scattered bushes of suppressed *Calluna vulgaris* within grassland and wet heath communities produced sufficient seed over time to ensure that a large, persistent, buried seed bank is present. Hence heathland restoration is not limited by propagule availability, despite the low abundance of *Calluna vulgaris* amongst surface vegetation.

Vaccinium myrtillus does not possess a persistent seed bank. Therefore 'Moorland Management' or 'Moorland Restoration' aimed at increasing or maintaining its cover relies on vegetative spread where the species is already extant. *Vaccinium myrtillus* is restricted to *Calluna vulgaris-Ulex* *gallii* heath, *Calluna vulgaris-Vaccinium myrtillus* heath, *Vaccinium myrtillus-Deschampsia flexuosa* heath and hybrids primarily on tors, although *Agrostis curtisii-Ulex gallii* heath also contains some *Vaccinium myrtillus*.

Most *Erica tetralix* seed was found in *Sphagnum*-rich wet heath and most *Ulex gallii* seed was found beneath *Festuca-Agrostis* grassland although differences in the abundance of *Erica tetralix* and *Ulex gallii* seed beneath the communities of Bodmin Moor were not significant. The density of *Ulex gallii* seed is low in comparison to other UK uplands. Hence propagule availability may hinder restoration attempts. Additionally, *Ulex gallii* seed was present where *Ulex gallii* was not present in the vegetation. This could indicate that the former distribution of *Ulex gallii* was different to the current distribution, although the lack of variation in seed abundance with depth suggests otherwise. It also suggests that factors other than seed availability are important in the establishment of *Ulex gallii*. It is known that fire plays an important role in the regeneration ecology of *Ulex* gallii. (Stokes, K. Centre for Ecology and Hydrology. *Pers. comm.* Nature Conservancy 2001). It is not clear whether there is sufficient seed for the regeneration of *Ulex gallii* or *Erica tetralix* because most work on heathland restoration has focused on *Callunetum*. More work is required to determine how many propagules of species other than *Calluna vulgaris* are required for successful heathland restoration and to understand the dynamics of heathland regeneration in all heathland communities, especially those restricted to South-west Britain.

Although there were sufficient propagules to achieve the objectives of 'Moorland Management' and 'Moorland Restoration', it is not clear if the management protocols will result in the creation of the safe-sites necessary for the propagules to germinate. Grazing can create safe-sites directly and indirectly. The consumption of biomass by herbivores can create safe-sites by reducing competition. Additionally, trampling, especially by cattle, can create bare ground where competition is reduced and also disturbs the soil exposing seed in the seed bank. It is not known if the stewardship prescription of light summer grazing is resulting in the creation of safe-sites on Bodmin Moor. It seems probable that light grazing creates more safe-sites than no grazing, but fewer safe-sites than heavy grazing, but this requires verification. It is ironic that the management most likely to produce safe-sites for germination will result in damage to existing dwarf-shrub vegetation. The dynamics of regeneration require further investigation in order to predict the outcome of stewardship management.

Species other than the CS target dwarf-shrubs may exploit safe-sites if they become available. On Bodmin Moor, seeds of *Molinia caerulea, Agrostis capillaris* and *Carex pilulifera* were abundant in the communities that contain *Calluna vulgaris* and *Ulex gallii.* These species may therefore compete with dwarf-shrub species for safe-sites and affect the outcome of stewardship prescriptions. These competitive interactions are less likely to be problematic for *Vaccinium myrtillus,* as fewer potential competitors were present in the seed bank. Although *Juncus squarrosus* seed was abundant beneath *Sphagnum*-rich wet heath in association with *Erica tetralix,* it is less likely to compete for safe-sites, as it was found predominantly in the 5 - 10 cm horizon. However, the effect of competition for safe-sites between germinating species is potentially serious for all dwarf-shrubs and requires investigation.

The influence of the mix of species and abundance of propagules on the success of heathland restoration remains unknown. This highlights the desirability for regeneration experiments under different conditions with different combinations and densities of propagules. Many variables other than propagule type and abundance affect the outcome of competition between seedlings including grazing. Once germinated, seedlings are particularly vulnerable to damage by grazing animals (Oesterheld & Sula 1990) and different species will have different responses to grazing. The likelihood of the emerging seedlings being damaged is determined in part by the composition of the surrounding vegetation (Oesterheld & Sula 1990). The effects of soil type, gap size, nutrient availability, burning or other disturbance, may modify the response of seedlings. Work on lowland heath has demonstrated that regeneration dynamics are extremely variable, suggesting that management regimes should be tailored to suit the conditions prevailing at individual sites (Britton *et al.* 2001). Thus agri-environment schemes aimed at restoring heathland on Bodmin Moor or any other area should be based on the results of detailed site-specific experimental work. The seed input component of this work has been undertaken on Bodmin Moor, but the other factors affecting regeneration dynamics and species composition following regeneration require investigation.

6.5 Conclusions

- The composition of vegetation and soil seed banks on Bodmin Moor was related at a large scale. However, some species exhibit disparities in abundance between vegetation and the seed bank. This is consistent with work from other areas.

- Propagule availability should not limit heathland restoration on Bodmin Moor except in *Eriophorum* mire and *Pteridium aquilinum*-dominated communities. However, the composition of heathland is limited by propagule availability. *Vaccinium myrtillus* heathlands are restricted largely to tors on Bodmin Moor and regeneration of *Vaccinium myrtillus* heathland is also restricted to tors. Further work is required to determine if the number of propagules of *Erica tetralix* and *Ulex gallii* are sufficient for heathland restoration, although it has been determined that they are present in the seed bank.

- Many non-heathland species are present in the seed bank on Bodmin Moor. Seeds of *Molinia caerulea, Carex pilulifera, Juncus squarrosus* and *Agrostis capillaris* are present at higher densities than other non-dwarf-shrub species. Further work is required to ascertain the effects of these species on heathland restoration but potentially they could inhibit dwarf-shrubs by competing for germination and establishment safe-sites should they become available. Work on regeneration dynamics is required over a long time-scale in order to predict the outcome of 'Moorland Management' and 'Moorland Restoration'.

- The distribution of species with depth in the seed bank of Bodmin Moor can be explained in terms of the number of seeds produced and persistence. There is a strong relationship between the composition of seed banks in the 0-5 cm and 5-10 cm horizons of Bodmin Moor. Therefore there is no evidence that the former distribution of vegetation differed from vegetation today. As heathland propagules are persistent, it is not possible to attribute their occurrence to the former extent of heathland.

- Several species have been identified as forming seed banks. *Sedum album* formed a seed bank, primarily in the 0-5 cm horizon on Bodmin Moor. *Sagina nodosa* had a persistent seed bank, primarily in the 5-10 cm horizon on Bodmin Moor. Seed banks have not previously been reported for either of these species. *Agrostis curtisii* had a seed bank on Bodmin Moor that is larger than previously reported seed banks on lowland heath. *Molinia caerulea* had a large persistent seed bank on Bodmin Moor, with seed distributed throughout the 0 -10 cm horizon. There is some debate about the persistence of seed banks of *Molinia caerulea*.

7 Countryside Stewardship monitoring

7.1 Introduction

7.1.1 General Introduction

In 1997 a monitoring program was initiated on Ivey & Hawkstor farms to evaluate the effect of a Countryside Stewardship (CS) agreement on the plant communities of Bodmin Moor (Dale & Dinsdale 1997). The monitoring program provided the opportunity to investigate temporal change in vegetation in response to reduced grazing pressure on both inbye (semi-improved) and semi-natural moorland vegetation on the two farms.

Ivey & Hawkstor farms are a beef cattle and sheep enterprise covering 424 hectares on the North Moor and are managed as one farm unit (Figure 2.2). The farms entered into CS in 1995, resulting in a change in grazing regime from heavy grazing to light summer-only grazing. The semi-natural vegetation on the farm consists of 282 hectares of grassland, grass-heath and bog and contains most of Bodmin Moor North SSSI. Since the inception of CS, 280 ewes and 90 cattle have grazed this vegetation from April to September, resulting in an overall prescription of 0.5 LU/ha (Mansfield 1998). From October to April no grazing occurs. A small number of ponies grazed intermittently on Hawkstor & Ivey farms by crossing valley mires from adjacent common land. The objective of the CS management is to allow *Calluna vulgaris* and other heathland dwarf-shrubs to regenerate. The semi-improved vegetation consists of 142 hectares and is grazed by 1000 ewes and 60 head of cattle from April to August (1.5 LU/ha) with no winter grazing (Mansfield 1998). The objective of CS on the semi-improved land is to re-establish acid grassland (Mansfield 1998).

7.1.2 Aims

The monitoring program initiated in 1997 by Dale & Dinsdale provided an opportunity to examine the effect of a reduced summer grazing and no winter grazing regime on both semi-natural and semi-improved vegetation on Bodmin Moor. In particular, the following questions were addressed:

- 1) How have the plant communities of Ivey & Hawkstor farm changed over the five-year monitoring period, when subject to no grazing or light summer grazing, having been subject to heavier grazing prior to 1995?
- 2) Has there been a significant increase in dwarf-shrub heath frequency or biomass within the semi-natural vegetation?
- 3) Has there been a significant increase in *Molinia caerulea* frequency or biomass within the semi-natural vegetation?

7.2 Methods

7.2.1 Data collection

The methodology employed in the monitoring follows Dale & Dinsdale (1997). Twelve 10 x 10m grazing exclosures were set up in six vegetation types across Ivey & Hawkstor farms. (Table 7.1, Figure 7.1.). Each exclosure was surrounded by a stock proof fence (Figure 7.2).

Table 7.1. The distribution of exclosures amongst the vegetation types of Dale & Dinsdale (1997).

Vegetation type	Number of replicates	Site identifiers
Semi-improved grassland	4	S1-4
Fine unimproved grassland	2	N1, 2
Coarse-grained *Molinia* with *Calluna*	2	N3, 4
Fine-grained *Molinia* mire	2	N5, 6
Molinia grassland with gorse	1	N7
Mixed valley mire	1	N8

Figure 7.1. The location of the twelve monitoring sites on Ivey & Hawkstor farms.

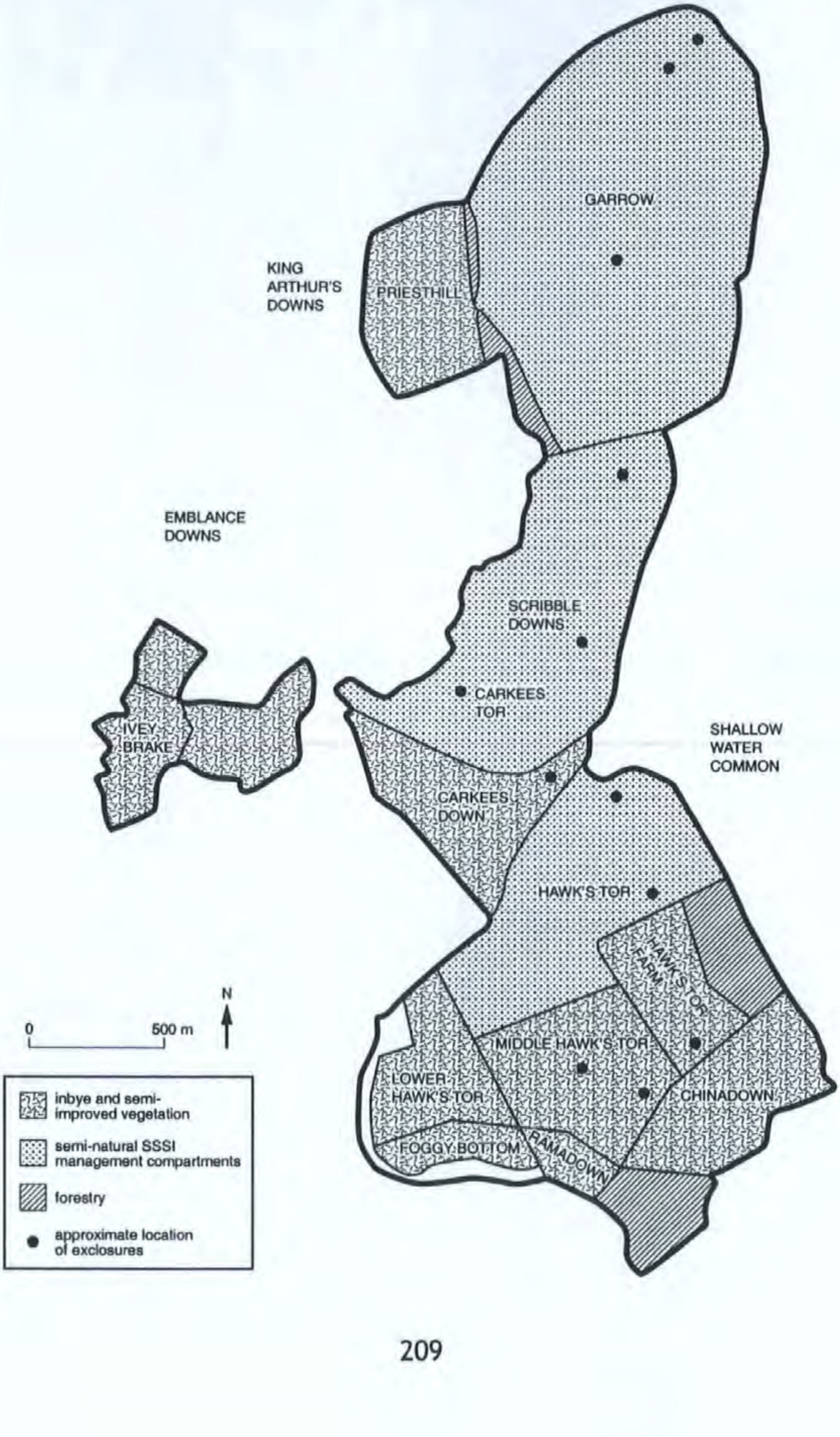


Figure 7.2. Monitoring exclosure of semi-natural vegetation with a stockproof fence.

Monitoring of vegetation composition

The frequency (or occupancy) of plant species inside and outside each grazing exclosure was determined by sampling fifty 0.25 x 0.25m quadrats at each of the twelve locations. Subjective stratification was employed to ensure roughly equal sampling intensity within the sampling area. Sampling outside the exclosure occurred in a 10-15 metre wide strip around the exclosure, constrained to visibly homogeneous vegetation within the vicinity and avoiding vegetation radically different to that inside the exclosure (e.g. seepage zones) (Dale & Dinsdale 1997).

Standing crop analysis

Standing crop analysis was undertaken by destructive harvest. At each of the eight semi-natural sites, one 0.5 by 0.5 metre quadrat was selected at random from inside the grazing exclosure and one from the homogenous vegetation outside (Dale & Dinsdale 1997). All above-ground biomass was removed and returned to the laboratory, where the material was sorted into: needle-leaved grasses (*Festuca ovina, Festuca* *rubra* and *Agrostis curtisii*), bryophytes, litter and each of the remaining individual species (Dale & Dinsdale 1997).

At each of the four semi-improved sites, a sward of 0.25 x 0.25m was selected at random and removed in its entirety from inside and outside each exclosure. Individual plants were sorted as for semi-natural samples (Dale & Dinsdale 1997). Biomass was oven dried to constant weight at 90 °C. In 1997, where the amount of biomass was substantial, sub-sampling was used to estimate the final proportion of each species within the whole sample and data were expressed as percentage of biomass within the whole sample. In subsequent years, the whole sample was sorted and data were expressed as biomass. Care was taken to ensure that biomass samples were not taken from the same location in subsequent years.

Monitoring was carried out between June and August by different recorders in different years (Table 7.2). Biomass analysis was undertaken in 1997, 1999 and 2001 (Table 7.2).

Table 7.2. The various recorders involved in the collection of frequency and biomass data from the exclosures on Ivey & Hawkstor farms. Foot-and-mouth disease and other access restrictions meant no frequency data were available for 2001.

Year	Frequency data	Biomass data
1997	Dinsdale, J., Dale, M.P.	Dinsdale, J.
1998	Dale, M.P., Dinsdale, J., Powe, C., Trodd, C.	
1999	Stewart, G., Croxton, P., Swankie, L., Dale, M.P.	Stewart, G.
2000	Stewart, G.	
2001		Stewart, G.

7.2.2 Data analysis

Detrended Correspondence Analysis (DCA) (Hill 1979b, Hill & Gauch 1980) was used to examine temporal change in plant community composition utilising botanical monitoring and standing crop data. Semi-improved vegetation consisting of *Lolium* sward in various stages of degeneration was analysed independently of semi-natural vegetation due to large differences in species composition and management. In the case of botanical monitoring data, species and sample outliers required consideration. *Pteridium aquilinum, Blechnum spicant, Campylopus introflexus, Poa pratensis, Bracathecium rutabulum, Thuidium tamariscum, Aira praecox,* and *Hyacinthoides non-scripta* were eliminated from semi-natural vegetation analysis. Changes in the frequency of mixed valley mire vegetation were analysed independently of other semi-natural vegetation as they created five outliers out of a possible total of eight, when combined with other semi-natural vegetation.

Trajectory analysis was used to quantify the consistency of vector direction and distance from year to year. The ratio of total distance in DCA ordination space to direct distance equals one, when there is uni-directional movement over time. The larger the ratio, the more deviation there is from uni-directional travel. Over a five-year period it is likely that deviation from uni-directional travel represents noise in the dataset.

Mantel's asymptotic approximation (Mantel 1967, algorithm based on Douglas & Endler 1982) was used to evaluate the null hypothesis of no relationship between dissimilarity matrices. Biomass matrices were compared from 1997 to 2001. Frequency matrices were compared from 1997 to 2000. Matrices derived using different parameters of abundance in 1999 were also compared with each other.

Analysis of variance (ANOVA) was used to assess the significance of changes in frequency and standing crop from year to year for *Calluna vulgaris, Erica tetralix, Vaccinium myrtillus, Ulex gallii* and *Molinia caerulea.* Seven replicates were utilised for frequency analysis, with mixed valley mire (N8) being excluded as an outlier in terms of floristic composition (see DCA above). Standing crop analysis was based on eight replicates.

7.3 Results

7.3.1 Temporal variation in plant community composition assessed by frequency

Semi-improved vegetation

When subject to no grazing, semi-improved vegetation showed a consistent trajectory from the right-hand side of the DCA ordination towards the left (Figure 7.3). The right-hand side of the ordination is associated with species such as *Prunella vulgaris*, *Lolium perenne* and *Trifolium repens* whilst species on the left include *Holcus lanatus*, *Dactylis glomerata* and *Succisa pratensis*. The ratio of total distance in DCA ordination space to direct distance for each ungrazed semi-improved site is relatively close to one, indicating relatively uni-directional movement over time (Table 7.3.). These data indicate that a consistent change has occurred in semi-improved vegetation year-on-year in response to the cessation of grazing. The relationship between the different semi-improved plots changed between 1997 and 2000 as there was no significant relationship between dissimilarity matrices of ungrazed semi-improved vegetation in 1997 and 2000 (Table 7.4).

Figure 7.3. Sample (top) and species (bottom) ordination (DCA) of semi-improved vegetation on Hawkstor & Ivey farms subject to no grazing and Countryside Stewardship regimes monitored over four years (based on frequency data).Coefficients of variation, axis one = 0.461, axis two = 0.103. For species abbreviations see Appendix 2.

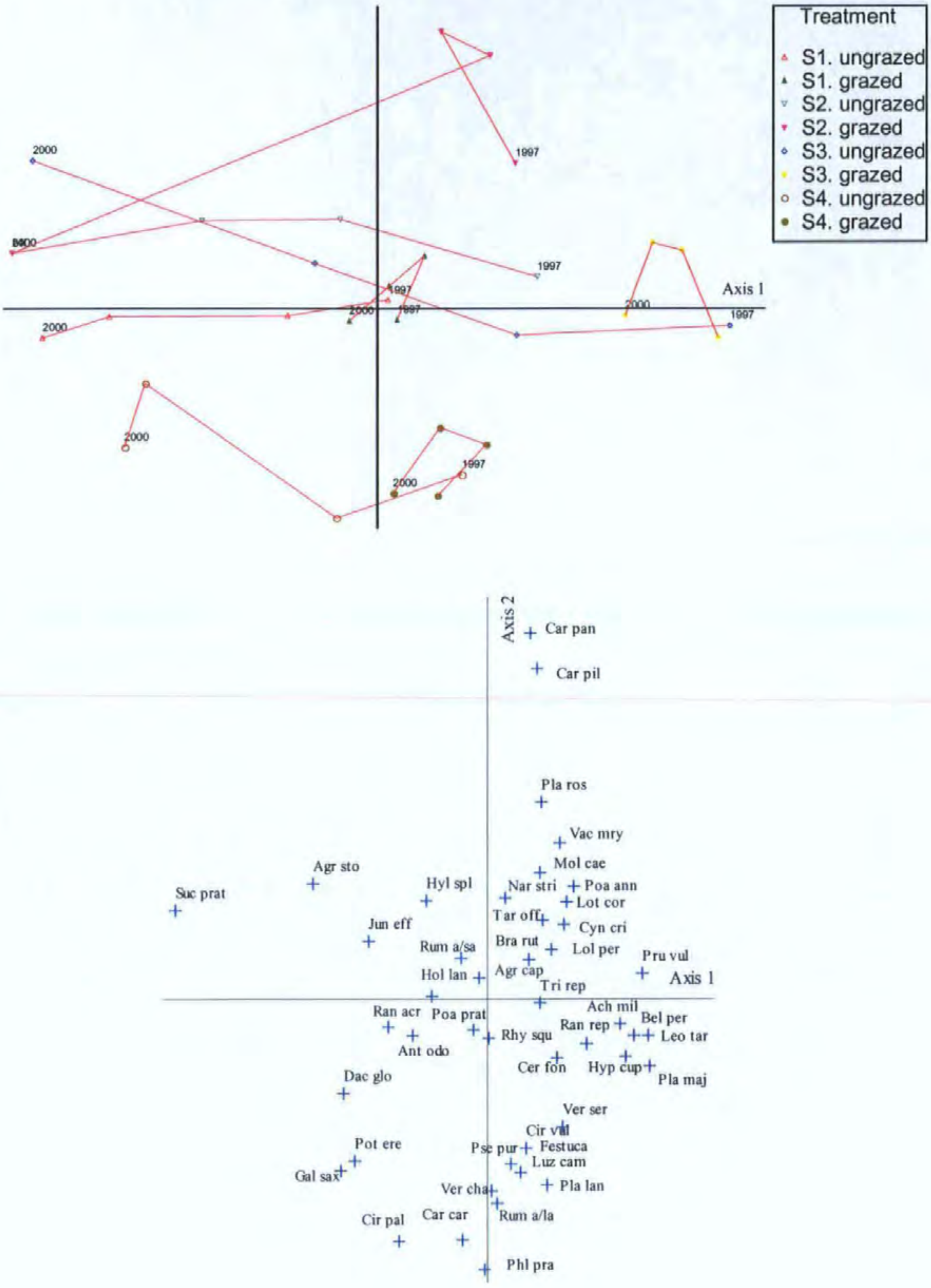


Table 7.3. The ratio of total distance in DCA ordination space to direct distance for each site. The ratio is closest to one (bold) when there is uni-directional movement over time. The larger the ratio, the more deviation from uni-directional travel.

Vegetation type (Dale & Dinsdale 1997)	Site	Parameter of abundance			
		Frequency		Biomass	
		Grazed	Ungrazed	Grazed	Ungrazed
Semi-improved grassland	S1	3.5	**1.03**	**1.02**	**1.01**
	S2	1.4	**1.02**	1.45	**1**
	S3	2.12	**1.04**	1.31	**1.02**
	S4	4.08	1.26	**1.02**	**1.06**
Fine unimproved grassland	N1	**1.075**	**1.06**	2.93	1.26
	N2	1.35	1.15	1.22	**1.09**
Coarse-grained *Molinia* with *Calluna*	N3	3.4	1.38	1.95	**1.04**
	N4	1.59	17.8	2.48	2.6
Fine-grained *Molinia* mire	N5	1.2	1.76	**1.04**	3.22
	N6	2	18	1.12	1.1
Molinia grassland with gorse	N7	1.29	1.5	1.13	2.5
Mixed valley mire	N8	2.18	1.77	1.5	1.16

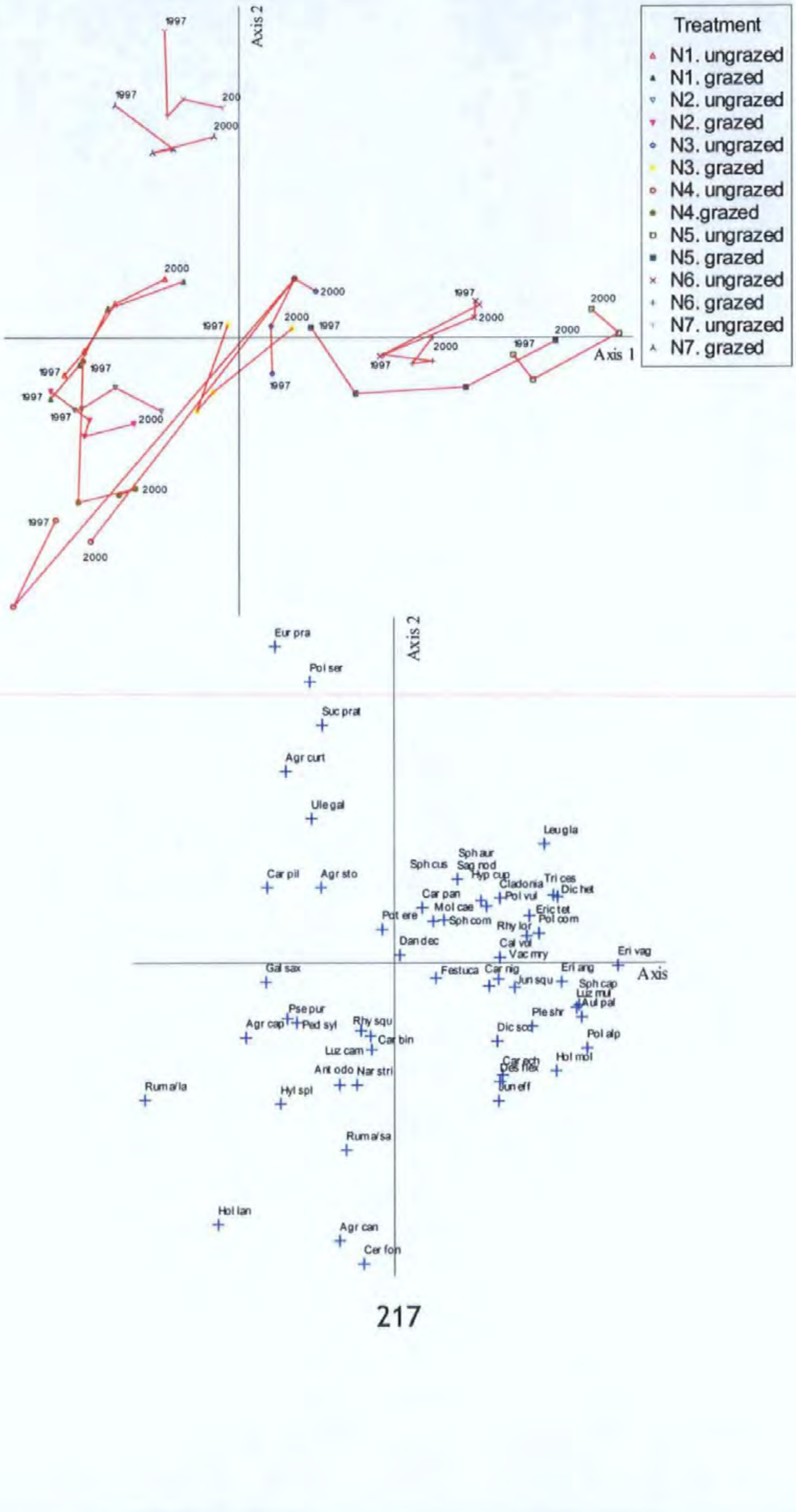
The response of grazed semi-improved vegetation was more complex. All four replicates initially increased in relation to the second axis prior to decreasing, whilst moving from the right-hand side of the ordination to the left (Figure 7.3). The magnitude of the changes was generally smaller in the grazed vegetation than ungrazed, although grazed site S2 had the largest change from 1999 to 2000 where it converged with ungrazed vegetation. The ratio of total distance in DCA ordination space to direct distance for each ungrazed semi-improved site was greater than one, indicating some deviation from uni-directional movement over time (Table 7.3.). As with ungrazed vegetation, the relationship between the different semi-improved plots changed between 1997 and 2000 (Table 7.4).

Semi-natural vegetation

In contrast to semi-improved vegetation, the trajectories of semi-natural vegetation appeared to be related to replicate rather than treatment

(Figure 7.4). Although variable, the pattern of change was similar within grazed and ungrazed plots but varied from replicate to replicate. Treatment did not have a consistent effect on the ratios of total distance in DCA ordination space to direct distance for semi-natural vegetation. There were many large deviations from uni-directional travel suggesting that the floristic changes from year to year are chaotic (Table 7.3).

Figure 7.4. Sample (top) and species (bottom) ordination (DCA) of semi-natural vegetation on Hawkstor & Ivey farms subject to no grazing and Countryside Stewardship regimes monitored over four years (based on frequency data). Coefficients of variation, axis one = 0.446, axis two = 0.069. For species abbreviations see Appendix 2.



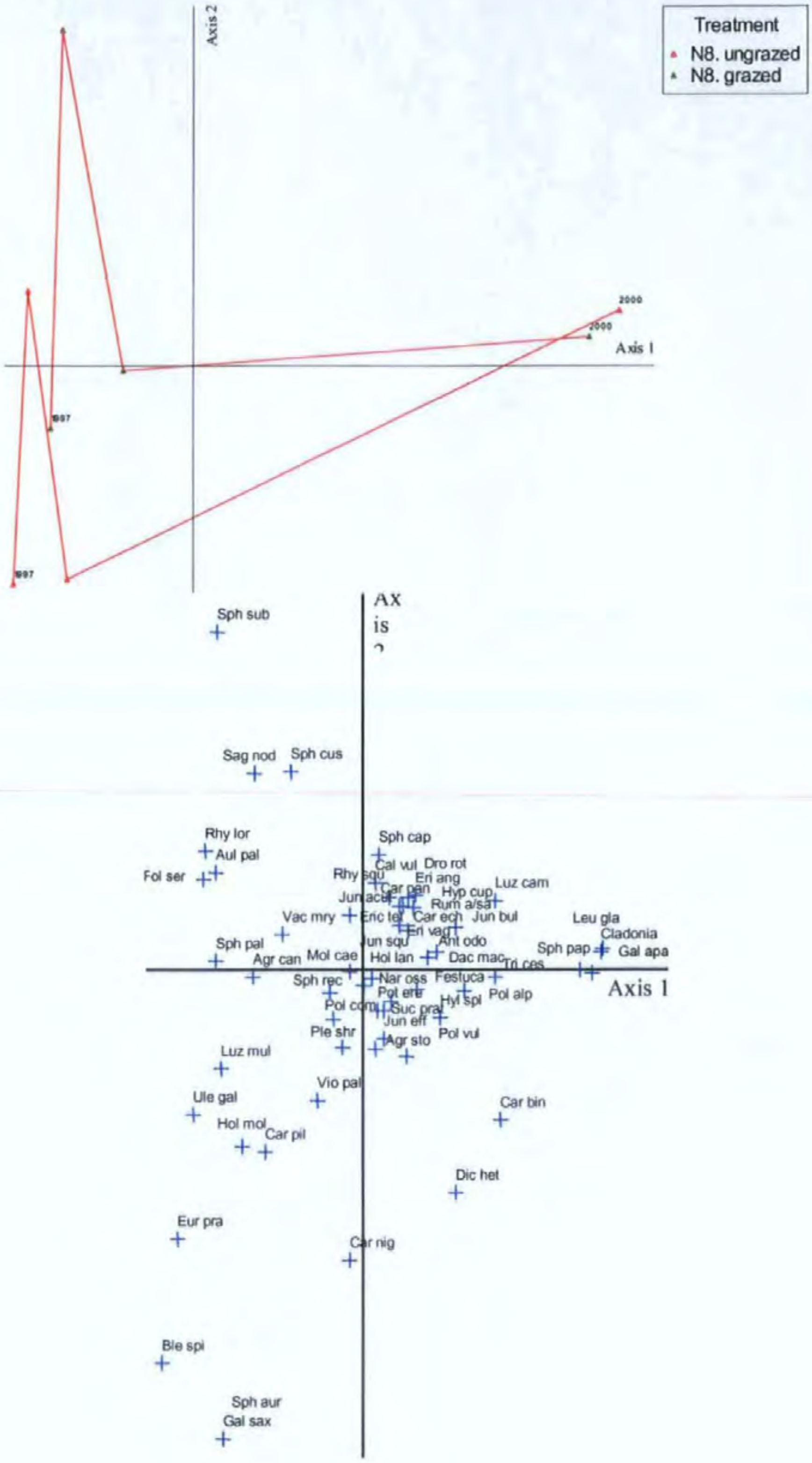
However, there was an overall shift from the left-hand side of the ordination to the right, although site N6 ungrazed moved from right to left. The species associated with the left-hand side of the ordination included *Agrostis capillaris, Galium saxatile, Agrostis curtisii* and *Ulex gallii*, whilst the right-hand side of the ordination was characterised by *Eriophorum* spp. and *Sphagnum capillifolium* amongst others. The relationship between the different grazed semi-natural plots changed between 1997 and 2000 but did not change in ungrazed plots (Table 7.4).

As with other semi-natural vegetation, the mire plot showed a similar pattern of change within both grazed and ungrazed vegetation (Figure 7.5). There was a rise and fall on the second axis, associated with a shift from the left-hand side of the ordination to the right. Species on the left-hand side of the ordination included *Sphagnum palustre* and *Agrostis canina*, whilst *Sphagnum papillosum* and *Leucobryum glaucum* were amongst those associated with the right. The ratios of total distance in DCA ordination space to direct distance were greater than one in both grazed and ungrazed mire vegetation suggesting some variation in the consistency of change from year to year (Table 7.3).

Table 7.4. The significance of correlations between matrices taken from the same sites at different times or utilising different parameters of abundance.

	Matrix one	Matrix two	Mantel test	Relationship
Overall, changes in proportion of biomass with time 1997-2001	Semi-improved 1997	Semi-improved 2001	T = 0.37 P = 0.71	Positive association between matrices but not significant
	Semi-natural 1997	Semi-natural 2001	T = 1.36 P = 0.17	
	Ungrazed Semi-natural 1997	Ungrazed Semi-natural 2001	T = 2.59 P = 0.009	Significant positive association between matrices
	Stewardship Semi-natural 1997	Stewardship Semi-natural 2001	T = 0.69 P = 0.48	Positive association between matrices but not significant
Overall, changes in frequency with time 1997 -2000	Semi-improved 1997	Semi-improved 2000	T = 1.79 P = 0.0734	
	Ungrazed semi-improved 1997	Ungrazed semi-improved 2000	T = 1.07 P = 0.282	
	Stewardship semi-improved 1997	Stewardship semi-improved 2000	T = 1.28 P = 0.199	
	Semi-natural 1997	Semi-natural 2000	T = 2.61 P = 0.009	Highly significant positive association between matrices
	Ungrazed semi-natural 1997	Ungrazed semi-natural 2000	T = 2.05 P = 0.04	Significant positive association between matrices
	Stewardship semi-natural 1997	Stewardship semi-natural 2000	T = 0.10 P = 0.91	Very slight positive association between matrices but not significant
Difference between parameters of abundance in 1999	Biomass (proportion)	Frequency	T = -0.69 P = 0.48	Negative association between matrices but not significant
	Biomass (proportion)	Cover	T = -0.02 P = 0.98	
	Cover	frequency	T = -1.5 P = 0.13	
	Biomass (weight)	Biomass (proportion)	T = 3.98 P =0.00007	Highly significant positive association between matrices

Figure 7.5. Sample (top) and species (bottom) ordination (DCA) of mixed valley mire on Hawkstor & Ivey farms subject to no grazing and Countryside Stewardship regimes monitored over four years (based on frequency data). Coefficients of variation, axis one = 0.707, axis two = 0.110. For species abbreviations see Appendix 2.

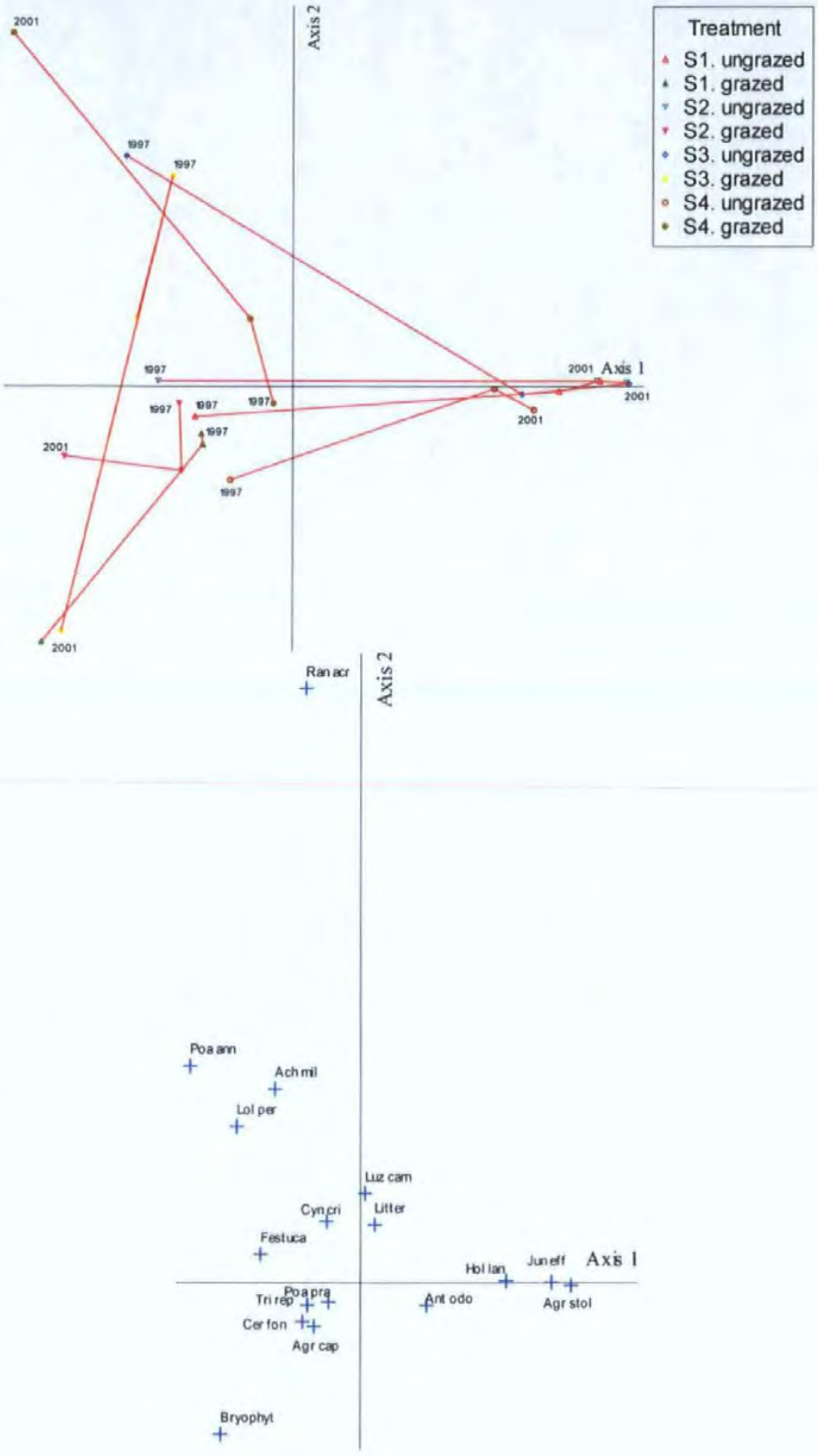


7.3.2 Temporal variation in plant community composition assessed by biomass

Semi-improved vegetation

When subject to no grazing, semi-improved vegetation showed a consistent trajectory from the left-hand side of the ordination to the right, with different sites converging (Figure 7.6). The response of grazed vegetation was less consistent. The grazed sites moved from the right-hand side of the ordination to the left, by varying amounts, whilst three sites moved down and the other moved up. The right-hand side of the ordination was characterised by *Agrostis stolonifera, Juncus effusus* and *Holcus lanatus*, whilst the left was associated with *Poa annua, Lolium perenne* and *Trifolium repens* amongst others. The ratio of total distance in DCA ordination space to direct distance was relatively low for biomass amongst semi-improved vegetation, indicating uni-directional movement over time, especially for ungrazed sites (Table 7.3). The relationship between the different semi-improved plots changed between 1997 and 2001 (Table 7.4).

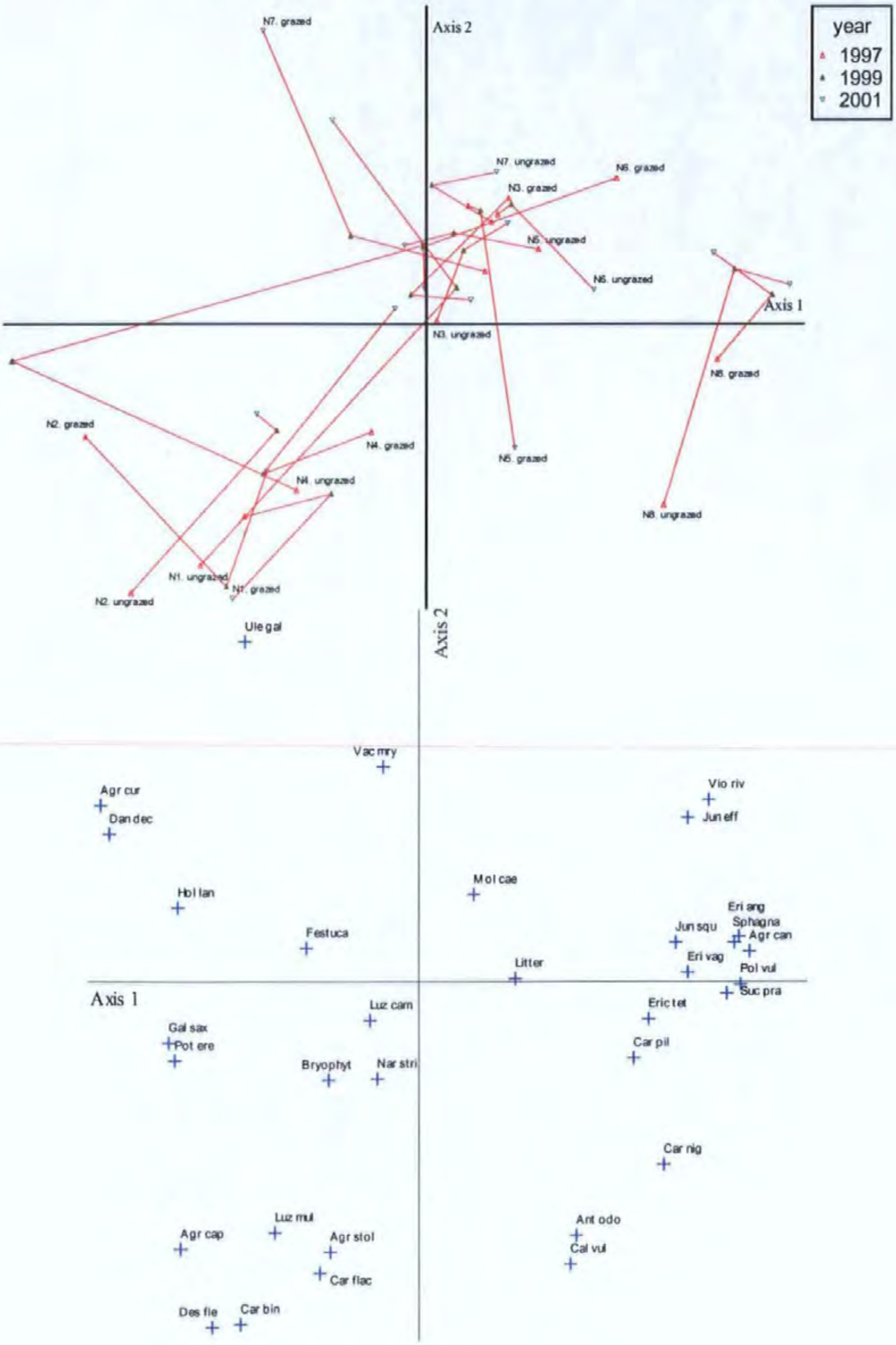
Figure 7.6. Sample (top) and species (bottom) ordination (DCA) of semi-improved vegetation on Hawkstor & Ivey farms subject to no grazing and Countryside Stewardship regimes monitored over four years (based on proportional biomass data). Coefficients of variation, axis one = 0.441, axis two = 0.279. For species abbreviations see Appendix 2.



Semi-natural vegetation

The biomass trajectories in semi-natural vegetation were complex and variable. Six out of eight grazed plots moved from the top-right of the ordination to the bottom-left, whilst five ungrazed plots moved from the left-hand side of the ordination to the right (Figure 7.7). The top-right of the ordination was associated with species including *Eriophorum angustifolium*, *Viola riviniana* and *Juncus effusus*. The bottom-left of the ordination was associated with *Agrostis capillaris*, *Deschampsia flexuosa* and *Carex binervis*. The ratios of total distance in DCA ordination space to direct distance for each site showed no consistent trends (Table 7.3). Ungrazed sites N2 and N3 had low ratios indicating uni-directional movement over time as did grazed site N5. Thus, the ratio did not appear related to treatment. However, it was not site-dependent either, as ungrazed site N5 had the highest ratio of all semi-natural biomass ratios. The relationship between the different semi-improved plots changed between 1997 and 2001 in grazed vegetation but did not change in ungrazed vegetation (Table 7.4).

Figure 7.7. Sample (top) and species (bottom) ordination (DCA) of semi-natural vegetation on Hawkstor & Ivey farms subject to no grazing and Countryside Stewardship regimes monitored over four years (based on proportional biomass data).Coefficients of variation, axis one = 0.415, axis two = 0.041. For species abbreviations see Appendix 2.



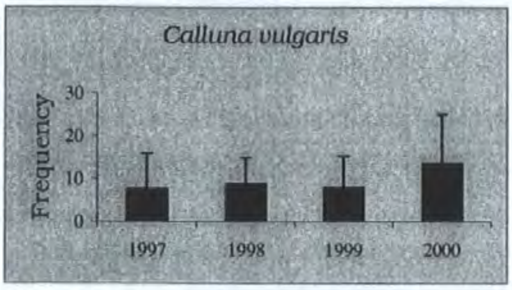
7.3.3 Differences between patterns of frequency and biomass

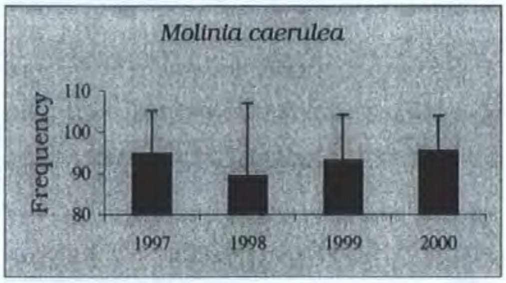
The patterns of temporal change generated were different when different parameters of abundance with different associated sampling strategies are used. Changes in biomass with time were generally consistent with changes in frequency but there were some discrepancies. Mantel's asymptotic approximation indicated that there was no significant relationship between biomass (proportional), frequency and percentage cover estimates taken from the same sites in 1999 (Table 7.4).

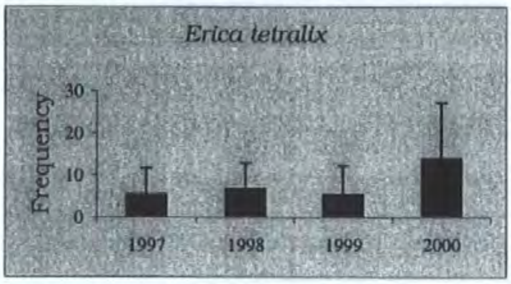
7.3.4 Temporal variation in abundance of individual species

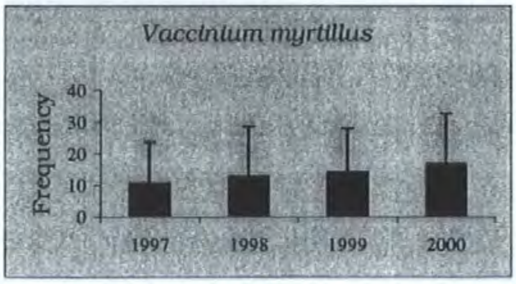
ANOVA was used to assess the significance of changes in the frequency and biomass of dwarf-shrub species and *Molinia caerulea* in semi-natural vegetation as a result of cessation of grazing or the adoption of CS management. Anderson-Darling tests indicated significant deviation from normality for all species in all analyses except *Molinia caerulea* biomass analyses (Figures 7.8-7.11). However, even with small sample sizes (seven - eight replicates), ANOVA is quite robust to non-normality (Box 1953, Underwood 1997). Levene's test indicated that heterogeneity of variance was not significant for any species in any of the analyses, thus ANOVA will not generate erroneous significant results. None of the changes in the frequency or biomass of *Calluna vulgaris*, *Erica tetralix*, *Vaccinium myrtillus*, *Ulex gallii* or *Molinia caerulea* were significant.

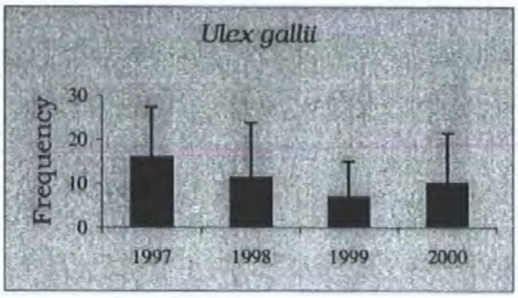
Figure 7.8. Variation in the frequency of selected species subject to Stewardship grazing on Ivey and Hawkstor Farms.There are no significant differences between years (ANOVA, n = 7). The data deviate from normality but are not subject to significant heterogeneity of variance.





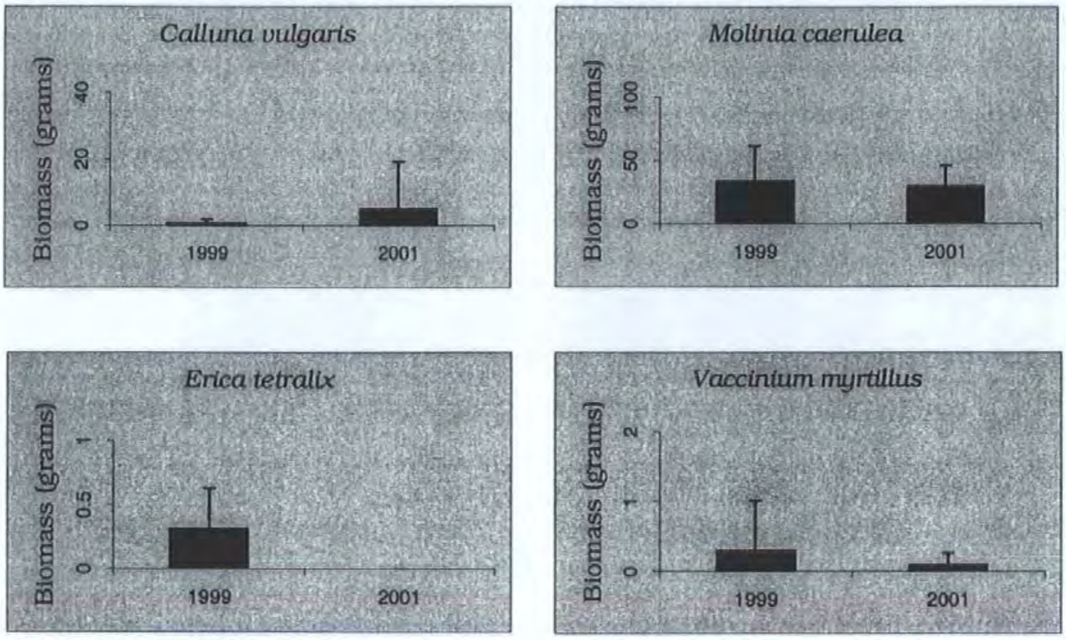


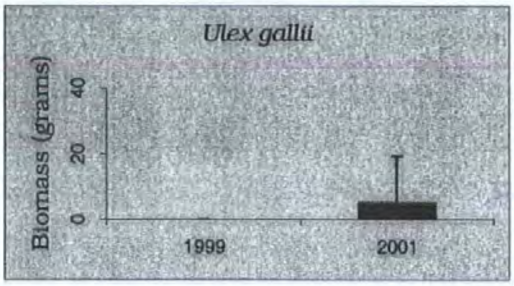




Species	ANOVA	Anderson-Darling	Levene's test
Calluna vulgaris	F = 0.94 P = 0.43	A2 = 0.88 P = 0.02	T = 0.55 P = 0.64
Erica tetralix	F = 1.79 P = 0.17	A2 = 1.85 P = 0.00	T = 1.44 P = 0.25
Vaccinium myrtillus	F = 0.32 P = 0.81	A2 = 2.04 P = 0.00	T = 0.11 P = 0.95
Ulex gallii	F = 1.11 P = 0.36	A2 = 1.13 P = 0.00	T = 0.31 P = 0.81
Molinia caerulea	F = 0.39 P = 0.75	A2 = 5.07 P = 0.00	T = 0.39 P = 0.75

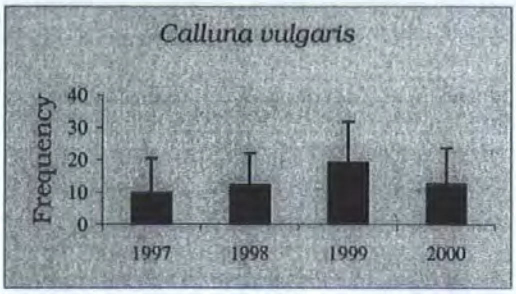
Figure 7.9. Variation in the biomass of selected species subject to Stewardship grazing on Ivey and Hawkstor Farms.There are no significant differences between years (ANOVA, n = 8). The data deviate from normality but are not subject to significant heterogeneity of variance.

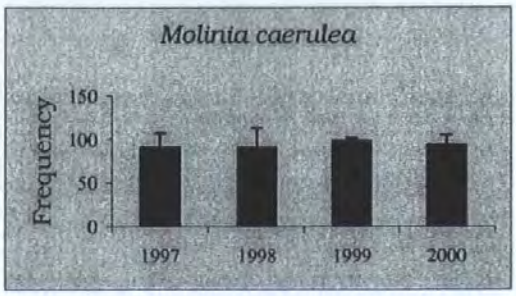


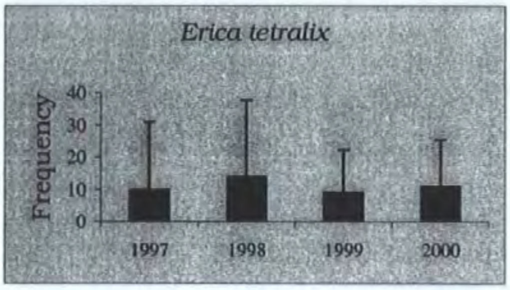


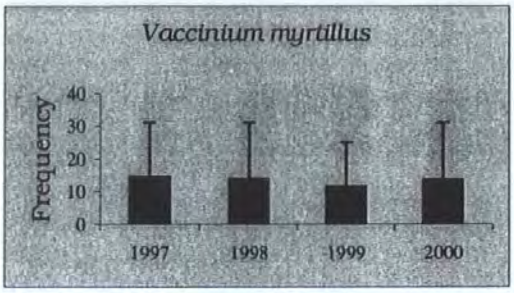
Species	ANOVA	Anderson-Darling	Levene's test
Calluna vulgaris	F = 0.72 P = 0.41	$A^2 = 4.97$ P = 0.00	T = 0.71 P = 0.41
Erica tetralix	F = 1.81 P = 0.19	$A^2 = 4.64$ P = 0.00	No variance
Vaccinium myrtillus	F = 0.53 P = 0.47	$A^2 = 3.94$ P = 0.00	T = 0.67 P = 0.42
Ulex gallii	F = 1.11 P = 0.30	$A^2 = 5.93$ P = 0.00	T = 0.97 P = 0.33
Molinia caerulea	F = 0.43 P = 0.52	$A^2 = 0.35$ P = 0.42	T = 3.58 P = 0.07

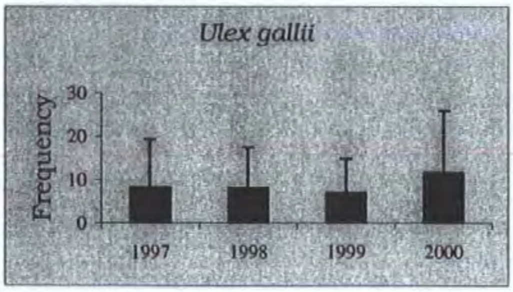
Figure 7.10. Variation in the frequency of selected species subject to no grazing on Ivey and Hawkstor Farms.There are no significant differences between years (ANOVA, n = 7). The data deviate from normality but are not subject to significant heterogeneity of variance.





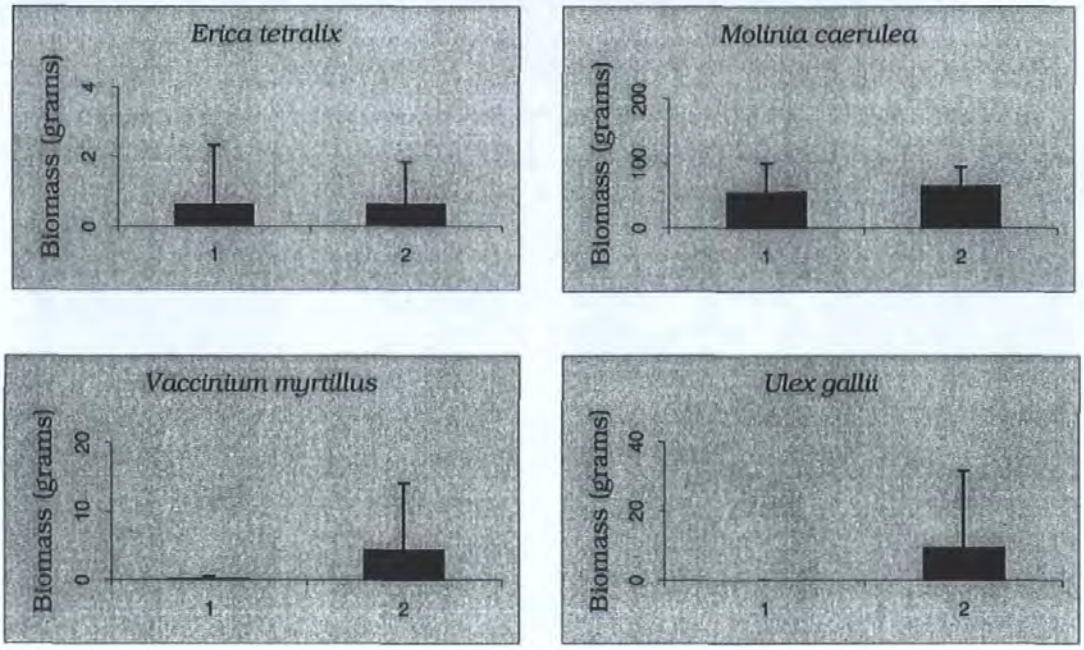






Species	ANOVA	Anderson-Darling	Levene's test
Calluna	F = 1.18	$A^2 = 0.77$	T = 0.14
vulgaris	P = 0.33	P = 0.03	P = 0.93
Erica	F = 0.12	$A^2 = 3.69$	T = 0.14
tetralix	P = 0.94	P = 0.00	P = 0.93
Vaccinium	F = 0.03	$A^2 = 2.27$	T = 0.08
myrtillus	P = 0.99	P = 0.00	P = 0.96
Ulex gallii	F = 0.24	$A^2 = 1.60$	T = 0.27
	P = 0.86	P = 0.00	P = 0.84
Molinia	F = 0.36	$A^2 = 6.25$	T = 0.36
caerulea	P = 0.78	P = 0.00	P = 0.78

Figure 7.11. Variation in the biomass of selected species subject to no grazing on Ivey and Hawkstor Farms.There are no significant differences between years (ANOVA, n = 8). The data deviate from normality but are not subject to significant heterogeneity of variance. *Calluna vulgaris* is absent from biomass samples in both 1999 and 2001.



Species	ANOVA	Anderson-Darling	Levene's test
Erica	F = 0.00	A^2 = 3.85	T = 0.00
tetralix	P = 0.98	P = 0.00	P = 0.98
Vaccinium	F = 1.51	A^2 = 4.45	T = 1.51
myrtillus	P = 0.23	P = 0.00	P = 0.23
Ulex gallii	F = 1.39	A^2 = 4.90	No
	P = 0.25	P = 0.00	variance
Molinia	F = 0.24	A^2 = 0.26	T = 3.20
caerulea	P = 0.63	P = 0.64	P = 0.09

7.4 Discussion

7.4.1 Plant community responses

Semi-improved vegetation

Plots of ungrazed semi-improved vegetation converged consistently from year to year in response to increases in the frequency and biomass of *Holcus lanatus* and *Agrostis stolonifera*. The frequency and biomass of species such as *Lolium perenne* and *Trifolium repens* declined. These species have high nutrient requirements (Grime *et al.* 1990, Hill *et al* 1999) and are very tolerant of grazing (Grime *et al.* 1990). In contrast

Holcus lanatus has lower nutrient requirements (Hill *et al.* 1999) and is a later colonist during sward deterioration (Grime *et al.* 1990). Thus all the plots were converging to a *Holcus lanatus*-dominated assemblage in response to the cessation of grazing and a decline in nutrient levels.

The response of semi-improved plots grazed at a reduced stocking rate of 1.5 LU/ha was more complex and variable, but essentially the same changes were occurring, albeit it to a lesser degree. The increased variation in response and speed of change may reflect increased variation in treatment. In ungrazed vegetation, the treatment is uniform, whereas in grazed vegetation the treatment varied because utilisation is not homogenous and therefore not directly synonymous with stocking rate.

Succession from *Lolium perenne* leys and *Lolium perenne-Cynosurus cristatus* grasslands are known to be grazing-mediated with undergrazing allowing coarser species to increase their cover (Rodwell 1992b). Transitions to *Holcus lanatus*-dominated vegetation are reported from base-poor podzolic soils, although more usually *Arrhenatherum elatius* becomes dominant (Rodwell 1992b). The development of a *Holcus lanatus*-dominated assemblage in response to cessation of grazing for five years is therefore consistent with successions from other areas. It is also consistent with the interpretation of survey results from Chapter Five, which associated the presence of a *Holcus lanatus-Deschampsia cespitosa* variant with reductions in grazing pressure on the sown swards of inbye or former inbye land. The results suggest that the effects of deintensification associated with CS might lead to sward deterioration and increasing abundance of *Holcus lanatus*. Further work is required to verify this and to determine whether *Holcus lanatus* dominated vegetation will become a polyclimax (*sensu* Tansley).

It appears that acidic grassland, from which the semi-improved vegetation was presumably derived, will take considerable time to re-establish and may not re-establish at all. Cessation of grazing leads to the creation of species-poor *Holcus lanatus*-dominated grassland. It is possible that grazing at 1.5 LU/ha will converge with ungrazed vegetation given time. It is equally possible that the vegetation will revert to acid grassland, as fertility levels drop. Other work (Smith *et al.* 2000) indicates that management to increase the number of plant species in agriculturally improved mesotrophic grassland requires a complex combination of management and restoration. Meadows require the joint implementation of appropriate cut date and grazing regimes to provide regeneration niches and the application of seed to provide species to fill these niches, with nutrient levels being of lesser importance (Smith *et al.* 2000). Management of this type could lead to the creation of species-rich meadows that would be more desirable than species-poor *Holcus lanatus*-dominated communities. Other stocking rates, changes in stock type or more time may be required if creation of acidic grassland is the objective of management. Alternatively, the inbye land could be grazed intensively, providing feeding grounds for Golden Plover and providing land managers with more flexibility over stocking rates in the more valuable semi-natural vegetation.

Semi-natural vegetation

Semi-natural vegetation exhibited similar patterns of changes in frequency irrespective of management, although individual replicates varied to some degree. Essentially the changes in frequency suggest that the communities were shifting towards wetter assemblages. Species such as *Agrostis capillaris, Galium saxatile, Agrostis curtisii* and *Ulex gallii* declined, whilst *Eriophorum* spp., *Trichophorum cespitosum, Erica tetralix* and *Sphagnum capillifolium* increased in frequency. Even in mire vegetation, a similar trend was seen with *Agrostis canina* decreasing whilst *Sphagnum papillosum* increased.

In contrast to the frequency data, the biomass response of grazed and ungrazed plots differed. Grazed vegetation appeared to be shifting towards drier assemblages with increases in *Agrostis capillaris, Deschampsia flexuosa* and *Carex binervis* and decreases in *Eriophorum* *angustifolium, Viola riviniana* and *Juncus effusus*. Ungrazed vegetation responded in the opposite manner with increased biomass of *Eriophorum angustifolium, Viola riviniana* and *Juncus effusus* and decreased abundance of *Agrostis capillaris, Deschampsia flexuosa* and *Carex binervis*.

The overall changes in abundance suggest that vegetation on Hawkstor & Ivey farms was shifting towards wetter assemblages. Mean annual precipitation on Bodmin Moor was higher throughout the five-year monitoring period than in the previous five years (NERC British Atmospheric Data Collection). It is therefore possible that the increase in wet species was a response to this increasing precipitation. However, if this is the case, it is difficult to understand why the biomass response of grazing is not consistent with the other responses. There are three possible explanations:

- The heterogeneity of the vegetation within plots at the scale of sampling resulted in high variance. It was therefore difficult to obtain consistent results. This is illustrated by the high ratios of total distance in DCA ordination space to direct distance, which indicate inconsistency of results from year to year.

- Frequency and biomass abundance measures pick up different aspects of vegetation response. The direct effect of grazing operates when grazing of taller or faster-growing species reduces their competitive ability or kills them, allowing smaller species which would be shaded out in the absence of grazing to coexist (Milne *et al.* 1998). Thus the initial response of vegetation to changing grazing management will be changes in biomass, resulting in new inter and intra-specific competitive relationships between species which may result in changes in frequency. More time may be required for trends in changing frequencies to become clear when comparing no grazing with light grazing, whereas the relative changes in biomass are likely to occur more rapidly and therefore be detected sooner.

Additionally frequency data were only available for 1997 - 2000 whereas biomass data were available from 1997 - 2001.

- The precision and replication of biomass and frequency measures were different. The biomass data were derived from a single sample at each site, whereas the frequency data were replicated. The precision of the frequency data was higher but the size of individual quadrats meant that many species had high frequencies. In particular, frequency measures did not identify increases in the abundance of *Molinia caerulea*, as the frequency was initially 100%. This could be responsible for the differential trajectories of grazed versus ungrazed vegetation in terms of biomass.

7.4.2 Individual species responses

There were no significant changes in the frequency or biomass of *Molinia caerulea* in the area that was monitored. This may not accurately reflect the true situation for the reasons outlined above. More work is required to establish the response of this species to grazing. However, it is clear that summer-only grazing at <0.5 LU/ha on Ivey & Hawkstor farm did not reduce *Molinia caerulea* abundance. Other work suggests that *Molinia caerulea* increases in dominance when ungrazed eventually excluding all other species (Hill 1982). Recent work at Redesdale demonstrates that implementing light summer grazing by sheep (0.15LU/ha and 0.006LU/ha) within *Calluna-Molinia* dominated upland heath resulted in increased *Molinia caerulea* abundance (Gardner *et al.* 2001).

There were also no significant changes in the frequency or biomass of *Calluna vulgaris, Erica tetralix, Ulex gallii* or *Vaccinium myrtillus* in the area that was monitored. Dwarf-shrub abundance was initially low. Therefore the monitoring would have identified significant increases in dwarf-shrub abundance had any occurred.

The CS agreement stipulates an overall stocking rate of 0.5 LU/ha in summer with no winter grazing (Mansfield 1998), although overall stocking rates have exceeded 0.83 LU/ha whilst stocking rates in individual management compartments have been as high as 1.5 LU/ha (Figure 7.12). There is evidence from other studies that stocking rates of 0.5 LU/ha cause a decline in *Calluna vulgaris* abundance. Grazing by sheep at 0.5 LU/ha resulted in a 9% decline in *Calluna vulgaris* cover over four years (Welch 1984a) and resulted in conversion of heathland to grassland (Miles *et al.* 1978) in NE Scotland. Recommended maximum sheep densities consistent with maintenance of *Calluna vulgaris* are all less than 0.3 LU/ha, including off wintering (Sibbald *et al.* 1987, Lance 1987, Felton & Marsden 1991, Bardgett & Marsden 1992, Smallshire *et al.* 1997). Cattle grazing at 1.2LU/ha caused a decline of 32% *Calluna vulgaris* cover over four years, with an associated reduction in cover from 80% to 5% in 10 years (Welch 1984a). It is therefore not surprising that there has been no significant increase in *Calluna vulgaris* cover on Ivey & Hawkstor farm given summer stocking well in excess of 0.3LU/ha and low initial abundance of *Calluna vulgaris*. Indeed one might have expected a significant decline in *Calluna vulgaris* abundance given such stocking rates.

The response of *Calluna vulgaris* under no grazing is also interesting, as regeneration is generally much faster in ungrazed situations than grazed (Fenton 1937), with increases in *Calluna vulgaris* cover in response to no grazing being common (Welch 1968, Hill 1982, Marrs *et al.* 1988, Milne *et al.* 1998). However, on *Molinia caerulea*-dominated vegetation, no grazing can result in the expansion of *Molinia caerulea* and the exclusion of other species after seven years (Hill 1982). *Molinia caerulea* is a virtual constant within the vegetation of Ivey & Hawkstor farm. The lack of increase in *Calluna vulgaris* abundance in response to no grazing is probably a result of competition from *Molinia caerulea* and replicates the result of Hill (1982) in Snowdonia.

There is a paucity of information concerning the response of *Erica tetralix* to grazing. What is known suggests that the response is similar to that of *Calluna vulgaris*, especially when cattle grazing is considered

(Putman *et al.* 1987). This appears to be the case on Ivey & Hawkstor farm.

Vaccinium myrtillus is tolerant of sheep grazing but release from grazing can lead to the development of tall phenotypes with many erect robust shoots (Grime *et al.* 1990). Total protection from grazing led to a fall in *Vaccinium myrtillus* cover but there was a significant increase in height in the Peak District (Welch *et al.* 1994). Other work shows that after 20 years of no grazing, the abundance of *Vaccinium myrtillus* increases (Hill 1982). Seasonal protection from grazing in winter has been shown to have no effect compared to year round grazing by sheep (Welch *et al.* 1994). This study suggests that both total protection and seasonal protection (CS prescriptions) had no effect on *Vaccinium myrtillus* abundance and is therefore consistent with Welch *et al.* (1994).

Very little is known about the response of *Ulex gallii* to upland grazing, as it has received little attention from ecologists. Further work is required to quantify the response of *Ulex gallii* to grazing.

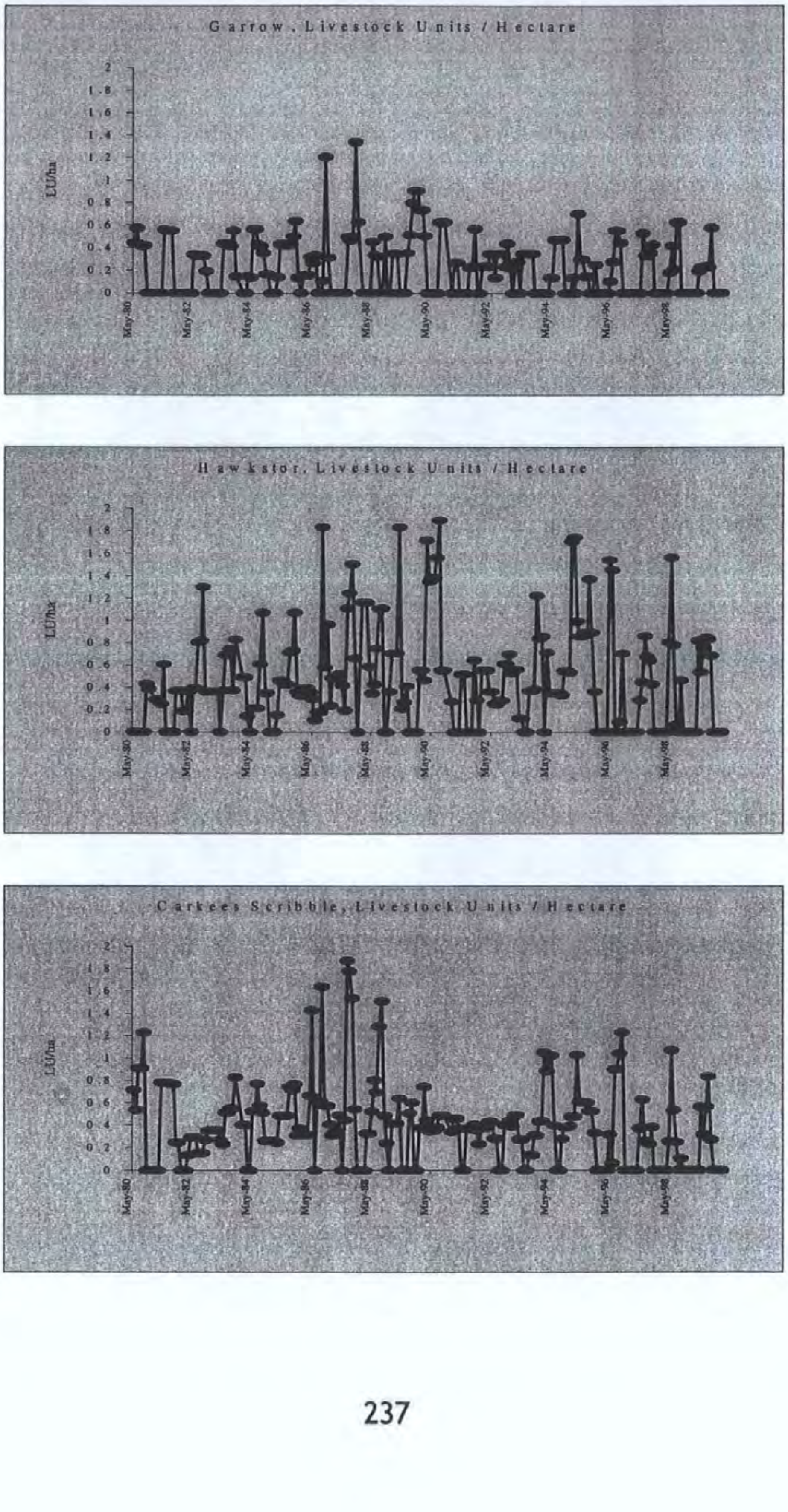
These individual species responses suggest that CS is not working on Bodmin Moor, as there were no significant increases in the abundance of any dwarf-shrub species over a 5-year period. Furthermore, these results suggest that it may not be possible to rehabilitate dwarf-shrub heathland on Bodmin Moor by the manipulation of stock alone because of the widespread presence of *Molinia caerulea.* When *Molinia caerulea* is not grazed it becomes dominant frequently excluding other species (Hill 1982, Hubbard 1984, Chambers *et al.* 1999, Taylor *et al.* 2001). *Molinia caerulea* therefore must be suppressed by grazing to release dwarf-shrubs from competition (Backshall *et al.* 2001). *Molinia caerulea* has been shown to increase in abundance under light summer grazing (0.15 LU/ha) but heavy grazing suppresses heathland (Miles *et al.* 1978, Welch 1984a, Sibbald *et al.* 1987, Lance 1987, Felton & Marsden 1991, Bardgett & Marsden 1992, Smallshire *et al.* 1997). This suggests that stocking levels must be high enough to suppress *Molinia caerulea* but low enough to allow dwarf-shrub survival. The monitoring results suggest that grazing levels must be in excess of 0.5 Lu/ha in order to suppress *Molinia caerulea*. This stocking level has been shown to be incompatible with dwarf-shrub heath in good condition.

7.4.3 Management implications

The precise objectives of Countryside Stewardship heathland rehabilitation vary, as do the details of the prescriptions. 'Moorland Management' has the highest stocking rate (0.3Lu/ha) and less than 30% dwarf-shrub heath initially. The objective is to increase dwarf-shrub cover to more than 30%. 'Moorland Restoration' has a lower stocking rate (0.17Lu/ha) but more than 30% dwarf-shrub heath initially. The objective is to increase dwarf-shrub cover to 50% or more. Neither of these Bodmin Moor prescriptions give a time-scale for this change or specify the composition of the resultant dwarf-shrub. However, national Countryside Stewardship options do provide time-scales. The objective of regeneration applies where *Calluna vulgaris* covers less than 25% of the area. Summer grazing must be less than 0.15LU/ha and the objective is to achieve at least 40%, preferably 50% *Calluna vulgaris* cover by year five of the agreement. The enhancing heather moorland option applies when *Calluna vulgaris* is initially between 25% and 50% and is in poor condition. Summer grazing must be less than 0.15LU/ha, whilst winter grazing must not exceed 0.075LU/ha with no cattle grazing. The aim is to improve the condition and extent of heather and other moorland vegetation.

A large body of evidence (Miles *et al.* 1978, Welch 1984a, Sibbald *et al.* 1987, Lance 1987, Felton & Marsden 1991, Bardgett & Marsden 1992, Smallshire *et al.* 1997) indicates that grazing above these stocking levels results in the loss of dwarf-shrubs. Unfortunately, grazing at levels above these stocking rates does not suppress *Molinia caerulea* on Bodmin Moor. This suggests that CS grazing prescriptions will not achieve the CS aims of increasing dwarf-shrub abundance on graminoid-dominated communities, because *Molinia caerulea* is not suppressed sufficiently to release dwarf-shrubs from competition.

Figure 7.12. Changes in livestock units per hectare in the three semi-natural management compartments on Hawkstor & Ivey farms from 1980-2000.



However, grazing systems are complex and variable. The use of stock other than sheep or cattle or mixed stock grazing may allow more effective control of *Molinia caerulea*, whilst not debilitating existing dwarf-shrub vegetation. The precise timing and intensity of grazing requires investigation, as it may prove possible to target *Molinia caerulea* more effectively. Likewise it is possible that burning or more likely, burning and grazing together, may provide a management solution to this problem. Alternatively, increasing atmospheric deposition of nitrogen may favour *Molinia caerulea* over dwarf-shrub species. The effects of climate on the intractability of this problem are also unknown.

The effects of grazing by different species of herbivore and interactions between them result in different offtake of vegetation even when the offtake is equivalent in terms of biomass and livestock unit density. It is generally acknowledged that cattle are more damaging than sheep to dwarf-shrub communities but they are also able to utilise *Molinia caerulea* to a greater extent (Grant *et al.* 1996). Ponies, however, eat less *Calluna vulgaris* than cattle in winter, and more *Molinia caerulea* in summer (Putman *et al.* 1987). Thus pony grazing has greater potential to control *Molinia caerulea* without damaging *Calluna vulgaris* than sheep or cattle. Unfortunately, ponies on both Bodmin Moor and Dartmoor are of low economic value, and graze in addition to other stock, thus increasing grazing pressure in terms of livestock units per hectare rather than replacing sheep or cattle and increasing grazing pressure on *Molinia caerulea*, whilst reducing it on *Calluna vulgaris*.

The history of burning could also be of critical importance in the response of the vegetation to management. The burning history on Hawkstor & Ivey farm is unquantified and largely unknown. There has been no burning in the last decade but previous management is known to have involved burning. Burning areas dominated by *Molinia caerulea* to replace dead and unpalatable plant matter with a flush of young palatable grass is a traditional management practice, particulary in

South-west England (Backshall *et al.* 2001). *Molinia caerulea* responds well to burning because the dense tussocks protect the buds from fire (Mowforth & Sydes 1989). Thus frequent burning perpetuates *Molinia caerulea*, whilst it debilitates *Calluna vulgaris* (Miles 1971).

Todd (1997) and Backshall *et al.* (2001) suggested that burning, then grazing intensively from mid-May to mid-July (the period of maximum *Molinia caerulea* growth and palatability) can reduce the dominance of *Molinia caerulea*. However burning with a follow up graze of less than 0.1 sheep per hectare (0.01LU/ha) reduced *Calluna vulgaris* productivity by 30-40% (Rawes & Williams 1973). Likewise, post-burn grazing allowed *Eriophorum vaginatum* to gain dominance at the expense of dwarf-shrubs on blanket bog (Rawes & Hobbs 1979). Thus, although burning with post-burn grazing may allow some control of *Molinia caerulea*, it will probably be detrimental to dwarf-shrubs. The effect of burning and post-burn grazing will be differential for the different species. *Vaccinium myrtillus* rhizomes are at greater depth than those of *Calluna vulgaris* (Grime 1990) Thus it is less vulnerable to frequent burning than *Calluna vulgaris* but no information exists on the response of *Vaccinium myrtillus* to post-burn grazing. There is even less information on burning, grazing and post-burn grazing of *Erica tetralix* and *Ulex gallii*, although a 16 year burning frequency is thought to be favourable to *Ulex gallii* (Stokes, K. Centre for Ecology and Hydrology. *Pers. comm.*).

Increased nitrogen deposition is reinforcing changes in management in upland grazing systems, with a detectable effect under light grazing having the same overall effect (grassland dominance) as heavy grazing (Emmett, B. Centre for Ecology and Hydrology. *Pers. comm.*). Thus it may not be possible to increase dwarf-shrub abundance by initiating light grazing regimes even if a control mechanism for *Molinia caerulea* is found.

Climate may also be a potential problem necessitating the use of regional prescriptions and possibly requiring new CS objectives altogether in regions with warm wet winters (Bodmin Moor, South Wales upland fringe, Galloway upland fringe). *Calluna vulgaris* may be vulnerable to grazing as a result of high winter temperatures resulting in depletion of carbohydrate reserves (Crawford 1997). Warm spring temperatures may encourage early growth of *Molinia caerulea*. These factors could be modifying the response of plant species to grazing on Bodmin Moor and possibly in other areas.

It is clear that more work is required to inform management decisions on Hawkstor & Ivey farm, Bodmin Moor and in other upland areas. In particular, increased understanding of the response of *Molinia caerulea* to changes in management regime may be critical. The effects of different grazers requires investigation, with information on less studied species such as ponies and cattle being essential in drawing up suitable management protocols on Bodmin Moor. The modifying effects of climate may also be of importance and may invalidate the use of studies in other climatic regions to inform management decisions.

7.5 Conclusions

- Semi-improved vegetation became dominated by *Holcus lanatus* at the expense of *Poa* spp. *Lolium perene* and *Trifolium repens*. More time is required to determine the outcome of grazing at 1.5LU/ha, as no baseline data existed prior to the change in management. However, cutting and seed addition with low spring and autumn stocking rates could result in the creation of species-rich hay meadows (Smith *et al.* 2000), whilst different stocking rates, stock types or more time could result in the re-establishment of acid grassland. Alternatively inbye could be heavily grazed, providing Golden Plover with feeding grounds and land managers with the flexibility to reduce stock or mob stock the more valuable areas of unimproved vegetation.

- The response of semi-natural vegetation was complex. Changes in frequency did not distinguish between grazed and ungrazed vegetation, whereas biomass had a differential response. This may reflect the faster response of biomass to changes in management or the inability of the frequency measures to detect increases in *Molinia caerulea* abundance. The overall interpretation suggests that species of wet conditions increase in abundance (with the exception of grazed biomass) at the expense of drier species. Mean rainfall was higher throughout the monitoring period indicating that conditions on Bodmin Moor were wetter. This is a potential explanation of the changes in community composition in semi-natural vegetation.

- Species response at the farm scale showed no significant changes in the abundance of any dwarf-shrub species. The objectives of CS are therefore not being met on Ivey & Hawkstor Farm. Other work suggests that a decline in the abundance of *Calluna vulgaris* would be expected under grazing by 0.5LU/ha and an increase in abundance when subject to no grazing. It is possible that, given more time, dwarf-shrub species may show an increase in cover, but this remains speculative.

- The presence of *Molinia caerulea* is known to modify the response of ungrazed vegetation, resulting in *Molinia caerulea* dominance (Hill 1982). Other work suggests that light grazing (0.15 LU/ha) may be effective in maintaining *Calluna vulgaris* where it is already abundant but it is insufficient to enable enhancement of *Calluna vulgaris* cover in areas where it has become sub-dominant or been replaced by grasses (Gardner *et al.* 2001). On Bodmin Moor, grazing in excess of 0.5 LU/ha did not reduce *Molinia caerulea* abundance. There is reason to doubt that that the current CS prescription is sufficient to suppress *Molinia caerulea* and enhance or maintain the cover of *Calluna vulgaris* and other dwarf-shrubs. Indeed, given that grazing to control *Molinia caerulea* must be in excess of 0.5 LU/ha and that this level of grazing has been shown to debilitate dwarf-shrub heath in other areas, an appropriate grazing intensity may not exist.

- Further work is required to inform management decisions. Little is known about the effects of species of grazers such as ponies and mixed stock management, and the responses of plant species such as *Ulex gallii*, *Erica tetralix*, and *Agrostis curtisii*, all of which are common on Bodmin Moor. Information on burning, particularly on wetter vegetation, and post-burn grazing is absent. The modifying effects of climate on species response to grazing is also largely a matter of conjecture, and may be important in explaining variation of response to management in different areas. Finally, competitive relationships between dwarf-shrubs and *Molinia caerulea* require further work, as does the response of *Molinia caerulea* to the different grazing regimes.

8 The response of *Molinia caerulea* to defoliation

8.1 Introduction

8.1.1 General Introduction

Molinia caerulea (hereafter referred to as *Molinia*) is a common constituent of moorlands throughout Britain. It is often abundant and frequently dominates large areas, often excluding other flowering plants (Hubbard 1984). The widespread dominance of *Molinia* is a problem, as it results in species-poor landscapes that are of low value in agricultural and conservation terms. *Molinia* begins growing in April and is of some value to foraging stock throughout spring. However, by July it begins to senesce, and is of limited value to grazing animals until the following April. The species-poor landscapes that result from *Molinia* dominance are not valued by conservationists partly because of their low floristic diversity, and partly because *Molinia* is perceived as invading dwarf-shrub heath communities (Chambers *et al.* 1999, Backshall *et al.* 2001). Dwarf-shrub heath including *Calluna vulgaris* heath is valued because of its rarity outside the Western seaboard of Europe. Therefore the alleged invasion of *Calluna* moorland by *Molinia* in the last century is a cause for concern in many areas of upland Britain (Chambers et al. 1999). Increased nutrient supply can cause a shift from *Calluna* moorland to grassland (Berendse *et al.* 1994, Pitcairn *et al.* 1995). However, changing management regimes can also cause a shift from *Calluna* dominance to *Molinia* dominance (Damblon 1992). Upland management in Britain involves both grazing and burning. Stock numbers have risen dramatically since the 1940s and it is generally recognised that this results in the loss of *Calluna* moorland. For example 36% of *Calluna* was lost between 1914 and 1979 in the Peak District (Anderson & Yalden 1981). According to Bardgett *et al.* (1995), 24% of *Calluna* moorland in England shows growth forms associated with overgrazing and other inappropriate management.

Paleoecological work on Exmoor (South West England), suggests a shift from *Callunetum* to *Molinetum* during the last century. The rise in *Molinia* dominance is associated with charcoal, indicating increased frequency of burning and is correlated with increased stock numbers (Chambers *et al.* 1999). However, over the last millenium, vegetation dominance has alternated between *Calluna* and *Molinia* with dominance determined partly by prevailing climate, and the *Callunetum* itself originated from a grass-heath community in the Mediaeval period (Chambers *et al.* 1999).

Brewster (1975), and Roberts & Edwards (1994) have interpreted written sources as suggesting that on Bodmin Moor dwarf-shrub heath was more abundant in the past than it is today. Roberts & Edwards (1994) suggested that increasing numbers of livestock have brought about the replacement of dwarf-shrub heath with acid grassland, of which *Molinia* is a virtual constant on Bodmin Moor. Bodmin Moor has seen a 38-fold increase in sheep numbers between 1940 and 1973, and a four-fold increase in cattle numbers between 1953 and 1974 (Brewster 1975). However, in the absence of aerial photography, ground truthing and paleoecological studies, the extent of losses of dwarf-shrub heath to grassland remain speculative.

In addition to understanding the long-term dynamics of *Molinia* grassland and dwarf-shrub heathland on Bodmin Moor, the short-term response of *Molinia* to grazing requires investigation. Agri-environment management prescriptions currently advocate a reduction in stocking levels, in an attempt to promote heathland restoration. This reduced grazing pressure may result in a detrimental increase in dominance of *Molinia*, as an inevitable consequence of attempts to improve the condition of dwarf-shrubs (Smallshire *et al.* 1997). Experiments at Langridge and Little Stannon (Dartmoor) showed increases in *Molinia* in ungrazed and reduced grazing controls compared to grazed treatments (Weaver *et al.* 1998). Monitoring at Redesdale also showed increases in *Molinia* abundance under light summer grazing, particularly where

Molinia was already prevalent (Gardner *et al.* 2001). Reducing stocking levels on Bodmin Moor, where *Molinia* is virtually ubiquitous, may therefore result in *Molinia* dominance rather than promoting the spread of dwarf-shrub heath. Monitoring on Hawkstor & Ivey lends support to this hypothesis (Chapter Seven).

Research indicates that winter and autumn grazing are detrimental to *Calluna*, as grass species are unavailable to stock and *Calluna* is preferentially grazed. *Molinia* is senescent throughout winter but begins to grow in early spring. Countryside Stewardship grazing protocols therefore consist of no winter grazing to avoid damage to *Calluna vulgaris* and light summer grazing to control *Molinia*. Information on the effects of frequency, timing and severity of defoliation on *Molinia* is required to ascertain how it may best be controlled. Experimental work in Southern Scotland indicates that the frequency and severity of defoliation are more important than timing in their effects on *Molinia* (Grant *et al.* 1996). This suggests that increasing the severity of grazing under Stewardship may be more appropriate for *Molinia* control than changing the timing of grazing. However, on Bodmin Moor, *Molinia* growth starts earlier in spring than in other areas because Bodmin Moor is the warmest upland area in Britain. Early spring grazing may therefore provide a mechanism for *Molinia caerulea* control on Bodmin Moor.

The findings of research are contradictory on the effects of reduced grazing on *Molinia* dominance in wet areas. *Molinia* on wet heath in Northumberland increased in cover when grazed by sheep at 1.2 ewes/ha for three years, compared to an ungrazed control (Nolan *et al.* 1995). In contrast, it is believed that in the valley and blanket mires of the South West, cattle grazing is necessary to prevent *Molinia* dominance (Smallshire *et al.* 1997). Further research is therefore required into the response of *Molinia* to grazing in different communities specifically in wet heath/mire and dry heath.

Population processes are often described as providing the key to understanding community compositional shifts in response to grazing (Briske & Silvertown 1993). Grant *et al.* (1996) discovered that defoliation was associated with reduced leaf production as a consequence of reductions in the size and number of *Molinia* tillers. The responsiveness of tiller density to grazing suggest that it is a useful variable for monitoring the response of grassland communities to disturbance (Briske & Silvertown 1993). Hence the use of tiller number in this investigation. Lamina extension provided a measure of leaf production. Height was also used as it provides information about competition for light.

8.1.2 Aims

The primary aim of the work described in this chapter was to examine the response of *Molinia* to variation in the timing, frequency and severity of defoliation (Table 8.1). A second aim was to determine if the response of *Molinia* to defoliation is modified by wetness. Variation in tiller density, lamina growth and plant height may provide information on the likely response of *Molinia* to various management options.

Table 8.1. Research questions and their management implications.

Research Question	Management Implications
What are the effects of timing of grazing on the growth and population dynamics of *Molinia*?	Should spring grazing be introduced to agri-environment schemes on Bodmin Moor or is summer grazing alone sufficient to control *Molinia*?
What are the effects of different grazing intensities in summer on the growth and population dynamics of *Molinia*?	Would increased summer grazing make any difference to the control of *Molinia*?
Does *Molinia* respond to grazing differently in wet areas and dry areas?	Should valley mires and wet heath be managed differently to drier habitats in order to control *Molinia*?

8.2 Methods

8.2.1 Fieldwork

An exclosure measuring 53m by 12m was erected on Hawkstor Farm in an area currently under Countryside Stewardship management. The exclosure was on a slope and incorporated a transition from dry (top of slope) to wet (Figure 8.1.). *Molinia* was overwhelmingly dominant throughout the exclosure (Figure 8.2). It was associated with other grass species and *Ulex gallii* at the top of the slope and *Eriophorum vaginatum* and *Sphagnum* species. at the bottom.

Figure 8.1. The transition from dry (top of slope) to wet (bottom of slope) with the experimental grid overlaid.

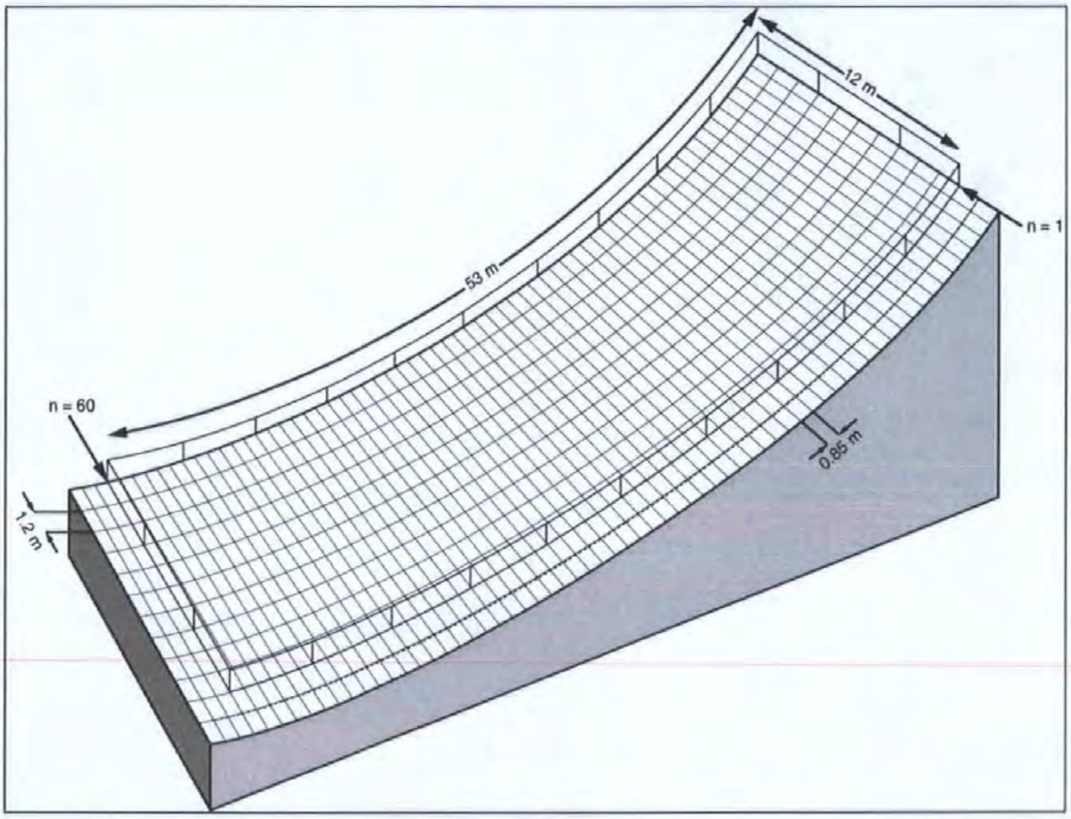


Figure 8.2. The experimental exclosure.

Six treatments were applied:

- **No grazing**
  Uncut control.
- **Countryside Stewardship** (CS)
  The effect of CS was monitored outside the experimental exlosure (Figure 8.1).
- **Spring grazing**
  Molinia cut to remove 50 % of lamina material in May
- **Summer grazing**
  Molinia cut to remove 50 % of lamina material in July
- **Spring & summer grazing** (Double cut)
  Molinia cut to remove 50 % of lamina material in May and July.
- **Severe summer grazing**
  Molinia cut to remove 80 % of lamina material in July.

Each treatment was replicated 60 times with each replicate occupying a different position on the experimental grid (Figure 8.1.). The treatments were fully randomised across the slope to allow for micro-environmental variation except for the Stewardship treatment, which was, of necessity outside the exclosure. On some occasions, no *Molinia* was present on the grid intercept and the sample point was moved to a suitable point within that square and marked with a peg. Soil moisture (theta probe) and slope angle (compass clinometer) were recorded at each sampling point together with an estimate of species composition using DAFOR cover abundance scores.

Each experimental unit consisted of a 10 cm by 10 cm area. Five tillers were measured at random in each experimental unit and the mean value used to ascertain the length of lamina that was cut. In each instance, the tillers were marked with acrylic paint, in order to allow tiller births and deaths to be recorded along with tiller number, lamina extension and overall height.

Monitoring was undertaken when the treatments were applied in May and July 2000. Final observations were taken in September 2000. Tiller number in each experimental unit was recorded. Lamina extension was measured from culms. Height was measured from the ground up.

8.2.2 Data analysis

Soil moisture categories were defined for subsequent analysis by ranking the rows of the experimental grid in order of mean soil moisture and dividing these rows into four equal-sized groups. One-way analysis of variance (ANOVA) and posthoc Student-Newman-Keuls (SNK) tests (Newman 1939, Keuls, 1952) confirmed the validity of the four categories. Canonical Correspondence Analysis (CCA) (ter Braak 1986, 1988, 1994, ter Braak & Smilauer 1998) was used to quantify the relationships between soil moisture, slope angle and species composition. Two-way ANOVA and posthoc SNK testing allowed the significance of changes in tiller number, lamina length and *Molinia* height to be determined.

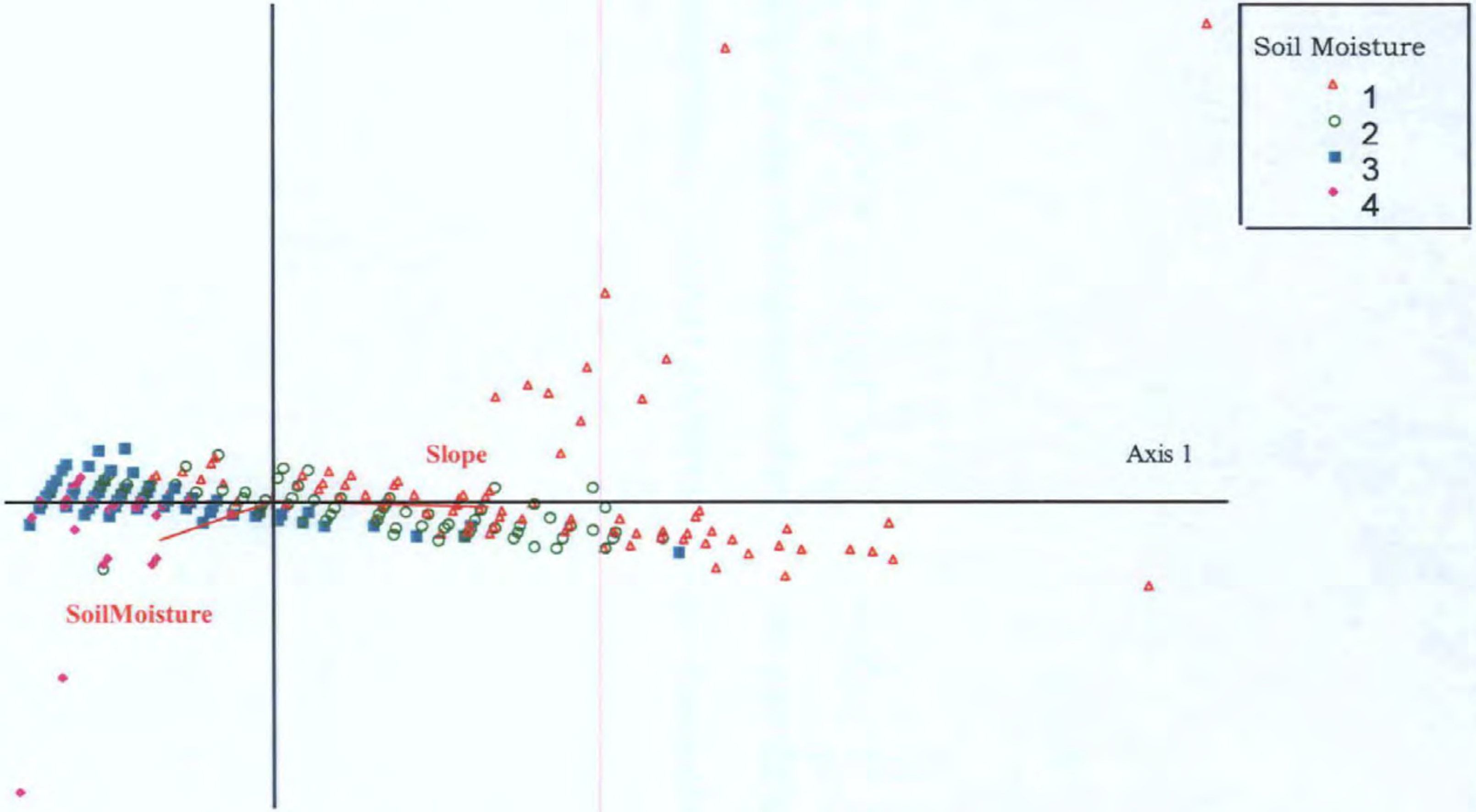
8.3 Results

8.3.1 Species composition within the experimental plot

The first axis of CCA explained only 4.7% of the variance, whilst the second axis explains 0.2%. The eigenvalue of the first axis and species-environment correlations differed significantly from random fluctuations (Monte Carlo test $p = 0.01$). However, subsequent axes did not differ significantly. Therefore only the first axis was interpreted.

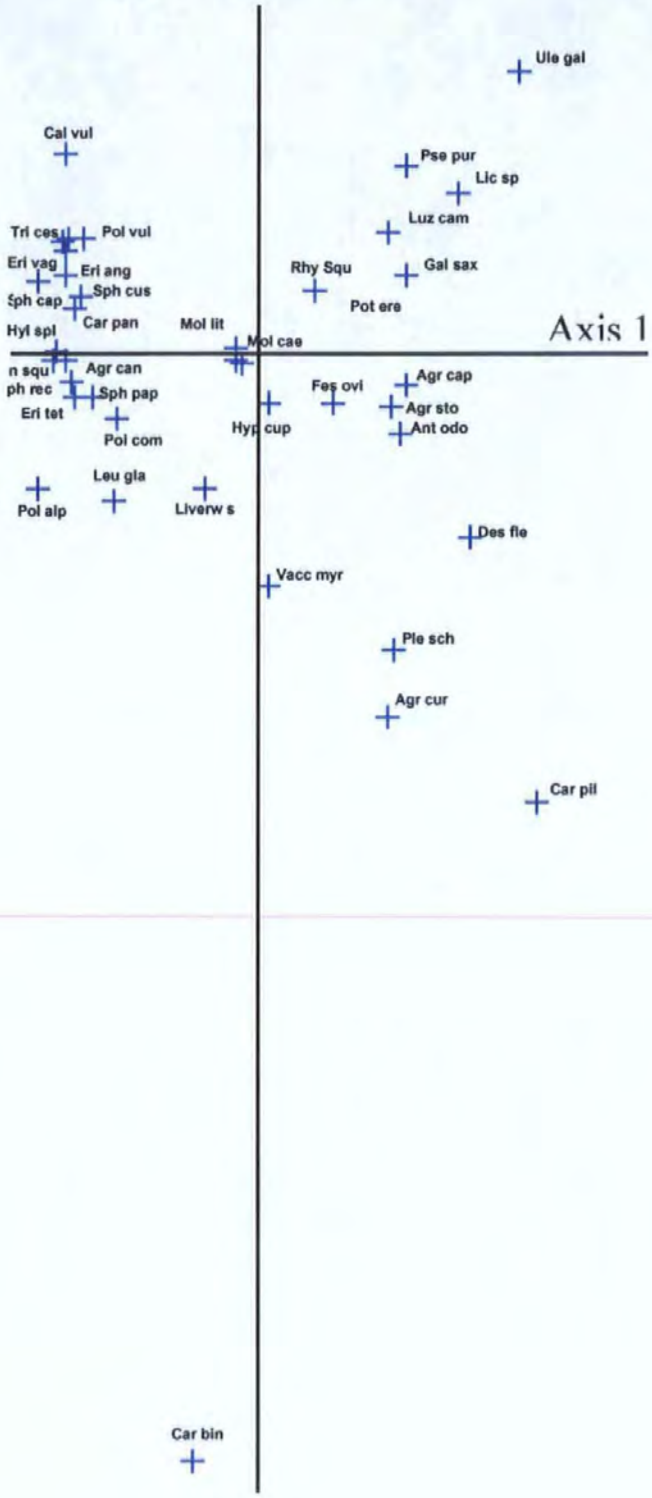
Axis one of CCA most closely corresponded to slope angle, followed by soil moisture (Figure 8.3). There was a correlation between slope angle and soil moisture ($r = -0.409$, $p < 0.01$) with the lower angled ground being wettest, but they made unique contributions to the regression coefficient (variance inflation factors were less than 20).

Figure 8.3. Sample ordination (CCA) of vegetation and environmental data from the *Molinia* defoliation experimental grid. Axis one, $\lambda = 0.244$, Axis two $\lambda = 0.011$. Soil Moisture 1 = dry, 2 = dry-intermediate, 3 = wet-intermediate, 4 = wet.



Axis one was most strongly associated with *Ulex gallii* (Pearson r = 0.506, Kendall tau = 0.387), *Galium saxatile* (Pearson r = 0.504, Kendall tau = 0.453), *Festuca ovina* (Pearson r = 0.439, Kendall tau = -0.402), *Agrostis stolonifera* (Pearson r = 0.360, Kendall tau = 0.336), *Eriophorum vaginatum* (Pearson r = -0.347, Kendall tau = -0.339) and *Sphagnum capillifolium* (Pearson r = -0.339, Kendall tau = -0.331) (Figure 8.4). *Ulex gallii, Galium saxatile, Festuca ovina* and *Agrostis stolonifera* were associated with the dry / dry-intermediate soil moisture categories, whilst *Eriophorum vaginatum* and *Sphagnum capillifolium* were associated with the wet / wet-intermediate soil moisture categories.

Figure 8.4. Species ordination (CCA) of vegetation and environmental data from the *Molinia* defoliation experimental grid.Axis one, λ = 0.244, Axis two λ = 0.011.



8.3.2 Molinia response to experimental treatments

ANOVA showed that there were significant differences in *Molinia* response to different treatments (Table 8.3). Soil moisture also had a significant effect on response and there were significant interactions between soil moisture and treatment for all the response variables investigated.

Table 8.2. Results of ANOVA on the response of *Molinia* to treatments and variation in soil moisture.

Response Variable	Source of variation	F value	P
Change in tiller number	Soil moisture	2.95	0.03
	Treatment	82.33	0.00
	Soil moisture x treatment	2.05	0.01
Change in lamina length	Soil moisture	4.75	0.00
	Treatment	69.24	0.00
	Soil moisture x treatment	2.26	0.00
Change in *Molinia* height	Soil moisture	3.30	0.02
	Treatment	78.14	0.00
	Soil moisture x treatment	1.75	0.04

Spring grazing, Spring & summer grazing and CS treatments all had fewer tillers at the end of the experiment than at the start (Figure 8.5). CS resulted in the largest decrease in tiller number and was significantly different to other treatments except in dry conditions. Tiller number increased in the summer grazing treatments (both intensities) and differed significantly from the other treatments in dry/dry intermediate conditions. The no grazing treatment showed a reduction in tiller numbers in drier conditions but a slight increase in wetter conditions resulting in a significant interaction effect.

CS treatment showed a reduction in lamina length, whereas all other treatments showed an increase (Figure 8.6). This difference was significant. Spring grazing and Spring & summer grazing showed increase in lamina length in wetter conditions and were significantly different to other treatments in wet-intermediate conditions.

CS and severe summer grazing treatments showed a reduction in *Molinia* height over the course of the experiment (Figure 8.7). These treatments were significantly different to the others which all showed height increases in all soil moisture catergories. Spring grazing and Spring & summer grazing treatments showed an increase in height in wetter conditions. They were significantly different from other treatments in the wet soil moisture category.

Figure 8.5. Changes in mean *Molinia* tiller number between May and September for six cutting treatments and four soil moisture levels. (error bars = sd)

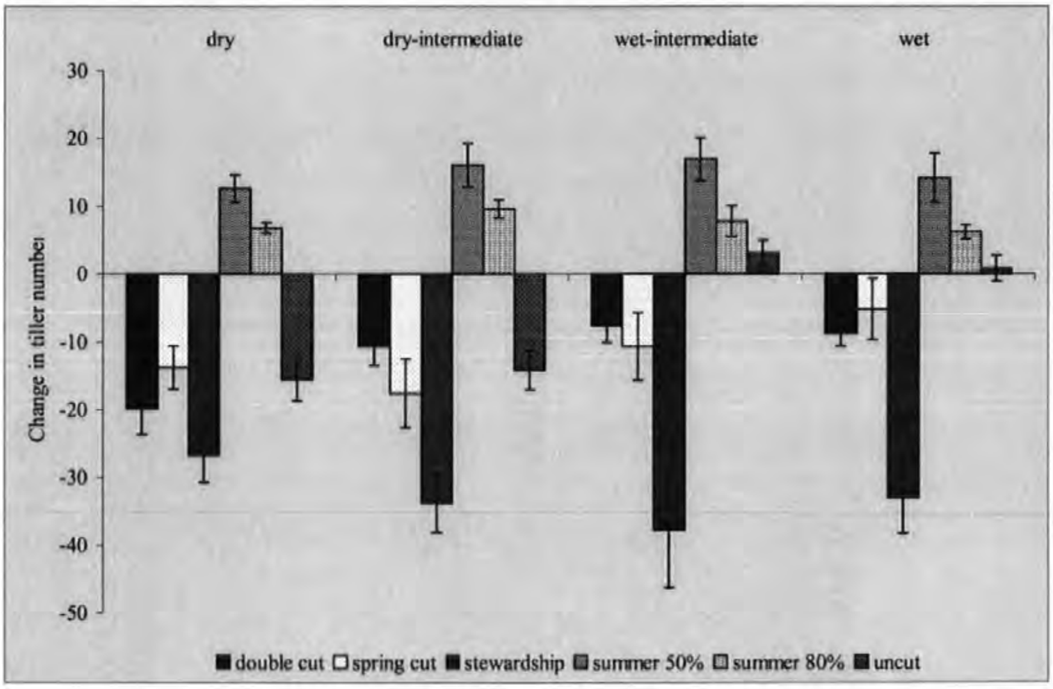


Figure 8.6. Changes in mean *Molinia* lamina length between May and September for six cutting treatments and four soil moisture levels. (error bars = sd)

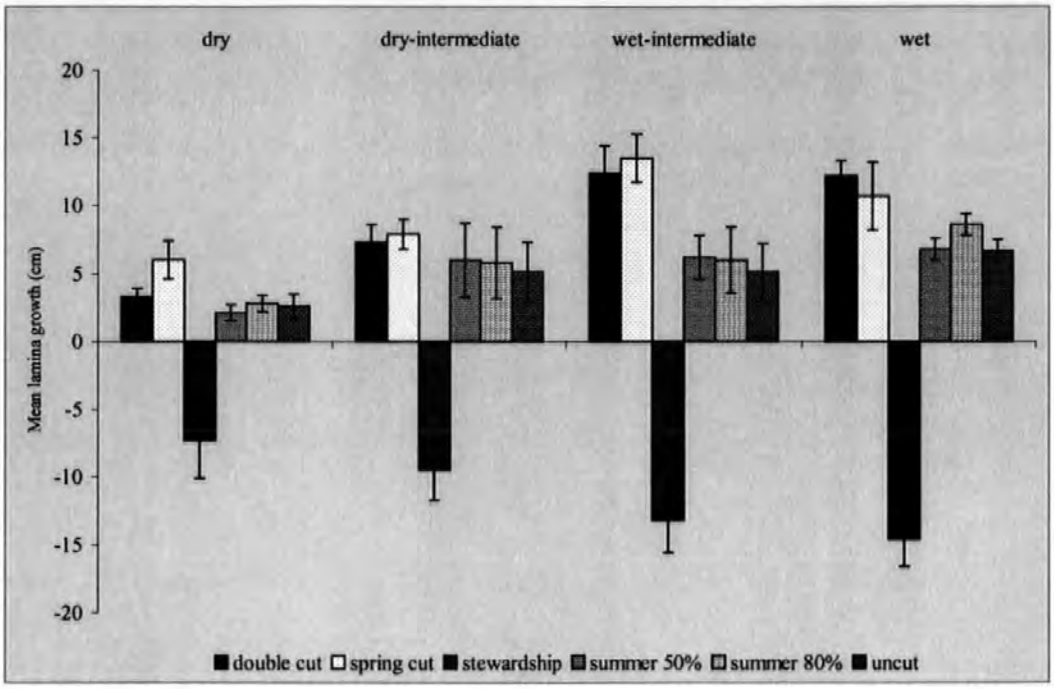
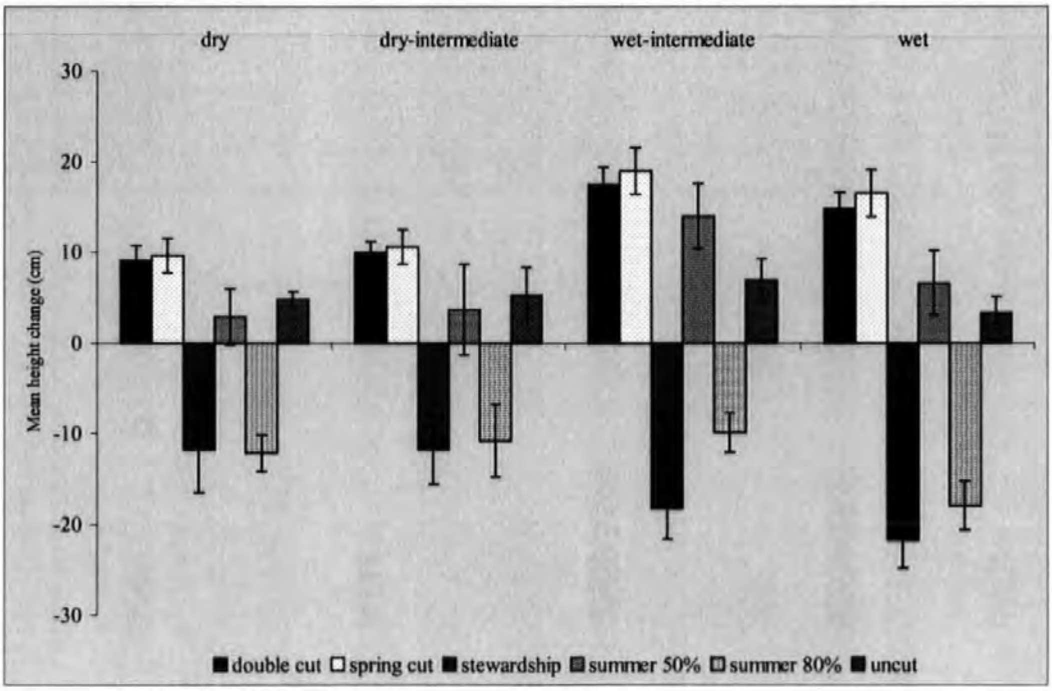


Figure 8.7. Changes in mean *Molinia* height between May and September for six cutting treatments and four soil moisture levels. (error bars = sd)



8.4 Discussion

8.4.1 The relationships between species composition, soil moisture and slope angle

Molinia is most abundant and vigorous on flat ground and slopes <40° suitable for the formation of peaty gleys or deep peats (Taylor *et al.* 2001), where there is ground-water movement, good soil aeration and an enriched nutrient supply (Rutter 1955, Webster 1962a, 1962b, Loach 1966, 1968a, 1968b, Sheikh 1969a, 1969b). The CCA demonstrated that slope angle and soil moisture were correlated with the lowest slope angles having the highest soil moisture values. Soil aeration was not measured but ground water movement and aeration were presumably higher on the sloping ground. On the flatter areas, water movement may have been more limited, but overland flow was observed during high rainfall events. The entire transition was therefore eminently suited to the growth of *Molinia* and this was reflected in its abundance across the experimental area.

There was very little floristic variation between dry and dry-intermediate categories, which represented acidic grassland and dry grass-heath characterised by species such as *Ulex gallii*, *Galium saxatile*, *Festuca ovina* and *Agrostis stolonifera* along with *Molinia*. Likewise wet and wet-intermediate categories were similar, representing wet heath and mire vegetation characterised by species such as *Eriophorum vaginatum* and *Sphagnum capillifolium*. Minor variation in soil moisture and slope angle therefore appears to exert little effect on floristics. The difference between dry, dry-intermediate and wet, wet-intermediate is therefore of greater management interest than the variation between all four categories, which require abiotic measurement for definition.

8.4.2 The response of *Molinia caerulea* to defoliation

Changes in tiller number

Spring grazing, Spring & summer grazing and CS treatments all had fewer tillers at the end of the experiment than at the start. This result is consistent with earlier work where the weights of storage organs were reduced by defoliation within a season (Latusek 1983, Torvell *et al.* 1988, Thornton 1991), whilst repeated within-season defoliation of *Molinia* resulted in declining tiller size and numbers over subsequent successive years (Jones 1967, Grant *et al.* 1996). Most species adapt to defoliation by producing large numbers of small tillers in response to raised red: far-red light ratios at tiller bases (Deregibus *et al.* 1983, Skalova & Krahulec 1992). Lack of tillering in *Molinia* is due either to lack of response to changed red: far-red light ratio or to very low inherent rate of tiller turnover for *Molinia* (Grant *et al.* 1996). As summer grazing resulted in increased tiller number on Bodmin Moor, *Molinia* must be able to respond to changes in red: far-red light ratio and/or tiller turnover must vary with grazing treatment. The red: far-red light ratio is not dependent upon seasonality but it is conceivable that differential mortality could be generated by variation in the timing of grazing. Likewise, birth rates could vary in response to grazing. On Bodmin Moor, tiller deaths exceeded tiller birth when grazing began in May, whereas births exceeded deaths when subject to grazing in July. Further work is required to separate out the effect of grazing on turnover rate from response to changes in the wavelength of light.

The no grazing treatment showed a reduction in tiller number in drier conditions but a slight increase in wet conditions. Changes in nutrient richness influence tillering and vigour of growth in *Molinia* (Thornton 1991, Grant *et al.* 1996, Taylor *et al.* 2001). Pot experiments on rooted basal internodes found that secondary tillers were produced at high N but not at low N (Thornton 1991). On Bodmin Moor the species occupying the wet habitat (such as *Eriophorum* spp., *Trichophorum cespitosum* and *Erica tetralix*) have extremely low Ellenberg N numbers indicating very infertile sites, whilst species of the drier sites (such as *Deschampsia flexuosa*, *Anthoxanthum odoratum*, *Galium saxatile* and *Carex pilulifera*) are indicative of "more or less infertile" conditions (Hill *et al.* 1999, p6). Thus, in contrast to Thornton (1991), the lower N sites exhibit more tillering than the higher N sites. This discrepancy is hard to explain, but factors other than nutrient level may have influenced the results on Bodmin Moor.

The CS treatment resulted in a larger decline in tiller number than other treatments suggesting that grazing is more severe in its effect on tiller number than defoliation. Grazing by cattle was concentrated in the experimental area due to a fenceline effect. Trampling may also have exerted an additional effect accounting for the severity of the CS treatment in comparison to the defoliation treatments.

Changes in lamina length

Lamina growth was significantly lower in the CS treatment than other treatments irrespective of soil moisture. The CS treatment exhibited negative values for lamina growth from May to September, as utilisation by livestock exceeded growth during this period. Other work suggests that repeated within-season defoliation results in lower leaf production in the long term (Grant *et al.* 1996).

The Spring and Spring & summer treatments showed significantly greater lamina growth in wet-intermediate conditions than other treatments. Leaf extension has been shown to increase on defoliated plants in the short-term (Latusek 1983, Thornton 1991) particularly at low nitrogen levels (Thornton 1991). Ellenberg numbers (Hill *et al.* 1999) indicate that nitrogen levels are low in the wet-intermediate soil moisture category. Thus this result is consistent with other work.

The other treatments were not significantly different to the uncut treatment suggesting that early cutting is required to elicit an increase in lamina extension. Late cutting (July/August) has been shown to reduce lamina mass in the long term, particularly if cutting is severe (Grant *et al.* 1996). Longer-term experiments are required to determine whether the short-term increase in lamina length persists in reponse to early cutting.

Changes in height

Change in *Molinia* height was significantly lower in CS and severe summer grazing treatments than other treatments. Any increase in plant height as a result of growth in the CS treatment was outweighed by reduction in height as a result of grazing (Figure 8.8).

Figure 8.8. A grazed *Molinia* tussock in the CS treatment area.

The decline in height in response to severe summer grazing was consistent with previous work, where reductions in productivity reflected the severity of leaf removal (Grant *et al.*1996). The Spring & summer and Spring treatments resulted in larger height increases in wet and wet-intermediate soil moisture categories than other treatments. This reflects the increased lamina extension in low nitrogen environments where defoliation occurs early in the year. If leaf production is increased, then plant height will also increase.

Interactions between variables

The interaction between different treatments, soil moisture categories and response variables involves the comparison of 72 means. Thus different variables respond to the same treatment in different ways modified by different conditions. There is generally a similar pattern between *Molinia* height and lamina extension, as might be expected, although summer grazing and no grazing treatments showed differences in lamina extension. However, the pattern of changes in tiller number is hard to relate to lamina extension or height change except in the case of the CS treatment, without biomass data. Unfortunately, the foot-and-mouth outbreak of 2001 coincided with the end of the experimental period, and the intended measurements of biomass were not possible.

Problems of Interpretation

The management implications of this work are difficult to elucidate for a number of reasons. Firstly, the effects of Stewardship are generally, although not always, more severe than the defoliation treatments. This suggests that defoliation does not equate to grazing in severity. More severe and frequent defoliation is required to simulate grazing. Additional effects of grazing such as trampling and more rapid nutrient cycling may also account for discrepancies between defoliation treatments and grazing (Backshall *et al.* 2001).

Secondly, the defoliation treatments were imposed on a site subject to Stewardship grazing for the previous four years. Although there are differences between treatments, all the vegetation subject to defoliation is responding to the cessation of grazing, as well as treatment whereas the Stewardship grazing was not. The effects of defoliation may be deferred in time (Grant *et al.* 1996), which could confound the effect of defoliation treatment.

Thirdly, the whole experiment was sited in just one area rather than using replicates from a number of different sites where CS had been applied. Extrapolating the results to the rest of Bodmin Moor must be done with a degree of circumspection.

8.4.3 Management Implications

Despite the problems of interpretation outlined above, it is nevertheless useful to discuss the management implications of this work. Grazing at

Stewardship levels reduces *Molinia* height, lamina length and tiller number relative to ungrazed vegetation and defoliation treatments. This suggests that CS may be controlling *Molinia*. However, further longer-term work would be necessary to confirm this. Monitoring over five years detected no decrease in *Molinia* abundance (Chapter 7). Thus reductions in tiller number, lamina extension and *Molinia* height may not necessarily equate to a reduction in *Molinia* biomass.

Spring and Spring & summer treatments resulted in increased lamina growth along with increased height but tiller number declined in wet conditions. This suggests that early defoliation is compensated for by increased lamina growth leading to increased height. There is, therefore, some evidence to suggest that spring grazing would not be a useful control mechanism for *Molinia* in wet, low nitrogen conditions common amongst wet heath and mires on Bodmin Moor. *Molinia*- domination in mires is often attributed to lack of grazing (Smallshire *et al.* 1997, Backshall *et al.* 2001) but could also reflect the use of mires for an early-bite by cattle. The results imply that early grazing by cattle could be detrimental rather than beneficial for *Molinia* control. Further work would be required to confirm that these results persist over time. The short-term response of *Molinia* to defoliation may differ from the long-term response because increased growth is reliant upon carbohydrate reserves in basal internodes and may be unsustainable in the long-term (Grant *et al.* 1996). However, other work does suggest that *Molinia* dominance is maintained by grazing at low levels in wet low nitrogen conditions (Nolan *et al.* 1995, Gardner *et al.* 2001). The effects of grazing timing and the use of different grazing species in wet heath and mire vegetation requires further experimentation if suitable management protocols are to be developed.

In drier higher nitrogen conditions, Spring grazing was not significantly different to the uncut control. This indicates that extending light grazing into the spring would not help to control *Molinia* amongst the dry heath and acidic grassland. Given that simulated grazing in this experiment was an imperfect representation of real grazing, real grazing in spring might assist in the control of *Molinia*.

Summer grazing represents the best form of *Molinia caerulea* control, on the basis of the results of this experiment. Summer defoliation resulted in a significant increase in tiller number from May-September in dry and dry-intermediate conditions compared to uncut *Molinia*. This was not associated with any significant differences in lamina growth, although heavy defoliation results in significantly lower height irrespective of conditions. The decrease in height under heavy grazing and lack of increased lamina growth suggest that heavy summer defoliation may be a good mechanism for *Molinia* control. This is consistent with work in Southern Scotland, where heavy grazing reduced *Molinia* biomass by 86%, compared to a 46-65% reduction under light grazing (Grant *et al.* 1996). Controlled grazing studies on small plots have demonstrated that heavy grazing can result in dominance of *Agrostis* species over *Molinia*, whilst light grazing or no grazing favours *Molinia* dominance (Jones 1967). However, heavy summer grazing is not compatible with the maintenance of dwarf-shrub heath.

There is abundant evidence that *Molinia* is a very variable species due to genecological variation and phenotypic plasticity (Taylor *et al.* 2001). Polyploid races exist with tetraploid and diploid subspecies identified as morphologically distinct (Trist & Sell 1988). Differences in growth in field conditions may represent edaphic ecotypes rather than phenotypic plasticity (Salim *et al.* 1995). Some research even suggests that some *Molinia* is '*r* selected' whilst some is '*K* selected'. It is therefore possible that *Molinia* may not respond uniformly to treatment. This could be exacerbated by the different environmental conditions in different upland regions. Bodmin Moor is the warmest upland in Britain throughout winter and spring (Chapter Two). There is therefore an argument for suggesting that different management may be required to control *Molinia* in different geographical areas. This could be particularly pertinent on Bodmin Moor.

The results of this short-term defoliation experiment suggest that spring grazing is an ineffective management protocol for *Molinia* control in acidic grassland and dry heath, whilst spring grazing may promote increased *Molinia* growth in wet heath and mire. Heavy summer grazing appears to offer the best method of controlling *Molinia* growth. However, further work is needed to confirm that these results persist over time and to determine the effect of real species of grazer.

The need for further work

It is clear that further work is required to inform management decisions both on Bodmin Moor and in other upland areas in order to fully understand the response of *Molinia* to defoliation and different grazing regimes. On Bodmin Moor, longer-term work involving measurement changes in both above and below ground biomass, and nitrogen availability would be useful. Monitoring of different Stewardship agreements on different farms would provide interesting data, especially if different species of grazers were studied.

Burning *Molinia*-dominant vegetation is often advocated as a management tool (Backshall *et al.* 2001). Research indicates that burning mixed grass and heather at 3-6 year intervals shifts dominance to *Molinia* (Miles 1988). Furthermore, where grass is already dominant, frequent burning favours *Molinia* at the expense of other grasses (Grant *et al.* 1963). However burning at a less intensive frequency could help to control *Molinia* dominance, especially if this is followed by mob stocking (intensive grazing) to inhibit *Molinia* regrowth.

On Bodmin Moor there is a large persistent seed bank containing *Molinia* and *Calluna vulgaris* (Chapter Six). Burning in March followed by heavy summer grazing and no winter grazing could conceivably allow seedling germination and inhibit *Molinia* as it germinates prior to dwarf-shrub species. Research is required to explore burning-grazing interactions.

8.5 Conclusions

- Short-term defoliation experiments and monitoring were carried out on a *Molinia*-dominated wet-dry transition at a site on Bodmin Moor to investigate the effect of various grazing management protocols on *Molinia*. Changes in tiller number, lamina extension and *Molinia* height were recorded. Unfortunately the experiment only ran for one year and it was not possible to collect biomass data, which hampers attempts to relate the findings to management.

- Tiller number decreased when grazing and defoliation treatments occurred before the end of May. This is consistent with other work (Latusek 1983, Torvell *et al.* 1988, Thornton 1991, Grant *et al.* 1996) and suggests that *Molinia* tillers do not respond to raised red: far-red light or that tillers have a very low rate of turnover. However, as summer defoliation on Bodmin Moor resulted in increased tiller number, *Molinia* must be able to respond to changes in red: far-red light ratio and/or tiller turnover must vary with grazing treatment. Further work is required to extend these findings over a longer time-scale and to determine their management implications.

- Summer-only grazing, primarily by cattle at 0.5LU/ha, resulted in significant decreases in tiller number, lamina length and height compared to no grazing or experimental defoliation irrespective of timing. However, monitoring over five years (Chapter 7) showed that *Molinia* abundance did not decline when subject to these grazing pressures. Further work is required in order to understand how the changes in tiller number, lamina length and height relate to grazing and *Molinia* abundance

- Experimental defoliation in spring encouraged lamina extension and height increase but decreased tiller number in wet conditions. This suggests that increased lamina extension may be able to compensate for vegetation offtake when subject to light spring grazing. Further work is required to determine whether this response is maintained over longer time-scales. If increased lamina extension is sustainable, then light spring grazing could increase *Molinia* dominance in wet heath vegetation. In drier vegetation, the response of spring defoliation was not significantly different to uncut *Molinia*.

- Experimental defoliation in summer generally resulted in decreases in tiller number, lamina extension and *Molinia* height, especially when defoliation was severe but tiller number increased in dry conditions. This suggests that heavy summer grazing may provide the best mechanism for *Molinia* control on Bodmin Moor, especially in wetter communities. However, declines in *Molinia* height, lamina extension and tiller number are not synonomous with reductions in *Molinia* abundance. Therefore further work is required.

9 Grazing management and plant community composition on Bodmin Moor

9.1 Introduction

9.1.1 The questions addressed by the thesis

The central aim of the research presented in this thesis was to reach an understanding of aspects of the ecology and dynamics of the upland vegetation of Bodmin Moor in response to grazing. This would allow evaluation of the suitability of Countryside Stewardship management for the rehabilitation of dwarf-shrub cover in the upland landscape of Bodmin Moor. Initial chapters reviewed the ecological character of Bodmin Moor, grazing management and vegetation in upland habitats and succession in relation to grazing in order to summarise current theory and identify gaps in knowledge. Chapter Five provided the first extensive and detailed phytosociological investigation of vegetation on Bodmin Moor providing a baseline for further work. It also examined the spatial distribution of the plant communities in relation to environmental gradients and grazing management. Chapter Six provided the first description of the soil seed banks on Bodmin Moor allowing assessment of the seedbank potential as sources of propagative material for the rehabilitation of dwarf-shrub cover. Chapter Seven utilised an existing monitoring scheme on Bodmin Moor North SSSI to identify the vegetation changes prompted by the establishment of a Countryside Stewardship management regime. Chapter Eight reported on *Molinia caerulea* defoliation experiments in an attempt to to inform management decisions regarding the control of *Molinia caerulea* using livestock.

9.2 Results and management implications

9.2.1 The nature of Bodmin Moor: implications for grazing management

The objectives of Chapter Five were to produce a phytosociological classification of the plant communities present on Bodmin Moor and to examine the relationships between species composition and a range of environmental factors including grazing management. The results conform to expectations and previous surveys of Bodmin Moor in terms of the range and type of communities present. The Natural Area is dominated by acid grassland and mire. There are also some small heathland fragments. *Calluna vulgaris* and *Vaccinium myrtillus*-dominated heath is mostly associated with granite tors, whilst *Ulex gallii*-dominated heath occurs more commonly in mosaics with grassland. These heathland fragments can generally be classified as grass-heath (*sensu* Ward *et al.* 1972), and the majority (with the exception of some tors, East Moor and areas around Minions) would be extremely hard to map at a landscape level (based on minimum polygons of $30m^2$). Wet heath is present on Bodmin Moor, often occupying an intermediate position in transitions from mire to grassland. However, dwarf-shrub species such as *Calluna vulgaris, Erica tetralix* and *Vaccinum myrtillus* are subordinate in cover to other species, notably *Molinia caerulea.* Bodmin Moor can therefore be defined as a grass-dominated moor lacking the cover of *Calluna vulgaris* that often defines moorland in the rest of the United Kingdom.

The nature of the heathland on Bodmin Moor poses some problems in the application of Countryside Stewardship and in assessing vegetation condition. Firstly, definition of the extent of existing heathland is scale-dependent. This is exacerbated by the rapidity of temporal change in response to burning. Thus, even where it is possible to map the distribution of areas of dominant dwarf-shrub, burning, particularly in combination with heavy continual grazing, could potentially change this distribution in one or two years. It is therefore difficult to assess the eligibility of land for 'Moorland Restoration' and 'Moorland Enhancement', where there must be >30% dwarf-shrub heath or potential for heathland restoration. It is equally difficult to determine vegetation condition in grass-heath mosaics as the definition of habitat types is not straightforward. For example, does grassland with dwarf-shrubs represent heathland in unfavourable condition or grassland in favourable condition? Additionally there is a lack of criteria for assessing the potential for heathland restoration. Propagule availability in the seed bank provides an easily quantified method of assessing the potential for heathland restoration (see Section 9.2.4.). Propagule availability and other objective criteria should be developed along with cover of dwarf-shrub heath in order to assess the eligibility of land for 'Moorland Management' or 'Moorland Restoration' and to assess its condition on Bodmin Moor.

The second difficulty in the application of Stewardship concerns the precision of the objectives. The current objectives are to increase dwarf-shrub cover to 50% or more ('Moorland Restoration') or the maintenance of a 70% grass: 30% dwarf-shrub mosaic ('Moorland Management'). The composition of this dwarf-shrub heath is not considered. Hence, as far as Stewardship is concerned, the nature conservation value of dwarf-shrub is dependent solely on cover rather than composition and cover in combination. The most definable heathland areas on Bodmin Moor consist of dense stands of *Ulex gallii* and to a lesser extent stands of *Ulex europeaus*. Although there is intrinsic value to all species and *Ulex* is known to support whinchats (Nature Conservancy 2001), this is considered to be of lower conservation value than more fragmented *Calluna-Vaccinium* heath on tors or more diverse *Ulex* heath incorporating other dwarf-shrub species (Backshall *et al.* 2001).

Further research is required to ascertain the relationships between these different heathland communities and management but the lack of distinction between them inherent in Stewardship prescriptions is an important issue. Although difficult to apply on Bodmin Moor, assessment of current condition (Jerram *et al.* 2001) could be used to determine eligibility for Stewardship. This would represent an improvement on the current criteria for eligibility and would also provide a means of assessing the success of Stewardship at a coarse level. However, further work is required to revise these criteria and monitoring programs are necessary to determine the precise impacts of Stewardship on upland vegetation.

9.2.2 Spatial variation in plant community composition in relation to grazing

Aside from phytosociology, another objective of Chapter Five was to examine the relationships between species composition and a range of environmental factors including grazing management. The distribution of the plant communities present on Bodmin Moor is controlled primarily by the interactions between soil depth, soil moisture and organic matter content. Grazing, soil pH and soil calcium are also of importance. The difficulty of finding objective measures of biotic pressure is a major problem in interpretation of grazing as a controlling variable. Variation in the timing of grazing and stock type is not differentiated, despite being of critical importance in determining the outcome of grazing. This is due to lack of uniform data and discrepancies between utilisation rate at the plant community scale and stocking rate at the management unit scale.

Rodwell (1992a, b) and Smallshire *et al.* (1997) suggest that heavy grazing converts *Ulex gallii*-dominated heathland to *Agrostis curtisii* grassland and that light grazing would allow establishment of *Ulex gallii* heathland. Further work is required for corroboration and to determine the precise impacts of variation in the timing and intensity of grazing and the effect of livestock type on the magnitude and direction of the changes. The role of burning in these transitions and grazing-burning interactions is also thought to be important (Rodwell 1992a, b). Burning every 16 years or so may favour *Ulex gallii* (Stokes, K. Centre for Ecology and Hydrology. *Pers. comm.*), whilst more frequent burning could favour grasses such as *Molinia caerulea* (Grant *et al.* 1963, Miles 1988) or *Agrostis curtisii* (Ivimey-Cook 1959).

It is also suggested that heavy grazing switches dominance in wet heath from dwarf-shrubs to *Molinia caerulea* (Godwin & Conway 1939, Bignal & Curtis 1981, Rodwell 1992a). Although reduction of grazing pressure generally results in increased dwarf-shrub abundance, cessation of grazing and light grazing can also result in *Molinia* dominance (Hill 1982, Rodwell 1992a, Gardner *et al.* 2001). Thus, reducing grazing intensity to increase dwarf-shrub abundance may inevitably increase *Molinia caerulea* abundance (Smallshire *et al.* 1997). Fence line boundaries encountered during phytosociological survey strongly suggest that Countryside Stewardship on Bodmin Moor will promote increased *Molinia caerulea* abundance rather than increasing the cover of dwarf-shrubs (Figure 9.1). Furthermore, the *Molinia caerulea* dominance is overwhelming and appears to suppress dwarf-shrubs when they are released from heavy grazing.

9.2.3 Temporal variation in plant community composition

The objectives of Chapter Seven were to determine how vegetation changed in response to cessation of grazing, or the implementation of a Countryside Stewardship agreement on Hawkstor & Ivey Farms over five years. The response of dwarf-shrub species and *Molinia* were of particular interest.

Changes in the composition of semi-natural vegetation assessed by frequency and biomass suggest that species of wet conditions increase in abundance (with the exception of grazed biomass), possibly in response to increased precipitation. However, change from one community to another can have many causes and lack of replication and scaling problems hampered the interpretation of these results.

Overall changes in dwarf-shrub abundance were not significant. Therefore, it is clear that dwarf-shrub abundance did not rise to 30% cover over the five-year monitoring period in the graminoid-dominated vegetation under study. Thus the objectives of CS are not being met. Furthermore, as there was no significant change in *Molinia* abundance, grazing at 0.5 LU/ha was not sufficient to supress *Molinia caerulea.* Work from other areas has shown that grazing at 0.5 LU/ha was not compatible with the maintenance of dwarf-shrub heath species. Thus

CS grazing levels on Bodmin Moor appeared to be too low to control *Molinia caerulea* unless they were too high to maintain dwarf-shrubs. It may therefore not be possible to increase dwarf-shrub heath cover on the grass-dominated communities of Bodmin Moor by the manipulation of grazing stock alone.

Figure 9.1. The boundary between Countryside Stewardship land (0.5 LU/ha, summer only) (right) and Common Land (>2 LU/ha non-agreement) (left), with detail of the vegetation in both (below). Note grazing-suppressed *Calluna vulgaris* amongst *Molinia caerulea* on the common land.

Further work is required to verify this. The overall changes are pseudoreplicated. Thus caution is required in extrapolating the effects of Stewardship to other areas. It is therefore safest to consider Hawkstor & Ivey farm as a unique case study rather than a general model. The initiation of rigorous, fully replicated CS monitoring programs is essential to determine the precise effects of Stewardship.

The effects of burning, livestock type and timing of grazing and interactions between these factors and grazing intensity remain largely unknown. It is possible that some form of extensive management could create heathland on these sites but this remains speculative. The effects of Stewardship management in areas of existing dwarf-shrub heath are also speculative. Areas of dense dwarf-shrub with more than 30% *Ulex gallii* cover on the North-East flank of Hawkstor and West-North-West flank of Carkees Tor have increased in cover since the initiation of Stewardship according to the perception of the land manager (Mansfield, A. Farmer. *Pers. comm.*). Likewise, areas of fragmented *Calluna-Vaccinium* heath on the West flank of Garrow Tor are also perceived to have increased in cover (Mansfield, A. Farmer. *Pers. comm.*). Unfortunately this cannot be confirmed by monitoring, as only grass-dominated communities on Hawkstor & Ivey Farm were subject to investigation. Work at Redesdale indicated that light grazing maintained the cover of cover of *Calluna vulgaris* where it was dominant but that *Molinia caerulea* increased in dominance where it was dominant (Gardner *et al.* 2001). This would suggest that the maintenance of existing heathland is possible by light summer only grazing but it remains to be seen if this is the case on Bodmin Moor. The response of mire vegetation to light grazing is also poorly understood both nationally (Shaw *et al.* 1996), and on Bodmin Moor.

Although heathland restoration is prevented, or at least held back by competition with *Molinia caerulea,* propagule availability may also limit the regeneration of dwarf-shrubs.

9.2.4 The Soil Seed Banks of Bodmin Moor

The objectives of Chapter Six were to examine spatial variability in the seed bank of Bodmin Moor to determine if there are sufficient propagules to allow heathland restoration and if the propagules of other species are present in sufficient numbers to potentially inhibit heathland restoration. Variability in the seed bank in relation to depth was also examined to assess the degree to which the vertical distribution of seeds relates to seed persistence.

Dwarf-shrub propagule availability was low on Bodmin Moor compared to other uplands, reflecting the abundance of grassland and dominance of graminoid species. However, *Calluna vulgaris* seed was present in sufficient quantities to allow heathland restoration on Bodmin Moor, except in the *Pteridium aquilinum* community and *Eriophorum* mire (Miles 1973, Gimingham, C. University of Aberdeen. *Pers. comm.*). The mire vegetation is too wet for *Calluna vulgaris* but it is suprising that little *Calluna vulgaris* seed is present beneath *Pteridium aquilinum,* as this community is often found on tors adjacent to extant *Calluna-Vaccinium* heath. *Erica tetralix* seed is most abundant in wet heath vegetation, reflecting both the above-ground distribution and edaphic preferences of *Erica tetralix. Vaccinium myrtillus* seed is scarce. Regeneration therefore relies on vegetative spread where the species is present. *Ulex gallii* seed is scarce and does not reflect the distribution of above-ground *Ulex gallii.* More work is required to elucidate the viability of regenerating *Ulex gallii* heath from seed, particularly as burning is known to be important in its distribution.

It was concluded that propagule availability should not limit the maintenance or enhancement of dwarf-shrub cover on Bodmin Moor in most communities, including acid grasslands. However, the species composition is limited by propagule availability. *Calluna-Vaccinium* heath can only be maintained or enhanced where it currently exists amongst surface vegetation on tors and further work is required to assess the viability of attempts to increase the cover of *Ulex gallii* using propagules present in the seed bank.

Assessing the potential for heathland restoration using above-ground vegetation without considering the seed bank as a source of regenerative propagules leads to erroneous conclusions concerning the capacity for restoration on Bodmin Moor. Heather condition survey on Bodmin Moor identified Tawna Downs (SX132664) as the best site for heathland restoration on Bodmin Moor, whilst East Moor (SX222775) was average (CTNC 1997). Seed bank studies show dwarf-shrub propagule availability to be lower on Tawna Downs than on East Moor, particularly when species other than *Calluna vulgaris* are considered (Table 9.1).

Table 9.1. Seed densities (mean number/ m^2) beneath *Ulex gallii-Agrostis curtisii* heath on Tawna Downs and East Moor, based on emergence from ten samples.

	Calluna vulgaris	*Erica tetralix*	*Ulex gallii*	*Agrostis curtisii*	*Molinia caerulea*
Tawna Downs	160	53	0	80	133
East Moor	213	266	27	186	293

In contrast to the distribution of current dwarf-shrub heath, propagule availability suggests that heathland restoration on East Moor is more likely to be successful than on Tawna Downs and would be less likely to result in dwarf-shrub monoculture resulting in more favourable condition (*sensu* Jerram *et al.* 2001). However, the impact of other species in the seed bank (Table 9.1) and other factors including current vegetation and management will also influence the success of any restoration attempts.

Numerous methods have been advocated to assess the condition of upland habitats (Jerram *et al.* 2001, Jerram & Drewitt 1998, Jerram & Drewitt 1997, Cox *et al.* 1998, Macdonald *et al.* 1998). Initially these methods were for use in SSSIs and SACs but they are also intended to aid general assessment of vegetation condition within agri-environment schemes. They are designed as pragmatic tools to define "existing state" but are also used to monitor gross change and to assess the impact of management (Jerram *et al.* 2001). Their utility for defining existing state has been recognised (above) but they would provide better descriptions of existing state and their predictive power could be increased if they included some quantification of propagule availability.

The presence of propagules in the seed bank could also help decisions regarding habitat definition. Grassland with little surface dwarf-shrub but large dwarf-shrub seed bank can be considered heathland in unfavourable condition, whereas the same grassland with a limited quantity of dwarf-shrub propagules can be considered as grassland. Increases in dwarf-shrub cover might occur under appropriate management (if it exists) in the former, but the latter would remain grassland unless planting was undertaken or propagules added to the site. Knowledge of the seed bank provides some information on the character of the previous vegetation on the site, although this is complicated by seed persistence and soil mixing. Paleoecological work is required if the history of the site is to be fully elucidated.

In general, seed bank investigations suggest that, although propagule availability is low in comparison to other areas, it is not limiting heathland restoration on Bodmin Moor, at least as far as *Calluna vulgaris* is concerned. The lack of increase in dwarf-shrub cover on Hawkstor & Ivey farm when subject to a Countryside Stewardship grazing regime is not due to lack of propagule availability. The existing dwarf-shrub is almost certainly suppressed by *Molinia caerulea*, which may also prevent safe-sites from becoming available for germinating seedlings. Competition within safe-sites may also hinder the germination of dwarf-shrub species. Results of greenhouse experiments show that *Molinia caerulea, Agrostis capillaris* and *Carex pilulifera* are abundant in the seed bank across Bodmin Moor and emerge earlier than dwarf-shrub species in the absence of competition from above-ground. Competition with these species and/or lack of safe-sites are feasible explanations for the lack of dwarf-shrub regeneration in grass-dominated communities on Bodmin Moor.

The role of burning and grazing in the creation of safe-sites requires further investigation. It is possible that heavy grazing or burning may create safe-sites and that follow up management can control the emergence of competitive species, allowing dwarf-shrubs to regenerate from seed. However, such management may not be compatible with the maintenance of existing dwarf-shrub cover and post-regeneration survival remains speculative.

Burning and follow-up grazing trials are underway on Bodmin Moor (Hazlehurst, D. English Nature. *Pers. comm.*). If successful regeneration is observed, the use of burning at a suitable frequency should be introduced to Countryside Stewardship schemes on Bodmin Moor.

9.2.5 **Molinia caerulea** *defoliation experiments*

The objectives of Chapter Eight were to examine the response of *Molinia caerulea* to variation in the timing, frequency and severity of defoliation and to determine if the response of *Molinia caerulea* to defoliation is modified by wetness. The results of the experimental defoliation are hard to interpret because different variables respond in different ways, biomass data were not available and the experiment only ran for one season due to the outbreak of foot and mouth disease. Additionally, CS resulted in reduced height, tiller number and lamina extension although monitoring showed that CS is not sufficient to suppress *Molinia caerulea*. It is therefore not easy to relate changes in these variables to management. Nevertheless some conclusions have been drawn.

As Bodmin Moor is the warmest upland in Britain, *Molinia caerulea* may begin growth earlier in the year here than in other upland areas. Therefore extending grazing into spring may help to control *Molinia caerulea* on Bodmin Moor. The defoliation experiment found that the response of *Molinia caerulea* to spring defoliation was no different to ungrazed *Molinia caerulea* in dry conditions. In wet conditions, increased lamina extension compensated for the loss of lamina material, increasing the height of *Molinia caeulea.* These results suggest that spring grazing may be ineffectual at inhibiting *Molinia caerulea* growth in dry conditions, whilst actually encouraging growth in the wet. However, further work is required to confirm this on longer time-scales.

The effects of summer defoliation are complex but heavy summer defoliation resulted in lower *Molinia caerulea* height. Heavy summer grazing therefore appears to be the best method for inhibiting *Molinia caerulea* growth, particularly in wet conditions. The problems posed by *Molinia caerulea* are recognised in current Stewardship prescriptions both nationally and specifically on Bodmin Moor. A summer purple-moor grass grazing supplement is available for all 'Moorland Management' options on Bodmin Moor. This allows an agreed stocking programme for cattle grazing on areas dominated by purple-moor grass between 16th April and 31st August. Unfortunately, summer grazing at levels that control *Molinia caerulea* are not compatible with the maintenance of existing dwarf-shrub vegetation (Chapter 7) and it appears from the results of short-term defoliation experiments that spring grazing will not be effective in controlling *Molinia caerulea* either.

It is clear that wet environments respond differently to different defoliation treatments than dry environments. Therefore they require different management. Most management units on Bodmin Moor are a mosaic of different communities and many include mire and wet heath vegetation as well as grassland. Stock, particularly cattle, graze mire and wet heath vegetation in spring for an early bite and thereafter generally avoid the wetter vegetation if more palatable forage is to be found on drier ground. More effective management for *Molinia caerulea* control may be to prevent grazing in mires and wet heath during spring. The control of stock movement would be essential for this form of management to occur. Fencing is one option, although this is expensive and raises important access issues. Shepherding is also costly but would provide maximum control and flexibility over where and when stock grazed, whilst avoiding problems of access. For example, shepherding would allow mob stocking on areas of dense *Molinia caerulea* and avoidance of heavy grazing in any areas of heathland where it would be detrimental. Shepherding is currently not economically viable, but the environmental benefits of such stock control could be high.

Horses and ponies are common on the moors of South-west England. Ponies are more effective than cattle for control of *Molinia caerulea* during summer and may be less damaging to *Calluna vulgaris* (Putman *et al.* 1987). The use of ponies rather than cattle should therefore be actively encouraged for Countryside Stewardship 'Moorland Management', although further financial incentives may be required as ponies are less economically viable than cattle. However, even with the use of these managemnt techniques, it may not be possible to control *Molinia caerulea* and increase dwarf-shrub abundance.

9.3 Assessing the nature conservation value of Countryside Stewardship in the uplands

9.3.1 Introduction

Assessment of nature conservation value is subjective and there are many problems involved in such evaluations (Hambler & Speight 1995, Spellerberg 1992). Conservation policy is usually defined *a priori* and scientists work on the manner in which these objectives may be met. However, science also allows the questioning of the objectives, which can deliver higher benefits or be more appropriate if informed by science. The primary objective of Countryside Stewardship 'Moorland Management' and 'Moorland Restoration' is to increase dwarf-shrub cover. However, the scope for increasing dwarf-shrub cover is extremely limited on most of the graminoid-dominated communities on Bodmin Moor using current Stewardship prescriptions. Unless *Molinia caerulea* is controlled, dwarf-shrub regeneration is not possible and grazing levels that suppress *Molinia caerulea* also suppress dwarf-shrub species. Modification of the management regime may increase the abundance of dwarf-shrub in grass-dominated communities but this is speculative and appears unlikely. In any case, this would be expensive, subject to landscape-level problems and possibly require long periods of time for success. The effects of light grazing on the grass-dominated communities of Bodmin Moor can have conservation value in the short term, even though they do not create heathland but instead promote the expansion of structurally diverse *Molinia caerulea*-dominated grassland. The objectives of Countryside Stewardship do not reflect this complexity. Recognition of the wider value of light grazing and other management regimes could allow the development of more flexible site-specific objectives for Countryside Stewardship. Management based on site-specific research is required to determine the precise effects of various management protocols in different communities in order to realize the full potential of Countryside Stewardship.

9.3.2 The value of heathland

The global significance of UK upland heath communities is widely recognised (Moffat 1994, Drewitt & Manley 1997). Dwarf-shrub heath is extensive in Britain but has become fragmented in the rest of Europe (Gimingham 1975). Likewise the national significance of heathland containing *Ulex gallii* restricted to South-west England and Wales is recognised (Rodwell 1991, Drewitt & Manley 1997). No continental mountains have a comparable extent of vegetation dominated by *Ulex gallii* (Moffat 1994).

CS grazing regimes appear to be too high for the maintenance of these communities and too low to control *Molinia caerulea*, which is detrimental to dwarf-shrubs. The optimal grazing regimes for these communities remain unknown and further work is required to ascertain how they would best be managed on Bodmin Moor.

9.3.3 The value of lightly grazed grassland

Acid grassland is generally considered to be of low ecological value particularly relative to heathland. Thus upland acidic grassland is in the lowest habitat priority for conservation (E), while upland heath is in the second highest (B), according to English Nature habitat conservation priorities (Moffat 1994). Conversion of communities dominated by dwarf-shrubs to grassland as a result of overgrazing in response to post-war livestock subsidies has been widespread in the British uplands. The advent of agri-environment schemes is intended to halt or reverse this decline by allowing low value grassland to revert to the higher value heathland. Although dwarf-shrub was undoubtedly more abundant in the past and declined last century due to inappropriate management, it was not the only vegetation that previously existed in the British uplands. Thus current agri-environment policy should not be aimed solely at heathland restoration. Unfortunately ESA and CS schemes do not reflect the value of other communities or consider local or regional variation in the former extent and naturalness of vegetation resulting in a blanket 'heathcentric' conservation policy across Britain.

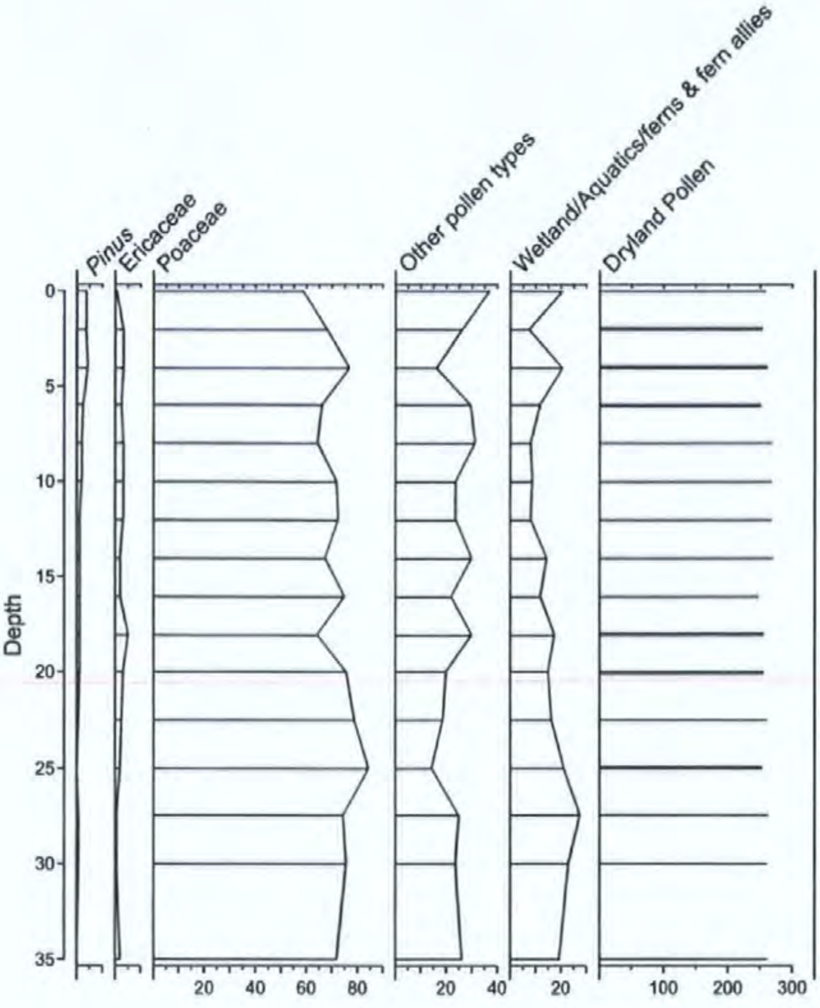
The *Molinia caerulea*-dominated grasslands that develop in response to Stewardship management on Bodmin Moor are more valuable than the heavily grazed suppressed sward from which they are derived and represent an element of an old cultural landscape of high conservation value. *Molinia caerulea* grassland on Bodmin Moor supports many species (Taylor *et al.* 2001), may be of great antiquity, and is of international conservation importance, as it is rare outside of the UK (Drewitt & Manley 1997).

Molinia caerulea supports at least 25 phytophagus insect and mite species. These herbivores include sap-suckers, leaf browsers, gall and mine producers (Taylor *et al.* 2001). *Molinia caerulea* also supports a number of plant parasites and diseases including *Claviceps microcephala* (Webster 1980), *Belonium hystrix*, *Hysteropezizella* *melatephroides*, and *Gloniella moliniae* (Ellis & Ellis 1985). On Bodmin Moor, *Molinia caerulea* provides a locus for large tick populations of unspecificed species. *Ixodes acuminatus* and *Dermacentor reticulatus* are largely restricted to South-west Britain and are present on Bodmin Moor (Martyn 1988). Numerous *Lepidoptera* occur on Bodmin Moor including the Marsh Fritillary (*Eurodryas aurinia*) (Annex 2 EC habitats and species directive, Biodiversity Action Plan priority species). It is not clear what the effect of reduced grazing on mire communities will have on the Marsh Fritillary, or other *Lepidoptera* species across Bodmin Moor. Voles (*Microtus agrestis*) show a preference for *Molinia caerulea* and *Juncus*-dominated communities and become the dominant herbivore in the absence of domestic stock (Hill *et al.* 1992). Large numbers of voles were observed in ungrazed areas where *Molinia caerulea* was dominant on Bodmin Moor. Thus less heavily grazed areas of *Molinia caerulea* may create valuable feeding territories for predators such as Adders (*Vipera berus*) and raptors such as Barn Owls (*Tyto alba*) and Buzzard (*Buteo buteo*), conceivably increasing their numbers. Rough grassland on Bodmin Moor also provides nesting areas for breeding birds such as Wheatear (*Oenanthe onenathe*), Skylark (*Alauda arvensis*) and Meadow Pippit (*Anthus pratensis*) (English Nature & Environmental Consultants Cornwall Trust for Nature Conservation 1994). However, Bodmin Moor is the most important site in Devon and Cornwall for Golden Plover (*Pluvialis apricaria*). Golden Plover favour heavily grazed open grassland and might be expected to decline if Stewardship was implemented on all semi-natural vegetation in the Bodmin Moor Natural Area. Thus some species of nature conservation value may benefit from reduced grazing pressure and the resultant increase in *Molinia caerulea* dominance, whilst some species of high nature conservation value may be adversely affected. It is clear that more work is required to determine which species are reliant on *Molinia caerulea* grassland, what their nature conservation value is and what management they require. However the assumption that *Molinia caerulea* grassland is of little value to other species must be questioned.

Work on Exmoor has shown that there was an increase in *Molinia caerulea* dominance at the expense of heathland during the last century (Chambers *et al.* 1999). This is correlated with increased stock numbers and frequency of burning as indicated by charcoal fragments (Chambers *et al.* 1999). This is consistent with the general paradigm of heathland loss due to overgrazing in the British Uplands in the last century. However, *Molinia*-dominated grassland was abundant on Exmoor around 1000BP (Chambers *et al.* 1999). This is when the present day character of Bodmin Moor and Dartmoor was established (Charman *et al.* 1998). On Exmoor, *Molinia caerulea* grassland was a precursor of heathland, which may have developed as a result of decreasing precipitation, before declining last century in response to heavy grazing and burning (Chambers *et al.* 1999). The post-Mediaeval paleoecology of Bodmin Moor is largely unknown. However, there is no evidence that dwarf-shrubs were more abundant than they are at present (Charman *et al.* 1998, Figure 9.2.). Recent palaeoecology suggests that dwarf-shrubs are more abundant now than 150 years ago (Stanlake 2002). Thus *Molinia caerulea* grassland is of greater antiquity than is often appreciated (Chambers *et al.* 1999) and there is no evidence to suggest that heathlands were formerly more abundant on Bodmin Moor than they are today.

Further paleoecological work is required to determine the post-Mediaeval paleoecology of *Molinia* grasslands both on Bodmin Moor and nationally. However, as on Exmoor, they may be older than heathland communities in other parts of Britain. *Molinia caerulea* grassland is an element in an old cultural landscape and reflects the long history of human impact on Bodmin Moor, as evidenced by the abundant archeological remains. Although heathland is another high value element in this relict landscape, it may never have been abundant across Bodmin Moor. Rigid adherence to conservation of heathland alone is inappropriate on Bodmin Moor, especially as the existing heathland may be derived from grassland in which *Molinia caerulea* is a prominent constituent.

Figure 9.2. Percentage pollen diagram for selected plant taxa from Roughtor Marsh (SX154816). *Ericaceae* pollen remains low throughout the profile (University of Plymouth, unpublished undergraduate dissertation). Dating is in progress but it is estimated that the top 35cm represent a time period from present day to AD1170-1290 (Charman *et al.* 1998).



Agrostis curtisii grassland is also present on Bodmin Moor. Like the *Ulex gallii-Agrostis curtisii* heath from which it is derived, it is restricted South-west England. Outside South-west England, *Agrostis curtisii* is only found in an upland context in the Cantabrian mountains (Ivimey-Cook, 1958). *Agrostis curtisii* grassland is therefore of global significance (Drewitt & Manley 1997). Although *Agrostis curtisii* grassland is a treatment-derived replacement for *Ulex gallii-Agrostis curtisii* heath, little is known about the actual management of the community. It is believed that when *Ulex gallii-Agrostis curtisii* heath is burnt, pure stands of *Agrostis curtisii* as large as 1000m^2 can develop, but after two years, other heath species re-establish (Ivimey-Cook, 1958). No large pure stands of *Agrostis curtisii* were encountered during the survey on Bodmin Moor, although from personal observation, they are present on Southern Dartmoor. More commonly *Agrostis curtisii* was seen on Bodmin Moor in some combination with *Agrostis capillaris, Festuca ovina / rubra, Anthoxanthum odoratum* and *Molinia caerulea* with or without a sub-shrub component. This results from variation in burning and grazing treatment and leads to problems regarding the definition of the communities (Rodwell 1992a, b). Where *Agrostis curtisii* occurs with *Agrostis capillaris* and *Festuca ovina / rubra,* it is referable to *Festuca-Agrostis-Galium* grassland, whilst vegetation in which *Molinia caerulea* abundance is higher than *Agrostis curtisii* is best considered a grassy *Molinia-Potentilla* mire (Rodwell 1992b). Grass-heath categories are used to cater for difficult intermediates or mosaics of grassland and heathland (Ward *et al.* 1972, Tubbs 1986). However, vegetation containing both *Agrostis curtisii* and *Molinia caerulea* became dominated by *Molinia caerulea* rather than dwarf-shrub under a Countryside Stewardship grazing regime. It is therefore unclear what management techniques should be used to promote the conservation of *Agrostis curtisii* grassland. Further work is required on the effects of burning and grazing on this heathland to create *Agrostis curtisii* grassland, and the control of any subsequent successional pathways. No experimental work has been undertaken on *Agrostis curtisii* grassland using a range of livestock types or densities or investigating the role of burning. Until such work is undertaken, optimal management regimes remain unknown.

9.3.4 The value of mire vegetation

Mire vegetation, specifically blanket bog, is generally more extensive and better developed in Scotland, Wales, the North of England, Exmoor and

Dartmoor than on Bodmin Moor. However, *Narthecium ossifragum-Sphagnum papillosum* mire is found in complex mosaics with other mire communities on Bodmin Moor and is of global significance, as it is restricted to South-west England (Drewitt & Manley 1997). Monitoring suggests that *Molinia caerulea* dominance increases in mire vegetation subject to Countryside Stewardship, but lack of replication and the complex nature of mire mosaics prevent generalisations being drawn. Other research suggests that stocking intensities that maintain dwarf-shrub cover on mire are lower than those of drier substrates. Thus competition between *Molinia caerulea* and dwarf-shrubs is likely at low stocking rates. Given that dwarf-shrub cover is low on mires, *Molinia caerulea* dominance might be expected at Stewardship stocking levels on Bodmin Moor especially if they are grazed in spring (Chapter 8). Little work has been undertaken on grazing in mire communities nationally (Shaw *et al.* 1996), whilst *Narthecium ossifragum-Sphagnum papillosum* mire has never been subject to grazing experiments. Further work is therefore required to inform management. However, there is debate concerning the optimal management of blanket bog and mire and what the objectives of such management should be. This uncertainty is reflected in Stewardship prescriptions. Blanket bog and mire are taken into consideration when setting stocking levels under the Enhancing Heather Moorland option. Likewise, diversity of habitat is important in the Management of Heather Moorland Habitat option but no specific objectives are stated beyond improving the condition and extent of *Calluna vulgaris*. In the absence of other criteria, those of Jerram *et al.* (2001) should be adopted (Table 9.2). Further work is required to ascertain the manner in which these targets can be achieved.

Table 9.2. Attributes and targets for favourable vegetation condition in blanket and upland raised mires (summarized from Jerram *et al.* 2001). * MacDonald *et al.* (1998) have developed standardized criteria for assessing grazing impact.

Abundant bryophytes including *Sphagnum* spp. in lawns or hummocks
Dwarf-shrub cover>33% except in *Sphagnum*-dominated areas
At least two dwarf-shrub species should be frequent and widespread
Graminoids should not dominate dwarf-shrub and should be <50% except over *Sphagnum* lawns
Little or no bare ground
No erosion features associated with human impact
Grazing impacts should be light* (MacDonald *et al.* 1998)

9.4 The effect of Countryside Stewardship management on Bodmin Moor

Determining the effects of Stewardship on the vegetation of Bodmin Moor is complex, as many interacting variables are operating in a range of plant communities. It is clear that graminoid-dominated communities have not increased dwarf-shrub extent in any biologically significant manner on Ivey & Hawkstor Farm where they have been subject to Stewardship for five years. Furthermore, the CS grazing levels are too low for the control of *Molinia caerulea* even when stocking rates are higher than those compatible with dwarf-shrub heath maintenance. This suggests that the objectives of CS may not be achievable at all, and that if they are, manipulation of stock alone will not maintain dwarf-shrub heath. Dwarf-shrub propagule availability is low on Bodmin Moor, but not low enough to account for the lack of heathland regeneration. This suggests that the *Molinia caerulea* dominance resulting from Stewardship prevents propagules in the seedbank from germinating or that other propagules in the seedbank including *Molinia caerulea* outcompete germinating dwarf-shrub species. Experimental work confirms that the frequency and severity of defoliation are primary controls on *Molinia caerulea* performance, but that timing also exerts an effect, with spring defoliation being less efficient for *Molinia* control than heavy summer defoliation, particularly in wetter communities. This suggests that *Molinia caerulea* dominance could be controlled in wet heath, mire and grassland communities by increasing Stewardship grazing intensity in summer but this is not compatible with the maintenance of existing dwarf-shrub. In any case, the desirability of increasing dwarf-shrub cover in all communities on Bodmin Moor and lack of alternative management objectives is questioned.

Bodmin Moor is of notable significance nationally due to the extensive areas of internationally scarce *Molinia caerulea-Potentilla erecta* grassland and *Agrostis curtisii* grassland according to a national assessment of the significance of vegetation in the uplands of Britain (Drewitt & Manley 1997). Some additional interest is provided by mire and heathland vegetation (Drewitt & Manley 1997), but it is the grassland which gives the Natural Area its character and also accounts for much of the conservation value.

Agri-environment schemes are focused on increasing dwarf-shrub abundance in order to address the replacement of heathland with grassland as a result of overgrazing during the last century. This 'heathcentric' approach does not reflect the value of communities other than heathland or species other than dwarf-shrub. It is particularly inappropriate on Bodmin Moor, which is dominated by grassland and mire communities of high conservation value. The full potential of Countryside Stewardship is not currently utilised largely as a result of the 'heathcentric' approach. There is also insufficient flexibility in setting and delivering objectives and a serious lack of scientific research.

9.4.1 Modifications to Stewardship

Adoption of the attributes and targets for favourable vegetation condition (Jerram *et al.* 2001) would diversify the objectives of Countryside Stewardship and could help decision-making regarding the eligibility of land for different management options. However, some problems still remain. Acid grassland is generally regarded as degraded heathland (Jerram *et al.* 2001) reflecting the 'heathcentric' conservation approach already inherent in Stewardship. There are therefore no criteria for determining the condition of grasslands. Such criteria are necessary to assess the value and effectiveness of Stewardship on grass-dominated communities that are unlikely to revert to heathland.

Many habitats, including grasslands, support rare species and they can represent important components of old cultural landscapes. This should be reflected in the value attributed to them, which must be assessed on a site-specific basis. For example, on Bodmin Moor *Euphrasia vigursii* (red data book), *Valerianella carinata, Parentucellia viscosa* and *Viola lactea* (nationally scarce) are present in grassland creating specific areas of high value grassland. The manner in which populations of these species respond to grazing is unknown but as they are present in grassland, converting it to heathland may not be desirable, even if it were possible. It is probable that acid grassland has dominated the landscape of Bodmin Moor since Mediaeval times. Thus grassland here represents an important component of an old cultural landscape. On Bodmin Moor there are sufficient propagules to convert this grassland to heathland but regeneration is not occurring even under Stewardship regimes.

The unique history and character of vegetation at a site should be reflected in its value and in the objectives for its management. Rigid adherence to blanket prescriptions could result in the loss of variation and hence value, in the very landscapes that Countryside Stewardship is attempting to conserve. The further development of precise yet diverse, site-specific criteria to assess the value of habitats is critical if the full potential of Countryside Stewardship is to be realized. Site-specific research is required to determine the paleoecology of the site, whilst knowledge of the seedbank is also required to determine the potential for propagules to modify succession.

Knowledge of the effects of management within habitats is also critical if appropriate management regimes are to be identified and implemented, in order to increase the value and condition of habitats. Although a vast literature exists concerning the effects of upland management, many fundamental gaps still exist. Thus CS is often operating beyond the limits of current scientific knowledge. Effective monitoring is therefore important to assess the success of Stewardship and to allow for its continued refinement. Monitoring could aid the implementation of revised and more effective management protocols, especially if a diverse range of management options are trialled. Flexibility in the delivery of Stewardship objectives is therefore desirable from a scientific viewpoint, as well necessary to deliver site-specific targets. The results of ESA monitoring are beginning to inform nature conservation agencies but dissemination of information amongst the scientific community is currently poor, due to lack of publications in refereed journals (Marrs 2001). The full potential of Countryside Stewardship cannot be realised unless more scientific work is undertaken.

9.4.2 Further science required

Further work is required to determine how different communities respond to modified management both on Bodmin Moor and nationally. The initiation of CS monitoring programs replicated in different Natural Areas is necessary to determine the precise effects of Stewardship.

On Bodmin Moor, further work is required to verify that heathland restoration is not possible in graminoid-dominated communities because grazing levels are either too low to suppress *Molinia caerulea* or too high for heathland maintenance. The response of dwarf-shrub-dominated communities to Stewardship management also requires investigation. The influence of Stewardship on the dynamics of seed germination and subsequent seedling survival requires investigation, as does the apparent lack of *Ulex gallii* propagules. Short-term experiments indicate that *Molinia caerulea* could not be controlled more effectively by extending grazing into spring. This requires verification over a longer time-scale preferably in a range of communities. Other work is needed to determine the effects of burning and the effects of grazing using different species of livestock.

Work is underway on the re-establishment of dwarf-shrubs on moorland previously dominated by *Molinia caerulea.* However, the control mechanisms involve sheep grazing at one density in combination with the application of herbicide. Glyphosate herbicide has been shown to be more effective than burning or grazing on *Molinia* control (Todd *et al.* 2000). Laboratory trials suggest that this could reduce regeneration via the roots but even low levels of glyphosate reduce shoot growth in *Calluna vulgaris* (Milligan *et al.* 1999). Quizalofopethyl (Pilot, AgroEvo UK) and sethoxydim (Checkmate, Rhone Poulenc) control *Molinia* to a lesser extent than glyphosate but do not damage *Calluna vulgaris* (Milligan *et al* 1999). They could therefore be used to reduce the dominance of *Molinia* without inhibiting the regenerative capacity of *Calluna vulgaris.* The effects of these herbicides on other dwarf-shrub species remain unknown.

Further work is required on methods utilising different intensities and types of stock in order that Stewardship can be effective in restoring heathland where appropriate. Such work is critical to the success of heathland restoration via Stewardship on Bodmin Moor. However, the management of other grasslands that do not result in heathland restoration under agri-environment management is of more concern nationally. In particular, the control of *Nardus stricta* grassland and restoration of *Calluna* moorland is a high priority for action (Marrs 2001). The re-establishment of *Calluna vulgaris,* once grass becomes dominant in grass-heath mosaics and the impacts of different grazing pressures is also a short-term priority (Marrs 2001). In the South-west, *Ulex gallii* is also of importance along with other dwarf-shrubs. Further work is therefore necessary, specifically on the grass-heath communities of the South-west, as they are very different to their Northern counterparts. The lack of research on burning is recognised as a serious omission and has become a short-term priority for research activity (Marrs 2001). No work is currently envisaged concerning the impact of different species of livestock. This is not a priority nationally, as upland grazing is primarily by sheep with some cattle grazing on upland fringes in the West. However, in the South-west, grazing is by a combination of sheep, cattle and ponies. Knowledge of the varying effects of different species is therefore essential for the regional implementation of Countryside Stewardship in South-west England.

Upland grazing systems involve complex interactions between many variables. Both regional and site-specific variables can affect the outcome of management. Bodmin Moor is a unique upland different to both the other South-west uplands and the more widespread and extensive Northern uplands. Other upland areas, especially those in the North, are of higher conservation value than Bodmin Moor (Drewitt & Manley 1997). Inevitably most research to inform management will be focused elsewhere but there is a clear need for further work on Bodmin Moor. This is recognised to some extent by policy makers. A £19,000 English Nature commissioned contract has been awarded to ADAS to study Agri-environment land management in Cornwall (MAFF 2001). Further work should be undertaken, as funding becomes available.

9.5 Conclusions

- Current Countryside Stewardship regimes do not result in increased dwarf-shrub abundance in grass-dominated communities on Bodmin Moor in the short-term (five years). The grazing pressure is not high enough to reduce the abundance of *Molinia caerulea,* which suppresses dwarf-shrubs. Levels of grazing which may control *Molinia caerulea* are in excess of those that are compatible with the maintenace of dwarf-shrub. Thus rehabilitation of heathland may not be possible on the graminoid-dominated communites of Bodmin Moor even though propagule availability is not limiting (at least in terms of *Calluna vulgaris*).

- Modification of the grazing regime to include grazing earlier in spring encourages *Molinia caerulea* growth according to short-term defoliation experiments. Thus extending grazing into spring may not control *Molinia* whilst grazing at levels that do control *Molinia* in summer debilitate dwarf-shrub heath. This suggests that management to rehabilitate heathland may not be possible at all and that if it is, complex management involving the use of burning, shepherding and different combinations of grazer at different times of year will need to be utilised.

- The 'heathcentric' approach to nature conservation inherent in Countryside Stewardship is inappropriate as a blanket prescription on Bodmin Moor. More precise and diverse targets than increasing dwarf-shrub abundance should be introduced to upland Countryside Stewardship measures. Flexibility in the application and delivery of targets should be allowed.

- Detailed and statistically rigorous monitoring is essential to determine the success of Countryside Stewardship and is necessary on Bodmin Moor to determine the effects of management and to corroborate the findings of this thesis.

- Further work is required to predict vegetation response to changing management. In particular, work on the effect of different species of grazer, the response of vegetation to burning, and regeneration dynamics is required to ensure that Countryside Stewardship does not continue to operate beyond the limits of current knowlege.

10 References

ADAS (1998) Environmental monitoring in the Dartmoor ESA 1994 – 1997. ADAS report to MAFF.

Andel, J. V. (1999) Herbivores and vegetation succession: introductory remarks. *Herbivores: between plants and predators.* (eds H. Olff, V.K. Brown, & R.H. Drent), pp. 169-174. 38th Symposium of the British Ecological Society, Blackwell Science, Oxford.

Anderson, P. & Radford, E. (1994) Changes in vegetation following reduction in grazing pressure on the National Trust's Kinder Estate, Peak District, Derbyshire, England. *Biological Conservation* **69**, 55-63.

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

Armstrong, H.M. & Milne, J.A. (1995) The effects of grazing on vegetation species composition. *Heaths and moorland: Cultural landscapes.* (eds D.B.A. Thompson, A.J. Hester and M.B. Usher), pp 162-173. SNH/HMSO, Edinburgh.

Armstrong, H.M., Gordon, I.J., Grant, S.A., Hutchins, N.J., Milne, J.A. & Sibbald, A.R. (1997) A model of the grazing of hill vegetation by sheep in the UK. 1. The prediction of vegetation biomass. *Journal of Applied Ecology* **34**, 186-207.

Atkinson, C.J. (1986) The effect of clipping on net photosynthesis and dark respiration rates of plants from an upland grassland, with reference to carbon partitioning in *Festuca ovina*. *Annals of Botany* **58**, 61-72.

Austin, M.P. (1981) Permanent quadrats: An interface for theory and practice. *Vegetatio* **46**, 1-10.

Avery, B.W. (1980) Soil classification for England and Wales. (Higher categories). *Soil survey technical monograph* No.**14**.

Backshall, J., Manley, J. & Rebane, M. (2001) *The Upland management handbook*. English Nature, Peterborough.

Bakker, J.P., Bie, S. de, Dallinga, J.H., Tjaden, P. & Vries, Y. de (1983) Sheep grazing as a management tool for heathland conservation and regeneration in the Netherlands. *Journal of Applied Ecology* **20**, 541-560.

Ball, D.F., Dale, J., Sheail, J. & Heal, O.W (1982) *Vegetation change in upland landscapes*. Institute of Terrestrial Ecology, Cambridge.

Ball, D.F., Radford, G.L., & Williams, W.M. (1983). A land characteristic databank for Great Britain. *Occassional paper no.***13**. Insititute of Terrestrial Ecology, Bangor.

Bannister, P. (1966) Biological Flora of the British Isles: *Erica tetralix* L. *Journal of Ecology* **54**, 795-813.

Bardgett, R.D. & Marsden, J.H. (1992) *Heather condition and management in the uplands of England and Wales*. English Nature, Peterborough.

Bardgett, R.D., Marsden, J.H. & Howard, D.C. (1995) The extent and condition of heather on moorland in the uplands of England and Wales. *Biological Conservation* **71**, 155-161.

Baskin, C.C. & Baskin, J.M. (1998) *Seeds: ecology, biogeography and evolution of dormancy and germination*. Academic Press, San Diego.

Bayfield, N.G. (1984) The dynamics of heather (*Calluna vulgaris*) stripes in the Cairngorm mountains, Scotland. *Journal of Ecology* **72**, 515-527.

Beals, E. W. (1984) Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* **14**, 1-55.

Beckett, S.C. (1981) Pollen analysis of the peat deposits. *The Shaugh Moor Project: Third Report.* (eds. K.Smith, J.Coppen, G.Wainwright & S.Beckett), pp. 205-273. Proceedings of the Prehistoric Society **47**

Begon,M., Harper, J.L., & Townsend, C.R. (1996). *Ecology.* (3rd edition). Blackwell Science, Oxford.

Belbin, L. & McDonald, C (1993) Comparing three classification strategies for use in ecology. *Journal of Vegetation Science* **4**, 341-348.

Berendse, F., Schimtz, M. & de Visser, W. (1994) Experimental manipulation of succession in heathland ecosystems. *Oecologica* **100**. 38-44.

Beresford, G. (1979) Three deserted Mediaeval settlements on Dartmoor. *Mediaeval Archaeology* **23**, 98-158.

Bignal, E.M. & Curtis, D.J. (1981) *Peat moss plant communities and site-types of Strathclyde Region, S.W. Scotland.* Nature Conservancy Council Report.

Birks, H.J.B. & Ratcliffe, D.A. (1980*). Classification of upland vegetation types in Britain.* NCC, Peterborough.

Birks, H.J.B. (1989) Holocene isochrone maps and patterns of tree spreading in the British Isles. *Journal of Biogeography* **16**, 503-540.

Birse, E.L. (1980) *Plant communities of Scotland: A preliminary Phytocoenonia.* Macaulay Institute for Soil Research, Aberdeen.

Birse, E.L. (1984) *The Phytocoenonia of Scotland: additions and revisions*. Macaulay Institute for Soil Research, Aberdeen.

Bowden, P.J. (1962) *The wool trade in Tudor and Stuart England.* Macmillan, London.

Box, G.E.P. (1953) Non-normality and tests on variances. *Biometrika* **40**, 318-335.

Bradshaw, M.E. & Jones, A.V. (1976) *Phytosociology in Upper Teesdale.* Durham University.

Brady, N.C. & Weil, R.R. (1999) *The nature and properties of soils.* 12th edition. Prentice-Hall Inc, New Jersey.

Braun-Blanquet, J. (1928) *Pflanzensoziologie. Grundzuge der Vegetationskunde.* Springer, Berlin.

Brewster, C. (1975) *Bodmin Moor – A synoptic study and report on a moorland area.* Volumes 1 & 2. Institute of Cornish Studies, Pool, Cornwall. Unpublished.

Bridgewater, P. (1970) *Phytosociology and community boundaries of the British heath formation.* PhD thesis, Durham University.

Briske, D.D. & Silvertown, J.W. (1993) Plant demography and grassland community balance: the contribution of population regulation mechanisms. *Grasslands for our world.* (ed. M.J. Baker), pp 105-111. SIR Publishing.

Bristow , C.M. (1993) *Bodmin Moor Natural Area. Potential geological / geomorphological conservation interest.* Unpublished notes to CTNC.

Britton, A.J., Carey, P.D., Pakeman, R.J. & Marrs, R.H. (2000) A comparison of regeneration dynamics following gap creation at two geographically contrasting heathland sites. *Journal of Applied Ecology* **37**, 832-844.

Brown, A. (1991) *The upland sites of South-west England.* Internal report. NCC, Truro.

Bullock, J. (1996) Plants. *Ecological census techniques - a handbook.* (ed. W.J. Sutherland), pp 111-138. Cambridge University Press, Cambridge.

Bunce, R.G.H. (1989) Heather in England and Wales. *ITE research publication no* **3**. HMSO, London.

Burrows, C.J. (1990). *Processes of vegetation change.* Unwin Hyman, London.

Cadbury, J. (1993) Grazing and other management of upland vegetation for birds in the UK. *RSPB Conservation Review* **7**, 12-21.

Carew, R. (1602) *Survey of Cornwall.* Published from the original with notes by T.Tomkin. Faulder, London.

Caseldine, C.J. & Hatton, J. (1993) The development of high moorland on Dartmoor: fire and the influence of Mesolithic activity on vegetation change. *Climate change and human impact on the landscape.* (ed. F.M. Chambers), pp 119-131. Chapman & Hall, London.

Caseldine, C.J. & Hatton, J. (1996) Into the mists? Thoughts on the prehistoric and historic environmental history of Dartmoor. *Proceedings of the Devonshire Archaeological Society* **52**, 35-47.

Chadwick, L. (1991) *Farm management handbook* 1991/1992. Scottish Agricultural College, Edinburgh.

Chambers, B.J., Critchley, C.N.R., Fowbert, J.A., Bhogal, A & Rose, S.C. (2001) *Soil Nutrient Status and Botanical Composition of Grasslands in Environmentally Sensitive Areas.* ADAS Final Project report BD1429.

Chambers, F.M., Mauquoy, D. & Todd, P.A. (1999) Recent rise to dominance of *Molinia caerulea* in environmentally sensititive areas: new perspectives from paleoecological data. *Journal of Applied Ecology* **36**. 719-733.

Chardy, P., Glemarec, M. & Laurec, A. (1976) Application of inertia methods to benthic marine ecology: practical implications of the basic options. *Estuarine Coastal Marine Science* **4**,179-205.

Charman, D., Gearey, B. & West, S. (1998) New perspectives on prehistoric human impact on the uplands of Devon and Cornwall. *Environmental Management and Change in Plymouth and the South West.* (eds. M. Blacksell, J. Matthews & P. Sims), pp 1-21. University of Plymouth, Plymouth.

Cherrill, A., & McClean, C. (1999) Between-observer variation in the application of a standard method of habitat mapping by environmental consultants in the UK. *Journal of Applied Ecology* **36**, 989-1008.

Chippendale, H.G. & Milton, W.E.J. (1934) On the viable seed present in the soil beneath pastures. *Journal of Ecology* **22**, 508-531.

Clarke, K. R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**,117-143.

Clements, F.E. (1916). *Plant succession: an analysis of the development of vegetation.* Carnegie Institute of Washington Publication, **242**.

Connell, J.H. & Slatyer, R.O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**, 1119-1144.

Coque-Delhuille, B. (1987) *Le massif du Sui Ouest Anglais et sa Bordure Sedimentaire: etude geomorphologique.* These d'Etat soutenue le 19 Decembre 1986 devant l'Universite de Paris 1-Pantheon-Sorbonne.

Cornwall Trust for Nature Conservation [CTNC] (1988-1993) *Habitat monitoring project.* Internal Report. CTNC, Truro.

Coulson, J.C., Fielding, C.A. & Goodyer, S.A. (1992) *The management of moorland areas to enhance their nature conservation interest.* JNCC Report no **134**. Joint Nature Conservation Committee, Peterborough.

Cox, J.H.S., Cooke, R. & Porter, K. (1998) *Guidance on heritage condition monitoring of lowland heathland restoration and recreation sites in Tomorrows Heathland Heritage Project areas.* English Nature, Peterborough.

Crawford, R.M.M. (1997) Oceanicity and the ecological disadvantages of warm winters. *Botanical Journal of Scotland* **49**(2), 205-221.

Critchley, C.N.R. & Poulton, S.M.C. (in preparation) A method to optimise precision and scale in vegetation monitoring and survey.

CTNC (1997) *English Nature Grazing Index Survey of Bodmin Moor Commons.*CTNC, Truro.

D.A. Skoog, D.M. West & F.J. Holler (2000) *Fundamentals of Analytical Chemistry.* Saunders College Publishing, Fort worth.

Dalby, M., Fidler, J.H., Fidler, A. & Duncan, J.E. (1971) The vegetative changes on Ilkley Moor. *Naturalist* **917**, 49-56.

Dale, M.P. & Dinsdale (1997) *Evaluation of the effect of a Countryside Stewardship agreement on the plant communities of Bodmin Moor North SSSI, Cornwall: A baseline assessment.* Unpublished report to English Nature, Truro.

Damblon, F. (1992) Paleobotanical analysis of *Eriophorum* and *Molinia* tussocks as a means of reconstructing recent history of disturbed mires in the Haute-Ardenne, Belgium. *Review of Paleobotany and Palynology* **75**. 273-288.

Daniell, J.J. (1854) *A geography of Cornwall.* Longman & Co, London.

Dartington Institute (1984) *Cornwall's heritage: The Minions Area Project.* Dartington Institute.

Deregibus, V.A., Sanchez, R.A. & Casal, J.J. (1983) Effects of light quality on tiller production in *Lolium* spp. *Plant Physiology* **72**. 900-902.

Diamond, J.M. (1983). Laboratory, field and natural experiments. *Nature* **304**, 586-587

Douglas, M. E. & Endler, J.A. (1982) Quantitative matrix comparisons in ecological and evolutionary investigations. *Journal of Theoretical Ecology* **99**, 777-795.

Drage, J. (1981) *Vegetation survey of Southern Bodmin Moor.* Internal report, NCC, South West Region.

Drewitt, A.L. & Manley, V.J. (1997) The vegetation of the mountains and moorlands of England. National assessment of significance. *English Nature Research Report* **218**. English Nature, Peterborough.

Drury, W.H. & Nisbet, I.C.T. (1973). Succession. *Journal of Arnold Arboreteum* **54**, 331-368

Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67** (3), 345-66.

Edmonds, E.A., McKeown, M.C. & Williams, M. (1985) *South-west England.* 2nd Edition. Natural Environment Research Council, British Geological Survey, London.

Egler, F.E. (1954). Vegetation science concepts 1.Initial floristic composition, a factor in old field vegetation development. *Vegetatio* **4**, 412-417

Ekins, J.R. (1989) *Forage resources of cattle and ponies in the New Forest, Southern England.* PhD Thesis, University of Southhampton, Southhampton.

Ellis, M.B. & Ellis, J.P. (1985) *Microfungi on Land Plants: an Identification Handbook.* Croom-Helm, London.

Embley, P.G. & Symes, R.F. (1987) *Minerals of Cornwall and Devon.* British Museum, London.

English Nature & Dartmoor National Park Authority. (1997). *The Dartmoor Natural Area Profile.* Dartmoor National Park / English Nature.

English Nature & Environmental Consultants Cornwall Trust for Nature Conservation (1994). *The Bodmin Moor Natural Area. A quality profile.* Report to English Nature, Truro.

English Nature (1991) *Citation for Bodmin Moor North SSSI.* Unpublished. English Nature, Truro.

English Nature (1995) *Bodmin Moor Natural Area Profile.* English Nature, Truro.

English Nature (1999). *Bodmin Moor Action Plan.* English Nature, Truro.

English Nature (1993). *Strategy for the 1990s. Natural areas – setting nature conservation objectives. A consultation paper.* English Nature, Peterborough.

European Community (1992) Council Directive 92/43EEC of May 1992 on the conservation of natural habitats and of wild flora and fauna. *Official Journal of the European Communities* **L206, 35. 22**. Office for Official Publications of the European Communities, Luxemboug.

Facelli, J.M. & Pickett, S.T.A. (1990) Markovian Chains and the role of history in succession. *Trends in Ecology and Evolution* **5**, 27-30.

Faith, D.P., Minchin, P.R. & Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**, 57-68.

Farming and Rural Conservation Agency [FRCA] (1999) *The feasibility of mapping the former extent of heathland on Dartnoor and Bodmin moor.* Internal report.

Farming and Rural Conservation Agency (FRCA) (2001) *Working instructions for field trial for moorland appraisal pilot project method* (with minor modifications 8 May 2001).

Felton, M. & Marsden, J.H. (1991) *Heather regeneration in England and Wales.* NCC, Peterborough.

Fenton, E.W. (1937) The influence of sheep on the vegetation of hill grazings in Scotland. *Journal of Ecology* **25**, 424-430.

Fielding, A.H. & Haworth, P.F. (1999) *Upland habitats.* Routledge, London.

Findlay, D.C., Colborne, G.J.N., Cope, D.W., Harrod, T.R., Hogan, D.V. & Staines, S.J. (1984) *Soils and their use in South-west England.* Soil Survey of England and Wales. Bulletin No **14**, Harpenden.

Finegan, B. (1984) Forest succession. *Nature* **312**, 109-114

Floyd, P.A., Exley, C.S. & Symes, M.T. (1993) *Igneous rocks of South West England.* Geological conservation review.**5**. Chapman and Hall, London.

Fox, F.J. (1977). Alternation and coexistance of tree species. *American Naturalist* **111**, 69-89

Fry, G.L.A. (1991) Conservation in agricultural ecosystems. *The scientific management of temperate communities for conservation.* (eds. F.F. Spellerberg, F.B. Goldsmith & M.G. Morris), pp 415-444. Blackwell, Oxford.

Gardner, S.M., Ross, S.Y. & Adamson, H.F. (2001) *Assessment of the effect of spatial variation in sheep grazing on Calluna vulgaris-Molinia caerulea interactions.* PROJECT BD1218, ADAS.

Gauch, H.G. & Whittaker, R.H. (1981) Hierarchical classification of community data. *Journal of Ecology* **69**, 135-152.

Gearey, B.R. & Charman, D.J. (1996) Rough Tor, Bodmin Moor: testing some archeological hypotheses with landscape paleoecology. *The Quaternary of Devon and East Cornwall: Field guide.* (eds. D.J. Charman, R.M. Newnham, & D. Croot), pp 101-119. Quaternary Research Association, London.

Gearey, B.R. (1996) *Human-environment relations on Bodmin Moor during the Holocene.* Unpublished Ph.D. Thesis, University of Plymouth.

Gearey, B.R. Charman, D.J. & Kent, M. (2000a) Palaeoecological evidence for the prehistoric settlement of Bodmin Moor, Cornwall, SouthWest England. Part 1: The status of woodland and early human impacts. *Journal of Archeological Science* **27**, 423-438.

Gearey, B.R. Charman, D.J. & Kent, M. (2000b) Palaeoecological evidence for the prehistoric settlement of Bodmin Moor, Cornwall, SouthWest England. Part 2: Land Use change from the Neolithic to the present. *Journal of Archeological Science* **27**, 493-508.

Gimingham, C.H. (1972) *Ecology of heathlands.* Chapman & Hall, London.

Gimingham, C.H. (1975) *An introduction to heathland ecology* Oliver & Boyd, Edinburgh.

Gimingham, C.H. (1995) Heaths and moorland: an overview of ecological change. *Heaths and moorland. Cultural landscapes* (eds. D.B.A. Thompson, A.J. Hester & M.B. Usher), pp 3-8. Edinburgh, HMSO.

Gimingham, C.H. (1997) Opening address: Burnett, 1964 and after. *Botanical Journal of Scotland* **49** (2), 117-126.

Gimingham, C.H., Spence, D.H.N. & Watson, A. (1983) Ecology. *Two hundred years of the biological sciences in Scotland.* (ed. W.W. Fletcher), pp 85-118. *Proceedings of the Royal Society of Edinburgh.* **84B**.

Gitay, H. & Noble, I.R. (1997) What are functional types and how should we seek them? *Plant functional types: their relevance to ecosystem properties and global change.* (eds. T.M. Smith, H.H. Shugart, & F.I. Woodward), pp 3-19. Cambridge University Press, Cambridge.

Gleason, H.A. (1927), Further views on the succession concept. *Ecology* **8**, 299-326.

Glenn-Lewin, D.C. & van der Maarel, E. (1992), Patterns and processes of vegetation dynamics. *Plant Succession: theory and prediction* (eds. D.C. Glenn-Lewin, K. Peet, & T.T. Veblen), pp 11-44. Chapman & Hall, London.

Godwin, H. & Conway, V.M. (1939) The ecology of a raised bog near Tregaron, Cardiganshire. *Journal of Ecology* **27**, 313-363.

Goldsmith, F.B., Harrison, C.M. & Morton, A.J. (1986), Description and analysis of vegetation. *Methods in plant ecology.* (eds. P.D. Moore & S. B. Chapman), pp 437-524. 2nd ed. Blackwell Scientific, Oxford.

Goodall, D.W. (1954) Objective methods for the classification of vegetation 1. The use of positive interspecific correlation. *Australian Journal of Botany,* **1**, 39-63.

Gordon, I.J. & Lascano, C. (1993) Foraging strategies of ruminant livestock on intensively managed grasslands: potential and constraints. *Grasslands for our world* (ed. M.Baker), pp 208-216. SIR Publishing, Wellington, New Zealand.

Gordon, I.J. (1989) Vegetation community selection by ungulates on the Isle of Rhum (Scotland, UK): 2. Vegetation community selection. *Journal of Applied Ecology* **26**, 53-64.

Gorham, E., Vitousek, P.M. & Reiner, W.A. (1979). The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Annual Review of Ecological Systematics* **10**, 53-84.

Grace, J. & Unsworth, M.H. (1988), Climate and microclimate of the uplands. *Ecological change in the uplands.* (eds. M.B. Usher & D.B.A. Thompson), pp 137-150. Special publication series of the British Ecological Society **7**, Blackwell Scientific Publications, Oxford.

Graham, D.J. & Hutchings, M.J. (1988) A field investigation of germination from the seed bank of a chalk grassland ley on former arable soil. *Journal of Applied Ecology* **25**, 253-263.

Granstrom, A (1987) Seed viability of 14 species during five years storage in a forest soil. *Journal of Ecology* **75**, 321-331.

Grant, S.A. & Armstrong, H.M. (1993) Grazing ecology and the conservation of heather moorland-the development of models as aids to management. *Biodiversity and Conservation* **2**, 79-94.

Grant, S.A. & Maxwell, T.J. (1988) Hill vegetation and grazing by domesticated herbivores: The biology and definition of management options. *Ecological change in the uplands.* (eds. M.B. Usher & D.B.A. Thompson), pp 201-215. Special publication series of the British Ecological Society **7**, Blackwell Scientific Publications, Oxford.

Grant, S.A., Barthram, G.T. & Marriott, C.A. (1986) The influence of sward conditions and nitrogen supply on the performance of white clover in continously stocked grass clover swards. *Grasslands Facing the Energy Crisis* (eds. F.M. Borba & J.M. Abreu), pp 352-

356. 11th General Meeting of the European Grassland Federation, Sociedade Portuguesa de Pastagens e Forragens, Elvas, Portugal.

Grant, S.A., Bolton, G.R. & Torvell, L (1985) The responses of blanket bog vegetation to controlled grazing by hill sheep. *Journal of Applied Ecology* **22**, 739-752.

Grant, S.A., Bolton, G.R., & Torvell, L. (1981) The effects of grazing by sheep on the structure, stability and productivity of blanket bog. *Hill Farming Research Organisation Biennial Report 1978-1981*, 68-70.

Grant, S.A., Hunter, R.F., & Cross, C. (1963) The effects of muirburning *Molinia*-dominant communities. *Journal of the British Grassland Society* **18**, 249-257.

Grant, S.A., Lamb, W.I.C., Kerr, C.D. & Bolton, G.R. (1976) The utilization of blanket bog vegetation by grazing sheep. *Journal of Applied Ecology* **13**, 857-869.

Grant, S.A., Suckling, D.E., Smith, H.K., Torvell, L., Forbes, T.D.A. & Hodgson, J. (1985) Comparative studies of diet selection by sheep and cattle: the hill grasslands. *Journal of Ecology* **73**, 987-1004.

Grant, S.A., Torvell, L., Armstrong, R.H. & Beattie, M.M. (1987a) *The manipulation of mat grass pasture by grazing management.* ITE symposium, Natural Environment Research Council UK. Institute of Terrestrial Ecology, 62-64.

Grant, S.A., Torvell, L., Common, T.G., Sim, E.M. & Small, J.L. (1996) Controlled grazing studies on *Molinia* grassland: effects of different seasonal patterns and levels of defoliation on *Molinia* growth and responses of swards to controlled grazing by cattle. *Journal of Applied Ecology* **33**. 1267-1280.

Grant, S.A., Torvell, L., Smith, H.K., Suckling, D.E., Forbes, T.D.A. & Hodgson, J. (1987b) Comparative studies of diet selection by sheep and cattle: blanket bog and heather moor. *Journal of Ecology* **75**, 947-960.

Grayson, B. & Beech, T. (2000) RDPs in the UK. *GAP NEWS. The Newsletter of the Grazing Animals Project.* **12**. English Nature, Peterborough.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**, 1169-1194.

Grime, J.P. (1979) *Plant strategies and vegetation processes.* John Wiley, Chichester.

Grime, J.P. (1989) Seed banks in ecological perspective. *Ecology of soil seed banks.* (eds. M.A. Leck, V.T. Parker & R.L. Simpson), pp xv-xxii. Academic Press, San Diego.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative plant ecology: A functional approach to common British species.* Chapman & Hall, London.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1990) *The abridged comparative plant ecology.* Chapman & Hall, London.

Grime, J.P., Mason, G. Curtis, A.V., Rodman, J. Bond, S.R., Mowforth, M.A.G., Neal, A.M. & Shaw, S. (1981) A comparative study of germination characteristics in a local flora. *Journal of Ecology* **69**, 1017-1059.

Gross, K.L. (1990) A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology* **78**, 1079-1093.

Grubb, P.J. (1977) The maintainence of species richness in plant communities. The importance of the regeneration niche. *Biological Reviews* **52**, 107-145

Grubb, P.J. (1985) Plant populations and vegetation in relation to habitat disturbance and competition: problems of generalization. *The population structure of vegetation.* (ed. J. White), pp 595-622. Junk, Dordrecht.

Hambler, C. & Speight, M.R. (1995) Biodiversity Conservation in Britain: Science Replacing Tradition. *British Wildlife* **6 (3)**. 234-240.

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

Harrison, S.J. (1997) Changes in the Scottish Climate. *The Botanical Journal of Scotland* **49** (2). 287-300.

Harrod, T.R., Hogan, D.V. & Staines, S.J. (1976) *Soils in Devon 2:* Sheet SX65 (Ivybridge). Soil Survey No **39**.

Hatcher, J. (1970) *Rural economy and Society in the Duchy of Cornwall 1300-1500.* Cambridge University Press, Cambridge.

Heal, O.W. & Grime, J.P. (1991), Comparative analysis of ecosystems: past lessons and future directions. *Comparative analysis of ecosystems: patterns mechanisms and theories.* (eds. J. Cole, G. Lovett & S. Findlay), pp 7-23. Springer-Verlag, New York.

Heath, M.J. & Oakes, H. (1990). *Woodland surveys in South-west England using the National vegetation classification.* CSD commissioned Research report **1239**. NCC, Peterborough.

Hendry, G.A.F. & Grime, J.P. (1993) *Methods in comparative plant ecology: a laboratory manual.* Chapman & Hall, London.

Herring, P. & Lewis, B. (1992) Ploughing up gatherer-hunters on Bodmin Moor: Mesolithic and later flints from Butterstor and elsewhere on Bodmin Moor. *Cornish Archaeology* **31**, 5-14.

Hester, A.J. & Sydes, C. (1992) Changes in burning of Scottish heather moorland since the 1940s from aerial photographs. *Biological Conservation* **60,** 25-30.

Hester, A.J. (1997) *Spatial pattern and process in the fragmentation of heather moorland.* Unpublished PhD concept note.

Hester, A.J., Gimingham, C.H. & Miles, J. (1991) Succession from heather moorland to birch woodland III. Seed availability, germination and early growth. *Journal of Ecology* **79**, 329-334.

Hester, A.J., Mitchell, F.J.G., Gordon, I.J. & Baillie, G.J. (1996) Activity patterns and resource use by sheep and red deer grazing across a grass:heather boundary. *Journal of Zoology* **240**, 609-620.

Hewson, R, (1976) Grazing by mountain hares *Lepus timidus* L., red deer *Cervus elaphus* L. and red grouse *Lagopus lagopus scoticus* L. on heather moorland in North-East Scotland. *Journal of Applied Ecology* **13**, 657-666.

Hewson, R. (1977) The effect on heather *Calluna vulgaris* of excluding sheep from moorland in North-East England. *Naturalist* **102**, 133-136.

Hewson, R. (1989) Grazing preferences of mountain hares on heather moorland and hill pastures. *Journal of Applied Ecology* **26**, 1-12.

Hill, M. O. & Gauch, H.G. (1980) Detrended correspondence analysis: an improved ordination technique. *Vegetatio* **42**, 47-58.

Hill, M.O. & Stevens, P.A. (1981) The density of viable seed in soils of forest plantations in upland Britain. *Journal of Ecology* **69**, 693-709.

Hill, M.O. (1979a) *TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of* *the individuals and attributes.* Ithaca, NY. Ecology and Systematics, Cornell University.

Hill, M.O. (1979b) *DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging.* Ithaca, NY. Ecology and Systematics, Cornell University.

Hill, M.O. (1982) *Effects of grazing in Snowdonia. Annual report.* Institute of Terrestrial Ecology, Natural Environment Research Council.

Hill, M.O. (1993) *TABLEFIT: version 0.0, for the identification of vegetation types.* Institute of Terrestrial Ecology, Huntingdon, UK.

Hill, M.O., Evans, D.F. & Bell, S.A. (1992) Long term effects of excluding sheep from hill pastures in North Wales. *Journal of Applied Ecology* **80**, 1-13.

Hill, M.O., Mountford, J.O., Roy, D.B. & Bunce, R.G.H. (1999) *Ellenberg's indicator values for British plants.* ECOFACT Volume 2 Technical Annex, HMSO, Norwich.

Hobbs, R.J. & Gimingham, C.H. (1980) Some effects of fire and grazing on heath vegetation. *Bulletin of Ecology* **11**, 709-715.

Hobbs, R.J. & Gimingham, C.H. (1987) Vegetation, fire and herbivore interactions. *Advances in Ecological Research* **16**, 87-173.

Hobbs, R.J., Mallik, A.U. & Gimingham, C.H. (1984) Studies on fire in Scottish heathland communities 3. Vital attributes of the species. *Journal of Ecology* **72**, 963-976

Hodgson, J. (1985) The control of herbage intake in the grazing ruminant. *Proceedings of the Nutrition Society* **44**, 339-346

Hodgson, J., Forbes, T.D.A., Armstrong, R.H., Beattie, M.M. & Hunter, E.A. (1991) Comparative studies of the ingestive behaviour and herbage intake of sheep and cattle grazing indigenous hill plant communities. *Journal of Applied Ecology* **28**, 205-227.

Holmes, J.S. (1991) *Bodmin Moor - Managing the commons for nature conservation.* Unpublished MSc Thesis, Imperial College of Science and Technology.

Homolka, M. (1985) The food of a wild rabbit population in Ceskomoravska Vrchovina Highlands. *Folia Zoologica* **34**, 303-314.

Hubbard, J.C.E. (1984) *Grasses. A guide to their structure, identification, uses and distribution in the British Isles.* Penguin books, London.

Hughes, A.D. & Staines, S.J. (1975) *Subsoiling on Bodmin Moor. Map at scale 1:63360.* MAFF-ADAS.

Hulbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**. 187-211.

Huston, M. & Smith, T. (1987) Plant succession: life history and competition. *American Naturalist* **130**, 168-198.

Institute of Terrestrial Ecology (1978) *Upland land use in England and Wales.* Desk Study. No CCP **111**. Countryside Commission.

Ivimey-Cook, R.B. (1959) Biological Flora of the British Isles: *Agrostis setacea* Curt. *Journal of Applied Ecology* **47**, 697-706.

Jackson, D.A. (1993) Stopping rules in PCA: a comparison of heuristical and statistical approaches. Ecology **74**, 2204-2214.

Jeffrey, D.W. (1987) *Soil - plant relationships: an ecological approach.* Croon Helm, London.

Jerram, R. & Drewitt, D. (1997) Optimal vegetation condition in the English uplands. Consultation draft *English Nature Research Reports No* **220**.

Jerram, R. & Drewitt, D. (1998) Assessing vegetation condition in the English uplands. *English Nature Research Reports No* **264**.

Jerram, R. Drewitt, A. & Backshall, J. (2001) Information note 1: Assessing vegetation condition in the English uplands. *The upland management handbook.* (eds. J. Backshall, J. Manley, M. Rebane). English Nature, Peterborough.

Jimaleh, A.A. (1985) *The use of cattle as a management tool on Woodwalton Fen NNR.* MSc Thesis, University College, London.

Johnson, N.D. & Rose, P. (1994) *The Bodmin Moor survey.* English Heritage, London.

Joint Nature Conservation Committee [JNCC] (1995) *Biodiversity: The UK steering group report.* Volume 2: action plans. HMSO, London.

Jones, D. & Essex, S. (1999) Landuse change in the British uplands: A case study of Bodmin Moor, Cornwall. *Geography* **84** (I), 11-23.

Jones, L.I. (1967) *Studies on hill land in Wales.* Technical Bulletin No. **2**, Welsh Plant Breeding Station, Aberystwyth.

Jongman, R.H.G., Ter Braak, C.F.J. & Van Tongeren, O.F.R. (1995) *Data analysis in community and landscape ecology.* 2nd edition. Cambridge University Press.

Keddy, P.A. & Shipley, B. (1989) Competitive hierarchies in herbaceous plant communities. *Oikos* **54**, 234-241.

Keddy, P.A. (1989) *Competition.* Population and community biology series. Chapman & Hall, London.

Keddy, P.A. (1990) Competitive hierarchies and centrifugal organisation in plant communities. *Perspectives on plant competition.* (eds. J.B. Grace & D. Tilman), pp 266-290. Academic Press, San Diego.

Kellman, M.C. (1970) The influence of accessibility on the composition of vegetation. *Professional Geographer* **22**, 1-4.

Kennet, P. & Ross, C.A. (1984) *Aspects of Geology*. Longman, York.

Kent, M. & Coker, P. (1992) *Vegetation description and analysis – A practical approach.* John Wiley & Sons, Chichester.

Kent, M. & Wathern, P. (1980) The vegetation of a Dartmoor catchment. *Vegetatio* **43**, 163-72.

Keuls, M. (1952) The use of studentized range in connection with an analysis of variance. *Euphytica,* **1**, 112-122.

Kiffe, K. (1989) The influence of rabbit grazing on vegetation as exemplified by *Agrostis* sand dune swards of East Fresian Islands. *Tuexenia* **9**, 283-291.

Lance, A.N. (1983) Performance of sheep on unburned and serially burned blanket bog in Western Ireland. *Journal of Applied Ecology* **20**, 767-775.

Lance, A.N. (1987) Estimating acceptable stocking levels for heather moorland. *Agriculture and conservation in the hills and uplands* (eds. M. Bell & R.G.H. Bunce), 109-115. ITE, Cambridge.

Latusek, E. (1983) *The autecology of* Molinia caerulea *(L) Moench. with particular reference to grazing.* PhD dissertation, Manchester Polytechnic.

Lawton, J.H. (ed) (1990) *Red grouse populations and 'Moorland Management'.* British Ecological Society, Ecological Issues No **2**. Field Studies Council, Shrewsbury.

Legg, C. J. (1995) Heathland dynamics: a matter of scale. *Heaths and moorland: Cultural landscapes.* (eds. D.B.A. Thompson, A.J. Hester and M.B. Usher), pp 117-134. SNH/HMSO, Edinburgh.

Legg, C.J. (1992) Putting concrete vegetation into abstract boxes. *Bulletin of the British Ecological Society* **xxiii**. **(1)**. 28-30.

Legg, C.J., Maltby, E. & Proctor, M.C.F. (1992) The ecology of severe moorland fire on the North York Moors: seed distribution and seedling establishment of *Calluna vulgaris*. *Journal of Ecology* **80**, 737-752.

Leland (1543) *Itineary*. Edited by L. Toulim - Smith. 5 Vols, London, 1907 - 1910.

Levene, H. (1960). *Contributions to Probability and Statistics*. Stanford University Press, Stanford.

Lindsay , R.A., Charman, D.J., Everingham, F., O'Reilly, R.M., Palmer, M.A., Rowell, T.A. & Stroud, D.A. (1988) *The Flow Country. The peatlands of Caithness and Sutherland*. Nature Conservancy Council.

Loach, K. (1966) Relations between soil nutrients and vegetation in wet heaths. 1. Soil nutrient content and moisture conditions. *Journal of Ecology* **54**. 597-608.

Loach, K. (1968a) Relations between soil nutrients and vegetation in wet heaths. 2. Nutrient uptake by the major species in the field and in controlled conditions. *Journal of Ecology* **56**. 117-127.

Loach, K. (1968b) Seasonal growth and nutrient uptake in a Molinietum. *Journal of Ecology* **56**. 433-444.

Loehle , C. (1983). Evaluation of theories and calculation tools in ecology. *Ecological modelling* **19**. 239-249.

Loudon, A.S.I., Darroch, A.D. & Milne, J.A. (1984) The lactation performance of red deer on hill and improved species pastures. *Journal of Agricultural Science* **102**, 149-158.

Luken, J.O. (1990) *Directing ecological succession*. Chapman & Hall.

Macdonald, A.J., Mayer, P., Armstrong, H., Immirzi, P. & Reynolds, P. (1998) *A guide to upland habitats: surveying land management impacts.* Scottish Natural Heritage, Perth.

MacLeod, A.C. (1955) Heather in the seasonal diet of sheep. *Proceedings of the British Society of Animal Production,* 13-17.

Malim, J.W. (1936) *The Bodmin Moors.* Methuen, London.

Mallan, A.U. (1888) Notes on the Neighbourhood of Brown Willy. *Journal of the Royal Institute of Cornwall,* **11** (**3**), 341-352.

Mallik, A.U., Hobbs, R.J. & Legg, C.J. (1984) Seed dynamics in *Calluna-Arctostaphylos* heath in North-Eastern Scotland. *Journal of Ecology* **72**, 855-871.

Malloch, A.J.C. (1971) *Analytical studies of cliff top vegetation in South West England.* PhD thesis, University of Cambridge.

Maltby, E. & Caseldine, C.J. (1982) Prehistoric soil and vegetation development on Bodmin Moor, South-western England. *Nature* **297**, 397-400.

Mansfield, A. (1998) *Ivey & Hawkstor Farms Stewardship Scheme. Progress review.*

Mantel, N. (1967) The detection of disease clustering and generalized regression approach. *Cancer Research* **27**, 209-220.

Marrs, R.H. & Pakeman, R.J. (1995) Bracken invasion – lessons from the past and prospects for the future. *Heaths and moorland. Cultural landscapes.* (eds. D.B.A. Thompson, A.J. Hester & M.B. Usher), pp 180-194. Scottish Natural Heritage HMSO, Edinburgh.

Marrs, R.H. (2001) *Programme advisor for the Uplands Assessment Unit Final Project Report.*BD1227. MAFF, London.

Marrs, R.H., Bravington, M. & Rawes, M. (1988) Long term vegetation change in the *Juncus squarrosus* grassland at Moor House, Northern England. *Vegetatio* **76**, 179-187.

Marrs, R.H., Pakeman, R.J. & Lowday, J.E. (1995), Bracken control and heathland restoration in Breckland. *Bracken: an environmental issue.* Proceedings of the 3rd International Bracken Conference, Aberystwyth. 166-172.

Marshall, W. (1796) *General survey of the rural economy of England.* Vol 2: The Western reprint (1970) David & Charles, Newton Abbott.

Martyn, K.P. (1988) *Provisional Atlas of the Ticks* (Ixodoidea) *of the British Isles.* Biological Records Centre. Huntingdon.

McClatchley , J. (1996) Spatial and altitudinal gradients of climate in the Cairngorms – observations from climatological and automatic weather stations. *Botanical Journal of Scotland,* **48**. 31-49.

McCook, L.J. (1994) Understanding ecological community succession: causal models and theories, a review. *Vegetatio* **110**, 115-147.

McCune, B. & Mefford, M.J. (1999*) PC-ORD. Multivariate analysis of ecological data, version 4.* MjM Software design, Gleneden Beach, Oregon, USA.

McIntosh, R.P. (1970) Community, competition and adaptation. *Quarterly Review of Biology* **45**, 259-280.

McIntosh, R.P. (1980) The relationship between succession and the recovery process in ecosystems. *The recovery process in damaged ecosystem* (ed. J.R. Cairns), pp 11-62 Ann Arbor Science Publications, Michigan.

McVean, D.N. & Ratcliffe, D.A. (1962) *Plant communities of the Scottish highlands.* HMSO, London.

Merchant, M. (1993) The potential for control of soft rush (*Juncus effusus*) in grass pastures by grazing goats. *Grass and Forage Science* **48**, 395-409.

Miles, J. Welch, D. & Chapman, S.B. (1978) Vegetation and management in the uplands. *Upland land use in England and Wales* (ed. O.W. Heal), pp 77-95. Countryside Commission, Leeds.

Miles, J. (1971) Burning *Molinia*-dominant vegetation for grazing by red deer. *British Grassland Society Journal.* **26**, 247-250.

Miles, J. (1973) Early mortality and survival of self-sown seedlings in Glenfeshie, Invernessshire. *Journal of Ecology* **61**, 93-98.

Miles, J. (1973) Natural recolonization of experimentally bared soil in *Callunetum* in North-East Scotland. *Journal of Ecology* **61**, 399-412.

Miles, J. (1979) *Vegetation Dynamics.* Chapman & Hall, London.

Miles, J. (1985) The pedogenic effects of different species and vegetation types and the implications of succession. *Journal of Soil Science* **36**, 571-584.

Miles, J. (1987) Vegetation succession: past and present perceptions. *Colonization, succession and stability.* (eds. A.J. Gray, M.J. Crawley & P.J. Edwards), pp 1-29. The 26th symposium of the British Ecological Society held jointly with the Linnean Society of London. Blackwell Scientific Publications, Oxford.

Miles, J. (1988) Vegetation and soil change in the uplands. *Ecological Change in the Uplands* (eds. M.B. Usher & D.B.A. Thompson), pp 57-70. Special Publication of the British Ecological Society. Blackwell Scientific Publications, Oxford.

Miles, J., Welch, D. & Chapman, S.B. (1978). *Vegetation management in the uplands.* Countryside Commission, Cheltenham.

Miller, G.R. & Cummins, R.P. (1981) Population dynamics of buried seeds on mountains. *Annual Report of the Institute of Terrestrial Ecology for 1980.* 75-76.

Miller, G.R. & Cummins, R.P. (1987) Role of buried viable seeds in the recolonization of disturbed ground by heather (*Calluna vulgaris*) in the Cairngorm mountains, Scotland, UK. *Arctic and Alpine Research* **19**, 396-401.

Milligan, A.L. Putwain, P.D. & Marrs, R.H. (1999) A laboratory assessment of the relative susceptibility of *Molinia caerulea* (L.) Moench and *Calluna vulgaris* (L.) Hull to a range of herbicides. *Annals of Applied Biology* **135**. 503-508.

Millward, R. & Robinson, A. (1980). *Upland Britain.* David & Charles, Newton Abbot.

Milne, J.A., Birch, C.P.D., Hester, A.J., Armstrong, H.M. & Robertson, A. (1998) *The impact of vertabrate herbivores on the natural heritage of the Scottish Uplands – a review.* Scottish Natural Heritage Review No **95**.

Minchin, P. R. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* **69**, 89-107.

Ministry of Agriculture, Food and Fisheries [MAFF] (2001) *A register of Agri-environmental R&D 1999/2000 update.* MAFF, London.

Ministry of Agriculture, Food and Fisheries [MAFF] (1998) Consultation paper – *environmental management in the uplands.*

Ministry of Agriculture, Food and Fisheries [MAFF] (1999a) www.maff.gov.uk/environ/envsch/cs.

Ministry of Agriculture, Food and Fisheries [MAFF] (1999b) The Countryside Stewardship Scheme. Information and how to apply. MAFF.

Mitchell, F.J.G. & Kirby, K.J. (1990) The impact of large herbivores on the conservation of semi-natural woods in the British uplands. *Forestry* **63**, 334-353.

Moffat, A.M. (1994) *Priorities for Habitat Conservation in England.* English Nature Research Report No **97**.

Moss, M.R. & Dickinson, G. (1979) Evolution of the dune and machair surface of South Uist, Outer Hebrides, Scotland. *Environmental Conservation* **6**, 287-292.

Mowforth, M.A. & Sydes, C. (1989) *'Moorland Management': a literature review.* Research and survey in nature conservation series No **25**. Nature Conservancy Council, Peterborough.

Nature Conservancy (2001) *Element Stewardship Abstract for Ulex europaeus.* Nature Conservancy, Virginia, USA.

Nature Conservancy Council [NCC] (1983) *The food and feeding behaviour of cattle and ponies in the New Forest.* Nature Conservancy Council, Lyndhurst.

Nature Conservancy Council [NCC] (1986) *Upland vegetation survey – Bodmin Moor.* Unpublished report. NCC, Edinburgh.

Nature Conservancy Council [NCC] (1987) *Changes in the Cumbrian countryside.* Research and survey in nature conservation series No **6**. Nature Conservancy Council, Peterborough.

Nature Conservancy Council [NCC] (1989). *Guidelines for the selection of biological SSSIs.* NCC, Peterborough.

Nature Conservancy Council [NCC] (1990) *A handbook for Phase 1 habitat survey.* A technique for environmental audit. NCC, Peterborough.

Newman, D. (1939) The distribution of the range of samples from a normal population expressed in terms of an independent estimate of standard deviation. *Biometrika,* **31**, 20-30.

Nicholson, I.A., Paterson, I.S. & Currie, A. (1970) A study of vegetational dynamics: selection by sheep and cattle in *Nardus* pasture. *Animal populations in relation to their food supplies* (ed. A. Watson), pp 129-143 Blackwells, Oxford.

Nobel, I. R. & Slatyer, R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**, 5-21.

Nolan, A.J., Henderson, D.J. & Merrell, B.G. (1995) The vegetation dynamics of wet heaths in relation to sheep graziing intensity. *Heaths and moorland: Cultural landscapes.* (eds. D.B.A. Thompson, A.J. Hester and M.B. Usher), pp 174-179. SNH/HMSO, Edinburgh.

Oates, M. (1994) *A review of the role of horses and ponies in habitat management for nature conservation.* National Trust, Cirencester.

Odum, E.P. (1969). The strategy of ecosystem development. *Science* **164**, 262-270.

Oesterheld, M. & Sula, O.E. (1990) Effects of grazing on seedling establishment: the role of seed and safe-site availability. *Journal of Vegetation science* **1**, 353-358.

Oksanen, J. & Minchin, P.R. (1997) Instability of ordination results under changes in input data order: explanations and remedies. *Journal of Vegetation Science* **8**, 447-454.

Osborne, B.C. (1984) Habitat use by red deer (*Cervus elaphus* L.) and hill sheep in the West Highlands. *Journal of Applied Ecology* **21**, 497-506.

Owen, N.W., Kent, M. & Dale, M.P. (2001) Spatial and temporal variability in seed dynamics of machair sand dune plant communities, the Outer Hebrides, Scotland. *Journal of Biogeography* **28**, 565-588.

Page, C.N. (1997) *The Ferns of Britain and Ireland.*(2nd Ed). Cambridge University Press, Cambridge.

Palmer, M. (2000) http://www.okstate.edu/artsci/botany/ordinate

Pearsall, W.H. (1941) The mosses of the Stainmore District. *Journal of Ecology* **29**, 161-175.

Pearsall, W.H. (1968) *Mountains and moorlands.* New Naturalist Series, 2nd Ed, Collins, London.

Perring, F.H. & Farrell, L. (1983) British Red Data Books:1 Vascular plants, 2nd ed, RSNC, Lincoln.

Pickett, S.T., Collins, S.L.& Armesto, J.J. (1987), A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* **69**, 109-114.

Pickett, S.T., Kolasa, J., Armesto, J.J. & Collins, S.L. (1989). The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* **54**, 129-136.

Pitcairn, C.E.R., Fowler, D. & Grace, J. (1995) Deposition of fixed atmospheric nitrogen and foliar nitrogen content of bryophytes and *Calluna vulgaris* (L.) Hull. *Environmental Pollution* **88**. 193-205.

Pons, T.L. (1989) Dormancy, germination and mortality of seeds buried in heathland and inland sand dunes. *Acta Botanica Neerlandica* **38**, 327-335.

Poore, M.E.D. & McVean, D.N. (1957) A new approach to Scottish mountain vegetation. *Journal of Ecology* **45**, 401-39.

Poore, M.E.D. (1955a) The use of phytosociological methods in ecological investigations. I. The Braun-Blanquet system. *Journal of Ecology* **43**, 226-44.

Poore, M.E.D. (1955b) The use of phytosociological methods in ecological investigations. II. Practical issues involved in an attempt to apply the Braun-Blanquet system. *Journal of Ecology* **43**, 245-69.

Poore, M.E.D. (1955c) The use of phytosociological methods in ecological investigations. III. Practical application. *Journal of Ecology* **43**, 606-51.

Poschlod, P. (1990) *Vegetationsentwicklung in abgetorften Hoochmooren des bayerischen Alpenvorlandes unter besonderer Berucksichtigung standortskundlicher und populationbiologische Faktoren.* Cramer, Berlin.

Poulton, S.M.C. (1991) *North Peak ESA biological monitoring 1990.* Unpublished ADAS report.

Pounds, N.J. G. (1947) *The historical geography of Cornwall.* PhD Thesis, London University.

Putman, R.J., Fowler, A.D., & Tout, S. (1991) Patterns of use of ancient grassland by cattle and horses and effects on vegetational composition and structure. *Biological Conservation* **56**, 329-347.

Putman, R.J., Pratt, R.M. Ekins, J.R. & Edwards, P.J. (1987) Food and feeding behaviour of cattle and ponies in the new forest, Hampshire. *Journal of Applied Ecology* **24**, 369-80.

Putwain, P.D. & Gillham, D.A. (1990) The significance of the dormant viable seed bank in the restoration of heathlands. *Biological Conservation* **52**, 1-16.

Quinnell, H. (1996) New perspectives on upland monuments – Dartmoor in early prehistory. *Proceedings of the Devonshire Archeological Society* **52**, 49-62.

Ranwell, D.S. (1960) Newborough Warren Anglesey 3. Changes in vegetation on parts of the dune system after loss of rabbits by myxomatosis. *Journal of Ecology* **48**, 385-395.

Ratcliffe, D.A. & Thompson, D.B.A. (1988) The British uplands: their ecological character and international significance. *Ecological change in the uplands.* (eds. M.B. Usher & D.B.A. Thompson), pp 9-36. Blackwell Scientific Publications, Oxford.

Ratcliffe, D.A. (1959) The vegetation of Carneddau, North Wales. 1. Grasslands, heaths and bogs. *Journal of Ecology* **47**, 371-413.

Ratcliffe, D.A. (1977) *A nature conservation review: the selection of biological sites of national importance.* Cambridge University Press (for the Nature Conservancy Council), Cambridge.

Ravenhill, G.J. (1967) Cornwall. *The Domesday geography of South-west England.* (eds. H.C. Darby & R.Welldon), pp 56-82 Cambridge University Press, Cambridge.

Ravensdale, J. (1974) Bodmin Moor. *Preliminary notes from field work only.* Unpublished notes. CTNC, Truro.

Rawes, M. & Heal, O.W. (1978) The blanket bog as part of a pennine Moorland. *Production ecology of British moors and montane grasslands.* (eds. O.W. Heal & D.F. Perkins), pp 224-243. Springer-Verlag, Berlin.

Rawes, M. & Hobbs, R. (1979) Management of semi-natural blanket bog in the Northern Pennines. *Journal of Ecology* **67**, 789-807.

Rawes, M. & Williams, R. (1973) Production and utilisation of *Calluna* and *Eriophorum.* Third Colloquium of the Potassium Institute Ltd. **3**, 115-119.

Rawes, M. (1971) Aspects of the ecology of Northern Pennine moorland. 1. The influence of agriculture. *Moor House occasional papers* No **1**.

Reichle, D.F., O'Neill, R.V. & Harris, W.F. (1975), Principles of energy and material exchange in ecosystems. *Unifying concepts in Ecology.* (eds. W.H. Van Dobben & R.H. Lowe-McConnell), pp 27-43 Junk, The Hague.

Rieley, J.O. & Page, S.E. (1990) *Ecology of plant communities.* Longman.

Roberts, H.A. (1981) Seed banks in soils. *Advances in Applied Biology* **6**, 1-55.

Roberts, N. (1998) *The Holocene. An environmental history.* (2nd Ed) Blackwell, Oxford.

Roberts, N., & Edwards, T. (1994) The Bodmin Moor Natural Area. A quality profile. Volume 1 report. Truro. Unpublished.

Rodwell, J. (1991) *British plant communities, volume 1. Woodlands and Scrub.* Cambridge University Press, Cambridge.

Rodwell, J. (1992a) *British plant communities, volume 2. Mires and heaths.* Cambridge University Press, Cambridge.

Rodwell, J. (1992b) *British plant communities, volume 3. Grasslands and montane communities.* Cambridge University Press, Cambridge.

Rodwell, J. (1994) *British plant communities, volume 4. Aquatic Communities, Swamps and Tall-herb Fens.* Cambridge University Press, Cambridge.

Rodwell, J. (2000) *British plant communities, volume 5. Maritime communities and vegetation of open habitats.* Cambridge University Press, Cambridge.

Rowell, D.L. (1994) *Soil science: methods and applications*, Longman Scientific & Technical, Harlow.

Royal Society for the Protection of Birds [RSPB] (1995) *Conservation management of blanket bog. A review.* Report to the Royal Society for the Protection of Birds by Scottish Wildlife Trust.

Rutter, A.J. (1955) The composition of wet heath vegetation in relation to the water table. *Journal of Ecology* **43**, 507-43.

Rutter, A.J. (1955) The composition of wet heath vegetation in relation to the water-table. *Journal of Applied Ecology* **43**. 507-543.

Salim, K.A., Gordon, D.B., Shaw, S. & Smith, C.A. (1995) Variation in *Molinia caerulea* (L.) Moench, the purple moor grass, in relation to edaphic environments. *Annals of Botany* **75**. 481-489.

Shaw, S.C., Wheeler, B.D., Kirby, P., Phillipson, P. & Edmunds, R. (1996) Literature review of the historical effects of burning and grazing of blanket bog and upland wet heath. *English Nature Research Report* No **172**.

Sheail, J. (1987) *Seventy five years in ecology: The British Ecological Society.* Blackwell Scientific Publications, Oxford.

Sheikh, K.H. (1969a) The responses of *Molinia caerulea* and *Erica tetralix* to soil aeration and related factors. 2. Gas concentrations in soil air and water. *Journal of Ecology* **57**. 727-736.

Sheikh, K.H. (1969b) Effects of competition and nutrition on wet heath plants. *Journal of Ecology* **57**. 87-99.

Shimwell, D.W. (1971) *Description and classification of vegetation.* Sidgewick & Jackson, London.

Shugart, H.H. (1984) *A theory of forest dynamics: the ecological implications of forest succession models.* Springer-Verlag, New York.

Shugart, H.H. (1997) Plant and ecosystem functional types. *Plant functional types. Their relevance to ecosystem properties and global change* (eds. T.M. Smith, H.H Shugart & I.F. Woodward), pp 20-46. Cambridge University Press, Cambridge.

Sibbald, A.R., Grant, S.A., Milne, J.A. & Maxwell, T.J. (1987) Heather 'Moorland Management'- a model. *Agriculture and conservation in the hills and uplands.* (eds. M. Ball & R.G.M. Bunce), pp 107-108. Institute of Terrestrial Ecology, Grange-over-Sands.

Silvertown, J. (1980) The dynamics of a grassland ecosystem: Botanical equilibrium in the park grass experiment. *Journal of Applied Ecology* **17**, 491-504.

Simpson, R.L., Leck, M.A. & Parker, V.T. (1989) Seed banks: General Concepts and Methodological Issues. *Ecology of soil seed banks.* (eds. M.A. Leck, V.T. Parker & R.L. Simpson), pp 3-8. Academic Press, San Diego.

Skalova, H. & Krahulec, F. (1992) The responses of three *Festuca rubra* clones to change in light quality and plant density. *Functional Ecology* **6**. 282-290.

Smallshire, D. (1996) *Heather utilisation at Dartmoor ESA prescribed stocking rates.* Unpublished ADAS report to MAFF.

Smallshire, D., Shorrock, D.J. & Halshaw, L. (1997) Sustainable grazing practices on the South West moors of England. *English Nature Research Reports* **254**. English Nature, Truro.

Smith, A.J.E. (1978) *The moss Flora of Britain & Ireland.* Cambridge University Press, Cambridge.

Smith, R.S., Shiel, R.S., Millward, D. & Corkhill, P. (2000) The interactive effects of management on the productivity and plant community structure of an upland meadow: an 8-year field trial. *Journal of Applied Ecology* **37**, 1029-1043.

Sparrow, C. (1994) *Bodmin Moor Natural Area [BMNA] Project. Mineralogical overview.* Unpublished notes to Cornwall Trust for Nature Conservation [CTNC], CTNC, Truro.

Spellerberg, I.F. (1992) *Evaluation and Assessment for Conservation.* Chapman & Hall, London.

Stace, C. (1997) *New flora of the British Isles.* 2nd Edition. Cambridge University Press, Cambridge.

Staines, B.W., Balharry, R. & Welch, R. (1995) The impact of red deer and their management on the natural heritage in the uplands. *Heaths and moorland. Cultural landscapes.*(eds. D.B.A. Thompson, A.J. Hester & M.B. Usher), pp 294-308. Edinburgh, HMSO.

Staines, S.J. (1976) Soils in Cornwall 1. Sheet SX18. *Soil Survey record* **34**. 92-121. Harpenden, Herts.

Stanlake, P. (2002) *Recent vegetation change on Bodmin Moor, are the management objectives correct?* MSc Thesis. University of Plymouth.

Stevenson, A.C. & Thompson, D.B.A. (1993) Long-term changes in the extent of heather moorland in upland Britain and Ireland. Paleoecological evidence for the importance of grazing. *The Holocene* **3**, 75-81.

Stewart, A.J.A. & Lance, A.N. (1991) Effects of moor draining on the hydrology and vegetation of Northern Pennine blanket bog. *Journal of Applied Ecology* **28**, 1105-1117.

Tansley, A.G. (1911) *Types of British vegetation.* Cambridge University Press, Cambridge.

Tansley, A.G. (1935). The use and abuse of vegetational concepts and terms. *Ecology* **16**, 284-307.

Tansley, A.G. (1939) *The British islands and their vegetation.* Cambridge University Press, Cambridge.

Taylor, A.J. (1976) Upland climates. *The Climate of the British Isles.* (eds. T.J. Chandler & S. Gregory), pp 132-145. Longman, London.

Taylor, J.A. (1993) Foraging strategy: summary. *Grasslands for our World.* (ed. M.J. Baker), pp 224-225. SIR publishing, New Zealand.

Taylor, K., Rowland, A.P., & Jones, H.E. (2001) Biological Flora of the British Isles: *Molinia caerulea* (L.) Moench. *Journal of Applied Ecology* **89**. 126-144.

Ter Braak, C. J. F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**,1167-1179.

Ter Braak, C.F.J. (1988) CANOCO - an extension of DECORANA to analyse species-environment relationships. *Vegetatio* **75**, 139-160.

Ter Braak, C.J.F. & Prentice, I.C. (1988) A theory of gradient analysis. *Advances in Ecological Research* **18**, 271-317.

Ter Braak, C.J.F. (1994) Canonical community ordination. Part I: Basic theory and linear methods. *Ecoscience* **1**,127-140.

Ter Braak, C.J.F. & Smilauer, P. (1998) *CANOCO reference manual and users guide to CANOCO for windows: Software for community ordination (Version 4).* Wageningen, Centre for Biometry.

Thompson, D.B.A. & Brown, A. (1992) Biodiversity in montane Britain: habitat variation, vegetation diversity and some objectives for conservation. *Biodiversity and Conservation* **1**, 179-208.

Thompson, D.B.A. & Horsfield, D. (1997) Upland conservation in Scotland: a review of progress and some proposals for action. *Botanical Journal of Scotland* **49**, 501-516.

Thompson, D.B.A. & Miles, J. (1995) Heaths and moorland: some conclusions and questions about environmental change. *Heaths and moorland. Cultural landscapes.* (eds. D.B.A. Thompson, A.J. Hester & M.B. Usher), pp 362-389. HMSO, Edinburgh.

Thompson, D.B.A. & Sydes, C. (1997) The British uplands. *Our natural heritage.* (ed. I.F.G. McLean), pp 15-26. Nature Conservancy Council, Peterborough.

Thompson, D.B.A., Macdonald, A.J., Marsden, J.H. & Galbraith, C.A. (1995) Upland heather moorland in Great Britain - a review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation* **71**, 163-178.

Thompson, K. & Grime, J.P. (1979) Seasonal variation in the seed banks of herbaceous species in 10 contrasting habitats. *Journal of Ecology* **67**, 893-921.

Thompson, K. (1985) Buried seed banks as indicators of seed output along an altitudinal gradient. *Journal of Biological Education* **19**, 137-140.

Thompson, K., Bakker, J. & Bekker, R. (1997) *The soil seed banks of North West Europe: methodology, density and longevity.* Cambridge University Press, Cambridge.

Thompson, M. & Walsh, J.N. (1983) *Inductively Coupled Plasma Specrometry.* Blackie, London.

Thornton, B (1991) Effect of nutrition on the short-term response of *Molinia caerulea* to defoliation. *Annals of Botany* **68**, 569-576.

Tilman, D. (1982) *Resource competition and community structure.* Princeton University Press, Princeton.

Tilman, D. (1990) Constraints and tradeoffs: towards a predictive theory of competition and succession. *Oikos* **58**, 3-15.

Todd, M. (1987) *The South-west to AD1000.* Longman, London.

Todd, P.A. (1997) The MAFF *Molinia* contract - Year two. *The Heather Trust Annual Report.* Kippen: The Heather Trust.

Todd, P.A., Phillips, J.D.P., Putwain, P.D. & Marrs, R.H. (2000) Control of *Molinia caerulea* on moorland. *Grass and Forage Science* **55**. 181-191.

Torvell, L., Common, T.G. & Grant, S.A. (1988) Seasonal patterns of tissue flow and responses of *Molinia* to defoliation. *Ecological Change in the Uplands* (eds. M.B. Usher & D.B.A. Thompson), pp 219-222. Special Publication of the British Ecological Society. Blackwell Scientific Publications, Oxford.

Trist, P.J.O. & Sell, P.D. (1988) Two subspecies of *Molinia caerulea* (L.) Moench in the British Isles. *Watsonia* **17**. 153-157.

Tubbs, C.R. (1986) *The New Forest.* Collins, London.

Underwood, A.J. (1997) *Experiments in ecology. Their logical design and interpretation using analysis of variance.* Cambridge University Press, Cambridge.

Usher, M.B. (1987) Modelling successional processes in ecosystems. *Colonization, succession and stability.* (eds. A.J. Gray, M.J. Crawley & P.J. Edwards), pp 31-57. 26th Symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford.

Van Groenewoud, H. (1992) The robustness of correspondence, detrended correspondence and TWINSPAN analysis. *Journal of Vegetation Science* **3**, 239-246.

Wainwright, G.J. (1960) Three microlithic industries from South-west Eire and their affinities. *Proceedings of the Prehistoric Society* **26,** 193-201.

Walker, D. (1970). Direction and rate in some British post glacial hydroseres. *Studies in the vegetational history of the British Isles.* (eds. D. Walker & R.G. West), pp 117-139. Cambridge University press, Cambridge.

Walker, F. & Elias, D. (1989) *Heather regeneration scheme: the Berwyn Mountains case study.* Nature Conservancy Council, Bala, Unpublished report.

Walker, L.R. & Chapin, F.S. (1987) Interactions among processes controlling successional change. *Oikos* **50**, 131-135.

Wallis, C. (1811) Evidence given to the board of Agriculture of the County of Cornwall. *Survey of the Board of Agriculture and Internal Improvement.* (ed. G.B. Worgan), pp 7.Barracuda Books Ltd, Buckingham.

Ward, S.D., Jones, A.D. & Manton, M. (1972) The vegetation of Dartmoor. *Field Studies* **3 (4)**, 505-533.

Warr, S.J., Kent, M. & Thompson, K. (1994) Seed bank composition and variability in five woodlands in South-west England. *Journal of Biogeography* **21**, 151-168.

Warr, S.J., Thompson, K. & Kent, M. (1993) Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Progress in Physical Geography* **17**, 329-347.

Watson, E.V. (1981) *British mosses and liverworts. 3rd ed.* Cambridge University Press, Cambridge.

Watt, A.S. (1947) Pattern and process in the plant community. *Journal of Ecology* **35**, 1-22.

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

Watt, K.E.F. (1975). Critique and comparison of biome ecosystem modelling. *Systems analysis and simulation in ecology* Vol **3** (ed. B.C. Pattern), pp 139-155. Academic Press, New York.

Weaver, R., Kent, M. & Goodfellow, S. (1998) Dynamics and management of semi-natural vegetation on Dartmoor. *Environmental Management and Change in Plymouth and the South West.* (eds. M. Blacksell, J. Matthews, P. Sims), pp 21-51. University of Plymouth, Plymouth.

Webster, J. (1980) *Introduction to Fungi.* 2nd edn. Cambridge University Press, Cambridge.

Webster, J.R. (1962a) The composition of wet heath vegetation in relation to aeration of the ground-water and the soil. 1. Field studies of ground-water and soil aeration in several communities. *Journal of Ecology* **50**, 619-637.

Webster, J.R. (1962b) The composition of wet heath vegetation in relation to aeration of the ground-water and the soil. 2. Responses of *Molinia caerulea* to controlled conditions of soil aeration and ground-water movement. *Journal of Ecology* **50**, 639-650.

Welch, D. & Rawes, M. (1966) The intensity of sheep grazing on high level blanket bog in Upper Teesdale. *Irish Journal of Agricultural Research* **5**, 83-111.

Welch, D. (1968) Sheep grazing in Northern England. some ecological considerations. *Occasional Symposium of the British Grassland Society No* **4**, 173-176.

Welch, D. (1984a) Studies in the grazing of heather moorland in North East Scotland. II. Response of heather. *Journal of Applied Ecology* **21**, 197-207.

Welch, D. (1984b) Studies in the grazing of heather moorland in North East Scotland. IV. Seed dispersal and plant establishment in dung. *Journal of Applied Ecology* **22**, 461-471.

Welch, D., Miller, G.R. & Legg, C, J. (1990) Plant dispersal in moorlands and heathlands in Britain. *Species dispersal in Agricultural Habitats* (eds. R.G.H. Bunce & D.C. Howard), pp 117-132. Belhaven Press, London.

Welch, D., Scott, D., Moss, R. & Bayfield, N.G. (1994) *Ecology of blaeberry and its management in British moorlands.* Institute of Terrestrial Ecology.

West, S. (1997) *Geochemical and palynological signals for paleoenvironmental change in South-west England.* PhD thesis, University of Plymouth.

Westhoff, V. & van der Maarel, E. (1978) The Braun Blanquet approach. *Classification of Plant communities.* (ed.R.H. Whittaker), pp 289-374. Junk, The Hague.

Westoby, M. & Leishman, M. (1997) Categorizing species into plant functional types. *Plant functional types. Their relevance to ecosystem properties and global change.* (eds. T.M. Smith, H.H. Shugart & F.I. Woodward), pp 104-121. Cambridge University Press, Cambridge.

Whittaker, R.H. (1962) Classification of natural communities. *Botanical Review* **28**, 1-24

Whittaker, R.H. (1977). Evolution of species diversity in land communities. *Evolutionary Biology* **10.**1-67.

Wiegleb, G. (1989). Explanation and prediction in vegetation science. *Vegetatio* **83,** 17-34.

Wolton, R.J., Edge, S., Keedle, R.M., Kendall, S. & Archer, R. (1994) *Vegetation and heather condition maps for the commons of Dartmoor. A practical aid to their sensitive management.* English Nature.

A1 Appendix 1: Phytosociological data

Table A1.1. Indicator value scores, relative abundance index (Dufrêne & Legendre 1997) and constancy of characteristic species of vegetation assemblage one (10 samples, TWINSPAN group 00).

Characterising species	Indicator values	% constancy	Relative abundance index
*Holcus lanatus****	93	100	93
*Lolium perenne****	60	60	100
*Trifolium repens****	59	60	99
*Cerastium fontanum****	40	40	100
*Cynosurus cristatus****	40	40	100
*Poa pratensis****	37	40	93
*Agrostis capillaris****	33	100	33
*Ranunculus acris****	21	30	71
*Bracathecium rutabulum****	20	20	100
*Poa annua****	17	20	85
Rhytideadelphus squarrosus	11	70	16
Cirsium vulgaris	10	10	100
Trifolium pratensis	10	10	100
*Achillea millefolium**	9	10	89
Bellis perennis	8	10	81

Table A1.2. Indicator value scores, relative abundance index (Dufrêne & Legendre 1997) and constancy of characteristic species of vegetation assemblage two (17 samples TWINSPAN group 0100).

Characterising species	Indicator values	% constancy	Relative abundance index
Pseudoscleropodium purum ***	52	71	74
*Pteridium aquilinum****	50	82	61
Agrostis capillaris	30	76	39
*Galium saxatile****	24	71	34
*Anthoxanthum odoratum****	21	53	40
*Sedum album****	21	24	89
Rhytideadelphus squarrosus	20	71	29
Festuca ovina	12	71	18
*Oxalis acetosella**	12	12	100
Potentilla erecta	11	71	16
*Rubus fruticosus**	10	12	84
Digitalis purpurea	8	12	67
Rumex acetosella	6	12	52
Plagiomnium rostratum	6	6	100
Luzula sylvatica	6	6	97
Aira praecox	3	6	50

Table A1.3. Indicator value scores, relative abundance index (Dufrêne & Legendre 1997) and constancy of characteristic species of vegetation assemblage three (87 samples, TWINSPAN group 0101).

Characterising species	Indicator values	% constancy	Relative abundance index
*Festuca ovina****	38	82	47
*Rhytideadelphus squarrosus****	27	90	31
*Potentilla erecta****	21	91	23
Anthoxanthum odoratum	15	62	23
Agrostis capillaris	14	77	18
*Danthonia decumbens**	14	26	52
Galium saxatile	11	61	18
*Euphrasia officinalis**	10	10	100
Molinia caerulea	6	78	8
Hieracium pilosella	6	6	100
Hypnum cupressiforme	5	52	11
Viola riviniana	5	7	73
Prunella vulgaris	5	6	94
Plantago major	2	2	100
Plantago lanceolata	2	2	100
Lotus corniculatus	2	2	86
Veronica chamedrys	1	1	100
Leontodon autumnalis	1	1	100
Cratageous monygyna	1	1	100
Veronica officinalis	1	1	100
Ulex europea	1	1	100
Aira caryopholea	1	1	100

Table A1.4. Indicator value scores, relative abundance index (Dufrêne & Legendre 1997) and constancy of characteristic species of vegetation assemblage four (66 samples, TWINSPAN group 01100).

Characterising species	Indicator values	% constancy	Relative abundance index
*Agrostis curtisii****	60	86	69
*Ulex gallii****	31	77	40
*Hypnum cupressiforme****	20	86	23
Potentilla erecta	19	94	20
Molinia caerulea	13	95	13
Calluna vulgaris	11	88	12
Agrostis capillaris	3	64	4
Eurhynchium praelongum	1	2	57

Table A1.5. Indicator value scores, relative abundance index (Dufrêne & Legendre 1997) and constancy of characteristic species of vegetation assemblage five (14 samples, TWINSPAN group 011010).

Characterising species	Indicator values	% constancy	Relative abundance index
*Festuca rubra****	25	43	58
Hypnum cupressiforme	18	79	23
*Montia fontanum**	18	50	36
Molinia caerulea	17	100	17
Carex binervis	15	57	26
Carex panicea	13	57	23
Juncus squarrosus	13	50	26
Festuca ovina	8	64	13
Calluna vulgaris	8	64	12
Racomitrium lanuginosum	7	7	100
Erica tetralix	6	64	9
Carex pilulifera	6	50	13
Potentilla erecta	5	64	8

Table A1.6. Indicator value scores, relative abundance index (Dufrêne & Legendre 1997) and constancy of characteristic species of vegetation assemblage six (15 samples, TWINSPAN group 011011).

Characterising species	Indicator values	% constancy	Relative abundance index
*Trichophorum cespitosum****	47	87	54
*Dicranella heteromalla****	36	67	53
Calluna vulgaris	18	93	19
Molinia caerulea	17	100	17
Hypnum cupressiforme	16	87	18
Carex panicea	11	80	14
Erica tetralix	11	80	13
Montia fontanum	8	60	14
Juncus squarrosus	8	60	13
Potentilla erecta	5	73	7
Festuca ovina	3	53	6

Table A1.7. Indicator value scores, relative abundance index (Dufrêne & Legendre 1997) and constancy of characteristic species of vegetation assemblage seven (32 samples, TWINSPAN group 0111).

Characterising species	Indicator values	% constancy	Relative abundance index
*Vaccinium myrtillus****	65	97	68
*Deschampsia flexuosa****	63	65	97
*Calluna vulgaris****	33	90	37
*Pleurozium shreberi****	31	55	57
*Cladonia impexa****	30	61	49
Galium saxatile	23	74	31
*Erica cinerea**	12	19	61
Potentilla erecta	11	77	14
*Cladonia uncialis**	11	13	81
Hypnum cupressiforme	9	58	16
Hypnum jutlandicum	8	13	59
Pteridium aquilinum	7	65	11
Festuca ovina	5	55	9
Agrostis capillaris	2	52	4
Ilex aquifolium	0	3	100

Table A1.8. Indicator value scores, relative abundance index (Dufrêne & Legendre 1997) and constancy of characteristic species of vegetation assemblag eight (26 samples, TWINSPAN groups 1000, 10010).

Characterising species	Indicator values	% constancy	Relative abundance index
*Juncus squarrosus****	34	69	49
*Sphagnum capillifolium****	32	77	42
Erica tetralix	18	81	22
*Aulaconium palustre**	15	23	63
Carex panicea	14	50	27
Molinia caerulea	12	100	12
Trichophorum cespitosus	10	65	16
Sphagnum papillosum	9	54	16
Eriophorum angustifolium	8	73	11
Sphagnum compactum	8	8	100
Carex dioica	8	8	100
Calluna vulgaris	6	69	9
Potentilla erecta	4	69	6
Drosera intermedia	4	4	100
Teucrium scorodonia	2	10	100

Table A1.9. Indicator value scores, relative abundance index (Dufrêne & Legendre 1997) and constancy of characteristic species of vegetation assemblage nine (13 samples, TWINSPAN group 10011).

Characterising species	Indicator values	% constancy	Rel abundance index
*Narthecium ossifragum****	39	86	45
*Erica tetralix****	25	93	26
Sphagnum capillifolium	24	64	37
*Eriophorum vaginatum****	24	43	55
Sphagnum papillosum	23	79	29
*Molinia caerulea****	19	100	19
*Lophoclea bidentata****	19	36	52
Trichophorum cespitosus	16	79	21
Eriophorum angustifolium	11	79	14
Sphagnum recurvum	9	57	16
Carex panicea	8	50	16
Drosera rotundifolia	7	50	14
Vaccinium oxycocus	6	7	79
Potentilla erecta	4	79	4
Hypnum cupressiforme	4	71	6
Cirsium palustre	4	7	61
Calluna vulgaris	3	71	4

Table A1.10. Indicator value scores, relative abundance index (Dufrêne & Legendre 1997) and constancy of characteristic species of vegetation assemblage ten (11 samples, TWINPAN group 101).

Characterising species	Indicator values	% constancy	Relative abundance index
*Eriophorum angustifolium****	59	100	59
*Sphagnum inundatum****	39	50	77
*Drosera rotundifolia****	39	80	48
*Sphagnum papillosum****	26	70	37
*Rhynchospora alba****	20	20	100
Erica tetralix	18	80	22
Narthecium ossifragum	17	60	28
*Carex nigra**	14	20	69
Sphagnum palustre	11	50	22
Carex rostrata	10	10	100
*Carex flacca**	9	10	90
Carex demissa	8	10	84
Potamogeton natans	8	10	79
Molinia caerulea	6	100	6
Lotus uliginosum	6	10	64

Table A1.11. Indicator value scores, relative abundance index (Dufrêne & Legendre 1997) and constancy of characteristic species of vegetation assemblage 11 (21 Samples, TWINSPAN group 110).

Characterising species	Indicator values	% constancy	Relative abundance index
*Juncus acutiflorus****	63	64	99
*Juncus effusus****	48	91	53
*Sphagnum recurvum****	40	64	62
*Politrichum commune****	31	55	57
*Galium palustre****	30	32	95
*Hypericum elodes****	29	32	92
*Ranunculus flammula****	27	27	100
*Hydrocotyle vulgaris****	23	23	100
*Viola palustris****	22	36	61
*Agrostis canina****	20	36	56
*Juncus bulbosus****	16	18	88
*Potamogeton polygonifolius****	14	14	100
*Epilobium palusris****	14	14	100
Eriophorum angustifolium	9	55	16
Myosotis scorpiodies	9	9	97
Dactylorhiza maculata	6	9	64
*Menyanthes trifoliata**	5	9	51
Ranunculus omiophyllus	5	5	100
Elatine hexandra	5	5	100
Cardamine pratensis	5	5	100
Glyceria fluitans	5	5	100
Chrysosplenium oppositifolium	5	5	100
Carex pulicaris	5	5	100
Molinia caerulea	4	68	6
Deschampsia cespitosa	4	5	84

Table A1.12. Proportion of First rank (column one) community within ten % of second rank communities (column two) assessed by TABLEFIT. Proportion is the percentage of first rank samples within 10 % goodness of fit of second rank samples.

First rank NVC community	Second rank NVC community	Proportion
U1 *Festuca ovina-Agrostis capillaris-Rumex acetosella* grassland	U4 *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland	50%
U3 *Agrostis curtisii* grassland	H4 *Ulex gallii-Agrostis curtisii* heath	32%
	M25 *Molinia caerulea-Potentilla erecta* mire	9%
U4 *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland	*U5Nardus stricta-Galium saxatile* grassland	20%
U5 *Nardus stricta-Galium saxatile* grassland	U4 *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland	29%
	H4 *Ulex gallii-Agrostis curtisii* heath	29%
U20 *Pteridium aquilinum-Galium saxatile* community	*U4Festuca ovina-Agrostis capillaris-Galium saxatile* grassland	42%
H4 *Ulex gallii-Agrostis curtisii* heath	U3 *Agrostis curtisii* grassland	22%
	U4 *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland	18%
	H8 *Calluna vulgaris-Ulex gallii* heath	22%
	M25 *Molinia caerulea-Potentilla erecta* mire	15%
H8 *Calluna vulgaris-Ulex gallii* heath	H4 *Ulex gallii-Agrostis curtisii* heath	15%
	M25 *Molinia caerulea-Potentilla erecta* mire	10%
H10 *Calluna vulgaris-Erica cinerea* heath	H1 *Calluna vulgaris-Festuca ovina* heath	29%
H12 *Calluna vulgaris-Vaccinium myrtillus* heath	H8 *Calluna vulgaris-Ulex gallii* heath	17%
M6 *Carex echinata-Sphagnum recurvum/auriculatum* mire	M15 *Scirpus cespitosus-Erica tetralix* wet heath	31%
M15 *Scirpus cespitosus-Erica tetralix* wet heath	H4 *Ulex gallii-Agrostis curtisii* heath	8%
	M17 *Scirpus cespitosus-Eriophorum vaginatum* blanket mire	16%
	M25 *Molinia caerulea-Potentilla erecta* mire	29%
	M16 *Erica tetralix-Sphagnum compactum* wet heath	6%
M17 *Scirpus cespitosus-Eriophorum vaginatum* blanket mire	M15 *Scirpus cespitosus-Erica tetralix* wet heath	67%
M21Narthecium ossifragum-Sphagnum papillosum valley mire	M15 *Scirpus cespitosus-Erica tetralix* wet heath	33%
	M25 *Molinia caerulea-Potentilla erecta* mire	33%
M25 *Molinia caerulea-Potentilla erecta* mire	U4 *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland	11%
	M15 *Scirpus cespitosus-Erica tetralix* wet heath	30%

A2 Appendix 2: Species abbreviations

Table A2.13. Species abbreviations used in ordination diagrams.

Species Name	Abbreviation(s)
Achillea millefolium	Ach mil
Agrostis canina	Agr can
Agrostis capillaris	Agr cap
Agrostis curtisii	Agr cur
Agrostis stolonifera	Agr sto
Anthoxanthum odoratum	Ant odo
Asplenium adiantum nigrum	Asp adi
Bellis perennis	Bel per
Blechnum spicant	Ble spi
Bryophyte (biomass combined)	Bryo
Calluna vulgaris	Cal vul
Carex binervis	Car bin
Carex echinata	Car ech
Carex flacca	Car fla
Carex nigra	Car nig
Carex panicea	Car pan
Carex pilulifera	Car pil
Cerastium fontanum	Cer fon
Cirsium vulgaris	Cir vul
Cladonia impexa	Cla imp
Cladonia species	Cla spe
Cladonia uncialis	Cla unc
Cynosurus cristatus	Cyn cri
Dactylis glomerata	Dac glo
Dactylorrhiza maculata	Dac mac
Danthonia decumbens	Dan dec
Deschampsia flexuosa	Des fle
Dicranum heteromalla	Dic het
Dicranum scoparium	Dic sco
Drosera rotundifolia	Dro rot
Erica cinerea	Eri cin
Erica tetralix	Eri tet
Eriophorum angustifolium	Eri ang
Eriophorum vaginatum	Eri vag
Euphrasia officinalis	Eup off
Eurhynchium praelongum	Eur pra
Festuca ovina	Fes ovi

Appendix 2: Species abbreviations

Species Name	Abbreviation(s)
Festuca spp.	Fes spp
Galium aparine	Gal apa
Galium palustre	Gal pal
Galium saxatile	Gal sax
Hieracium pillosela	Hie pil
Holcus lanatus	Hol lan
Holcus mollis	Hol mol
Hydrocotyle vulgaris	Hyd vul
Hylocomium splendens	Hyl spl
Hypnum cupressiforme	Hyp cup
Hypnum jutlandicum	Hyp jut
Juncus acutiflorus	Jun acu
Juncus bulbosus	Jun bul
Juncus effusus	Jun eff
Leontodon autumnalis	Leo aut
Leucobryum glaucum	Leu gla
Litter (dead biomass)	litter
Lolium perenne	Lol per
Lophoclea bidentata	Lop bid
Luzula campestris	Luz cam
Luzula multiflora	Luz mul
Luzula sylvatica	Luz syl
Menyanthes trifoliata	Men tri
Molinia caerulea	Mol cae
Montia fontanum	Mon fon
Myosotis scorpiodies	Myo sco
Nardus stricta	Nar str
Narthecium ossifragum	Nar oss
Oxalis acetosella	Oxa ace
Pedicularis sylvatica	Ped syl
Phleum pratensis	Phl pra
Plagiomnium rostratum	Pla ros
Plantago lanceolata	Pla lan
Plantago major	Pla maj
Pleurozium shreberi	Ple shr
Poa annua	Poa ann
Poa pratensis	Poa pra
Polygala serpyllifolia	Pol ser
Polygala vulgaris	Pol vul
Potentilla erecta	Pot ere

Appendix 2: Species abbreviations

Species Name	Abbreviation(s)
Prunella vulgaris	Pru vul
Pseudoscleropodium purum	Pse pur
Pteridium aquilinum	Pte aqu
Ranunculus acris	Ran acr
Rhytidiadelphus loreus	Rhy lor
Rhytidiadelphus squarrosus	Rhy squ
Rubus fruticosus	Rub fru
Rumex acetosa	Rume acsa, Rum/sa
Rumex acetosella	Rume acel, Rum a/la
Sagina nodosa	Sag nod
Sagina procumbens	Sag pro
Scirpus cespitosa (Trichophorum cespitosum)	Sci ces
Sedum album	Sed alb
Sphagnum subsecundum	Sph sub
Sphagnum auriculatum	Sph aur
Sphagnum capillifolium	Sph cap
Sphagnum cuspidatum	Sph cus
Sphagnum palustre	Sph pal
Sphagnum papillosum	Sph pap
Sphagnum recurvum	Sph rec
Succisa pratensis	Suc pra
Trifolium repens	Tri rep
Ulex europeaus	Ule eur
Ulex gallii	Ule gal
Vaccinum myrtillus	Vac myr
Veronica officinalis	Ver off
Viola riviniana	Vio riv

Copyright Statement

Author's Declaration

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

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Relevant scientific conferences were attended at which work was presented and external institutions were visted for consultation purposes.

Presentation and Conferences Attended:

British Ecological Society Winter Meeting 2000
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External Contacts:

Department of Environment, Farming and Rural Affairs, Exeter
Agricultural Development and Advisory Service, Star Cross, Exeter
Rural Development Service, Leeds
English Nature. Peterborough and Cornwall Office
Scottish Natural Heritage, Edinburgh
Macaulay Land Use Research Centre, Aberdeen
Centre for Ecology and Hydrology, Wareham and Banchory
Cornwall Trust For Nature Conservation, Bodmin

Signed. Sam ....

Date. 6/1/03 ....

Scotland Small?

Scotland small? Our multiform, our infinite Scotland small?
Only as a patch of hillside may be a cliché corner
To a fool who cries 'Nothing but heather!' where in
September another
Sitting there and resting and gazing round
Sees not only the heather but blaeberries
With bright green leaves and leaves already turned scarlet,
Hiding ripe blue berries; and amongst the sage-green leaves
Of the bog-myrtle the golden flowers of the tormentil shining;
And on the small bare places, where the little Blackface sheep
Found grazing, milkworts blue as summer skies;
And down in neglected peat-hags, not worked
Within living memory, sphagnum moss in pastel shades
Of yellow, green, and pink; sundew and butterwort
Waiting with wide-open sticky leaves for their tiny winged
prey;
And nodding harebells vying in their colour
With the blue butterflies that poise themselves delicately
Upon them,
And stunted rowans with harsh dry leaves of glorious colour.
'Nothing but heather!' – How marvellously descriptive! And
incomplete!

Hugh MacDiarmid