Restoration of blanket bog vegetation as a habitat for red grouse following clearance of immature Sitka spruce forest on the west coast of Scotland.

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Abstract

Blanket bog habitat is a globally scarce resource and as a result is amongst the most important of British vegetation types in an international context. The habitat supports four Annex 1 bird species including golden eagle (*Aquila chrysaetos*) as well as red grouse (*Lagopus lagopus*) which is only found on heather moorland habitats and provides an important food source for golden eagle. The habitat is a Biodiversity Action Plan habitat with a target to restore 845,000 hectares of degraded blanket bog by 2015. At least 190,000 hectares of blanket bog habitat have been planted with conifer plantation, mainly Sitka spruce (*Picea sitchensis*), which is unlikely to mature until 2020-2030. This thesis explores the potential for restoring blanket bog, to provide habitat for red grouse, through the removal of immature Sitka spruce plantation. Three different tree clearance techniques are considered in terms of impact on the developing vegetation plant community. The most cost effective method of clearance, *in situ* chipping using an excavator mounted flail, is investigated in detail; in particular the effect of wood-chip depth on changes in wood chip decomposition, plant colonisation, plant community development and vegetation structure. Monitoring and experimental data were analysed using multivariate methods including Principal Response Curves, Detrended Correspondence Analysis and Redundancy Analysis, and univariate methods including linear mixed effects and spatio-temporal models. Restoration of blanket bog vegetation is clearly achievable within a relatively short timescale that is dependent on the size of the trees and hence depth of wood chip. Plant community recovery following *in situ* chipping of trees (yield class 10) that are 20, 25 and 30 years old is predicted to take 7, 9 and 10.5 years respectively. Vegetation structure is linked to plant community, with the cover and age of *Calluna vulgaris* being particularly important. As a result it seems likely that suitable red grouse habitat will be achieved as the target blanket bog plant community is reached.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Blanket Bog, extent and importance

1.1.1 Blanket Bog

Blanket bog is the dominant form of ombrotrophic peatland habitat in the British Isles (Lindsay et al. 1988). All ombrotrophic mires are rain-fed (Gk. ombros = a storm of rain, trophos = feeder, nurse) (Lindsay et al. 1988; Wheeler 1993; Anonymous 1995; Tallis et al. 1997), and there are essentially two types of ombrogenous bog in Britain, raised bog and blanket bog, although intermediate or transitional forms also occur (Goode and Ratcliffe 1977; Hulme 1980). Blanket bog formation is controlled primarily through climate, whilst raised bog formation is more closely related to topography (Lindsay et al. 1988).

Blanket bog forms in situations where the climate ensures that the soil is maintained in a waterlogged condition. This encourages the growth of a specific type of vegetation which decays slowly and causes peat to be formed in a process known as paludification (Sjors 1983). Peat accumulation occurs directly over a waterlogged mineral soil that is said to be paludifying (Joosten and Clarke 2002). As a result this type of peat formation is not confined to the level terrain or basins required by raised bogs, but can occur on slopes and often covers the land in a smothering mantle (Lindsay 1995). Blanket bog is common in the north and west of Britain where the climate and the underlying rock creates highly suitable conditions for peat formation. Rainfall is consistently high and the temperatures are generally low ensuring low evapotranspiration, production and decomposition. Poor decomposition is also attributable to the low numbers of bacteria that occur in acidic organic surface horizons on peatland (Maltby 1989). The prevalence of hard, acidic rocks and base-deficient soils, coupled with the leaching and podsolisation characteristic of the cool, wet climate helps to promote the development of acidophilous bog vegetation and subsequent formation of peat (Lindsay 1995).

Intact blanket bog is differentiated into two functional layers (Clymo 1978; Ingram 1978; Ingram 1983; Clymo 1984; Clymo 1984a). The accumulation of dead plant material which gives the bog its overall shape and depth is called the catotelm and is permanently waterlogged (Proctor 1993). This is sealed and protected by the acrotelm which is no more than 30cm deep and provides the bog with a small scale surface pattern. This layer is at least intermittently aerobic and is the region where organic matter is progressively broken down and added to the surface of the catotelm as the bog grows (Proctor 1993). Decay rates of organic material, from the surface vegetation, decrease down the profile until permanent waterlogging reduces it to very low levels (Doyle and Dowding 1990). Hydrological processes in the acrotelm are rapid compared to the catotelm, with water flow rates up to 1000 times faster (Ivanov 1981; Lindsay 1995).

Blanket bogs have evolved as part of the British upland landscape for at least the last 7000 years, the exact time varying from one region to another (Tallis 1993). It is thought that many blanket bogs originated following human destruction of higher altitude forest and scrub during the new stone age (Jacobi et al. 1976; Tallis 1991; Moore 1993). Since that period peat has accumulated between 1cm and 12cm per hundred years to achieve depths of 5m or more in some places (Clymo and Reddaway 1971; Tallis 1993) .

Blanket bog remains completely waterlogged for most of the year (Lindsay 1995). This occurs because water enters the bog from above via rainfall, its downward progress through the peat is very slow but losses by evapotranspiration are also limited because this only occurs from the surface actrotelm. In addition air temperatures are typically low where blanket bog accumulates, further reducing evapotranspiration. As a result blanket bog tends to be made up of 95-98% rainwater and 2-5% peat, by weight (Lindsay 1995). The slow rate of water movement through peat is a result of the amorphous nature of the peat matrix and the water retaining properties of blanket bog species, for example *Sphagnum* sp. which retains water even when dead (Lindsay 1995). It is also thought that water movement is restricted because some of the interstitial spaces between peat particles are blocked by microscopic bubbles of methane (Brown 1989).

As a result of the high water table, low pH and low concentrations of many essential nutrients blanket bog is a relatively hostile environment for plant growth. Although peat contains a large reserve of organic nitrogen only a small proportion is mineralised each year due to the waterlogged and acid conditions that limit microbial activity (Williams 1989). Primary production of ombrogenous bog vegetation is generally low compared with other upland vegetation types (Bradbury and Grace 1983) and ombrogenous bog vegetation often shows minimal response to nutrient-addition experiments on ombrogenous peat (Proctor 1993). It is thought that this is, in part, due to the inherently slow growth rate and efficient nutrient retention characteristic of wild species adapted to nutrient-poor habitats (Chapin et al. 1979).

Bog vegetation is characterised by a dominance of acidophilous plants (Lindsay 1995). On the wetter areas the *Sphagnum* species that are adapted to highly stagnant waterlogged and acidic conditions including *S. papillosum, S. capillifolium* and *S. magellanicum* form a carpet which higher plants grow within. Surfaces which are naturally drier or disturbed have a greater abundance of vascular plants including *Calluna vulgaris, Eriophorum vaginatum* and *Scirpus cespitosus* (Lindsay 1995). The National Vegetation Classification (NVC) (Rodwell et al. 1991) defines eight major bog communities (M15, M16, M17, M18, M19, M20, M21 & M2) which provides a valuable summary of bog plant communities at a site level, although bogs are know to have more detailed variation according to the pattern of the bog surface (Lindsay 1995).

1.1.2 Extent of blanket bog

Blanket bog is a globally restricted habitat confined to cool, wet and typically oceanic climates where precipitation exceeds evaporation (Tallis 1993; Tallis et al. 1997). A precise figure for the area of blanket bog, both nationally and worldwide, is not currently available because different authors refer to different habitat definitions. However, there is generally considered to be between 1 and 2 million hectares of blanket bog in the British Isles (Tallis 1993) depending on peat depth. Lindsay (1995) reports a total area of 1.4 million hectares of 1 metre deep blanket bog.

There are problems determining the distribution and extent of blanket bogs in other parts of the world because the floristics of blanket bog can vary widely depending on geographical location (Stroud et al. 1987). Even if blanket bog vegetation is identified there may be little published information about the extent of the habitat. The common features are peat characteristics, bog structure and relationships to topography (Stroud et al. 1987). Based on this information and climatic information blanket bog is thought to exist on the East coast of Canada, the North American Pacific coast, the southern-most tip of South America, New Zealand and other Southern Ocean islands, North-east Asia and in the mountainous region of central equatorial Africa. A number of European countries have extensive areas of blanket bog including Iceland, north-western France, western Norway and Finland, but the blanket mire in Ireland and Scotland is better developed than anywhere else in Europe (Stroud et al. 1987). The total global extent of the resource is thought to be in the region of 10 – 12 million hectares (Lindsay et al. 1988) indicating that the British Isles have between 10-15% of the global resource (Tallis 1993; Lindsay 1995; Coupar et al. 1997). Indeed blanket mires are among the most important of British vegetation types in an international context (Tallis 1993) and the habitat is considered to be a globally scarce resource (Lindsay 1993; Tallis et al. 1997).

1.1.3 Importance of blanket bog

Lindsay (1995) highlights the importance of blanket bog listing twelve features of the habitat that are either beneficial or worthy of note. These include global rarity of the habitat, support for a number of rare plant, invertebrate and bird species, importance in local and regional hydrological cycles, significance as a carbon sink and value as an historic archive.

In a report on heather moorland loss from the UK, a habitat description which includes many of the blanket bog and mire communities, 40 species of birds are identified as being associated with the habitat (Thompson et al. 1995). These include 8 species listed under Annex 1 of the EC Directive on the Conservation of Wild Birds (79/409/EEC), which requires the UK Government to take special measures, including the designation of Special Protection Areas to ensure the survival and reproduction of these species throughout their area of distribution. Four of these species, golden plover (*Pluvialis apricaria*), merlin (*Falco columbarius*), hen harrier (*Circus cyaneus*) and golden eagle (*Aquila chrysaetos*), are currently decreasing in numbers with one of the reasons stated as afforestation (Thompson et al. 1995). Other bird species supported by blanket bog that are either uncommon or not found in other habitats include wigeon, greenshank, dunlin, curlew, snipe, red grouse and raven (Stroud et al. 1987).

Blanket bog in general, and some specific blanket bogs, are protected by various international legislation including The Ramsar Convention, The Bern Convention (The Convention on the Conservation of European Wildlife and Natural Habitats), The EC Directive on the Conservation of Wild Birds (Directive 79/409/EEC), The EC Directive on the Conservation of Natural and Semi-natural Habitats and of Wild Fauna and Flora (Directive 92/43/EEC) and The United Nations Biodiversity Convention.

Extensive areas of blanket mire are given legal protection by being designated as Special Site of Scientific Interest (SSSI) or Special Area of Scientific Interest

(ASSI) (Anonymous 1995). Precise UK-wide data on the extent protected are lacking because the presence of blanket mire is often part of the general interest of a site, rather than being the specific reason for site designation in its own right. Current estimates suggest that SSSIs/ASSIs which include blanket mire as part of the designated interest extend to around 160,000 ha in England, 350,000 ha in Scotland, 12,000 ha in Northern Ireland and 15,700 ha in Wales (Anonymous 1995). The largest and most intact areas of blanket bog in the world are found in Caithness and Sutherland where 150,000 hectares of blanket bog and associated habitats are designated as SSSI's under the Wildlife and Countryside Act (1981) (Anonymous 2005). Much of this area has now been classified as a Special Protection Area under the EU's Birds Directive on account of the populations of breeding waders, wildfowl and raptors, a Special Area of Conservation under the EU's Habitat Convention and it is designated as a Wetland of International Importance under the Ramsar Convention. The area is also being considered as a World Heritage Site, of which there are only 3 sites in the whole of Scotland (Anonymous 2005).

Another important aspect of peat is its composition, containing a high proportion of carbon. One hectare (100x100m) of 1m deep peat contains 1000 tonnes of carbon which could be released if the bog were damaged through drainage or cutting (Lindsay 1995). Drainage of peatland has been shown to increase carbon dioxide emissions by between 2.5 and 3.4 times due to decomposition of the peat (Moore and Knowles 1989). As a result water level drawdown is predicted to enhance the greenhouse impact (Laine et al. 1996). However, drainage of peatland reduces methane production, a gas that has a far greater impact on the greenhouse effect than carbon (Byrne et al. 2000). Although new evidence suggests that undamaged blanket bogs have a closed methane cycle and that it is only after disturbance that methane begins to be released. Research is currently ongoing to examine the greenhouse gas balances of a number of management options of cutaway peatlands (Byrne et al. 2000).

1.2 Red grouse and blanket bog

One third of the area of grouse moor in the British Isles is located on blanket bog (Butterfield and Coulson 1975), a habitat that is defined along with dry heath and acid grassland as 'upland heather moorland' by Thompson *et al.* (1995). Red grouse require *Calluna vulgaris* in their diet and studies indicate that they will consume between 90 - 98% (Jenkins et al. 1963) even when *C. vulgaris* cover is relatively low (Lance and Mahon 1975). In general blanket bog plant communities tend to have a lower percentage cover of *C. vulgaris* due a high water table but this species is present in all of the NVC blanket bog plant communities (Rodwell et al. 1991).

The health and breeding success of adult red grouse are dependent on the nutrient content of their food (Moss 1969; Moss et al. 1972), particularly *C. vulgaris.* There is also evidence to suggest that nitrogen and phosphorus may be critical to successful breeding and subsequent survival of the young (Moss et al. 1972). It is thought that insects may provide an important supply of nitrogen and phosphorus for grouse living on blanket bog sites where *C. vulgaris* may be limited and relatively low in nutrients (Butterfield and Coulson 1975). Indeed insects contain considerably more nitrogen and phosphorus than *C. vulgaris* for example the species *Tipula subnodicornis* (cranefly) contains 9 and 7 times more nitrogen and phosphorus respectively (Butterfield and Coulson 1975). Insects such as the cranefly are notably absent from dry heathland sites where *C. vulgaris* tends to dominate.

Despite the requirement of red grouse for a diet composed largely of *C. vulgaris* there is considerable evidence to suggest that the percentage cover of heather or *C. vulgaris* is not related to red grouse numbers. For heather covers between 46-94% Smith *et al.* (2001) found no relationship between cover and grouse numbers and Moss (*pers. comm.*) suggests that a cover of 30% is adequate to support red grouse.

1.3 The causes and extent of blanket bog damage

1.3.1 Classification of bog damage

Bogs can be classified into two groups, primary and secondary bogs (Lindsay 1995), depending on their overall status and any damage they exhibit. A primary bog retains all the original peat depth and a surface formed through natural growth, although it does not necessarily need to be actively growing. Secondary bogs have had part of the original expanse of peat removed so this includes cut bogs through to those where the land has claimed for agriculture that involves cultivation. Both these classifications can then be further subdivided to describe their surface condition in more detail. This provides a more accurate view of the current land-use and conservation value of the bog (Lindsay 1995).

1.3.2 The causes and extent of damage

There are a number of factors that have caused damage to blanket bog and these include peat mining or cutting, drainage, afforestation, agriculture, climate change and pollution deposition.

1.3.2.1 Peat mining

Peat mining or cutting is a major anthropogenic disturbance (Lavoie et al. 2005). Peat extraction covers approximately 5 million hectares or 10% of the worlds peatland resource (Joosten and Clarke 2002). This includes all peatlands, both ombrotrophic and minerotrophic. The main uses for mined peat is in horticulture, agriculture, domestic heating and energy generation, although there are other small scale uses. Peat mining on a commercial scale often involves draining the site, removal of the vegetation and the extraction of a thick layer of peat. This is done over a relatively long period of time leaving an extremely hostile environment where vegetation establishment is not straightforward (Lavoie et al. 2005). For example most sites that have been mined using vacuum machines, a practice commonly used in Canada, are almost totally devoid of vegetation after decades of abandonment (Lavoir et al. 2003). This is probably due to a combination of factors including a low water table, lack of necessary propagules (Salonen 1987; Huopalainen et al. 1998), altered chemical conditions (Wind-Mulder et al. 1996) and the extreme conditions which retard plant colonisation (Campeau and Rochefort 1996; Lavoie and Rochefort 1996). Peat is laid down over many thousands of years so it is likely that the lower levels of peat have a different chemical composition to the surface layers. Similarly different surface conditions following peat extraction will influence the chemical composition of the peat (Wind-Mulder et al. 1996).

Peat mining or cutting has had a major impact on blanket bog habitats in a range of different countries including UK, Ireland, Finland, Sweden, Estonia and Canada (Wind-Mulder et al. 1996; Farrell and Doyle 2003; Vasander et al. 2003; Waddington et al. 2003). In many countries, particularly Ireland, peat mining is still ongoing, primarily for electricity generation. For example an active extraction site at Bellacorick, County Mayo, includes 8000 hectares of blanket bog (Farrell and Doyle 2003). 25% of this site has now been exhausted and taken out of production. There are remnants of the original blanket bog vegetation on the site and some areas of regeneration on cut away sites where the water table has been accidentally increased due to impeded drainage channels. However, active peat formation is not occurring although experimentation has indicated that a programme of re-wetting the cut away peat would allow this to occur (Farrell and Doyle 2003).

1.3.2.2 Drainage

The main requirement for carbon accumulation in peatland is that dead plant material is exposed to anaerobic conditions, associated with a high water table (Clymo 1984; Charman et al. 1994). This limits decomposition and hence allows the build up of peat. Drainage can lower the water table so that it descends into the catotelm during dry weather (Ingram 1989). This causes peat to decompose, releasing CO_2 (Charman et al. 1994) and causing the colloidal constituents of the catotelm to undergo irreversible physical alteration which manifests itself as shrinkage, cracking and mechanical weakening for the structure supporting the acrotelm (Ingram 1989). Where drainage on boreal peatlands in Finland is considered effective it has been shown to cause in the order of 100% increase in CO2 fluxes (Silvola et al. 1996). These effects are most obvious close to the drain where the peat of the catotelm can begin to fragment in a process of structural disintegration. The acrotelm becomes more sharply drained so that mosses become suppressed by dwarf shrub species and peat formation is disrupted. These effects spread outwards from the drain until a new hydraulic equilibrium supervenes (Stewart and Lance 1983).

The impact of drainage on the water levels of mires is not clearly understood (Smith et al. 1995). However, direct measures of water table lowering on either side of ditches show that its extent is negligible where annual rainfall exceeds 1200mm/annum (Coulson et al. 1990). Other research supports these findings and demonstrate that the effect of drainage on peat is very localized with the water table depression being restricted to within a few meters of ditches, regardless of peat depth (Robinson and Newson 1986; Stewart and Lance 1991).

Open drains are frequently referred to as grips and it is a technique that has been used for over 100 years to drain land. However, the extent of gripping only really increased significantly when mechanical techniques replaced manual digging. The 'feed Britain' post World War II era saw government grants for expansion of drainage works paid at 70%, particularly on agriculturally marginal upland areas (Holden et al. 2004). It was in the 1960's and 1970's that most of the drainage or gripping of blanket bog took place (Coulson et al. 1990; Holden et al. 2004). A study of aerial photographs indicate that over 50% of hill land in England and Wales has been drained (Coulson et al. 1990). In Scotland it is estimated that, in addition to the forested areas 5000km^2 of the uplands have been drained with open ditches (Coulson et al. 1990).

1.3.2.3 Afforestation

The impacts of afforestation on blanket bog occur over a relatively long period of time from ground preparation for planting until canopy closure, which may be 20 years later (Anderson 2001). Firstly there is a discontinuation of the burning and grazing regimes that were used to manage the site prior to afforestation, allowing more litter to accumulate and a thicker layer of vegetation to develop (Shotbolt et al. 1998). Recent forest practice, when planting conifers on blanket bog, involved ploughing the site to create drainage channels and subsequent application of phosphate, potassium and sometimes nitrogen (Taylor 1991). Drainage is thought to cause a slight lowering of the water table (Anderson et al. 1995) although this effect is minimal in very high rainfall areas (Coulson et al. 1990). It is thought that the application of phosphate and potassium increases microbial activity, particularly if waterlogging is reduced by drainage, so that nitrogen mineralisation occurs more rapidly (Williams 1989). Even if fertilizer is not applied there is evidence to suggest that plant nutrient element concentrations in the upper 50cm of the peat profile increase after drainage for forestry (Laiho and Laine 1994).

During the first 10-20 years of growth the plantation will have an increasing influence on blanket bog vegetation with a gradual increase in shade, shelter, rainfall interception and pollutant deposition from the foliage (Anderson 2001). In addition water uptake by the trees has a significant drying effect on the peat (Anderson et al. 1995). Most studies on the effect of drainage and afforestation on peat have concentrated on tree growth however one study (Anderson et al. 1995) compared the water content profile of peat under 30 year old forest with that in failed plots that were drained (Anderson et al. 1995). The plots where the tree crop had failed demonstrated almost no drying effect due to drainage alone.

Pyatt and John (1989) report that tree growth on peat can cause eventual shrinkage and cracking of the peat which is irreversible and contributes to further drainage of the site (Anderson et al. 1995). A study at Rumster Forest, Caithness showed that closely spaced furrow ploughing lowered the water table sufficiently to allow a tree crop to become established but that the main drying effect was caused by the 20 year old trees which caused irreversible reductions in peat water content and consequent subsidence (Pyatt et al. 1989).

In the north-west of England and the majority of Scotland, more than half of all forestry planting up to 1978, was done on peat soils (Taylor 1983). During the 1980s this proportion increased considerably due to Foresty Commission grants and government tax incentives for private forestry companies, which promoted planting forest on this type of ground (Lindsay 1995). By 1993 approximately 190,000 hectares of plantation forest was located on blanket bog that is over 45cm deep, which represents 9.5% of the British resource (Pyatt 1993).

Extensive areas have been planted in Wales, the Cheviots, the Southern Scottish Uplands, flow-lands in the Wigtown district, Caithness and Sutherland and scattered areas in the western and eastern highlands. 30% of the blanket peat on the Kintyre peninsula has been lost to forestry since 1945 (NCC 1982). In Ireland 75% of all peatland has been lost to afforestation with only high level blanket bog, that is totally unsuitable for forestry, being left unplanted (Anonymous 2004). Approximately 84% of all afforestation in Ireland during 1990-2000 has taken place on peat bogs (Anonymous 2004).

A Forestry Commission policy guidance note that was published in July 2000 states that the Forestry Commission will not approve applications for planting on active, raised or blanket bogs where the peat averages 1m or more in depth or any associated peatland where afforestation could alter the hydrology of such areas (Patterson and Anderson 2000). In addition they will encourage the conservation of peatland within forests and may support restoration of former bog habitats through re-structuring, drain blocking and the removal of unwanted natural regeneration. They have also commited to do similar work in Forestry Commission forests where it is considered appropriate to do so.

1.3.2.4 Agriculture

In some situations bogs have been converted to agricultural use and there is no evidence today from the vegetation that the ground was ever a peat bog (Lindsay 1995). This type of agricultural improvement has not really affected blanket bog which tends to be located at higher altitudes and in high rainfall areas where cropping is not feasible (Lindsay 1995). However, more extensive agriculture is widely practiced on blanket bog where it provides rough grazing for livestock (Lindsay 1995). Due to slow vegetation growth and poor nutritional quality, blanket bogs can only support low densities of grazing animals (Anonymous 2005). Because of this stocking rates tend to be low but there are examples where burning and draining has been used in an attempt to improve the quality of the vegetation, causing considerable damage to the blanket bog surface. Overgrazing and excessive trampling can both lead to erosion, where the slow growth of vegetation and a cool wet climate slows or prevents vegetation recovery (Anonymous 2005). However, a study including seven water catchment sites in the UK and Ireland concluded that burning and excessive grazing on blanket bog is not clearly implicated in causing peat erosion (Rhodes and Stevenson 1997). There is also evidence to suggest that a certain level of grazing is necessary to maintain a diverse ombrogenous plant community on blanket bog, particularly on shallower peats in order to prevent scrub encroachment (Chapman and Rose 1991).

Much of the blanket bog managed within agricultural livestock systems has been drained at one time or another (Vasander et al. 2003) but the extent of this type of management has not been documented.

1.3.2.5 Climate change

Climate change is believed to have affected mire vegetation during the twentieth century with summer temperature changes causing water table declines (Hendon and Charman 2004). Changes in mire hydrology and vegetation on the Border Mires in northern England was studied using palaeoecological data for the last 200 years (Hendon and Charman 2004). Although the mires surrounded by plantation forestry have become drier over the last 40 years there is also clear evidence to suggest that mires outside the direct influence of forestry have also become drier during the twentieth century. The extent of the drying suggests that forestry is not the main cause of changes observed on sites near forestry and that water table declines began earlier than the main phase of forest planting. Future projections for regional climate change suggest a summer temperature increase of 2-4°C and summer precipitation decrease between 30-50% for Northern England (Hulme et al. 2002). Given these predictions it seems likely that mires in the UK will continue to become drier whatever management is applied (Hendon and Charman 2004).

1.3.2.6 Pollution

Increased nitrogen and sulphur deposition is thought to have caused considerable changes to blanket bog pH and vegetation composition in many places (Hogg et al. 1995; Gunnarsson et al. 2000). Acid deposition leads to the lowering of peat pH and this acidification appears to be associated with a reduction in litter decomposition rates (Cresser et al. 1997). Detailed assessments of vegetation change and pH on a lowland bog in Yorkshire showed acidification of around 0.5 pH units between 1978 and 1991. The site is located downwind of a major industrial area and a large group of coal burning power stations and as a result, is considered to have the greatest depositions of hydrogen ions in the UK (Laboratory 1990). Vegetation composition on the bog changed considerably over the experimental period indicating not only increased acidity but also increased nitrogen availability (Hogg et al. 1995). In the South

Pennines a long history of atmospheric pollution has caused extensive modification of large areas of blanket bog with the virtual elimination of the once dominant Sphagnum cover (Baxter et al. 1989). This loss of sphagnum cover has in turn led to serious peat erosion and loss of the blanket bog habitat.

1.4 Blanket Bog Restoration

Environmental management of peatlands, landscape ecology, reduced economic viability of forestry on peatland and the protection of key habitats have created needs and pressure to restore damaged peatlands to natural mire ecosystems (Vasander et al. 2003). The UK Biodiversity Action Plan includes action plans for key habitat types including blanket bog (Anderson 2001) and there is a target of 845,000 hectares of blanket bog to be restored by 2015 (Anonymous 1995). This represents 75% of the total area of blanket bog in the UK that is considered to be restorable (Anonymous 1995). This 75% target is also an integral part of the Ireland Biodiversity Action Plan for blanket bog (Anonymous 2003). Other countries including Finland, Sweden, Estonia, USA and Canada have large scale restoration plans for forested and cut away peatlands (Succow and Lange 1984; Steiner 1985; Vasander et al. 1992; Heikkila and Lindholm 1995; Anonymous 2003; Vasander et al. 2003). In Finland, where approximately 60% of the original peatland area has been drained for forestry (Paavilainen and Paivanen 1995), at least 60,000 hectares is within existing or planned national parks (Heikkila and Lindholm 1995) and will therefore be subject to restoration policy (Vasander et al. 1992).

The main aim of most habitat restoration projects is to shorten the successional pathways towards plant communities that are functionally similar to the pre-disturbance state (Lockwood and Pimm 1999). In the case of blanket bog this process may be relatively simple, involving grazing reductions or cessation of burning management, or it may be more involved requiring a programme of re-wetting and the removal of unwanted plant species i.e. forest plantation or scrub or the introduction of suitable propagules to establish the desired bog vegetation (Salonen 1987; Wilkie et al. 1997; Komulainen et al. 1999; Tuittila et al. 2000b; Anderson 2001; Vasander et al. 2003; Waddington et al. 2003).

The majority of documented bog restoration projects have involved restoring cut away or drained bogs where general conservation of an important habitat or reducing CO^2 emissions is the main aim of the work (Heikkila and Lindholm 1995; Komulainen et al. 1999; Rochefort et al. 2003; Waddington et al. 2003).

1.4.1 Restoration of cut away bogs

Cut away peatlands have shown some ability to recover through spontaneous re-vegetation, although this depends on the peat mining technique used and how much drainage has been done (Lavoie et al. 2003). Despite this it is recognized that peat mining seriously hampers the natural capacity of the bog to regenerate and a proactive approach to restoration is often required (Rochefort et al. 2003). This usually involves re-wetting and perhaps the introduction of diaspores from an intact natural bog. It is estimated that a significant number of characteristic bog species can be established in 3-5 years, a stable high water-table in about a decade, and a functional ecosystem that accumulates peat in perhaps 30 years (Rochefort et al. 2003). However, periods of restoration have been too short to determine whether or not the appropriate ecosystem structure, function, trophic organization and biodiversity will ultimately be restored (Gorham and Rochefort 2003).

The two plant species that are considered the most useful in restoring cut away peatland are *Sphagnum sp.* and *Eriophorum vaginatum* (Lavoie et al. 2003). *Sphagnum sp.* the most abundant and important component of ombrogenous bog vegetation (Lindsay 1995) provides the means for active peat formation and *Eriophorum vaginatum* stabilizes the peat surface (Campbell et al. 2002) and increases relative humidity levels near the peat surface that may improve conditions for moss establishment (Lavoie et al. 2003; Lavoie et al. 2005).

Several studies indicate that it is possible to re-establish *Sphagnum* vegetation cover on post-extracted *Sphagnum* bogs (Rochefort et al. 1995; Campeau and Rochefort 1996; Rochefort et al. 2003). Experiments to investigate *Sphagnum* growth in natural peatland compared with experimentally-restored cut over peatland indicate that growth and capitula density is greater in the restored peatland, probably due to lack of competition (Waddington et al. 2003). There is also evidence to suggest that under optimal water level conditions *Sphagnum* production can revert a restored peatland to a net carbon sink (Tuittila et al. 1999) indicating that active peat production is occurring.

Eriophorum vaginatum or cotton grass has many characteristics that facilitate its establishment and survival in nutrient poor environments. These include the ability to produce numberous seeds, as many as 24 million seeds per hectare, (Lavoie et al. 2005) that are dispersed efficiently by wind (Salonen 1987; Campbell et al. 2003); a deep root system that allows the plant to tolerate prolonged periods of drought (Wein 1973); a constant plant root/leaf biomass ratio (Kummerow et al. 1988) with long-lived tussocks (Mark et al. 1985) where nutrients are translocated from dying leaves to support new leaves (Jonasson and Chapin 1985; Cholewa and Griffith 2004). Lastly the plant can absorb and utilise organic nitrogen directly from the soil (Chapin et al. 1993).

When the water table is less than 40cm below the soil surface massive cotton grass growth and expansion has been recorded (Komulainen et al. 1998; Komulainen et al. 1999; Tuittila et al. 1999; Tuittila et al. 2000b; Price et al. 2003; Lavoie et al. 2005). In fact, there is clear link between cotton grass cover and water table (Lavoie et al. 2005). A number of researchers have suggested that cotton grass can facilitate the colonization and establishment of other bog plants on exposed peat, particularly *Sphagnum* species (Grosvernier et al. 1995; Tuittila et al. 2000a; Lavoie et al. 2003) and paleoecological studies also support this (Buttler et al. 1996; Hughes and Dumayne-Peaty 2002). However, Lavoie (2005) found no evidence for this facilitation hypothesis and suggest that the establishment of mosses and liverworts were associated more with particular hydrological characteristics than with the presence of a dense cotton grass cover. It is certain that cotton grass contributes to stabilising the peat surface (Campbell et al. 2002) and increasing relative humidity levels near the peat surface (Lavoie et al. 2003) and this may improve establishment conditions for moss (Lavoie et al. 2005). However, cotton grass tussocks can intercept between 30-80% of precipitation and lose significant amounts of water through transpiration which may negate the benefits provided by cotton grass for moss establishment (Lavoie et al. 2005). It may improve establishment conditions for other species which prefer drier conditions, such as *Calluna vulgaris.*

Fertilisation increases growth of *Eriophorum vaginatum* (Heikkila and Lindholm 1995). In fertilisation experiments NPK (25:25:30.6g m^{-2}) fertilisation on Alaskan tundra more than doubled the total biomass per unit area of tussock (Shaver et al. 1986). The increase was due mainly to higher tiller density, although tiller size also increased. N was found to be the most strongly limiting element (Shaver et al. 1986). In a laboratory experiment researchers found that applications of 3 or 60kg N ha^{-1} yr^{-1} increased tiller production in *Eriophorum vaginatum* but did not affect shoot elongation or flowering (Leith et al. 1999). These application levels were used as the authors estimate that most upland sites will receive in excess of 10kg N ha^{-1} yr^{-1} and approximately 5% of upland sites will receive up to 30 kg N ha^{-1} yr^{-1} (Leith et al. 1999).

1.4.2 Restoration of drained bogs

When damaged bogs have retained their acrotelm and catotelm, and mire species are found either on the site or nearby, then restoration can rely on natural regeneration of mire vegetation (Komulainen et al. 1999). Rewetting of an ombrogenous bog in Finland had a clear effect on vegetation with the cover of *Sphagnum* species increasing and the cover of *Cladonia* and *Calluna vulgaris* decreasing. The water table rose by an average of 20cm so hollows were considerably wetter than before and this caused the *Calluna vulgaris* to die off (Komulainen et al. 1999). The rates of CO2 efflux from the soil surface also decreased after rewetting (Komulainen et al. 1999).

A number of the drained border mires in Kielder Forest, Northumberland have been dammed with various types of dams including peat dams, plywood dams and large elmboard dams on larger drains or gullies. Subsequent changes in plant species composition have revealed rapid changes on some of the mires (Smith et al. 1995) with the restoration of ombrogenous vegetation.

1.4.3 Restoration of forested bogs

There are a number of documented bog restoration projects involving tree clearance from raised bogs (Anderson 2001). The best examples are the Langlands Moss rehabilitation project in South Lanarkshire (Brooks and Stoneman 1997) and the Border Mires Project (Burlton pers comm.) where a number of raised mires have been or are in the process of being restored (Smith and Charman 1988; Smith et al. 1995). The Langlands Moss rehabilitation project, following tree clearance and drain blocking, reports an increase in *Sphagnum* cover. There is no published information relating to vegetation development on the Border Mires. Results from Scandinavia have been mixed although sites where the water table was successfully increased report vegetation changes in keeping with the restoration of bog vegetation (Anderson 2001). On a damaged ombrogenous mire in Finland, where trees were removed and drains dammed, the vegetation changes indicate a shift towards a functional mire ecosystem (Jauhiainen et al. 2002).

The only documented restoration attempt of afforested blanket bog in Britain is the EU Life Peatlands Project in Caithness and Sutherland (Wilkie et al. 1997; Anonymous 2005). A partnership of the Royal Society for the Protection of Birds, Scottish Natural Heritage and Caithness and Sutherland Enterprise received funding for the project in 1994. Since then the project has cleared over 2000 hectares of conifer forest from blanket bog (Wilkie *pers. comm.*). For the most part trees have been cut, either by chainsaw or using an excavator mounted shears and dropped into the plough furrows. During 2004 10 hectares of forest were cleared using a forest mulcher, a tracked machine with a large flail at the front, operating at ground level. This technique was effective in clearing the trees but completely obliterated all ground vegetation which may delay vegetation restoration and could facilitate erosion (Wilkie *pers. comm.*).

Although tree clearance has been extensive in the EU Life Peatlands project only a small area is being scientifically monitored to determine the effect of the work on blanket bog restoration and vegetation development (Cowie *pers. comm.*). A vegetation monitoring programme has been set up on one restoration area, the Talaheel plantation on the RSPB Forsinard Researve (Maier 2004). The Talaheel plantation was planted with a mixture of Sitka spruce and Lodgepole pine between 1983 and 1985 (Maier 2004). Tree growth was poor and canopy cover remained open even after 15 years of growth with elements of bog vegetation still present within the conifer blocks. Most of the site is covered by blanket peat with a depth of at least 1 metre. The site was cleared of trees early in 1998 and the cut trees were placed into the forestry plough furrows in an attempt to impede drainage. A few very deep or eroded drainage channels were dammed using plastic or wooden dams.

The vegetation monitoring programme involved a baseline survey which was done in winter 1997, prior to tree clearance, with a follow up survey done during the winter of 2003/2004, 6 years later (Maier 2004). In 1997, species indicative of blanket bog were only present at low cover values and *Calluna vulgaris* was the most abundant species in all compartments. By 2003, many blanket bog species had increased substantially, notably *Eriophorum vaginatum, Eriophorum angustifolium* and *Sphagnum capillifolium*. Pleurocarpous mosses, commonly found on blanket bog, such as *Hylocomium splendens* and *Pleurozium schreberi* had also increased and the vegetation cover for the whole of the site was much more continuous with little bare ground (Maier 2004). Vegetation community change was not investigated as part of the follow up work and species or community change was not considered in relation to environmental variables including slope, soil type, peat depth and soil moisture (Maier 2004).

Despite these documented cases of bog restoration following forest clearance evidence of successful restoration is limited and little has been published on the results of attempts to restore blanket bog vegetation (Anderson 2001). There are some signs that forested bogs can be restored but there has been, as yet, no clear demonstration of success (Anderson 2001).

A large scale habitat management plan to restore over 280 hectares of blanket bog in Central Kintyre was agreed in 1999 (ScottishPower 1998; ScottishPower 2000). The main aim of the plan was to restore blanket bog vegetation to an area of immature Sitka spruce forest through removal of the trees and in so doing create habitat suitable for red grouse and ultimately golden eagle foraging (ScottishPower 2000). This project provided an opportunity to investigate the restoration potential of forested blanket bog on the west coast of Scotland. This is of particular interest to Scottish Power and other wind farm development companies as a large number of proposed on-shore wind farm sites are likely to be built on forested blanket bog (Mortimer *pers. comm.*). These sites are usually very windy, they have limited conservation potential as they are under forest but at the same time offer clear opportunities to improve the conservation value of the site (Mortimer *pers. comm.*) by restoring an internationally important habitat (Anonymous 1995).

1.5 Thesis aims and objectives

The main aim of this thesis is to investigate the development of blanket bog vegetation, as potential habitat for red grouse, following the clearance of immature Sitka spruce plantation from blanket bog peatland in Central Kintyre. This aim will be addressed by the following objectives that relate to the four experimental chapters within the thesis.

1. To investigate plant community development in relation to forest clearance method and the environment.

Taking the most cost effective forest clearance method, 'in situ' chipping with an excavator mounted flail...

2. Assess the impact of forest age/tree size on vegetation development.

3. Assess how differences in blanket peat micro-site influence germination and growth of *Calluna vulgaris*.

4. Investigate the development of vegetation structure in relation to red grouse habitat preferences.

CHAPTER 2

PROJECT AND SITE DESCRIPTION

2.1 The Central Kintyre Habitat Management Project

The work described in this thesis was completed as part of an ongoing project to create new foraging areas for a pair of golden eagles in Central Kintyre. The project was initiated to mitigate the negative effects of a 30MW wind farm that was installed within the golden eagle territory (ScottishPower 2000). The likely negative effects of the wind farm were thought to be disturbance, displacement and collision so the mitigation proposals aimed to replace foraging areas one and a half times larger than the ground lost within the windfarm.

The land lost to the windfarm comprised approximately 260 hectares of blanket bog vegetation that was dominated by heather and rough grass. The main aim of the habitat creation project was to recreate this type of vegetation on an immature forest site. It is widely agreed that one of the main causes of decline in golden eagle populations on the West coast of Scotland is afforestation (ScottishPower 1998). In Kintyre the forest area increased twelve fold between 1980 and 2000 and the eagle population declined from 8 to 3 pairs (ScottishPower 1998). As a result, clearance of immature forestry was considered by Scottish Natural Heritage, the Royal Society for the Protection of Birds and Argyll and Bute Council to be the best approach to help mitigate the effects of the new wind farm. This is a management option for a large number of other sites where conservation objectives are now considered to be more important than timber production. For example in Caithness and Sutherland where extensive areas of blanket bog were planted during the 1980's (Anonymous 2005).

Over 280 hectares of immature *Picea sitchensis* (Sitka spruce) forest, located on deep peat blanket bog, were cleared during the first two years of the project (1999-2001) and this opened up 450 hectares of new foraging ground for the eagles. The cleared area had been planted during the 1980's following ground preparation that involved general drainage of the site as well as ploughing using a double mouldboard plough to create a series of plough furrows that were 50cm deep, at approximately 3 m intervals across the site. Two rows of trees were planted on the ridge between each plough furrow. Some areas were ploughed but left unplanted so there were islands of partly-drained, semi-natural vegetation within the forest. These areas amounted to 170 hectares in total but were mainly small patches surrounded by forest and consequently unavailable to the eagles (Madders *pers.comm.*).

Several different methods of tree removal and land management can be used in forest clearance projects to restore blanket or raised bog. These include whole-tree chipping, chainsawing, and mechanical tree removal (see section 2.2.2). Such schemes have sometimes included drain blocking measures (Wilkie 2005 *pers. comm.* Burlton 1993 *pers. comm.*). Drain blocking is done to increase water levels and hence encourage peat forming species, such as *Sphagnum sp.* to colonise the site and restore the bog to an active state. Drain blocking was not considered necessary in this situation for a number of reasons:

a) almost all the drains had been rendered inactive by vegetation growth

b) chipping of the trees using an excavator mounted flail allowed the chip to be directed into the plough furrows which further prevented any surface run off of water

c) the average annual rainfall on the hill ground in Kintyre is over 2000mm, and since it is well distributed throughout the year, peat drying is unlikely.

d) tree removal from blanket bog is known to reduce evapotranspiration significantly, which would further contribute to raising the water table on the cleared blanket bog (Anderson et al. 1995).

2.2 Site Description

The project area is located in Central Kintyre between Carradale on the East side of the peninsula and Glenbarr on the West side of the peninsula (Grid Reference for centre of area – NR 175 639). A map of this area is shown at Appendix 1. The forest clearance area extends to 450 hectares including 280 hectares of cleared forest and 170 hectares of unplanted open ground. The altitude ranges from 150-362m although the majority of the site is around 300m. Peat depth varies enormously but a large proportion of the area has depths well over 2m. There are numerous rock outcrops on the site where peat depth is as little as 2-3cm. The considerable variation in peat depth is reflected by the vegetation on site which includes mire National Vegetation Classification (NVC) communities such as M15 (*Scirpus cespitosus-Ericetum tetralix* wet heath), M17 (*Scirpus cespitosus-Eriophorum vaginatum* blanket mire), M18 (*Erica tetralix-Sphagnum papillosum* raised and blanket mire), M19 (*Calluna vulgaris-Eriophorum vaginatum* blanket mire) but also some dry heath and acid grassland communities including H10 (*Calluna vulgaris-Erica cinerea* heath), H12 (*Calluna vulgaris-Vaccinium myrtillus* heath), H18 (*Vaccinium myrtillus-Deschampsia flexuosa* heath), H21 (*Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* heath) (Rodwell et al. 1991; Rodwell et al. 1992). Much of the ground is highly acidic with pH ranging from 2.7 to 4.2. There are a few nutrient-rich flushes on the site where pH may be a little higher but they do not have sufficiently high pH to be classified as base-rich.

The climate in Central Kintyre is strongly oceanic with higher than average wind speeds and precipitation. The long term average rainfall for the area is approximately 1250mm per annum although the annual average for the 5 year period 2000-2004, on the hill ground is considerably higher than this at over 2000 mm/annum (results from on-site weather station). There is good distribution of precipitation throughout the year, with reasonably high summer rainfall. Although winter temperatures are generally higher than average, with very little snow or frost, summer temperatures are often relatively cool which limits growth, evapotranspiration and decay (Lindsay et al. 1988).

2.2.1 Management

Domestic livestock are excluded from the forest clearance area although there is limited grazing by the wild deer population which is controlled by Forestry Commission Scotland. Since the grazing pressure was and still is very low the patches of vegetation on open ground that existed within the forest plantation are in relatively good condition with some areas of active blanket bog where peat formation is occurring. Blanket bog vegetation on drier areas is dominated by *C.vulgaris* but heather burning is not practised due to the close vicinity of forested ground. In many locations the *C. vulgaris* is layering well so burning is not necessary anyway.

2.2.2 Forest Clearance

Yield class of the forest varied considerably over the whole site but it was generally very poor and tree growth was often patchy. Tree height varied between 2 and 8 m with trunk diameter at breast height varying between 5 and 20 cm. Because of the poor yield class and inaccessibility of the site the cost of extracting timber to clear the forest would have been prohibitive. Instead the site was cleared using three methods.

1. Chipping 'in situ' using an excavator-mounted flail.
2. Felling to waste using a chainsaw where the branches were removed and the trunk cut up into several pieces.
3. Whole tree harvesting where the tree was removed at ground level and used in its entirety to create a corduroy road for improved excavator access around the site. As a result no part of the tree was left on the area where it was harvested from.

Photographs of the three different tree clearance techniques and the type of material left on site following clearance are shown below in Figure 2.1. Table 2.1 highlights the differences between the three different clearance techniques.

Figure 2.1: Photographs of the three tree clearance methods, along with the state of the ground following tree clearance.

'In situ' chipping with an excavator mounted flail

Manual felling and branch removal using a chainsaw

Whole tree removal using a conventional harvester (for corduroy brash track construction as shown below)

Table 2.1: Comparison of the Three Different Tree Clearance Techniques

Clearance method	**Size and description of material left on site**	**Ground disturbance**	**% of clearance area**	**Type of ground**
Excavator-mounted flail	Wood chips from 1 cm^2 to chunks between 10-40cm long. Small pieces of branch & leaf (10-20 cm)	Considerable as excavator tracks frequently cut into peat and caused some compaction	80%	Variety of slopes, peat depths and wetness. (very steep or boggy areas avoided as excavator access poor)
Chainsaw to waste	All branches removed and the tree trunk cut into 1-1.5 m lengths	No disturbance or compaction as all done manually	15%	Mainly steep slopes and very boggy ground although some flatter areas that were inaccessible to excavators
Whole tree harvesting	Whole trees removed for building tracks so no material left on site	No disturbance where tree removed as machinery on track adjacent to cleared area.	5%	Variety of slopes, peat depths and wetness.

2.3 Materials & Methods

Data collected from a series of permanent monitoring quadrats form the basis of the work presented in Chapters 3, 5 & 6. Methods relating to quadrat sampling design and set up are provided here with further methods relating to specific data collection detailed in the relevant chapters. Species nomenclature used is according to Jermy *et al* (1982) for sedge species, Smith (1978; 1990) for mosses and liverworts, Hubbard (1954) for grasses and Rose (1981) for other vascular plants.

QUADRAT SAMPLING DESIGN

Eighty 10x10 m permanent monitoring quadrats were established during July and August 2001 on the tree clearance area. The quadrats were arranged using a stratified-random design, to ensure good geographical distribution over the treatment area and to include three different tree clearance methods (flail, chainsaw and harvested) and two different controls (existing blanket bog vegetation or 'target' vegetation and uncleared 15 year old Sitka spruce). The number of quadrats on each tree clearance method or control is shown in Table 2.2.

Table 2.2 Number of quadrats on each tree clearance method or control

Tree clearance method or control	**No. Quadrats established**
Flail	46
Chainsaw	10
Harvested	4
Existing blanket bog vegetation (target vegetation)	10
Uncleared 15 year old Sitka spruce	10

Three quadrats were lost during the monitoring period, one each from the three tree clearance methods. All three were lost due to excessive growth of vegetation so that the markers could not be re-located. They were, however, located in very fertile areas and as the vegetation developed it became apparent that they were not representative of the rest of the site.

The tree clearance programme extended over a period of 20 months from October 1999 until June 2001. All the monitoring quadrats were established during the summer of 2001 so that the time since tree clearance varied for each quadrat. In order to determine a 'time since tree clearance' for each quadrat three tree clearance years were defined and this was done according to the season in which the clearance work was completed (Table 2.3)

Table 2.3: Tree clearance periods

Tree Clearance Year	**Period of Tree Clearance**
1999	1st Oct. 99 – 30th April 00
2000	1st May 00 – 30th September 00
2001	1st March 01 – 31 May 01

The first vegetation assessments were done in 2001 when the quadrats were established and these were repeated annually for four years. The combination of three different tree clearance years and four sampling years creates a chronological sequence of data that spans six years since tree clearance (year 0 – year 5). Table 2.4 below shows how this chronological sequence is comprised and Table 2.5 shows the number of quadrats in each year since clearing category.

Table 2.4: Chronological sequence of year since tree clearance of monitoring quadrats

Clearance Yr	Years Since Tree Clearance			
	Sampling Year			
	2001	2002	2003	2004
1999	2	3	4	5
2000	1	2	3	4
2001	0	1	2	3

Table 2.5: Number of quadrats in each year since tree clearance category

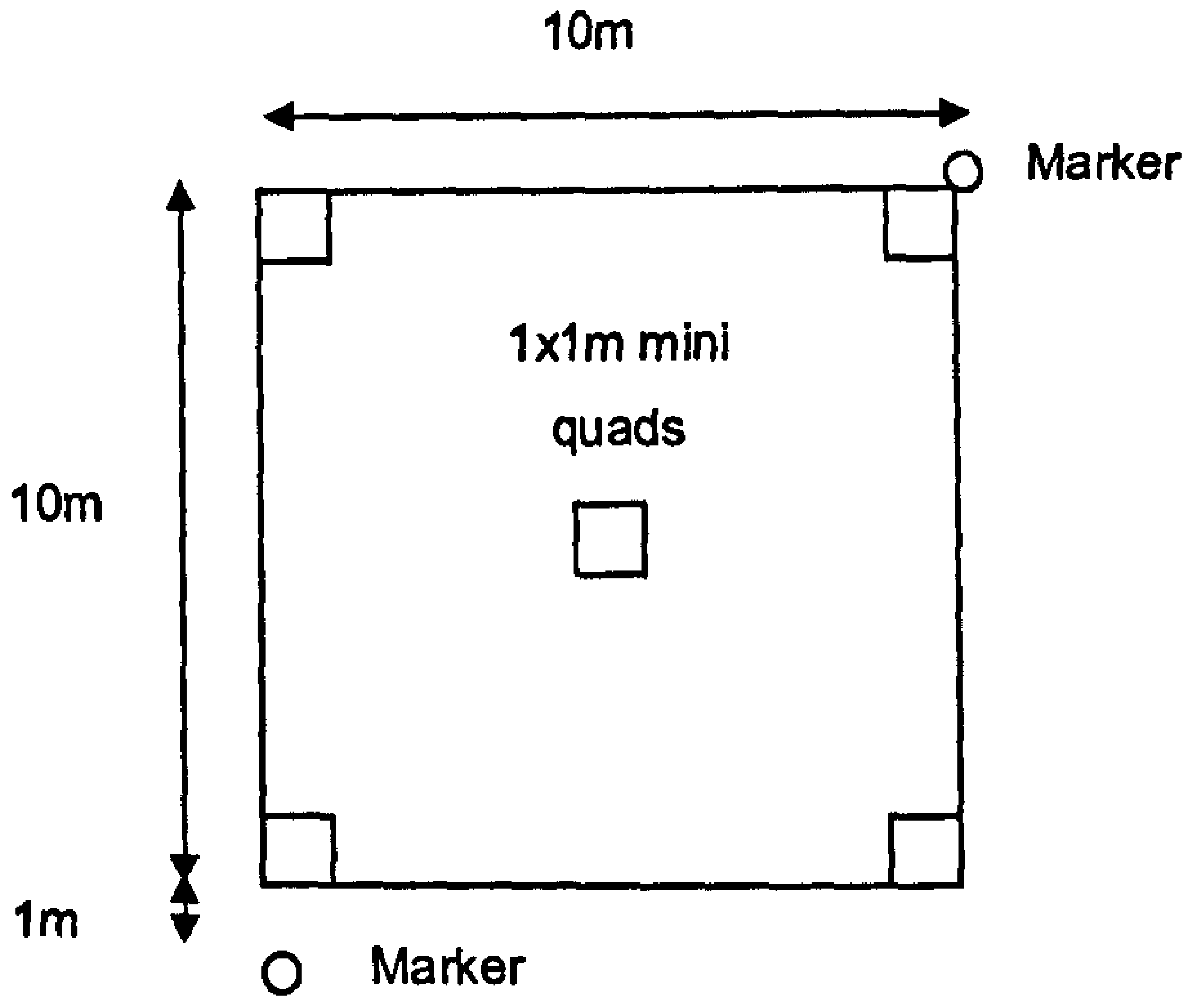
Yr. Since Clearance	No. of Quadrats		
	Flail	Chainsaw	Harvester
0	8	3	1
1	21	7	2
2	45	9	3
3	45	9	3
4	37	6	2
5	24	2	1

QUADRAT SET UP

The tree clearance area was divided into 5 geographic units (see Appendix 2). Initially these units were used to prioritise felling but they were also used to stratify the tree clearance area to ensure good distribution of quadrats. Between 10 and 25 grid references, depending on the size of the unit, were generated at random. Each grid reference was located using a hand held GPS and this point was marked with a wooden stake (5 x 5 x 75 cm). Treatment quadrats were rejected if they had greater than 50% cover of existing vegetation. For control quadrats 100% existing vegetation was required.

The 10x10m quadrat was established with the SW corner 1m due north of the wooden stake, as shown in Figure 2.2. A sighting compass and tape measure were used to achieve this and an exact square was marked out by measuring the hypotenuse and creating two contiguous right angled triangles. Once the square had been marked the NE corner was also marked with a stake to facilitate re-location of the quadrat in subsequent years.

Figure 2.2. Quadrat layout and method of permanent marking (not to scale) showing main 10 x 10 m monitoring quadrat, containing five 1 x 1 m mini-quadrats.



Five 1x1m 'mini-quadrats' were established within the main 10x10m quadrat. These were located in each corner and in the centre, as shown in Figure 2.2 above. The central mini quadrat was located by dividing the main quadrat into quarters using canes and string so the centre of the quadrat could be pinpointed. When the quadrats were established the following environmental data were recorded at each 10x10 main quadrat: tree clearance method and estimated clearance date, peat depth (to the nearest cm, mean of five depth readings [1]), slope (from the highest to the lowest point of the quadrat), number and diameter of tree stumps and pH (mean of 5 readings).

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[1] The depth and pH measurements were taken in each of the five mini-quadrats.

CHAPTER 3

PLANT COMMUNITY DEVELOPMENT OVER SIX YEARS FOLLOWING DEFORESTATION OF FORMER BLANKET BOG HABITAT

3.1 Introduction

Clearance of immature conifer forest from blanket bog is a necessity if the UK is to meet its Biodiversity Action Plan target to restore 845,000 hectares of degraded blanket bog by 2015 (Anonymous 1995). During the 1980's Forestry Commission grants and government tax incentives encouraged planting of conifer forest on marginal land (Lindsay 1995) and by 1993 190,000 hectares of plantation forest had been planted on blanket bog (Pyatt 1993). The age range of these plantations is not available but it seems likely that a significant proportion of the area will not reach economic maturity until at least 2020-2030, if at all. If this is the case then there is a considerable area of immature conifer forest that could be cleared during the next 8 years to start the process of restoring blanket bog habitat and contribute to the BAP restoration target.

Blanket or raised bog restoration that involves the removal of plantation forestry has been done in a few places in the UK (Burlton 1993; Brooks and Stoneman 1997; Wilkie et al. 1997). In all of these cases it was deemed necessary to remove the trees prematurely before it was economically viable to do so. As a result there was a net cost which varied from £250 to £9,000/ha depending on timber volume and value, accessibility and how much material could be left on site. Costs can certainly be reduced by delaying restoration until the trees are more valuable but it is generally thought that this will reduce the chances of achieving successful blanket bog restoration (Anderson 2001). The cheapest method of clearing trees is felling to waste using a chainsaw which may involve dropping the tree and leaving it intact or removing the branches and cutting up the trunk into small pieces. Either way the method still leaves whole trees or portions of trees on site that can obscure the ground for many years. The most expensive method of clearing trees is cutting with a chainsaw and removing the whole tree with a helicopter or skyline winch. Trees can be cut and extracted more cheaply using conventional forest harvesting machinery although the costs are still relatively high, especially if the timber that is being extracted has little or no value.

Scientific monitoring data relating to vegetation development post forest removal is virtually non existent and those data that do exist have not been published (Wilkie *pers comm.,* Burlton *pers comm.*). As a result there is a need to investigate the impact of different tree removal methods on re-vegetation of blanket bog and to determine likely timescales for achieving blanket bog restoration. Other factors that will influence the speed of recovery are the forest plantation species, age and yield class although Sitka spruce is the most widely planted species on blanket bog (Anderson 2001). It is the main commercial timber species in the UK (Taylor 1991) and since the species has some tolerance to waterlogged soil conditions it is the most commonly planted species on blanket bog (Anderson 2001).

The tree clearance project in Kintyre involved the removal of 280 hectares of 18-20 year old Sitka spruce forest (yield class 6-14) from former blanket bog habitat, using three different methods of tree clearance: whole tree removal with a conventional tree harvester, in situ chipping with an excavator mounted flail and cutting by hand using a chainsaw. A detailed monitoring programme was set up to investigate the development of blanket bog vegetation following tree clearance. The investigation was targeted primarily at the in situ chipping removal technique as this method was the most cost and time effective method. It was also used to clear the majority of the trees on the tree clearance area (80% of area). The other two removal techniques were included in the study to provide some comparisons to the results of in situ chipping although sample sizes were considerably lower for these techniques. The impact of various environmental variables, including slope, pH and peat depth, on vegetation development were also investigated to determine where blanket bog restoration is likely to be most successful.

3.2 Materials and Methods

DATA COLLECTION

Sampling design and quadrat set up is described in detail in Section 2.3.1. The 77 monitoring quadrats were assessed annually from 2001 – 2004. Each year the quadrat was marked out using the same method, as described in Section 2.3.1.

A visual estimate of percent cover was recorded for all plant species, rock, bare peat, water and tree remains (chip or brash). All vascular plants and bryophytes were identified to species level. In order to make percent cover estimates as accurate as possible each 10x10m quadrat was divided into four 5x5m quarters using canes and string. Each quarter was searched carefully and a species list recorded. 10 minutes (2.5 mins/quarter) was allocated to searching the quadrat for different plant species and becoming familiar with the plant community. After the 10 minute familiarisation period a percent cover estimate was made for each species recorded in the species list.

Percent cover estimates for all plant species, rock, bare peat, water and tree remains were also recorded for each of the five mini quadrats (1m^2 quadrats). This was done with the aid of a 1x1m grid divided into one hundred 10x10cm cells.

DATA ANALYSIS

A series of multivariate analysis techniques were used to investigate the monitoring quadrat data. These included Detrended Correspondence Analysis (DCA), Canonical Correspondence Analysis (CCA), and Redundancy Analysis (RDA) using CANOCO version 4.5 (Braak and Smilauer 1998).

DCA (Hill 1979) was used to investigate the development of vegetation over a six year period since tree clearance. Data from the monitoring quadrats were analysed in conjunction with computer generated random 'pseudo quadrats' (Rushton et al. 1996; Critchley et al. 2002a; Critchley et al. 2002b; Smith et al. 2002) of the 4 main National Vegetation Classification (NVC) communities found on the tree clearance site. The appropriate NVC communities on which to apply the pseudo quadrat technique were determined by running the existing blanket bog ('target') vegetation control quadrat data (all years) through MATCH (Malloch 1990). DCA was used instead of Principal Components Analysis (PCA) because the gradients of axis 1 and 2 were greater than 3.5 (Leps and Smilauer 2003). The DCA analyses were done using data from the main 10x10m quadrats and repeated with the mini quadrat data in order to investigate the effects of sampling scale. All treatment and control monitoring quadrats and the pseudo NVC community quadrats were included as active samples within the analysis.

The DCA analysis described above includes vegetation samples that were collected over four years (2001-2004) but represent 6 years since tree clearance (see section 2.3.1 for more details). Each group of 'year since tree clearance' samples contains samples collected in up to three different years. The variation between sample year but within 'year since tree clearance' was explored using RDA. To do this each 'year since tree clearance' group was analysed with sample year as a nominal variable. Significance of the first canonical axis was tested using a Monte Carlo permutation test (999 permutations) to determine any significant variation between sample years. This was only done for quadrats where tree clearance occurred and was not possible for control quadrats or NVC pseudo quadrats.

RDA was used to investigate the influence of a series of measured environmental variables on the vegetation development. The environmental variables include slope, peat depth, pH and estimated fresh weight of chip (for flailed quadrats only). In addition, year since tree clearance was included as a continuous variable. Loess smoothing models (Hastie and Tibshirani 1990) were used to create species response curves for each individual environmental variable and the Shannon Diversity index was used to calculate species diversity for each quadrat in each year.

RDA was selected for this constrained analysis, rather than CCA, because an initial DCA analysis had relatively short gradient lengths, all less than 3. This analysis was done using the main 10x10m quadrat data only and a separate analysis was done for the flailed and chainsawed quadrats. As there were only 3 harvested quadrats there was insufficient data to complete this analysis separately. The mini quadrat data were not used for this analysis as the environmental variables were measured at the main quadrat level.

3.3 Results

3.3.1 DCA analysis of main and mini quadrat data

NVC COMMUNITIES

The four main NVC communities that were used to generate the pseudo NVC quadrats are detailed below:

M15 *Scirpus cespitosus – Erica tetralix* wet heath
M19 *Calluna vulgaris – Eriophorum vaginatum* blanket mire
H18 *Vaccinium myrtillus – Deschampsia flexuosa* heath
H21 *Calluna vulgaris – Vaccinium myrtillus – Sphagnum capillifolium* heath

MAIN QUADRATS

In the DCA analysis of all main quadrats and the pseudo NVC quadrats 20.4% of variation was explained by the first 4 axes. Most of this variation was explained by axis 1 and 2 at 8.3% and 6.3% respectively. Sample results from the first two axes (Figs 3.1a-d), show a clear movement of the post tree clearance vegetation towards the pseudo NVC communities and the 'target' vegetation on site. Axis 1 appears to represent a gradient of species diversity with high scores for low diversity and Axis 2 shows a dry to wet gradient with wetness increasing with the axis score. Axis 3 and 4 provided little additional information about the post tree clearance vegetation development so it has not been included here. In order to aid interpretation of the DCA ordination diagram in Figures 3.1a-d not all the samples, included in the analysis, are shown on the diagram. All the pseudo NVC community samples are shown so that the distribution and relationship to the 'target' vegetation on site can be seen clearly. Only year one samples for the 'target' vegetation and Sitka control samples are shown because there was no change over the four assessment years (Table 3.1). For the tree clearance samples the mean DCA scores for each tree clearance method in each year since tree clearance are shown together (a) and in separate diagrams (b-d) with standard error bars to indicate variation.

Table 3.1: p-values from ANOVA to compare DCA scores in four different sample years.

Control quadrats	p-values from ANOVA on sample year	
	DCA Axis 1	DCA Axis 2
Target vegetation	0.953	0.986
Sitka	0.933	0.967

It is clear that there are substantial changes over time since tree clearance for all tree clearance methods. The post tree clearance vegetation is certainly developing into plant communities that already exist on site although there appears to be little difference between tree clearance methods. The 'target' vegetation control quadrats that represent existing blanket bog vegetation on site are mostly similar to the M19 NVC community (Rodwell et al. 1991), although one quadrat is clearly more like the H18 community. The Sitka control samples that represent vegetation in immature Sitka spruce forest are spread out along Axis1. This is because these quadrats were located in forest of differing densities from complete canopy cover, with only dead spruce needles for ground cover ('litter') to sparse tree cover where a fully developed blanket bog community exists underneath the trees.

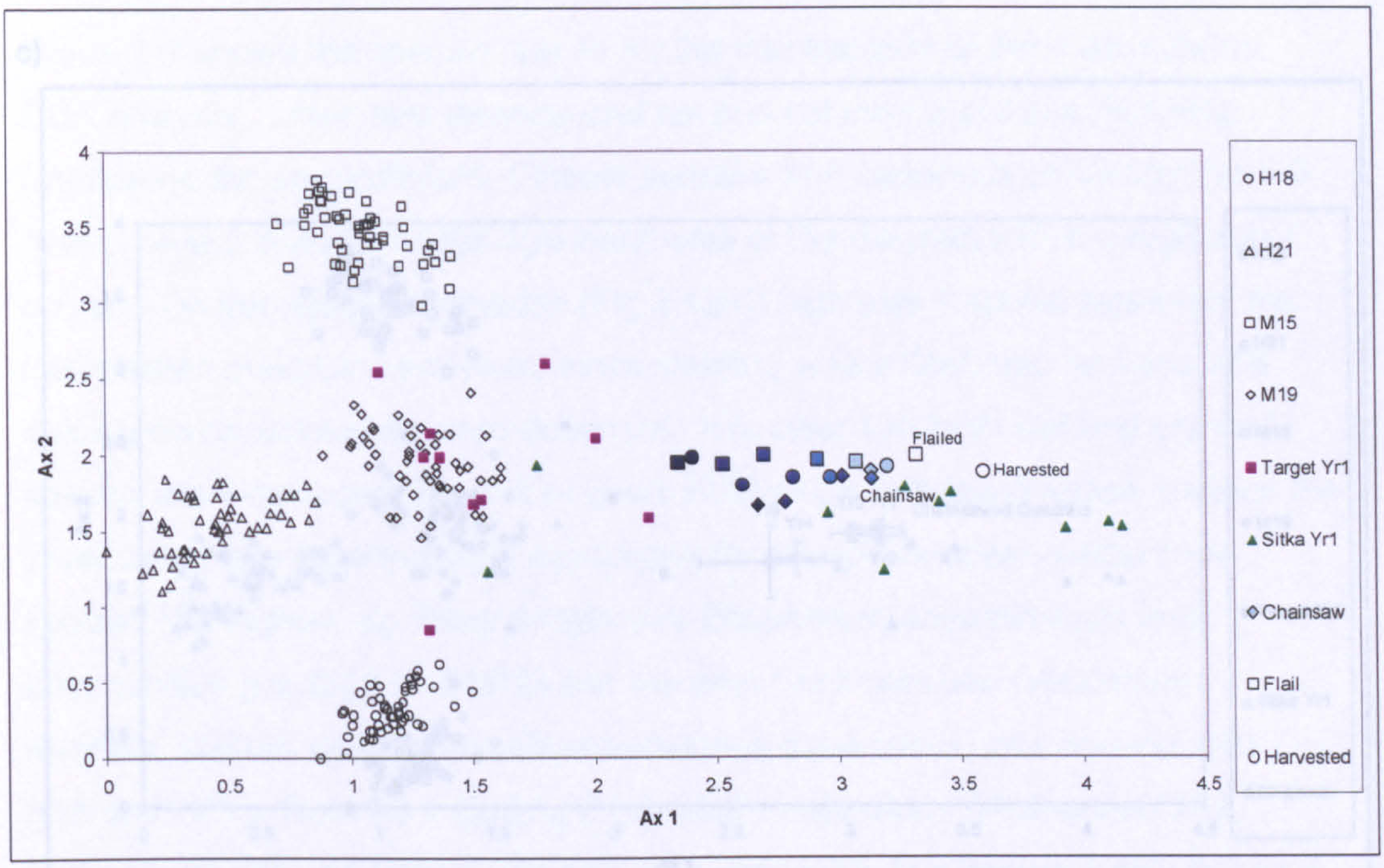
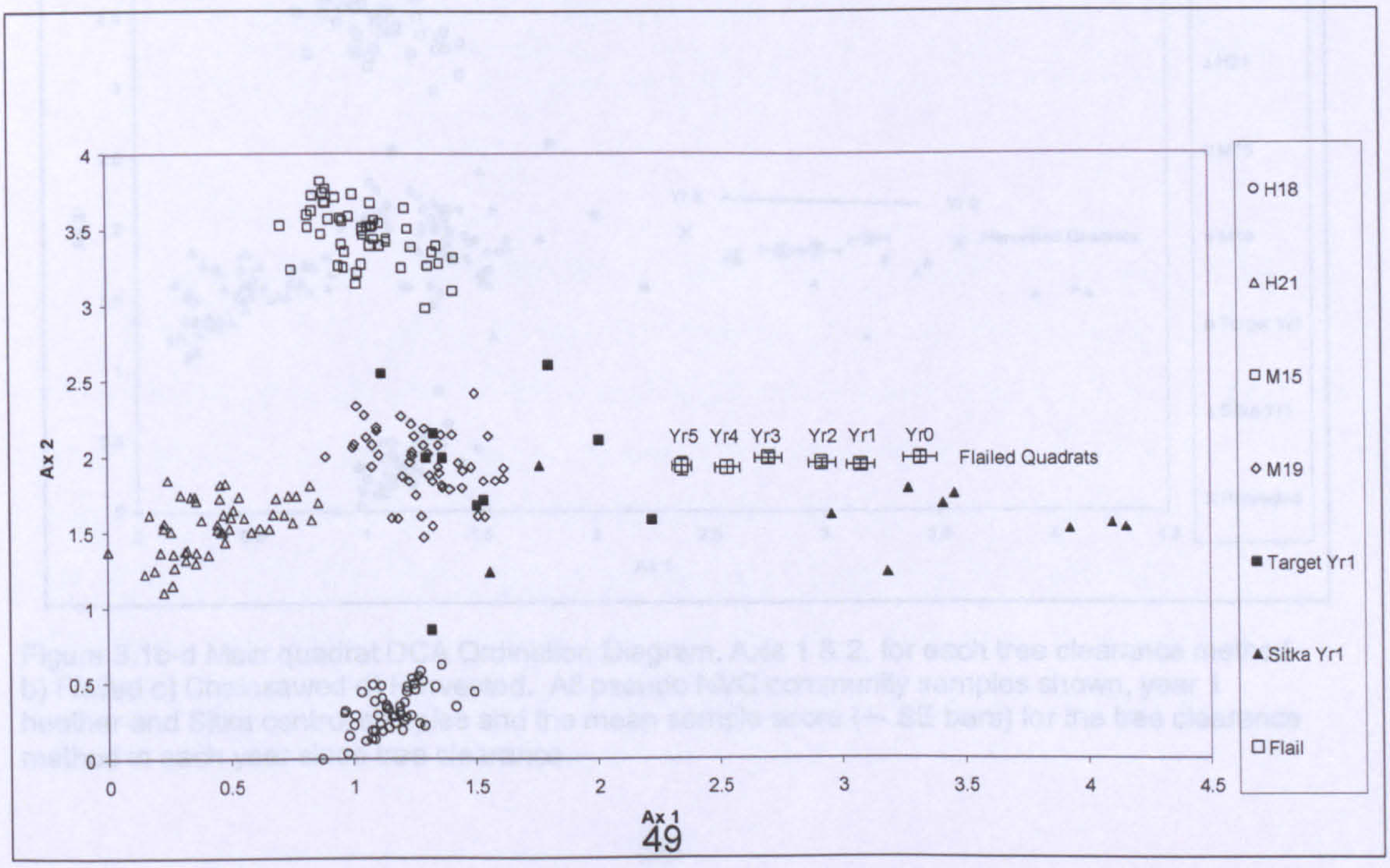


Figure 3.1a Main quadrat DCA Ordination Diagram, Axis 1 & 2. All pseudo NVC community samples shown, year 1 heather and Sitka control samples and the mean sample score for each tree clearance treatment in each year since tree clearance.

b)



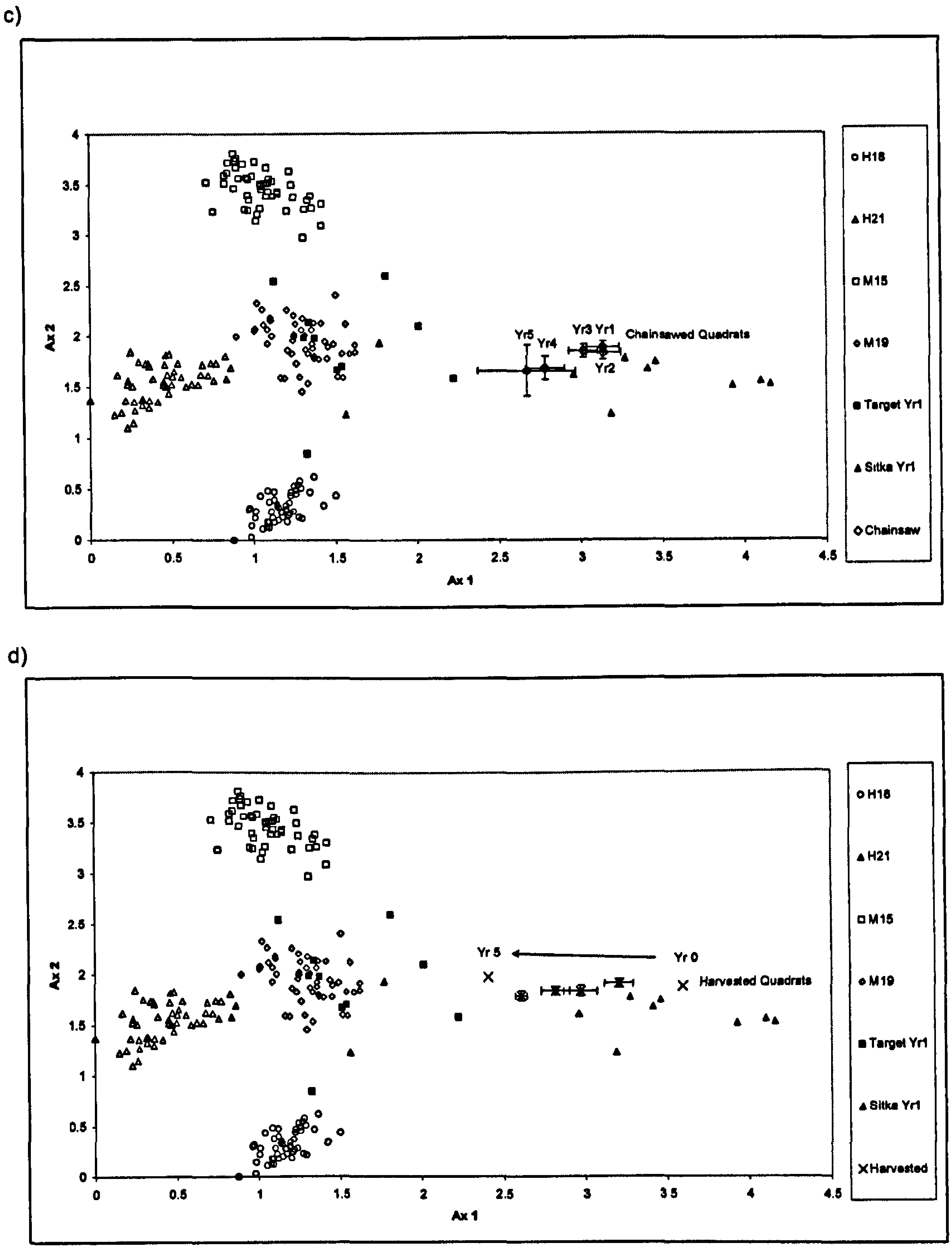


Figure 3.1b-d Main quadrat DCA Ordination Diagram, Axis 1 & 2, for each tree clearance method b) Flailed c) Chainsawed d) Harvested. All pseudo NVC community samples shown, year 1 heather and Sitka control samples and the mean sample score (+- SE bars) for the tree clearance method in each year since tree clearance.

Figure 3.2 shows the species results for the first two axis of the main quadrat DCA analysis. Litter, tree remains and several colonising species including *Chamaenerion angustifolium*, *Cirsium palustre* and *Dicranella cerviculata* and *D. heteromalla* dominate the far right hand side of the diagram with the high axis 1 scores. On the sample ordination (Fig 3.1a-d) high axis 1 scores represent the tree cleared quadrats zero years since clearing where litter, tree remains and quick growing colonisers were dominant. It is clear that both wet and dry mire species are influencing the shift of quadrats through ordination space towards the lower axis 1 scores with axis 2 accounting for the split between wetter mire species (*Sphagnum* sp. *Erica tetralix* and *Eriophorum angustifolium*) and communities (i.e. M15 and M19) and the drier heath species (*Vaccinium myrtillus, Galium saxatile* and *Rhytidiadelphus squarrosus*) and communities (i.e. H18 and H21). Species including *Eriophorum vaginatum, Molinia caerulea, Potentilla erecta,*and *Carex echinata* were very quick to colonise during the early years following tree clearance and were reasonably ubiquitous across the site.

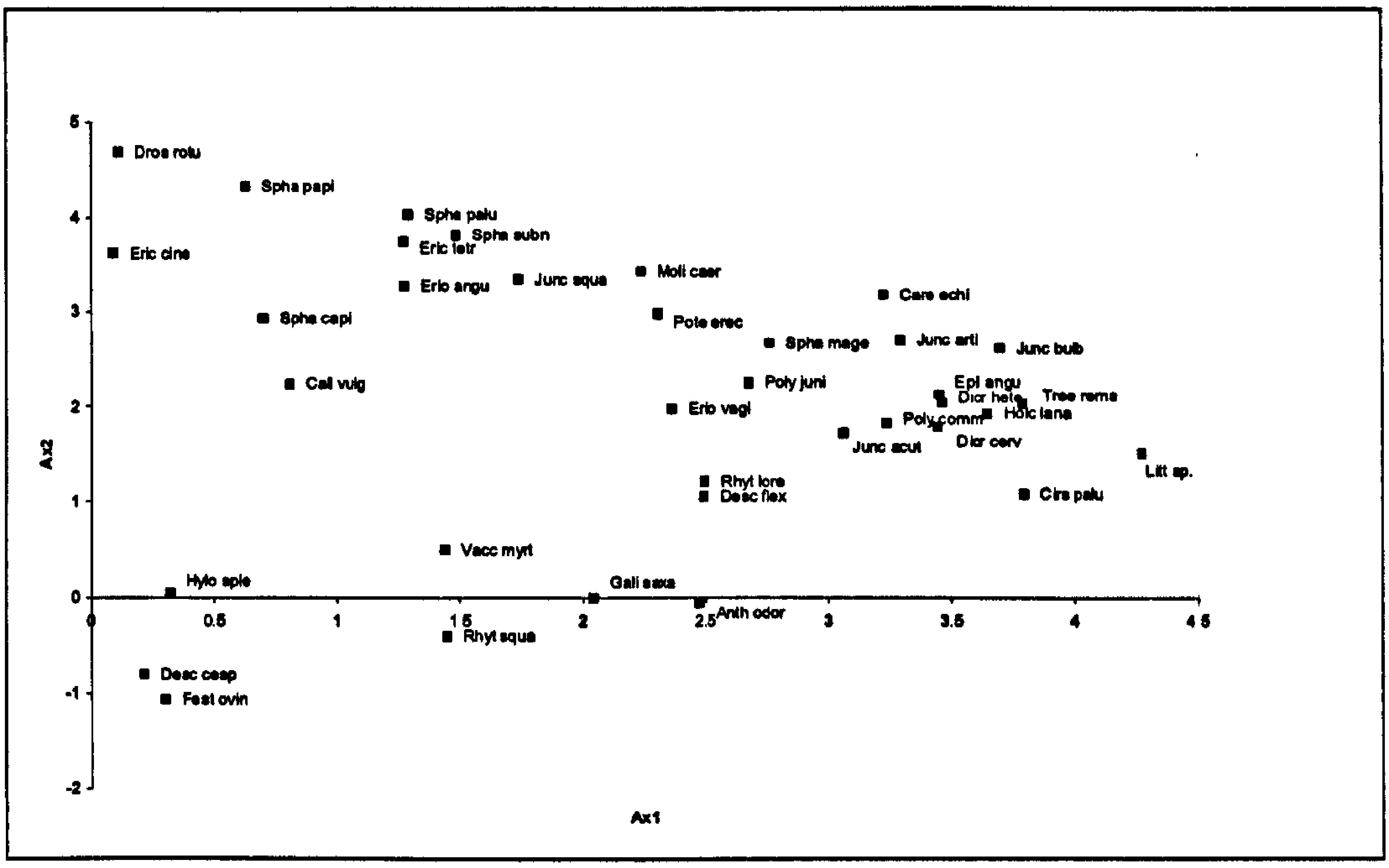


Figure 3.2 Main quadrat DCA Species Ordination Diagram for Axis 1 & 2 showing key species. Dros rotu = Drosera rotundifolia; Spha papi = Sphagnum papillosum; Spha palu = Sphagnum palustre; Spha subn = Sphagnum subnitens; Eric tetr = Erica tetralix; Eric cine = Erica cineria; Spha capi = Sphagnum capillifolium; Call vulg = Calluna vulgaris; Erio angu = Eriophorum angustifolium; Junc squa = Juncus squarrosus; Moli caer = Molinia caerulea; Pote erec = Potentilla erecta; Spha mage = Sphagnum magellanicum; Care echi = Carex echinata; Junc arti = Juncus articulatus; Junc bulb = Juncus bulbosus; Epil angu = Chamaenerion angustifolium; Dicr hete = Dicranella heteromalla; Tree rems = Tree remains; Holc lana = Holcus lanatus; Poly comm. = Polytrichum commune; Dicr cerv = Dicranella cerviculata; Junc acut = Juncus acutiflorus; Cirs palu = Cirsium palustre; Litt sp. = Litter; Poly juni = Polytrichum juniperinum; Erio vagi = Eriophorum vaginatum; Rhyt lore = Rhytidiadelphus loreus; Desc flex = Deschampsia flexuosa; Gali saxa = Galium saxatile; Anth odor = Anthoxanthum odoratum; Vacc myrt = Vaccinium myrtillus; Rhyt squa = Rhytidiadelphus squarrosus; Hylo sple = Hylocomnium splendens; Desc cesp = Deschampsia cespitosa; Fest ovin = Festuca ovina

MINI QUADRATS

A DCA ordination was also performed on the mini-quadrat data using exactly the same options as the analysis of the main quadrat data and including the pseudo NVC community quadrats. 13.4% of variation was explained by the first 4 axes with 4.7 and 3.2 percent explained by axis 1 & 2 respectively. These results suggest greater variability in the mini quadrat vegetation data compared with the main quadrat data and there were a number of outliers that probably reduced the proportion of variability explained by each of the axis. The general pattern of movement towards the pseudo NVC communities and the 'target' vegetation, which is clear in the main quadrat analysis, is more obvious for the mini quadrats.

Diagrams 3.3 and 3.4 demonstrate this differential clearly where a proportion of the mini quadrat samples have reached the far left of the ordination diagram amongst the pseudo NVC and established heather samples. This indicates that patches of vegetation at a 1x1m scale have developed into a plant community similar to nearby mature blanket bog vegetation within 6 years. However, at the 10x10m scale the vegetation is still not fully mature. Similarly there is considerably more variation along Axis 2 of the mini quadrat ordination diagram compared with the main quadrat ordination. If this is viewed in conjunction with the species ordination diagrams (3.2 and 3.6) it would suggest that there is a wider range of vegetation along the wet/dry gradient represented by the mini quadrats, with *Juncus bulbosus* and *Juncus effusus* having a big influence on the ordination in the first two years.

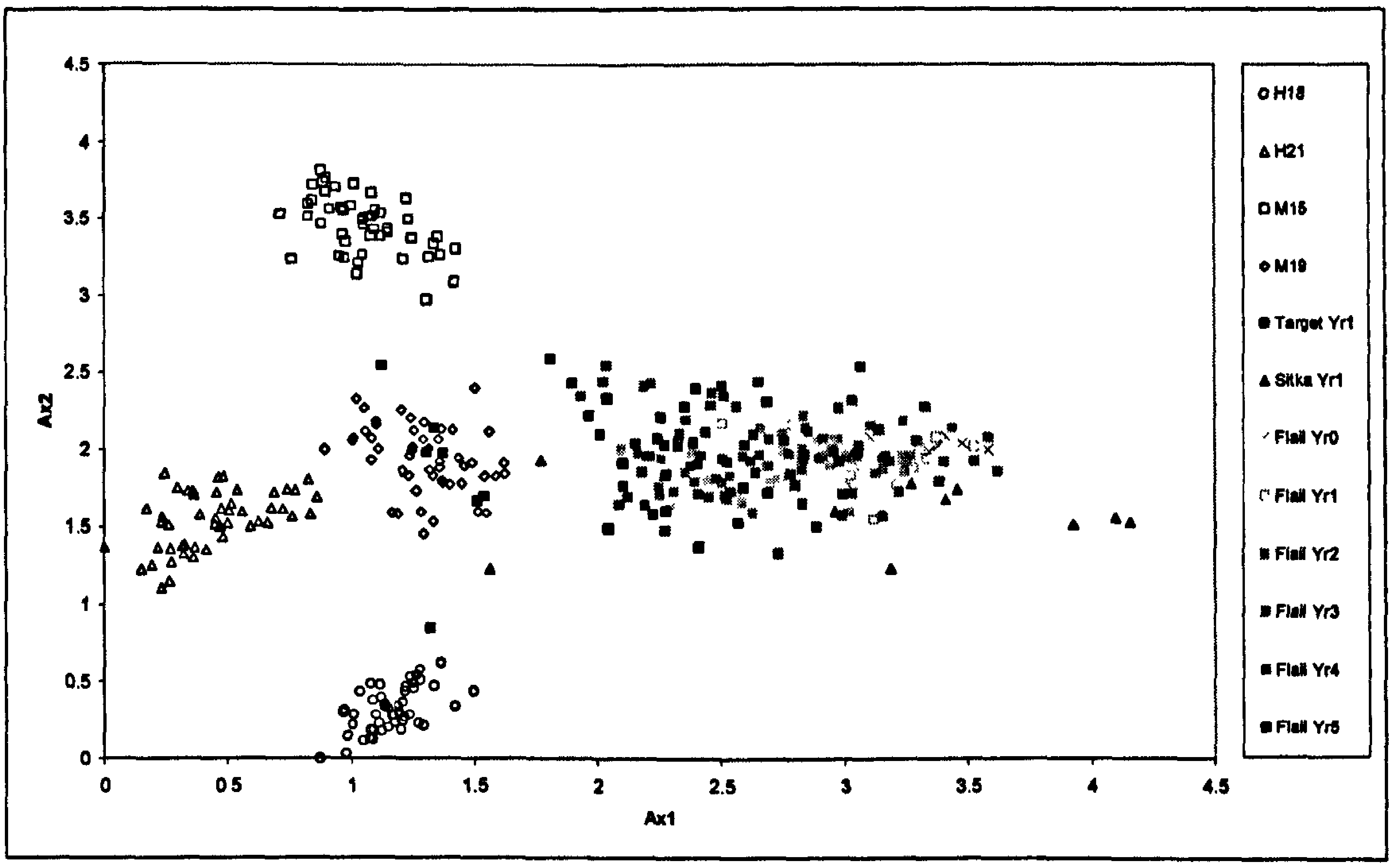


Figure 3.3: Main quadrat DCA Ordination - flailed only samples shaded depending on year since tree clearance. Pseudo NVC samples and year 1 heather and Sitka control samples are included.

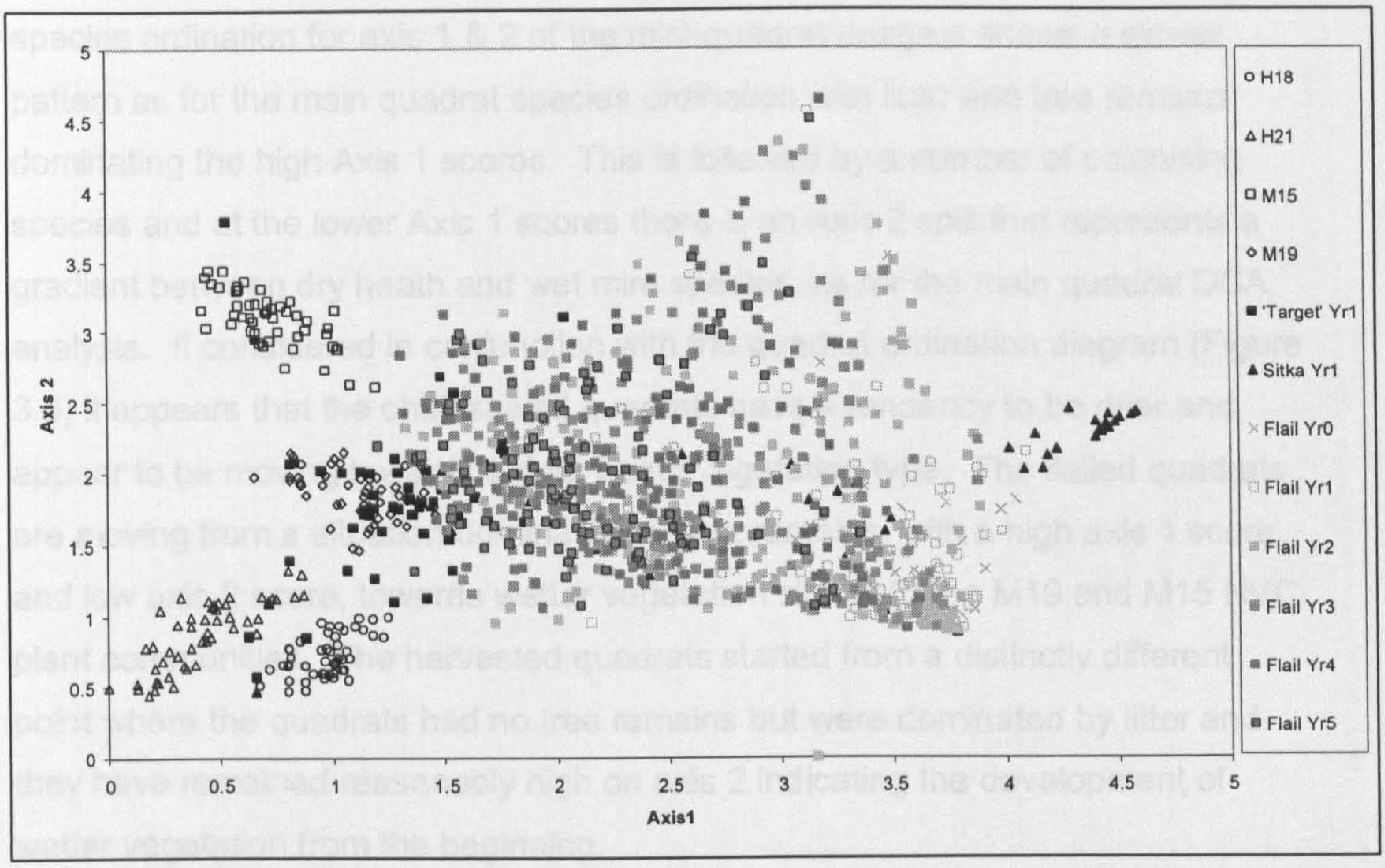


Figure 3.4: Mini quadrat DCA Ordination - flailed only samples shaded depending on year since tree clearance. Pseudo NVC samples and year 1 heather and Sitka control samples are included.

The DCA ordination of the mini quadrats compared with the main quadrats shows much greater variability along the third and fourth axis. However, as for the main quadrat analysis these axes do not provide any additional information about the development of the vegetation because most of the samples are located in the same part of the ordination diagram. Only very few samples cause the gradient of the axis to be lengthened and these respresent mini quadrats that have a large amount of one particular species i.e. *Molinia caerulea* . As it is only relevant to very few samples it is not worth looking at these axes in more detail.

Diagram 3.5 shows the mini quadrat DCA ordination results with the mean sample score for each tree clearance treatment in each year since tree clearance. Compared with the same diagram for the main quadrat DCA ordination (Diagram 3.1) it shows larger differences between tree clearance methods and between years for each tree clearance method. Figure 3.6 the species ordination for axis 1 & 2 of the mini-quadrat analysis shows a similar pattern as for the main quadrat species ordination with litter and tree remains dominating the high Axis 1 scores. This is followed by a number of colonising species and at the lower Axis 1 scores there is an Axis 2 split that represents a gradient between dry heath and wet mire species, as for the main quadrat DCA analysis. If considered in conjunction with the quadrat ordination diagram (Figure 3.5) it appears that the chainsawed quadrats have a tendency to be drier and appear to be moving towards a drier heath vegetation type. The flailed quadrats are moving from a situation dominated by tree remains, with a high axis 1 score and low axis 2 score, towards wetter vegetation similar to the M19 and M15 NVC plant communities. The harvested quadrats started from a distinctly different point where the quadrats had no tree remains but were dominated by litter and they have remained reasonably high on axis 2 indicating the development of wetter vegetation from the beginning.

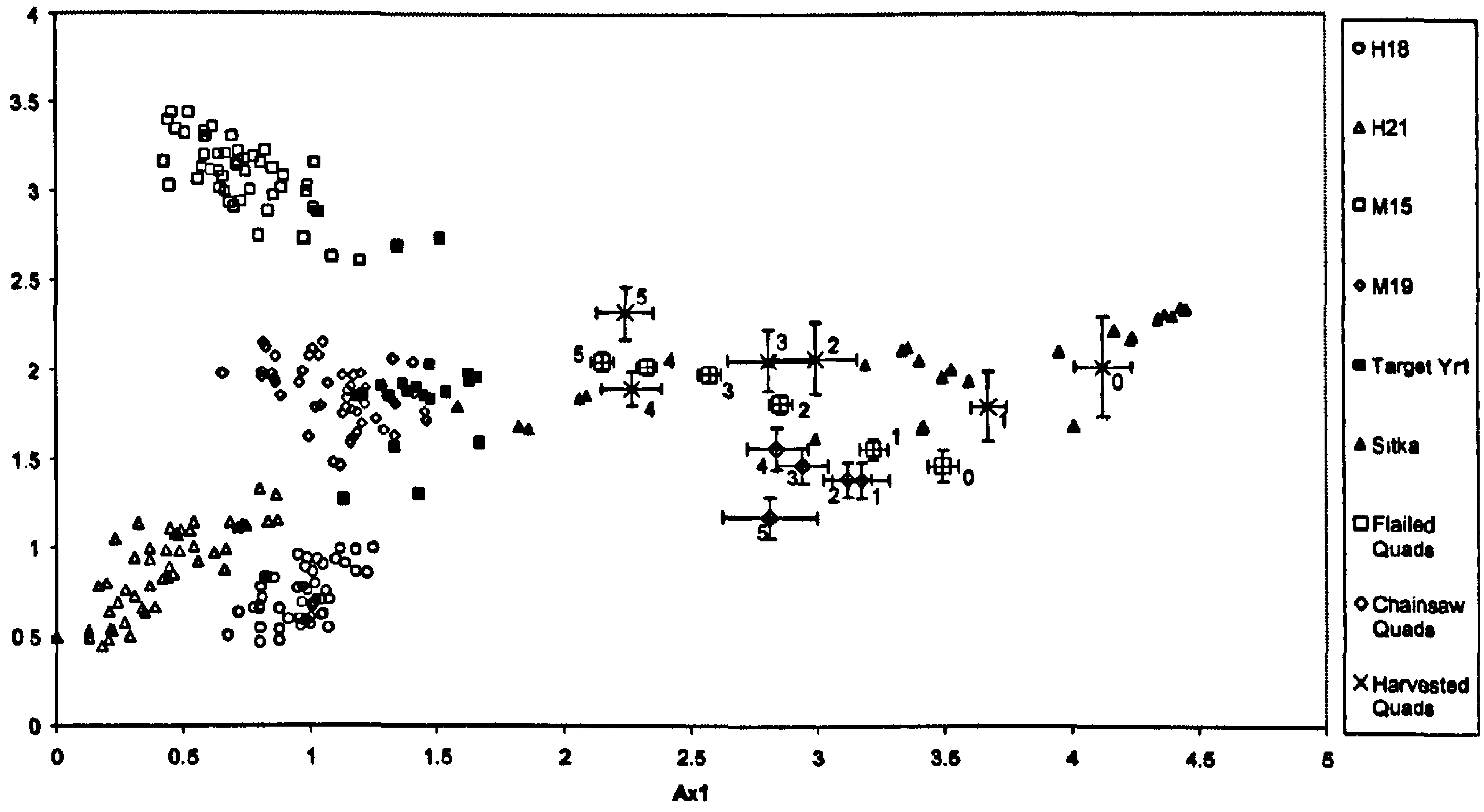


Figure 3.5: Mini-quadrat DCA ordination diagram for Axis 1 & 2 showing all pseudo NVC community samples, year 1 heather and Sitka control samples and the mean sample score (+-SE bars) for each tree clearance method in each year since clearance. Each tree clearance

method is represented by a different symbol as shown on the key and each year since tree clearance is indicated by a corresponding number i.e. '0' years since clearance

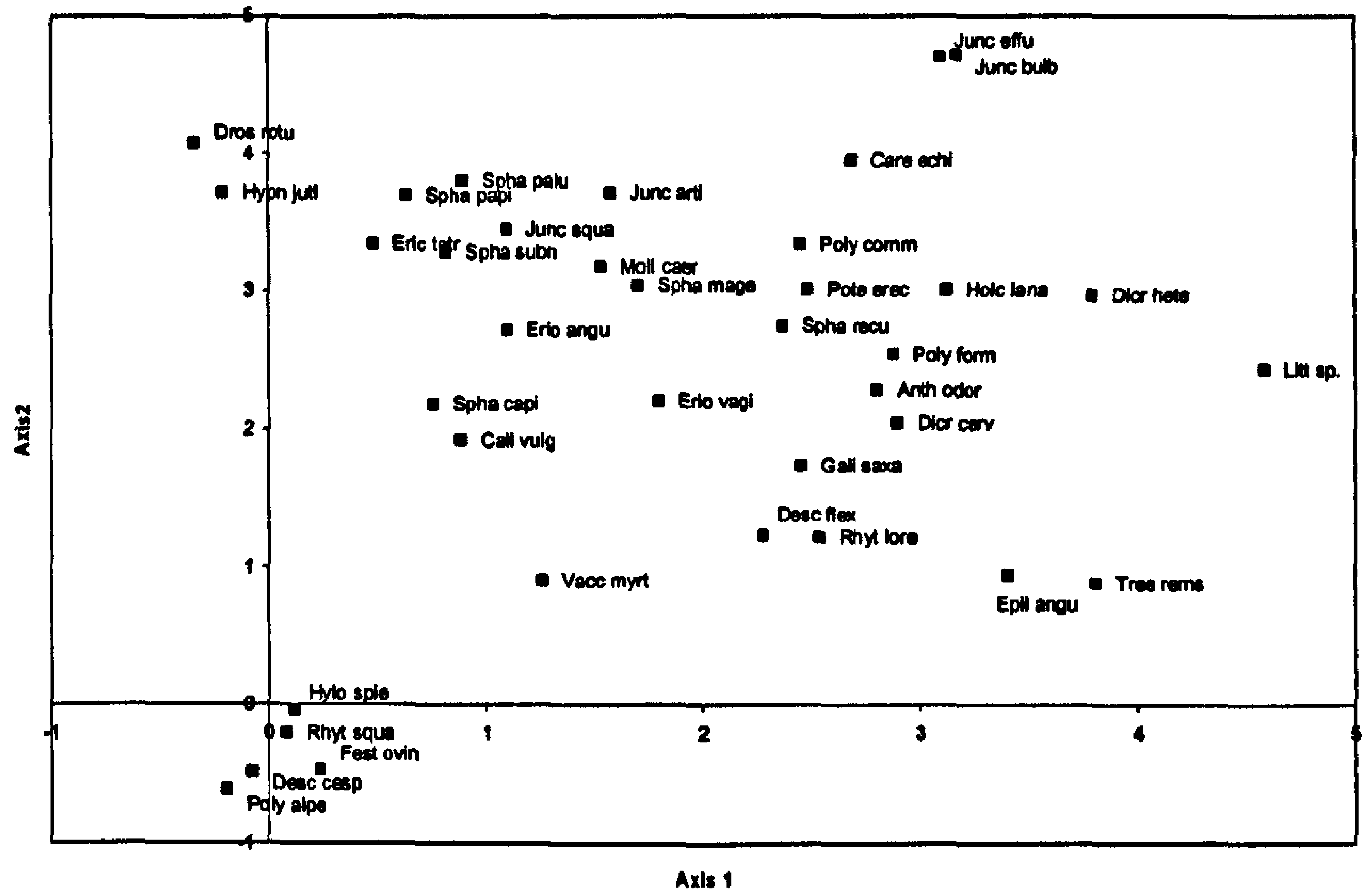


Figure 3.6: Mini quadrat DCA Species Ordination Diagram for Axis 1 & 2 showing key species. Dros rotu = Drosera rotundifolia; Spha papi = Sphagnum papillosum; Spha palu = Sphagnum palustre; Spha subn = Sphagnum subnitens; Spha recu = Sphagnum recurvum; Eric tetr = Erica tetralix; Spha capi = Sphagnum capillifolium; Call vulg = Calluna vulgaris; Erio angu = Eriophorum angustifolium; Junc squa = Juncus squarrosus; Moli caer = Molinia caerulea; Pote erec = Potentilla erecta; Spha mage = Sphagnum magellanicum; Care echi = Carex echinata; Junc arti = Juncus articulatus; Junc bulb = Juncus bulbosus; Epil angu = Chamaenerion angustifolium; Dicr hete = Dicranella heteromalla; Tree rems = Tree remains; Holc lana = Holcus lanatus; Poly comm. = Polytrichum commune; Dicr cerv = Dicranella cerviculata; Litt sp. = Litter; Poly form = Polytrichum formosa; Poly alpe = Polytrichum alpestre; Erio vagi = Eriophorum vaginatum; Rhyt lore = Rhytidiadelphus loreus; Desc flex = Deschampsia flexuosa; Gali saxa = Galium saxatile; Anth odor = Anthoxanthum odoratum; Vacc myrt = Vaccinium myrtillus; Rhyt squa = Rhytidiadelphus squarrosus; Hylo sple = Hylocomnium splendens; Desc cesp = Deschampsia cespitosa; Fest ovin = Festuca ovina

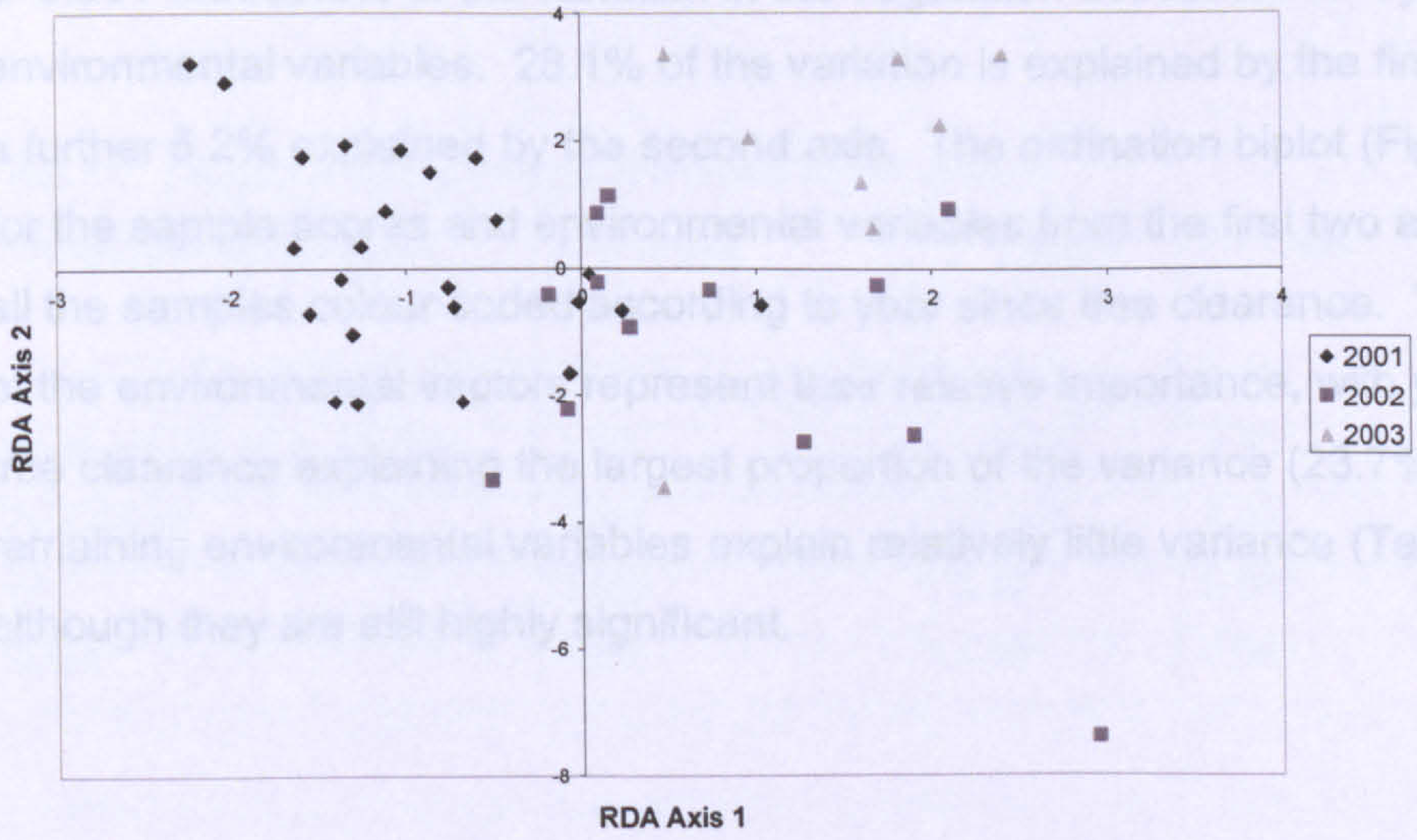
3.3.2 RDA analysis of 'year since clearance' sample groups

Table 3.2 below shows how each 'year since tree clearance' group of main quadrat samples is composed. Zero years since clearance only has samples taken in 2001, one year since clearance includes samples taken in 2001 and 2002 and so on. The Monte Carlo tests that were applied during the RDA indicate that in all cases, except one, the between sample year variation is not significant. There is a significant difference between samples on ground that was cleared in 1999 compared with 2000 or 2001 but this is only evident in the first sample year and is only just significant with a p-value of 0.0426. By the second sampling year (2002) the effect had disappeared. Two RDA ordination plots for the '2 years since' and the '3 years since' (Figure 3.7 a & b) tree clearance groups show how the difference between sampling year diminishes with the samples mixed to a greater extent in Fig 3.7b, 3 years since chipping.

Table 3.2: Between sampling year differences within 'year since tree clearance' group. Numbers represent year in chronosequence and letters represent the year that trees were cleared i.e. a, b & c equals ground cleared in 1999, 2000 & 2001.

Clearance Yr	Year Since Tree Clearance			
	Sampling Year			
	2001	2002	2003	2004
1999	2a (F = 2.138, P = 0.0426)	3a	4a	5
2000	1a	2b	3b	4b
2001	0	1b	2c	3c

a)



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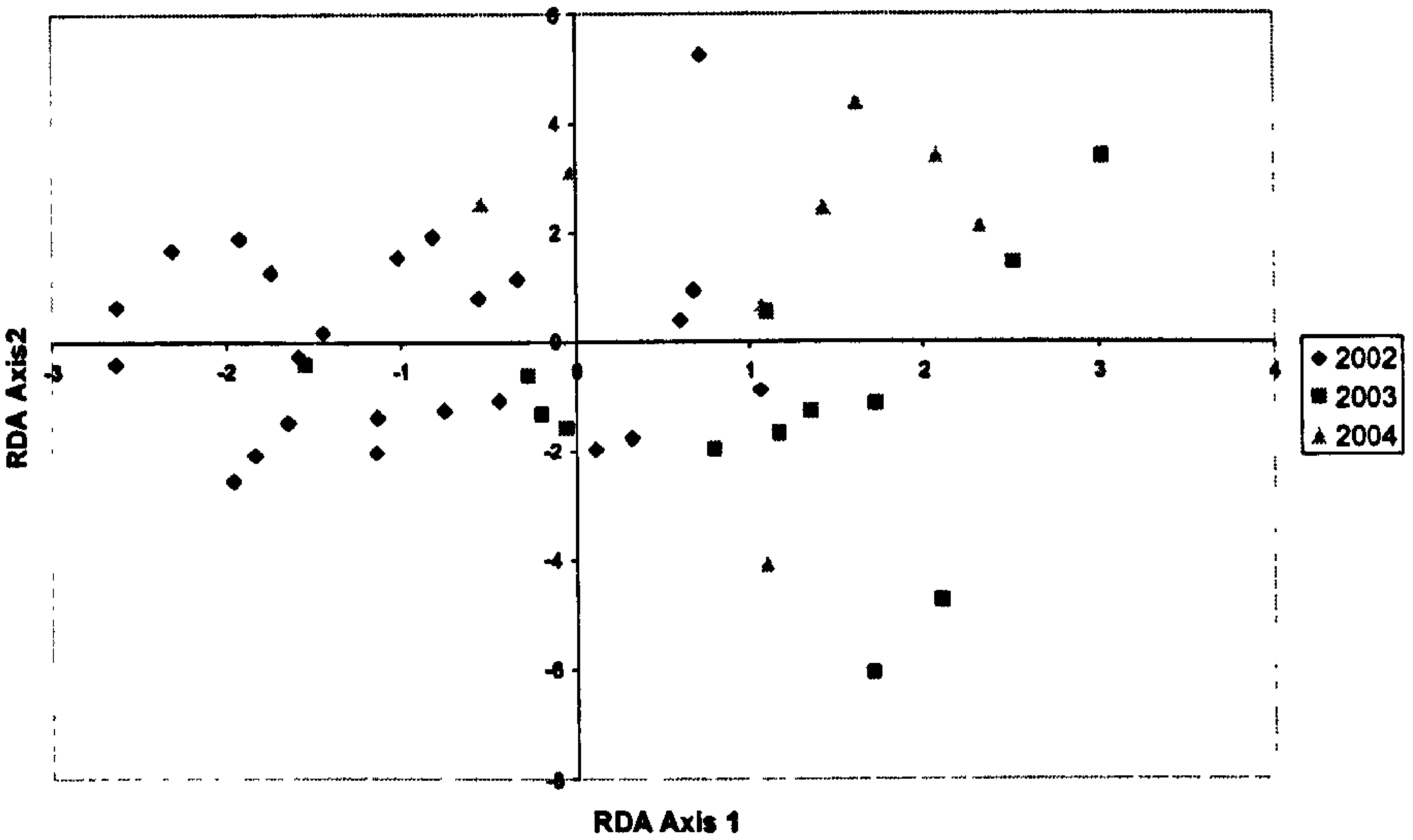


Figure 3.7a & b: RDA Ordination diagrams for a) two years since tree clearance and b) three years since tree clearance with different sample years indicated by different symbols.

3.3.3 RDA analysis of main quadrat data with environmental variables

FLAILED QUADRATS

The unrestricted Monte Carlo test on all axes of the ordination was significant at p=0.001 with 35.2% of the variation in the vegetation accounted for by the environmental variables. 28.1% of the variation is explained by the first axis with a further 5.2% explained by the second axis. The ordination biplot (Figure 3.8) for the sample scores and environmental variables from the first two axes show all the samples colour coded according to year since tree clearance. The lengths of the environmental vectors represent their relative importance, with year since tree clearance explaining the largest proportion of the variance (23.7%). The remaining environmental variables explain relatively little variance (Table 3.3) although they are still highly significant.

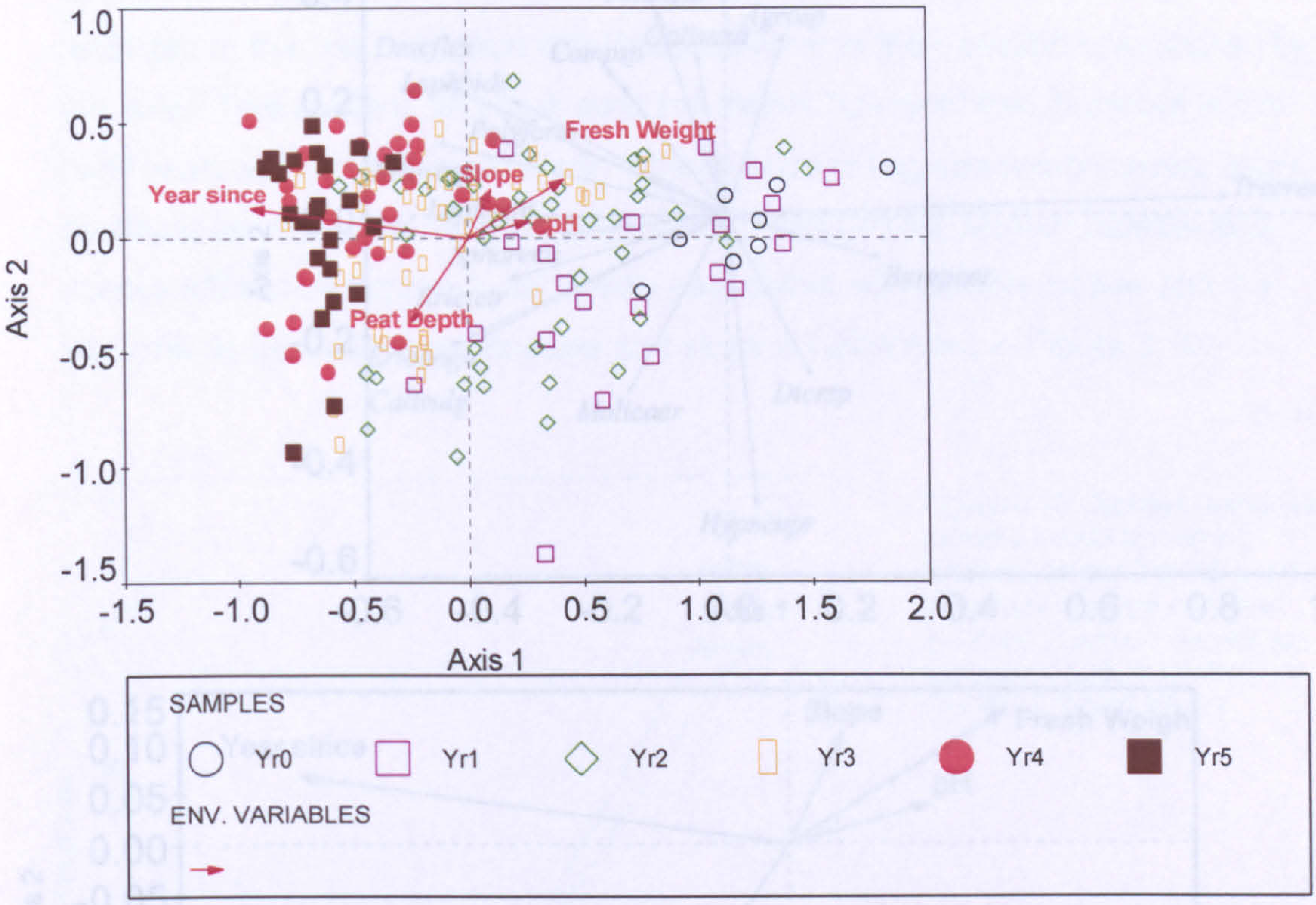


Figure 3.8: Ordination diagram from the RDA analysis of flailed quadrats showing samples and environmental variables for axis 1 & 2. Samples are colour/shape coded according to the number of years since tree clearance took place. Year since = year since tree clearance; Fresh Weight = estimated fresh weight of wood chip on quadrat; Peat depth = average peat depth; pH = average pH; Slope = slope from highest to lowest point of quadrat.

Table 3.3: Explained variance by each environmental variable

Environmental Variable	**Explained Variance**	**F – value**	**P - value**
Year since tree clearance	23.7%	55.308	0.001
Fresh weight of wood chip	4.3%	11.286	0.001
Peat depth	4.5%	11.092	0.001
pH	2.0%	5.43	0.001
Slope	1.3%	3.59	0.001

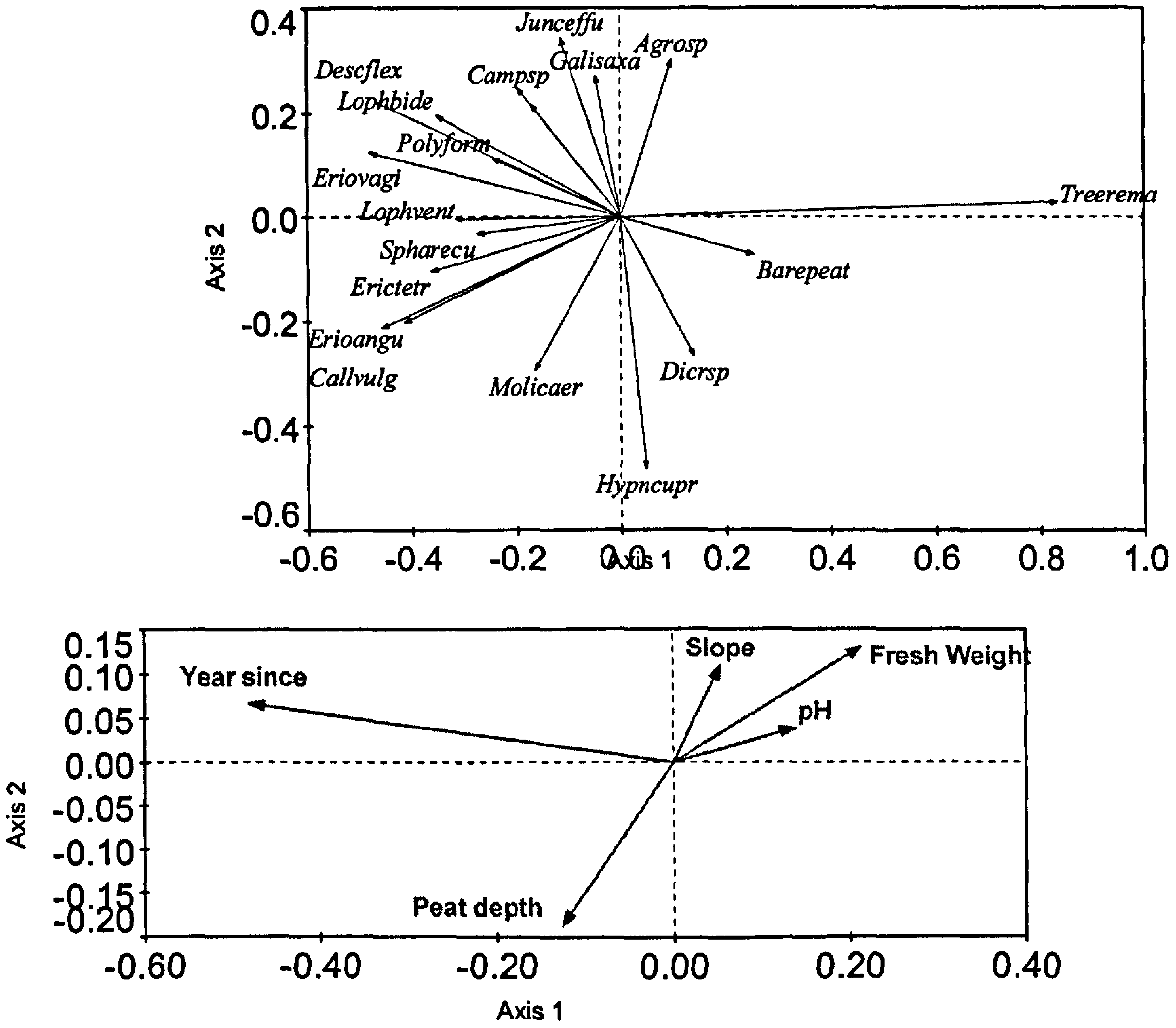


Figure 3.9a & b: Ordination diagrams from the RDA analysis of flailed quadrats showing a) species with most influence in the ordination and b) environmental variables for axis 1 & 2. Year since = year since tree clearance; Fresh Weight = estimated fresh weight of wood chip on quadrat; Peat depth = average peat depth; pH = average pH; Slope = slope from highest to lowest point of quadrat. Agrosp = Agrostis sp; Barepeat = Bare peat; Call vulg = Calluna vulgaris; Campintr = Campylopus introflexus; Campsp = Camplylopus sp; Desc flex = Deschampsia flexuosa; Dicrsp = Dicranum sp; Eric tetr = Erica tetralix; Erio angu = Eriophorum angustifolium; Erio vagi = Eriophorum vaginatum, Gali saxa = Galium saxatile; Hypncupr = Hypnum cuppresiformi; Junceffu = Juncus effusus; Lophbide = Lophocolea bidentata; Lophvent = Lophozia ventricosa; Moli caer = Molinia caerulea; Poly form = Polytrichum formosa; Spha recu = Sphagnum recurvum; Tree rems = Tree remains.

The ordination plots for species and environmental variables (Axes 1 & 2) are shown separately because the species completely obscure the environmental variables when plotted on the same biplot (Figure 3.9 a & b). The species plot shows 19 species that have the most influence over the ordination. As RDA is a linear ordination method, species positions are indicated with arrows, the length of which indicates importance within the ordination. These species fall within the species fit range 7-100% of the first ordination axis. The species fit range is restricted to the first ordination only because most of the variation is explained by this axis. Tree remains and bare peat are clearly "species" that dominate in the early years after tree clearance with various blanket bog species becoming more dominant as year since clearance increases. *Agrostis* sp, *Galium saxatile* and *Juncus effusus* all appear to be closely associated with steeper slopes and the relationship between these species and slope is highlighted in Figure 3.10.

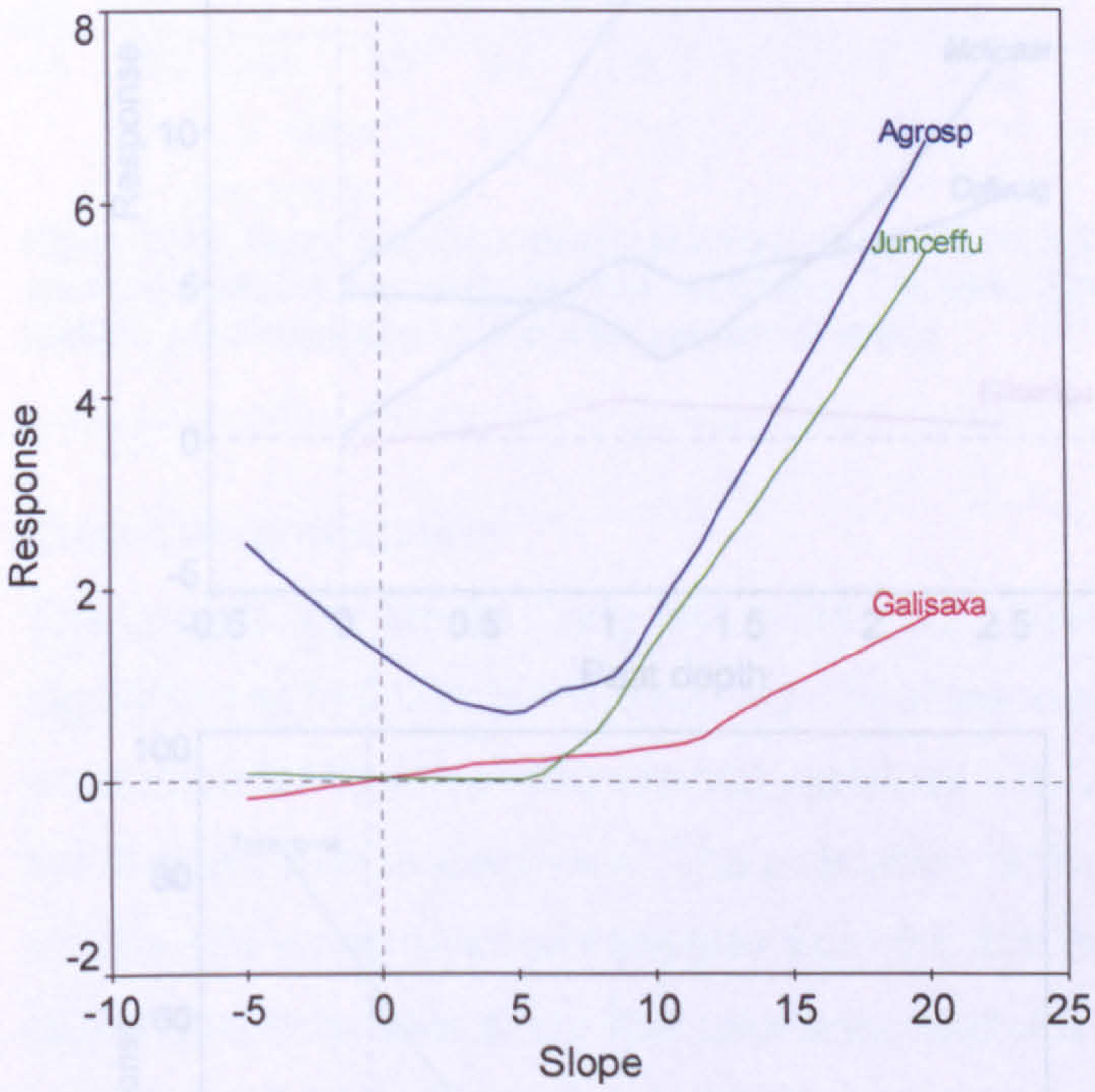


Figure 3.10: Species response (using a Loess smoothing function) on the first RDA axis to increased slope on flailed quadrats. Agrosp = Agrostis sp; Gali saxa = Galium saxatile; Junceffu = Juncus effusus.

Similarly *Molinia caerulea*, *Dicranum* sp, *Hypnum cupressiforme*, *Calluna vulgaris* and *Eriophorum angustifolium* are associated with deeper peat and this relationship is shown in Figure 3.11. The species that show the most significant change over time since tree clearance (Figure 3.12) are *Calluna vulgaris*, *Deschampsia flexuosa*, *Eriophorum vaginatum* and Tree remains. As the RDA ordination described above represents the development of vegetation following tree clearance an increase in species number over time would be expected. However, this trend is not as obvious as expected as can be seen in Figure 3.13a. What is more pronounced is the increase in species diversity (Figure 3.13b)

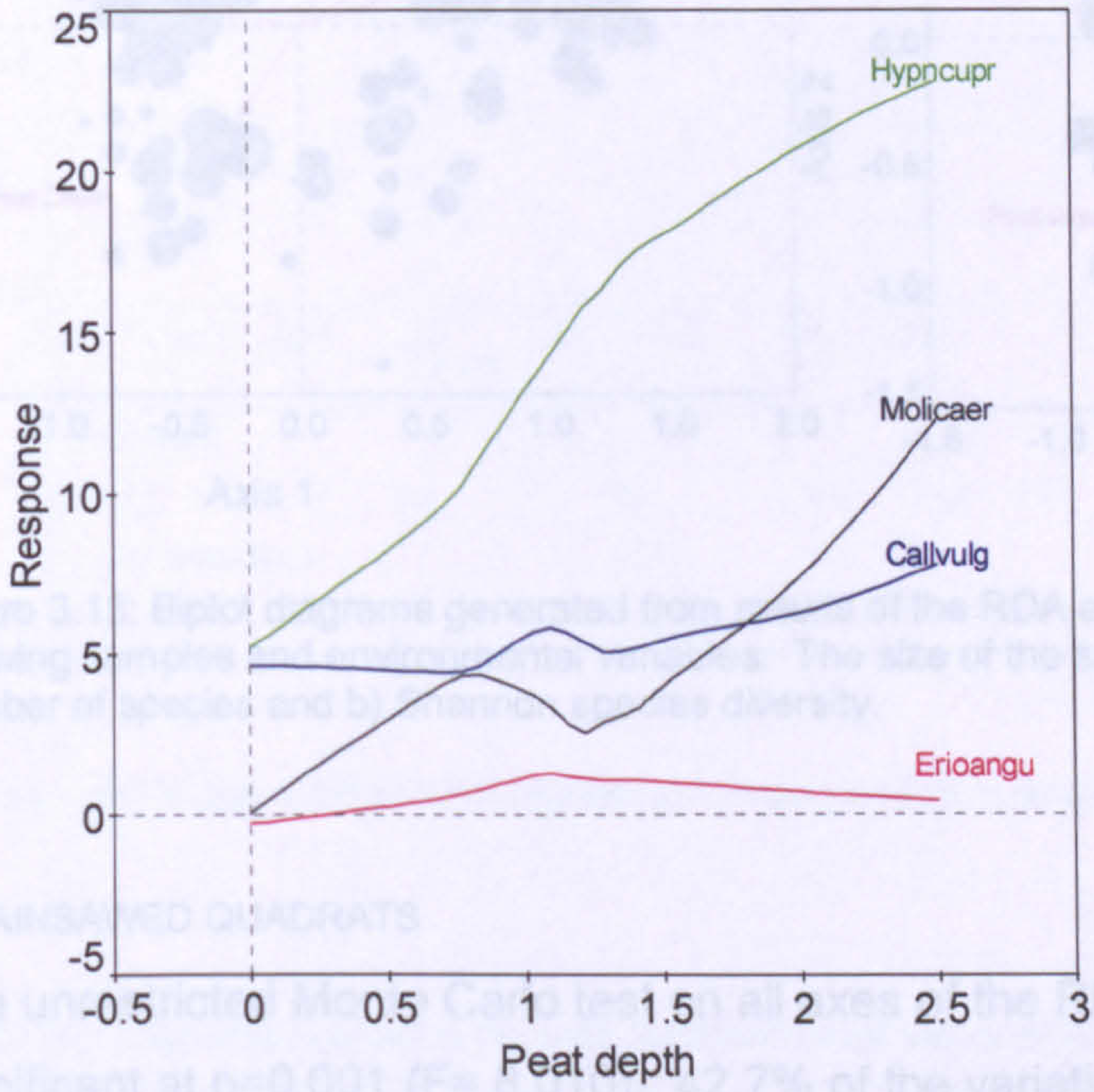


Figure 3.11: Species response (using a Loess smoothing function) on the first RDA axis to increased peat depth on flailed quadrats. Call vulg = Calluna vulgaris; Dicrsp = Dicranum sp; Erio angu = Eriophorum angustifolium; Hypncupr = Hypnum cuppresiformi; Moli caer = Molinia caerulea;

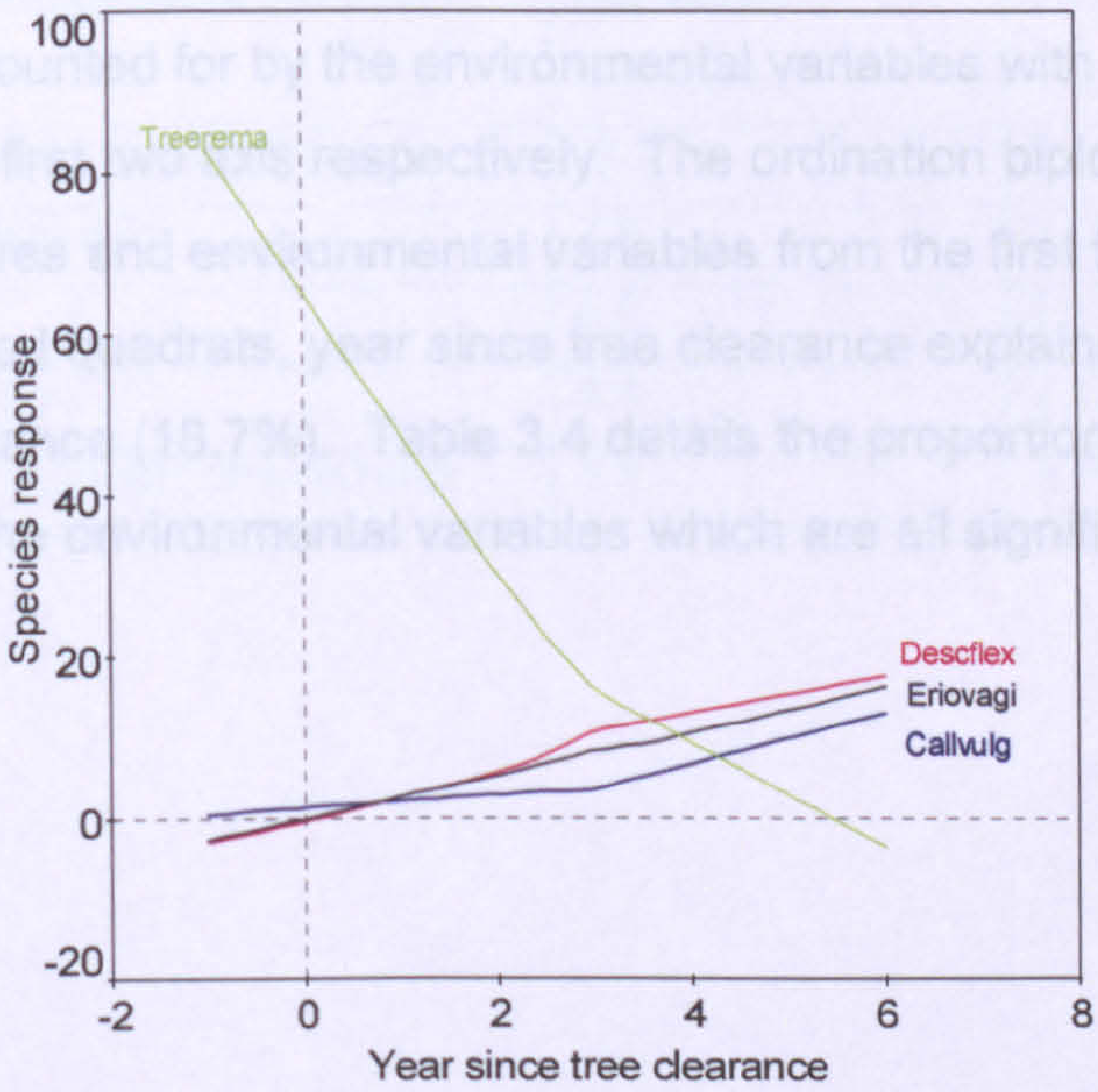


Figure 3.12: Species change on the first RDA axis over time since tree clearance. Call vulg = Calluna vulgaris; Desc flex = Deschampsia flexuosa; Erio vagi = Eriophorum vaginatum; Tree rems = Tree remains.

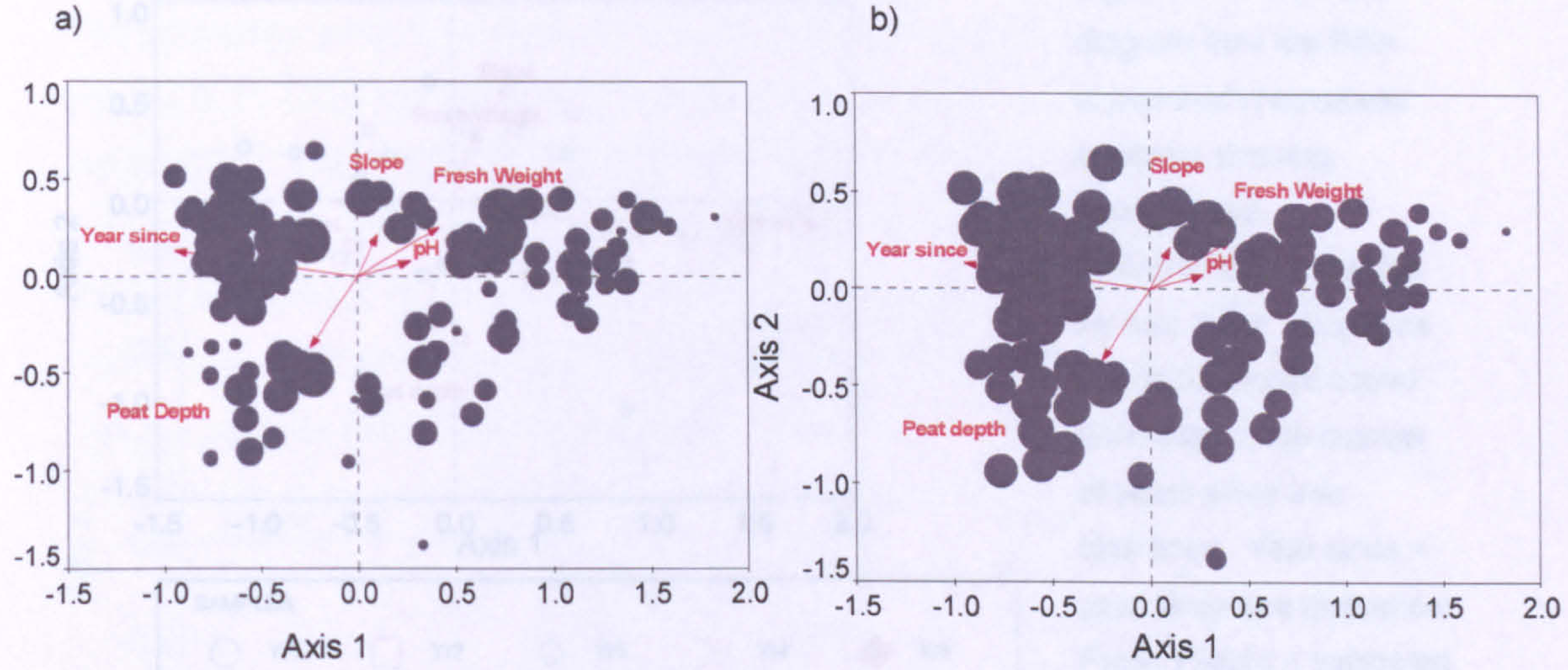


Figure 3.13: Biplot diagrams generated from results of the RDA analysis of flailed quadrats showing samples and environmental variables. The size of the sample symbols correspond to a) number of species and b) Shannon species diversity.

CHAINSAWED QUADRATS

The unrestricted Monte Carlo test on all axes of the RDA ordination was significant at p=0.001 (F= 8.010). 42.7% of the variation in the vegetation was accounted for by the environmental variables with 22.9% and 7.8% explained by the first two axis respectively. The ordination biplot (Figure 3.14) for the sample scores and environmental variables from the first two axes shows that, as for the flailed quadrats, year since tree clearance explains the largest proportion of the variance (18.7%). Table 3.4 details the proportion of variance explained by each of the environmental variables which are all significant.

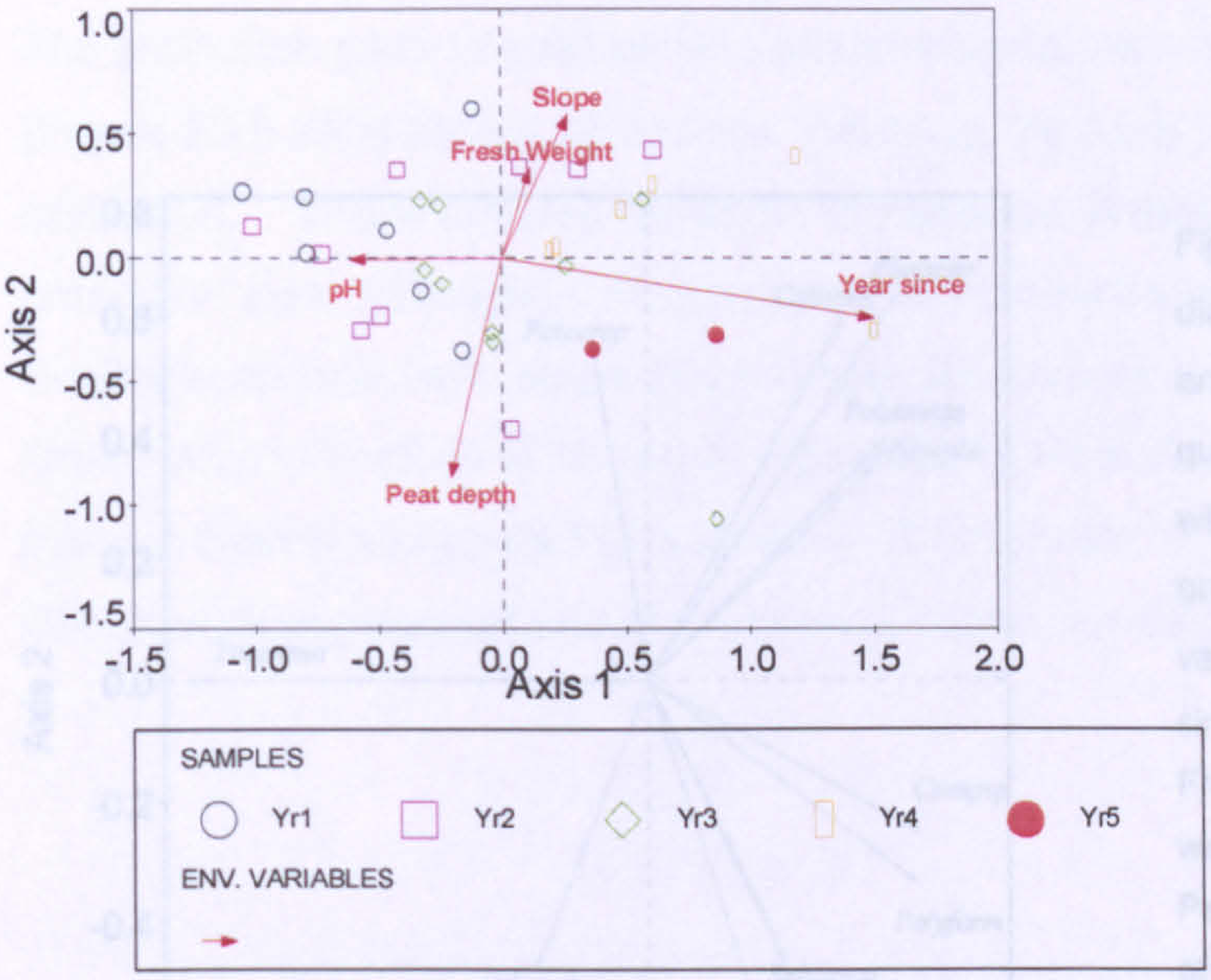


Figure 3.14: Ordination diagram from the RDA analysis of chainsawed quadrats showing samples and environmental variables for axis 1 & 2. Samples are colour/shape coded according to the number of years since tree clearance. Year since = year since tree clearance; Fresh Weight = estimated fresh weight of wood chip on quadrat; Peat depth = average peat depth; pH = average pH; Slope = slope from highest to lowest point of quadrat.

Table 3.4: Explained variance by each environmental variable for the chainsawed quadrats

Environmental Variable	**Explained Variance**	**F - value**	**P - value**
Year since tree clearance	18.7	7.11	0.002
Peat depth	7.2	2.195	0.008
pH	6.1	2.610	0.018
Slope	5.4	2.427	0.030
Fresh weight of wood chip	5.3	2.482	0.020

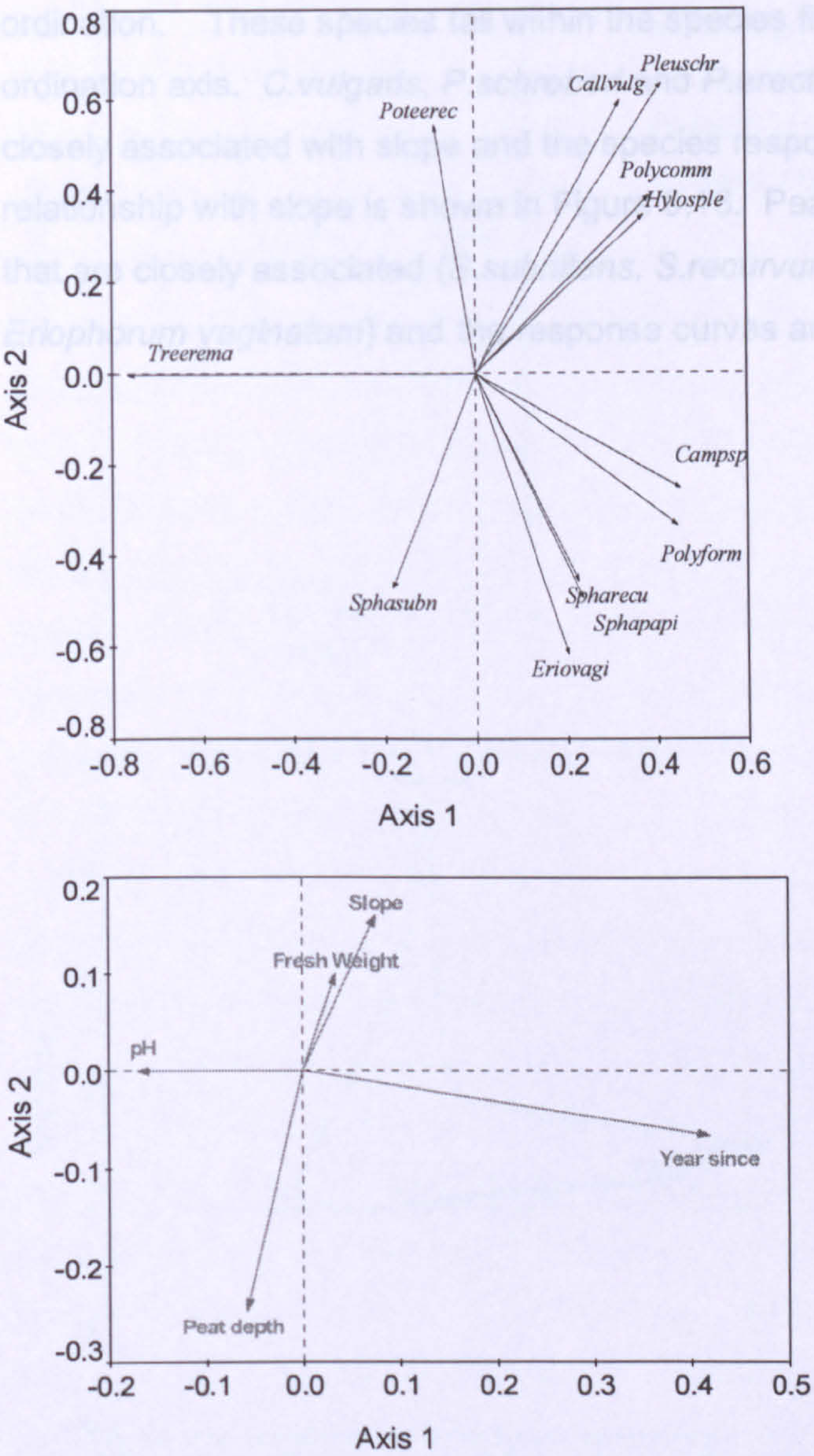


Figure 3.15a & b: Ordination diagrams from the RDA analysis of chainsawed quadrats showing a) species with most influence in the ordination and b) environmental variables for axis 1 & 2. Yr since = year since tree clearance; Fresh Weight = estimated fresh weight of wood chip on quadrat; Peat depth = average peat depth; pH = average pH; Slope = slope from highest to lowest point of quadrat. Call vulg = Calluna vulgaris; Campsp = Camplylopus sp; Erio vagi = Eriophorum vaginatum, Hylosple = Hylocomium splendens; Pleu schr = Pleurozium schreberi; Poly comm = Polytrichum commune; Poly form = Polytricchum formosum; Potentilla erecta; Spha papi = Sphagnum papillosum; Spha recu = S. recurvum; Spha subn = S. subnitens; Tree rems = Tree remains.

The ordination plots of species and environmental variables for axes 1 & 2 (Figure 3.15 a&b) shows 12 species that have the most influence over the ordination. These species fall within the species fit range 25-100% of the first ordination axis. *C.vulgaris, P.schreberi* and *P.erecta* are the three species most closely associated with slope and the species response curve that describes their relationship with slope is shown in Figure 3.16. Peat depth also has four species that are closely associated (*S.subnitens, S.recurvum, S.papillosum* and *Eriophorum vaginatum*) and the response curves are shown in Figure 3.17.

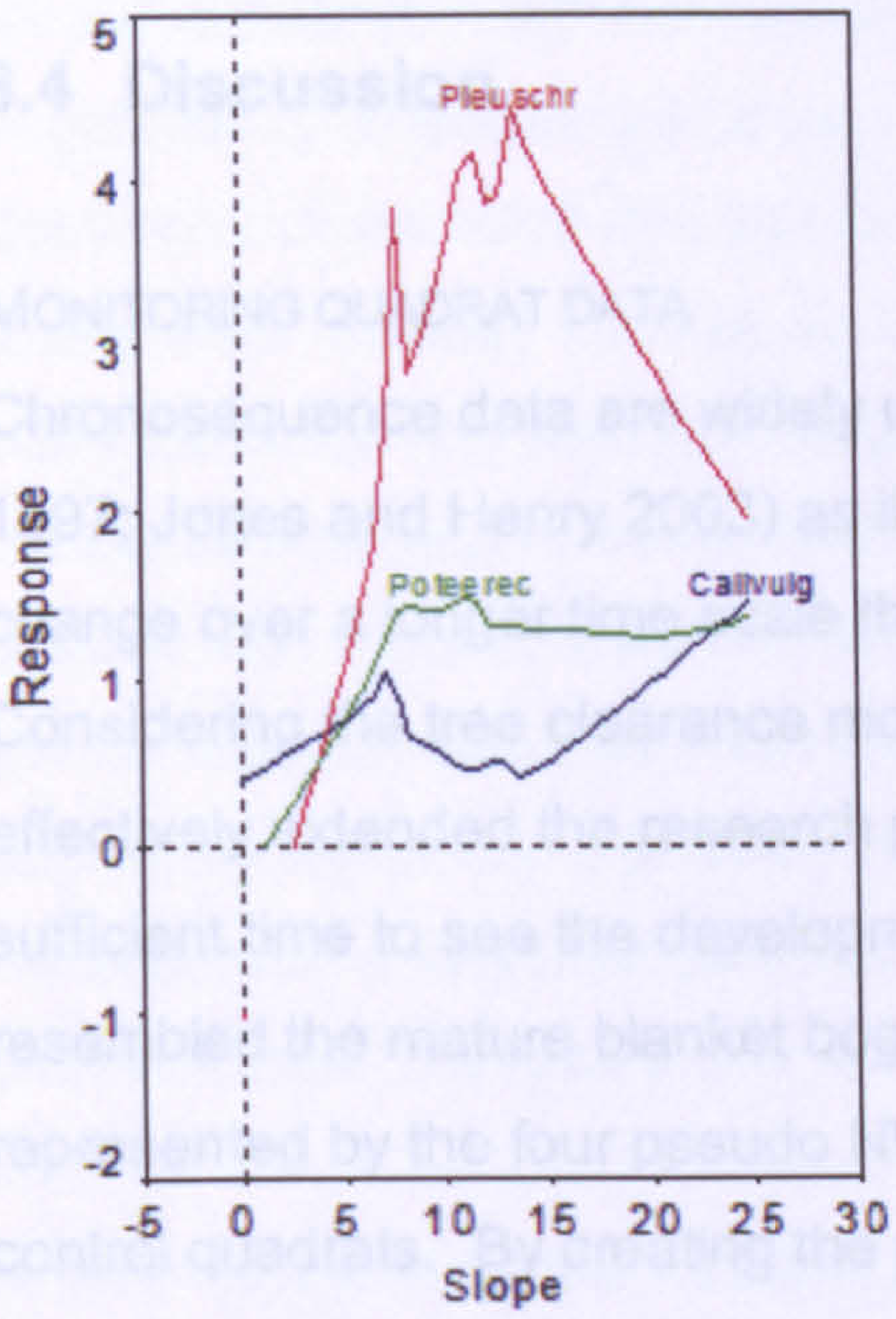
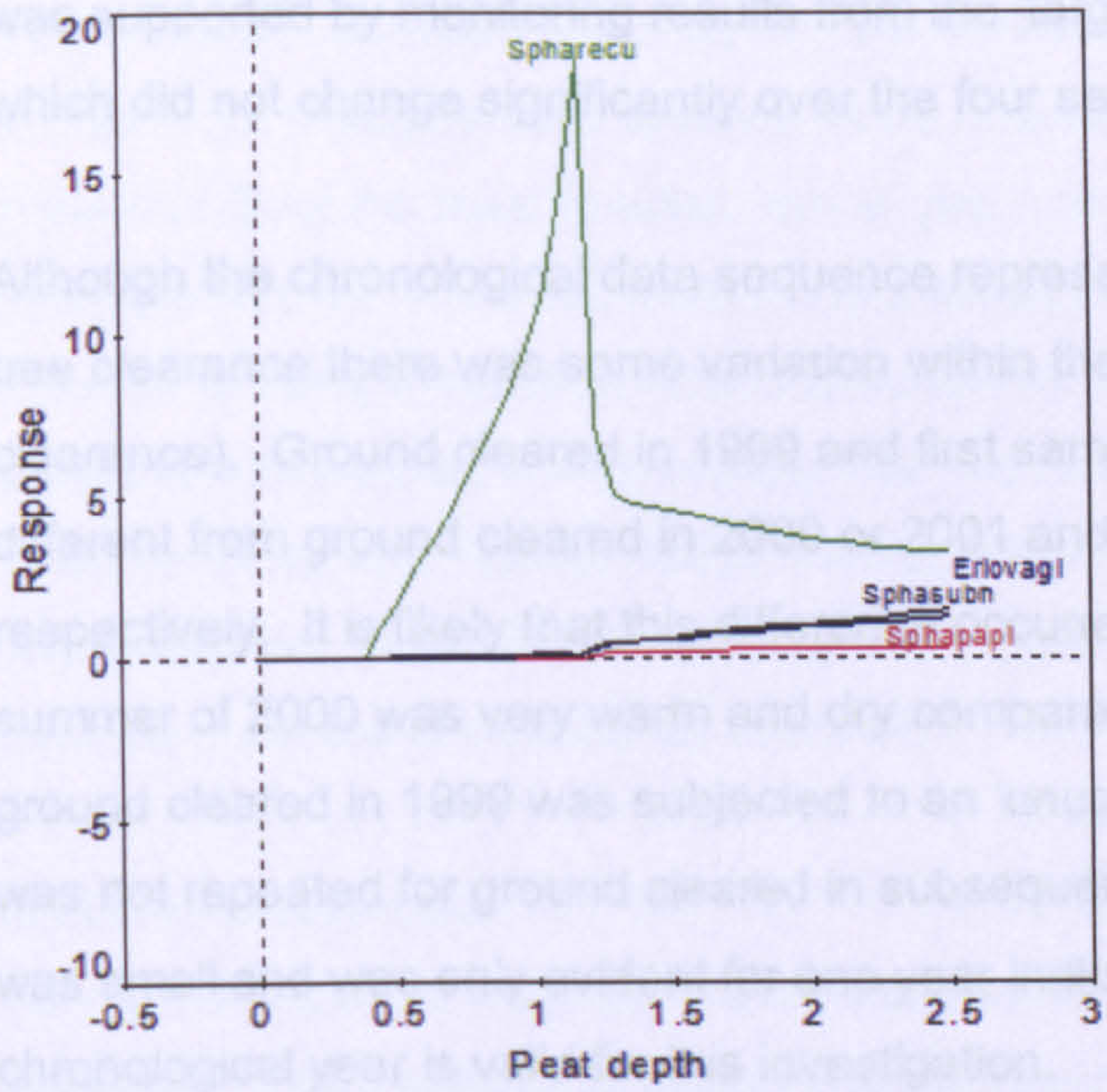


Figure 3.16: Species response (using a Loess smoothing function) on the first RDA axis to increased slope on chainsawed quadrats. Callvulg = Calluna vulgaris; Pleuschr = Pleurozium schreberi; Poteerec = Potentilla erecta.



3.17: Species response (using a Loess smoothing function) on the first RDA axis to increased peat depth on chainsawed quadrats. Erio vagi = Eriophorum vaginatum; Spha recu = Sphagnum recurvum; Spha subn = Sphagnum subnitens; Spha papi = Sphagnum papillosum.

3.4 Discussion

MONITORING QUADRAT DATA

Chronosequence data are widely used in ecological research (Zou and Gonzalez 1997; Jones and Henry 2003) as it is an effective way to investigate ecological change over a longer time scale than is available for the research project. Considering the tree clearance monitoring data as a chronological data sequence effectively extended the research period from four to six years. This was sufficient time to see the development of patches of blanket bog vegetation that resembled the mature blanket bog vegetation on site. This vegetation was represented by the four pseudo NVC communities and the 'target' vegetation control quadrats. By creating the pseudo NVC communities it was assumed that there was no change in the mature plant community during the project and this was supported by monitoring results from the 'target' vegetation control quadrats, which did not change significantly over the four sample years.

Although the chronological data sequence represented zero to five years since tree clearance there was some variation within the chronological year 2 (since clearance). Ground cleared in 1999 and first sampled in 2001 was significantly different from ground cleared in 2000 or 2001 and sampled in 2002 or 2003 respectively. It is likely that this difference occurred because the spring and summer of 2000 was very warm and dry compared with other years. As a result ground cleared in 1999 was subjected to an 'unusual' first growing season which was not repeated for ground cleared in subsequent years. However, the effect was small and was only evident for one year indicating that the use of chronological year is valid for this investigation.

The importance of scale in vegetation monitoring has long been recognized (Greig-Smith 1983) and it is not appropriate to sample sub-shrub heaths and woodland field layers with the same sized quadrat as that which would be used for a dwarf-shrub heath community (Rodwell et al. 1991). Although the target vegetation type following tree removal was a blanket bog community and this does not include scrub and tree species, a certain amount of scrub growth was anticipated. Species such as *Sorbus aucuparia*, *Salix caprea* and *Betula pubescens* are very common on ground immediately adjacent to the tree clearance area and as some drying of the peat was evident colonisation by these species was thought to be very likely. In addition it was thought that some Sitka spruce regeneration may occur following forest clearance and all of these tree species would create a scrubby vegetation community. The National Vegetation Classification project sampled this type of community using a 10x10m quadrat (Rodwell et al. 1991) so it was selected as the main sampling unit for this project.

In order to capture more detailed information about the developing blanket bog community five 1x1 m 'mini' quadrats were nested within the main quadrat. The NVC project used 2x2m quadrats for dwarf-shrub heath communities (Rodwell et al. 1991) but it was decided that five 1x1m quadrats, one in each corner and one in the middle of the main quadrat, would give more information about small scale heterogeneity within the main sampling unit. More complex monitoring techniques using a series of nested quadrats would have allowed the variation in scale to be measured more precisely than the chosen technique (Hodgson et al. 1993; Critchley and Poulton 1998) but these techniques are extremely time consuming to conduct (approximately 6 hours per stand of nested quadrats) and the data collected are difficult to interpret.

CONTROL VEGETATION

Two types of control vegetation were included within the monitoring programme, existing mature blanket bog vegetation, which is referred to as 'target' vegetation and the vegetation found beneath Sitka spruce plantation. The DCA ordinations indicated that the 'target' vegetation quadrats are mostly similar to the M19 NVC community (Rodwell et al. 1991) although there are some similarities with the other three pseudo NVC communities. This control vegetation provided the most sensible reference for the tree cleared ground as it could be considered as a 'target' for vegetation developing post tree clearance. The Sitka control quadrats were less informative although they do demonstrate the range of plant communities that existed on apparently forested ground. In some locations the trees had achieved canopy cover so the ground cover was limited to litter and possibly some shade tolerant mosses. At the other end of the scale tree growth was very patchy with a mature blanket bog plant community existing between the stunted Sitka spruce trees. These locations tended to be the wettest areas where Sitka spruce growth would have been severely inhibited due to lack of nutrients associated with constantly waterlogged conditions (Taylor 1991).

TREE CLEARANCE METHODS AND VEGETATION DEVELOPMENT

Vegetation development occurred at different rates depending on the tree clearance methods. The most rapid change was seen on the harvested quadrats which have the greatest difference in Axis 1 scores from year 0 to year 5. There were only three 'harvested' quadrats so the results must be viewed with caution. However, the results are not surprising given that the clearance method removes whole trees leaving an undisturbed ground surface for plant colonisation. Bare peat was unlikely to be present after clearance by harvesting because machinery would not have travelled over the ground. There was a layer of dead Sitka spruce needles that may have hindered plant germination but not in the same was as wood chip or brash remains. Vegetation on the flailed quadrats showed a similar response to the harvested quadrats moving consistently towards the 'target' vegetation on site. The chainsaw method of tree clearance left a huge quantity of brash on the ground, often at depths greater than one metre. This is almost certainly the reason why there was very little change in the vegetation over the first three years following tree clearance with only relatively small movements in years 4 and 5.

Although the main and mini quadrat ordinations are similar the mini quadrat ordination identifies differences between the tree clearance methods which are not obvious at the larger scale. It appears that vegetation on flailed ground is becoming increasingly wet with years since tree clearance and this is probably the result of peat re-wetting. Twenty year old plantation forest on blanket bog has been shown to cause significant drying (Anderson et al. 1995) so it would follow that tree removal with the cessation of evapo-transpiration and rainfall interception will certainly have increased the amount of water reaching the peat surface. In addition the wood chip created during the flailing process was directed into the plough furrows which also enhanced water retention of the peat. Vegetation on harvested ground showed a similar response to the flailed ground although the vegetation appeared to be wetter from the start. Vegetation developing on ground cleared with chainsaws tended to be slightly drier than on harvested or flailed plots. This was almost certainly because the majority of ground that was cleared with chainsaws was sloping and hence better drained. The excavator mounted flail and harvester could not access steeply sloping ground so chainsaws were the only available option.

In general all the main quadrat ordination diagrams indicate that although the developing vegetation is moving towards existing vegetation on site it has not yet reached the target point for any of the treatments. However, the mini quadrat ordination shows considerable variation in the vegetation with many of the quadrats already similar to existing vegetation. There are mini quadrats 2, 3, 4 and 5 years since tree clearance occupying the same ordination space as the 'target' vegetation control quadrats and the NVC pseudo quadrats. This indicates that small patches of the vegetation (1x1 m) are already fully developed but this is not the case for the larger scale main quadrats (10x10 m). There are two explanations for the apparent difference in plant community development and the first is related to heterogeneity in wood chip depth which appears to influence speed of vegetation development. In addition the main quadrats were sited based on randomly generated grid references with a selection criterion that there had to be greater than 50% cover of wood chip. As a result some of the main quadrats were located with a small part of the quadrat on existing mature vegetation so in some instances one or more of the mini quadrats contained 'target' vegetation when monitoring started.

The NVC plant community M19 is clearly the most dominant plant community on site and a large proportion of vegetation developing on the tree cleared ground moving towards this community. Plant community type appears more varied at the small scale of 1x1 metre indicating that there is an intimate mix of wet mire and drier heathland communities with the former being more dominant. This was certainly evident on site both on existing vegetation and on ground which had been cleared of trees. Microtopography of the tree cleared ground provided the sort of terrain that might encourage this type of plant community heterogeneity. Due to ground preparation prior to tree planting the ground immediately adjacent to the tree stump was much higher than surrounding areas and this was colonized by drier species such as *Rhytidiadelphus* sp. *Vaccinium myrtillus* and *Deschampsia flexuosa*. Initially *C. vulgaris* also dominated in these patches probably because there was only limited wood chip on the ground so light was reaching the peat surface. Light is required to stimulate germination in *C. vulgaris* seed (Mallik et al. 1984a; Pons 1989).

Away from the tree stumps the ground sloped down to plough furrows located between each double row of trees. During the chipping process wood chips were directed into the plough furrows which caused them to fill with water fairly rapidly after tree clearance. The most hydrophilic plant species started to colonise these areas including *Eriophorum vaginatum, C. angustifolium, Sphagnum palustre, S. recurvum* and *S. magelanicum.* In general the site is very wet with a high annual rainfall so much of the peat quickly became waterlogged following tree clearance but drier patches were still obvious even after five years.

PLANT COLONISATION

The species ordination diagrams for both the main and mini quadrats clearly demonstrate the process of colonization. Tree remains and litter are on the far right of the ordination diagrams and these were the dominant ground cover immediately after tree clearance. The first species to colonise were *Cirsium palustre, Chamaenerion angustifolium, Juncus bulbosus* and *Dicranella* sp. (*D. cerviculata* and *D. heteromalla*). These are all species that are commonly found in new or damaged acidic habitats with the first three species frequently found on spoil and wasteland (Hodgson et al. 1995) and the two species of *Dicranella* found on partially dried peat, especially peat cuttings (Smith 1978). *J. bulbosus* was particularly prevalent on very wet areas of completely bare peat, especially where small areas of open water had accumulated. Work done on the recolonisation of mine spoils (Pietsch 1996) and lakes resulting from coal mining operations (Chabbi 1999) has showed that *J.bulbosus* initiates aquatic colonization in highly acidic conditions. *J. bulbosus* growth is promoted by high CO_2 and ammonium concentrations (Roelofs et al. 1994) which may have occurred following tree clearance as the peat was disturbed and hence exposed to weathering processes and oxygen. These conditions would enhance peat decomposition creating CO_2 and possibly NH_3. The species is relatively mobile and appears to be encouraged by habitat disturbance (Grime et al. 1988).

There is no particular reference to using *J. bulbosus* as a species for peatland restoration work but it may be an appropriate species if the conditions are very acid and wet, particularly with areas of open water. *E. vaginatum* has been used for this purpose (Campbell et al. 2002; Lavoie et al. 2003; Lavoie et al. 2005) and the species did colonise wetter ground on the tree clearance area very quickly. Individual plants also grew very quickly and produced a mass of seed within the first growing year. This was particularly obvious on peat that was waterlogged for most of the year.

None of the initial colonizing species are recorded in any of the four NVC communities that were located on site, except *J. bulbosus* which is only 'scarce' in the M15 community (Rodwell et al. 1991). There are some similarities between the 'primary ecological strategies' (Grime et al. 1988) of these species which might indicate why they all colonised the site quickly but did not persist in the developing plant community. *C.palustre* and *J.bulbosus* are both classed as 'stress tolerant ruderals' (Grime et al. 1988) and *Dicranella sp* would probably come in this category as well. Seed/spore production is reasonably high and either transported by wind or maintained as a persistent seed bank (Grime et al. 1988). As a result germination was relatively rapid following exposure of bare ground. As the plant community developed with more 'competitive' and 'stress tolerant' species such as *C.vulgaris* and *E.vaginatum* the competition for resources almost certainly caused the initial colonisers to decline. In addition the development of permanently waterlogged conditions would have had an adverse affect on *C.palustre* (Grime et al. 1988). *C. angustifolium* is classed a 'competitor' which represents a different ecological strategy to the other colonizing species. However, the species does produce a large number of seeds which are transported by the wind (Grime et al. 1988) and hence quickly distributed to newly exposed ground. The reason why this species did not persist in the developing community is probably due to the highly acidic and anaerobic conditions that developed as the water table increased following tree removal.

In the second growing season following tree clearance many of the community defining species started to appear with some growing more quickly than others. For example *Carex echinata, Molinia caerulea, E. vaginatum* and *Potentilla erecta* covered the ground very quickly in the wetter communities and these are all 'constant species' found in abundance within the two NVC mire communities (M15 and M19) on site (Rodwell et al. 1991). *Deschampsia flexuosa, Rhytidiadelphus loreus, Galium saxatile* and *Anthoxanthum odoratum* quickly colonised drier ground and again, with the exception of *A.odoratum,* these are all 'constants' within the NVC heath communities (H18 and H21) on site (Rodwell et al. 1991). Other species such as many of the *Sphagnum* species, *Calluna vulgaris, Vaccinium myrtillus and Hylocomium splendens* appeared within a couple of years of tree clearance and expansion of these species was steady but relatively slow.

VEGETATION AND THE ENVIRONMENT

All of the environmental variables included within the RDA analysis of flailed quadrats had a significant effect on variation in the vegetation community composition. Year since tree clearance, although not strictly an environmental variable, explained two thirds of the explained variation which is not surprising given the results from the DCA analysis. Four species showed a clear response to year since tree clearance, these were 'tree remains' which decreased rapidly over time, *D. flexuosa, E. vaginatum* and *C. vulgaris* which all increased consistently with time. Fresh weight of wood chip explained a further 5.8% of the variation but it was not closely associated with any particular species. The effect of weight of wood chip is discussed in more detail in Chapter 4 but vegetation development did appear to be inhibited as the amount of wood chip increased. Peat depth, pH and slope all had small but significant affects on variation in the vegetation with a few key species closely linked to peat depth and slope. For example, *Agrostis* sp, *Juncus effusus* and *Galium saxatile* all increased in cover with increasing slope. These species are all typical of the drier heathland communities which one might expect to occur on sloping ground. Although deep peat can occur on slopes this is not the case on the tree clearance area where the slopes tended to be associated with a shallow peat cover, better drainage and hence drier conditions. Deeper peat occurred on flatter ground and in basins and the species that were closely associated with these conditions were *Hypnum cupressiforme, Molinia caerulea* and *C. vulgaris*. pH had the smallest effect on the vegetation, probably because the pH range was relatively limited and highly acidic.

The RDA analysis for the chainsawed quadrats showed broadly similar results to the equivalent analsysis for the flailed quadrats with year since tree clearance explaining the highest proportion of variation in the vegetation. There were only 9 chainsawed quadrats included in the analysis and they were not really representative of a range of different environmental variables. Chainsaws were only used to clear trees on ground that was not accessible to the flail or harvester. As a result most of the ground was steeply sloping (over 7° degrees) and 6 of the quadrats were located on steep slopes with a shallow peat cover (less than 20cm). The remaining three quadrats were located on completely flat ground that was also very deep peat. In effect the quadrats were located at extremes of a slope and peat depth gradient with no representation along the rest of the gradient. This, coupled with the small number of quadrats included in the analysis, is almost certainly why the species response curves are not particularly interpretable. *C.vulgaris* cover appears to increase with increasing slope to 7 degrees then declines with slopes up to 14 degrees and then increases again. These results suggest that it is not possible to generalise about species response to environmental variables following tree clearance by chainsaws on this experimental site.

IMPLICATIONS FOR THE RESTORATION OF BLANKET BOG FOLLOWING FOREST CLEARANCE

The restoration of blanket bog vegetation following the clearance of 15-20 year old immature Sitka spruce is clearly achievable within a relatively short period of time. At a small scale, patches of the 'target' vegetation may develop within 6 years, although it will take a few years longer for whole areas to develop. This heterogeneity in time taken for various plant communities to develop, post tree clearance, is probably a reflection of the heterogeneity in Sitka spruce size. Where trees have reached the thicket growth stage, with the ground vegetation completely shaded out, the plant community will take more than six years to develop. However, where patches of mature vegetation still exist between stunted Sitka spruce trees the plant community quickly recovers after tree clearance operations.

Vegetation development following the three different tree clearance methods showed some differences in response. Clearance of trees using chainsaws creates a deep covering of brash and tree remains on the ground and this appeared to inhibit vegetation development compared with the harvesting and flail clearance methods. In general the chainsawed ground was located on steep slopes so the developing vegetation was different to that on less sloping ground and deeper peat. However, where slopes were cleared with a flail the vegetation did respond more quickly than after chainsaw clearance. Similarly vegetation on flat chainsawed ground responded more slowly than equivalent areas that were flailed. This indicates that the brash inhibited vegetation development rather than a factor inherent in the ground that was cleared by chainsaws. Whole tree harvesting, as a method of clearing trees from blanket bog, would allow blanket bog restoration to occur most rapidly as there are no tree remains left on the ground at all. However, this method of clearance was only used to create corduroy tracks (a track created by placing tree trunks side by side in a corduroy pattern) for flails to travel over boggy ground and it was not considered to be a cost effective method for clearing large areas. In general blanket bog sites are not particularly accessible so, removing trees with no timber value from the site would be prohibitively expensive in most situations. In addition the results clearly demonstrated that although vegetation development was initially much quicker, following whole tree harvesting compared with flail clearance, the vegetation was at a similar point for both clearance methods 6 years post tree removal. Therefore, unless the site is extremely important in conservation terms it is not worth the substantial extra cost to clear the trees by whole tree harvesting.

CHAPTER 4

THE EFFECT OF WOOD-CHIP DEPTH ON THE DEVELOPMENT OF BLANKET BOG VEGETATION FOLLOWING IN SITU CHIPPING OF IMMATURE SITKA SPRUCE

4.1 Introduction

There are a small number of blanket and raised bog restoration projects in the UK where tree removal has been an integral part of the restoration work (Burlton 1993; Brooks and Stoneman 1997; Wilkie et al. 1997). 'In situ' chipping of trees has been used on two of the sites (Burlton 1993; Wilkie 2005) although this was achieved in two separate operations where the trees were felled, either manually or mechanically and then fed into a stand alone chipping machine. Although the tree clearance project in Kintyre reviewed a number of different tree clearance techniques 'in situ' chipping using an excavator mounted flail appeared to offer a solution that balanced cost with likelihood of achieving successful blanket bog restoration. The method was considerably cheaper than whole tree harvesting with the associated costs of extracting low value timber from a highly inaccessible site and it provided a more acceptable way of leaving woody debris on site than the manual chainsaw felling option. Whole trees, including the trunk, branches and brash were reduced to relatively small wood chips and woody debris that was spread around in the immediate vicinity of the flail.

The excavator mounted flail as a wood chipping device had been used for *Rhododendron* clearance in woodland but it had never been used to clear conifer forest growing on blanket bog. Consequently there were no results relating to the success or otherwise of this technique for blanket bog restoration. A number of specialists had voiced concerns about the potential nutrient release associated with leaving material on site whether it was whole trees, bits of trees, brash or wood chips (Burlton 1993; Brooks and Stoneman 1997; Anderson 2001). Ombrotrophic vegetation has very low nutrient requirements and the concern is that increased nutrient levels would encourage the growth of nutrient demanding species that are not native blanket bog species (Anderson 2001). The ecological consultant employed to advise on the tree clearance project in Kintyre was also concerned that if a dense layer of wood chip was left on site germination and growth of blanket bog vegetation would be inhibited (Moss *pers. comm.*).

This study was set up to investigate the main concerns relating to 'in situ' chipping of trees to facilitate blanket bog restoration. The objectives of the experiment were firstly to investigate the effect of different wood chip depths on the development of blanket bog vegetation, including speed of recovery and the type of plant community and secondly to measure decomposition rates of wood chip at different chip depths so that the relationship between decomposition and vegetation development could be investigated. The chip depth treatments were selected to represent the size/age of trees that are too big to fell to waste (i.e. cut down with a chainsaw and leave as whole trees on site) and too small to have any value as timber/wood fuel. In addition, a six-year chronosequence of vegetation change is analysed in the context of estimated depth of wood chip deposited on the ground after tree-clearance.

4.2 Materials and Methods

4.2.1 Wood chip depth experiment

A randomised block experiment was set up to investigate the effect of wood chip depth on vegetation development and wood chip decomposition following 'in situ' chipping of immature plantation forest planted on former blanket bog habitat. The experiment was established on the forest clearance area, the exact location is indicated on the map at Appendix 2. The location was chosen because tree growth prior to forest clearance had been good and complete canopy cover had been achieved. Trees in the area were 18 years old when they were cleared with an average diameter at breast height of 15cm. As a result there was no ground vegetation present at the beginning of the experiment. The trees were chipped using an excavator mounted flail as part of the tree clearance programme over the whole area.

EXPERIMENTAL DESIGN

The experiment comprised four treatments plus a control, each replicated three times within three blocks. The blocks were located to control for variation in peat depth and wetness. Plot size was 3x3 metres, with 15 randomly-located plots within each block. Prior to applying the chip treatments all wood chip was raked up and removed and the treatments were applied as shown in Table 4.1. The exception was Treatment 4 (control) where the pre-existing woodchip on the site was left undisturbed.

Table 4.1: Treatments/control used in the chip experiment

Treatment No.	Description
0	No wood chip
1	Normal rate (8 kg/m^2)*
2	Double rate (16 kg/ m^2)
3	Triple rate (24 kg/m^2)
4	Control: Natural - no woodchip removed or re-applied

* normal rate is the average amount of wood chip present per m^2 on this part of the forest clearance area assessed using 20 randomly located 1m^2 plots.

After tree clearance and raking (except Treatment 4) the chip treatments were applied and two samples of chip were taken from the upper layer of chip on each plot. A small feed scoop (500ml) was used to take each sample. The samples were oven dried and the % moisture content calculated. Chip treatments were applied within a period of 1 week across all plots, and since the weather conditions were consistent chip moisture contents were within 1% across all samples. As a result it was assumed that replicates of the wood chip treatments, in terms of their initial moisture content, are comparable.

DATA COLLECTION

On each of the 45 experimental plots two permanent 1x1m quadrats were established and assessed annually from 2001-2004. These were located immediately adjacent to each other, either side of a middle line running through the centre of each 3 x 3 m plot. The middle line was permanently marked with wooden stakes at either end of a block of plots and re-established each year using a tape measure. Each plot was 3m long so the quadrats were located between 1-2m, exactly central along the length of the plot as shown in Figure 4.1.

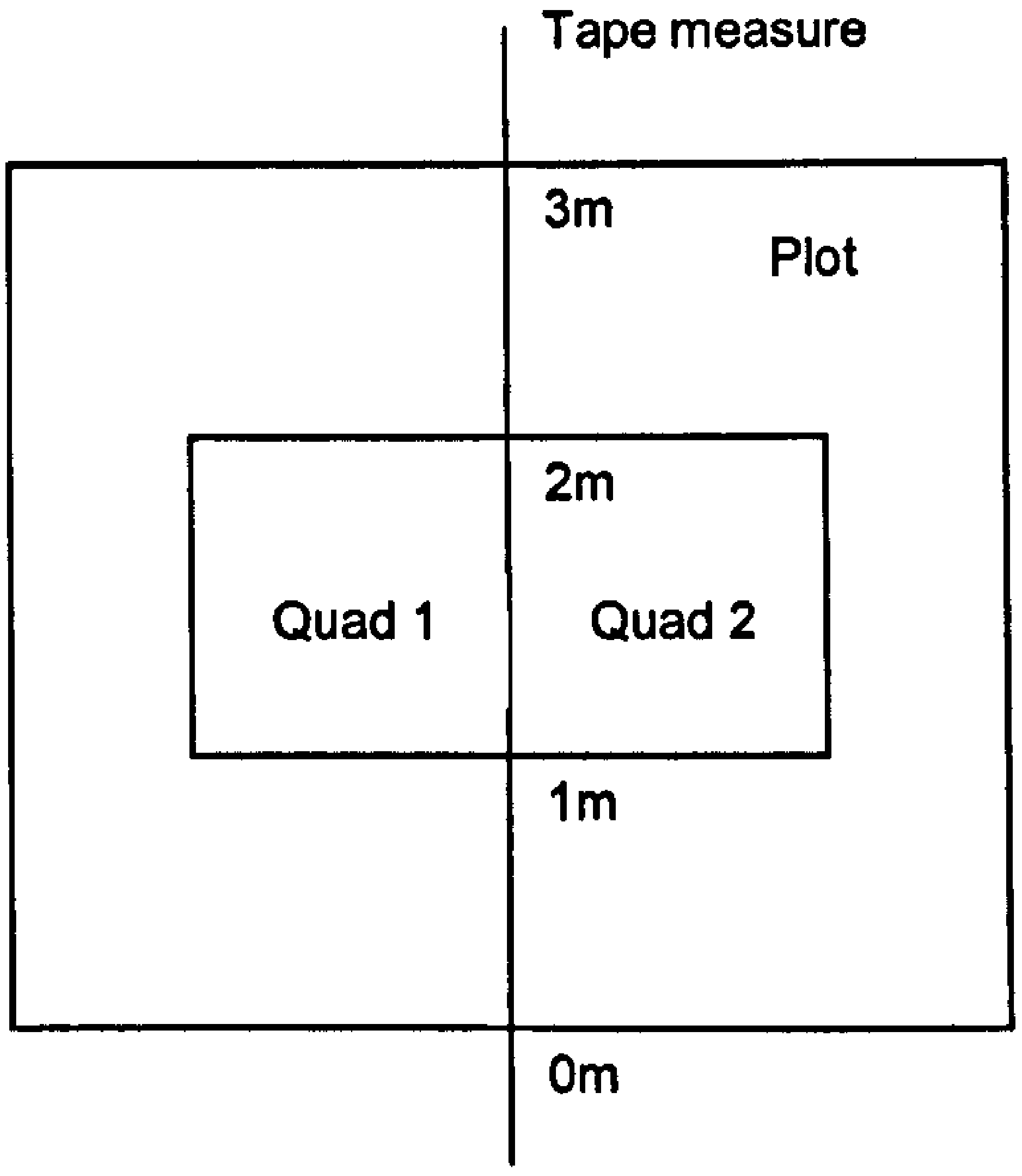


Figure 4.1: Plot and quadrat layout on the experimental plots

A visual estimate of percent cover was recorded for all plant species, rock, bare peat, water and tree remains (chip or brash) within each quadrat. This was done with the aid of a 1x1m grid divided into one hundred 10x10cm cells. All vascular plants and bryophytes were identified to species level. Assessments were carried out in July in 2001-2004.

DATA ANALYSIS

Two statistical methods were used to analyse the data from the chip depth experiment, depending on whether the response of individual species was being tested in univariate analyses via linear mixed effects models (Pinheiro & Bates, 2000), or all species simultaneously in multivariate tests through constrained ordination (Ter Braak and Smilauer 1998).

Linear mixed effects modelling

Percentage cover of individual species was subjected to linear mixed effects (LME) modelling (Pinheiro and Bates 2000) to test the effect of chip depth treatment on plant establishment at the species level. Six species that were found across all treatments and on more than 70% of the experimental plots, were selected for this analysis. The species were *Calluna vulgaris*, *Eriophorum vaginatum, Hypnum cupressiforme, Deschampsia flexuosa, Polytrichum sp. (P.commune & P.formosum)* and *Campylopus sp.* (*C. pyriformis, C. atrovirens* and *C. introflexus*). The two species of *Polytrichum* have similar ecology and were frequently found in an intimate mix on the experimental plots so they were considered as one species for the purposes of this analysis. This was also the case for *Campylopus* species.

For all species except *Campylopus* sp. the percentage cover data were log transformed (log(cover+1)) as there were a large number of zeros in year 0 and 1 of the experiment with rapid increase in cover in years 2 and 3. This transformation was considered appropriate, rather than an arcsine transformation which is commonly used on percentage cover data, because no individual species exceeded 30% cover in any year. For *Campylopus* sp. the response was unimodal for three of the treatments so the data were not transformed and a quadratic term for year was included within the model. Two designs of LME models were fitted for each species and all models included fixed and random effects. The first model included 4 chip depth treatment levels as fixed effects (Tmt 0 - all chip removed, Tmt 1 – normal, Tmt 2 – double and Tmt 3 – triple) and the second included only two chip depth treatment levels (Tmt 1 - normal and Tmt 4 – Natural) as fixed effects. Both models included year as a fixed effect. The random effects were year nested within individual plots. Hence, species abundance in treatment i, plot j, and year k, S_{ijk} could be modelled as:

$$S_{ijk} = t_i + p_j + y_k + ty_{ik} + T_j + P_j + Y_k + \varepsilon_{ijk}$$

where t is the treatment effect, p the plot effect, y the year effect, T the random error associated with treatment, P the random error associated with plot, Y the random error associated with year, and ε the overall residual across all treatments, plots and years.

Where necessary temporal autocorrelation was accounted for within models using a first-order autoregressive function (Pinheiro and Bates 2000; Crawley 2002), this was done by specifying residual correlation that decays exponentially with distance between years. Similarly, where appropriate, differences between treatment variances were accounted for, by specifying separate error terms for each level of chip depth. In all cases, the simplest possible model that gave the best fit to the data, and most appropriate residual error distribution was sought. Different models were compared by likelihood ratio tests and if models were significantly different ($p<0.05$), the model with the lower Akaike's information criterion (Burnham and Anderson 2002) was selected:

$$AIC = -2\log Lik + 2n$$

where n is the number of parameters in the model, and is effectively a 'penalty term' related to the complexity of the model.

For the species where treatment effect was significant, an orthogonal contrast analysis (Crawley 2002) was performed on model 1. The following contrasts were made; Tmt 0 compared with Tmts 1, 2 & 3, Tmt 2 compared with Tmt 3 and Tmt 1 compared with Tmts 2 & 3. It was not necessary to repeat the orthogonal contrast analysis for the LME model 2 as they only contained two treatments, Tmts 1 and 4.

Principle Response Curve Analysis

For analysis of the vegetation community data the multivariate technique Principal Response Curve (PRC) analysis (Frampton et al. 2001; Pakeman et al. 2003) was used to display temporal changes in species composition between treatments. PRC analysis is based on the multivariate ordination technique redundancy analysis (RDA) but is designed to evaluate the extent of differences among individual time steps and also among individual treatments (Van den Brink and Ter Braak 1998; Frampton et al. 2001). One problem with displaying multivariate patterns that change over time in an RDA plot, is that with several treatments over a number of years, the plots often become complex and difficult to interpret. This difficulty is compounded by the fact that time is represented by a haphazard trajectory within the plot, rather than a single axis. PRC analysis simplifies the presentation of such time-based analyses by plotting the differences in community composition for each treatment relative to a baseline treatment (typically a control) against time. In a PRC analysis the basic model (following the syntax of Van den Brink & Ter Braak, 1999) is:

$$y_{d(j)tk} = \bar{y}_{0tk} + b_k c_{dt} + \varepsilon_{d(j)tk}$$

where $y_{d(j)tk}$ is the abundance of species k in replicate j of treatment d at time t; y_{0tk} is the mean abundance of species k at time t in the control (d=0); b_k is the weight of each species, fitted to the basic response c_{dt} ; $\varepsilon_{d(j)tk}$ is an error term with zero mean and σ^2_k variance. Note that c_{0t}=0 for every treatment t and species k, i.e. all values on the control for every species are deliberately constrained to zero on each date, and all other PRC response values for the remaining treatments (i.e. c_{dt} where d is not the baseline control) are scaled relative to this. The partial least-squares estimates of these c_{dt} coefficients can be determined through partial RDA (redundancy analysis), and the c_{dt} values plotted as PRC axis 1 (on the y-axis) against sampling time (x-axis) for each treatment. The resulting curves for each treatment show the principal community response over time, in comparison with the baseline treatment. The species weights (b_k) show how closely each species matches the overall community change with time, and can also be plotted on the PRC graph.

The practicalities of performing a PRC analysis within CANOCO software are described in detail by Leps and Smilauer (2003) and this method was followed using the same selection of options. The significance of the whole PRC can be tested via a Monte Carlo permutation test of the samples (i.e. permuting whole time-series) in the partial RDA used to develop the PRC. Multiple comparison testing of each treatment at each time point on the PRC (Frampton et al. 2001) was done by performing a series of normal RDA analyses at each sampling point including only the two treatments to be compared. These treatments were then included as the environmental variables, with block as a covariable. This allowed letters a, b, c etc. to be used to demonstrate where significant variation between treatments exists (Van den Brink *pers. comm.*). Differences were only recorded as significant where the p-value was lower than 0.008 (Bonferroni correction to avoid Type I statistical error).

Two PRC analyses were done using different 'control' or 'reference' data. Firstly, only experimental data were included in the PRC and the natural treatment was taken as the reference. This is the most obvious treatment to use as a control because no chip was removed or returned to the plot. However, in order to provide a reference line that represented mature vegetation i.e. completely untreated with no trees planted and none removed/chipped the 'target' vegetation monitoring quadrats were used as the reference data in the second set of PRC analyses. These quadrats were clearly not part of the experiment but it is useful to visualise how the vegetation is likely to develop in the short- to medium- term.

4.2.2 Wood chip decomposition

EXPERIMENTAL DESIGN

An experiment to investigate the decomposition of wood chip at different chip depths was nested within the main experiment described in section 4.2.1 (Experimental design). One of the three plots for each treatment, in each block was selected at random to be included in this investigation (randomised block design but no within-block replication). Sixty 'chip decomposition' bags were made up using specially made medium weight nylon net bags. These were 20x20cm with a drawstring cord that could be tied to prevent wood chip being lost from the bag. The mesh size was 5x5mm which was sufficiently small to prevent wood chip from falling out of the bag. Enough wood chip to fill all the bags was collected and mixed to ensure homogeneity of the sample. Each bag was then filled with approximately 300g of wood chip and the exact weight of the chip was recorded. The bag was then closed and a numbered marker attached to the end of the cord so the bag could be identified during the investigation. Three additional samples were taken and oven dried at 100°C for 24 hours. These were used to calculate a dry weight for wood chip in each of the bags.

Four bags were placed on each of the 15 plots included in the investigation (5 treatments, 3 blocks) and pegged to the ground using a plastic peg. The bags were located in the NW corner of each plot in a group together. They were placed underneath the wood chip treatment on each plot so the bags on the 'triple' treatment plots (Tmt 3) were underneath three times as much woodchip as the bags on the 'normal' treatment plots. The bags on the 'all removed' treatment were not covered at all. The bags were always located in the same position (NW corner) on each plot so for the natural treatment the bags were under whatever wood chip was present in this part of the plot.

DATA COLLECTION

The bags were put out on the plots in October 2001 and one bag was then removed from each plot in October of the four subsequent years (2002, 2003, 2004 & 2005). These samples were oven dried at 100°C for 24 hours and weighed to obtain the dry weight of wood chip. This figure was then subtracted from the estimated dry weight calculated at the beginning of the experiment to give a percentage wood chip remaining and hence a measure of chip decomposition.

An attempt was made to collect temperature data on each of the plots where the chip decomposition bags were located. Tinytag Transit temperature loggers (Gemini Data Loggers (UK) Ltd) were used and placed immediately adjacent to the chip bags. For example loggers on the triple, double, normal and natural treatment plots were underneath different depths of wood chip and the loggers on the all removed treatments were placed on directly on the peat. Unfortunately a large number of problems were encountered with these loggers due to malfunction and feral sheep damage. As a result the data set had too many missing data points for any sensible analysis to be completed.

DATA ANALYSIS

The percentage of woodchip remaining in each of the four years was subjected to linear mixed effects modelling (Pinheiro and Bates 2000) to test the effect of chip depth treatment on wood chip decomposition. The method is described in detail in section 4.2.1 (Data analysis, univariate analysis) and the same model was fitted although the data were not transformed. The series of models were fitted all of which showed no significant difference between treatments. The residual error distribution was normal.

4.2.3 Chip depth and vegetation change on the 6 year chronosequence of monitoring quadrats

DATA COLLECTION

The number and diameter of all tree stumps on each of the monitoring quadrats was recorded when the quadrat was established. In order to transform these data into an estimate of wood chip on each quadrat the relationship between trunk diameter just above ground level and the weight of the trunk and branches was determined by doing a calibration using 15 trees. A range of different sized sample trees were chosen to be destructively sampled. They were harvested using a conventional harvesting machine and then cut into manageable pieces (approximately 1m lengths). The diameter just above ground level was recorded and the weight of the tree was determined by weighing each piece of the trunk and the branches.

DATA ANALYSIS

The stump diameter vs. tree fresh weight calibration was calculated using linear regression. The diameter measurement was converted to radius cubed (r^3) because the relationship between diameter increase and fresh weight increase is most similar to a cubic relationship. The regression model was then used to convert all the stump diameters on each monitoring quadrat to fresh weight of wood chip and a total weight for each monitoring quadrat was calculated. The normal, double and triple wood chip treatments in the chip depth experiment were equivalent to 8, 16 & 24kg woodchip/m^3 and these were used to categorise the monitoring quadrats (flailed only) by the estimated weight of wood chip on the quadrat. Up to 12kg/m^3 was classed as normal, between 12-20kg/m^3 was classed as double and over 20kg/m^3 was classed as triple.

The wood chip weight categories were used as a 'treatment' factor within a PRC analysis on the 6 year chronosequence of monitoring quadrats. The heather control monitoring quadrats were included as the control / reference data (a mean of all four sample years was used for each of the six time points). It was not possible to do a single permutation test of the whole PRC as described by Leps and Smilauer (2003) where each annual assessment on each quadrat is treated as a split plot and whole plots are permuted at random but split plots are not permuted. This is because the data used represented a chronosequence of years so quadrats in year 0 are not the same as those in year 5. Instead of the split plot approach the plots were considered as a time series and permuted using cyclic shifts. The resulting diagram can be interpreted as other PRC diagrams but the overall Monte Carlo test is not valid. However, the mulitple comparison testing of each treatment at each time point on the PRC is still valid as this is done in a separate RDA analysis, as described in section 4.2.1 (multivariate analysis) above.

A linear regression model was fitted to each of the 6 year chronosequence PRC curves in order to predict the number of years for the three treatments to reach the 'target' vegetation (where the modelled line intersects the 'target' vegetation line on the PRC). Confidence intervals for each of the PRC curves were calculated as detailed in Zar (1996) for an inverse prediction procedure.

4.3 Results

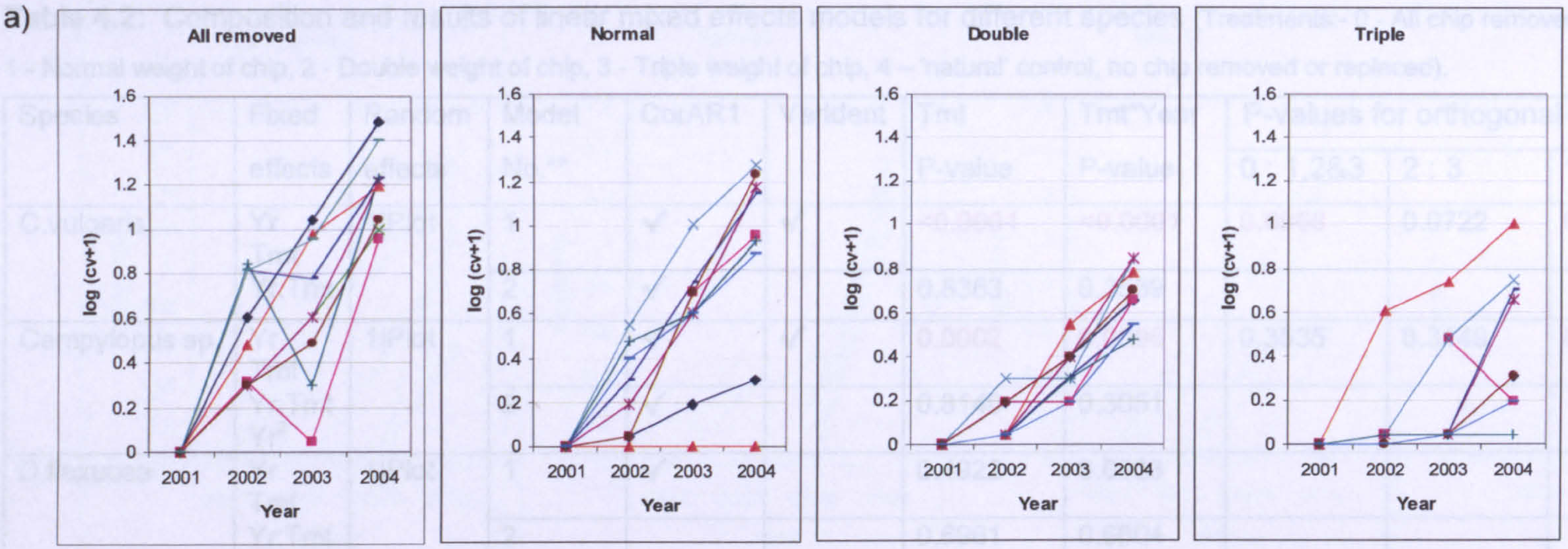
4.3.1 Wood chip depth experiment

Linear mixed effects modeling

69 species were recorded in the experimental plots over the four sampling years including the pseudo species; tree remains, bare peat, water and rock. Of these only 6 species were found (>1% cover) in 70% or more of the experimental plots in the final assessment year, 2004. These include *Calluna vulgaris, Campylopus sp. Deschampsia flexuosa, Eriophorum vaginatum, Hypnum cupressiforme, Polytrichum sp.*

The LME models showed that four of the species (*C.vulgaris, Campylopus sp., E.vaginatum, Polytrichum sp.*) demonstrated significant differences in response over time between treatments. The other two species (*D. flexuosa* and *H. cupressiforme*) increased in cover over the four year experiment but no treatment effect was evident. The composition of each LME model is summarised in Table 4.2 along with the analysis of variance p-value for the treatment effect and the treatment*year interaction effect. The necessity of accounting for first-order temporal correlation and/or differences in treatment variances in the model, as well as the P-values for the orthogonal contrasts are also detailed in Table 4.2.

Of the four species that showed a treatment and treatment*year interaction effect *C.vulgaris* and *Polytrichum sp.* showed the most dramatic differences between treatments with all treatments significantly different from each other except normal and the natural control. The absolute differences between treatments were as might be expected with the most rapid increase in the species cover seen on the all chip removed treatment followed by the normal, double and triple treatments (see Figure 4.2 for the *C.vulgaris* response curves). The response of *E.vaginatum* (Figure 4.3) was fairly similar to that of *C.vulgaris* although growth occurred more rapidly on the natural control (Tmt 4) compared with the normal treatment (Tmt 1) (p=0.0245). The differences between other treatments were not as great and the only significant difference was between normal and double/triple. This indicates that the response was the same on the all removed and normal treatments and the same on the double and triple treatments. *Campylopus sp* response (Figure 4.4) was noticeably different from the other three species showing a unimodal response to the shallower wood chip depth treatments/control (all removed, normal & natural). In general the cover of *Campylopus sp* increased very quickly in the first year, for example 0 to 30% in some plots, and then started to decrease in years 2 or 3. The response to the double and triple treatments was exponential as for the other species.



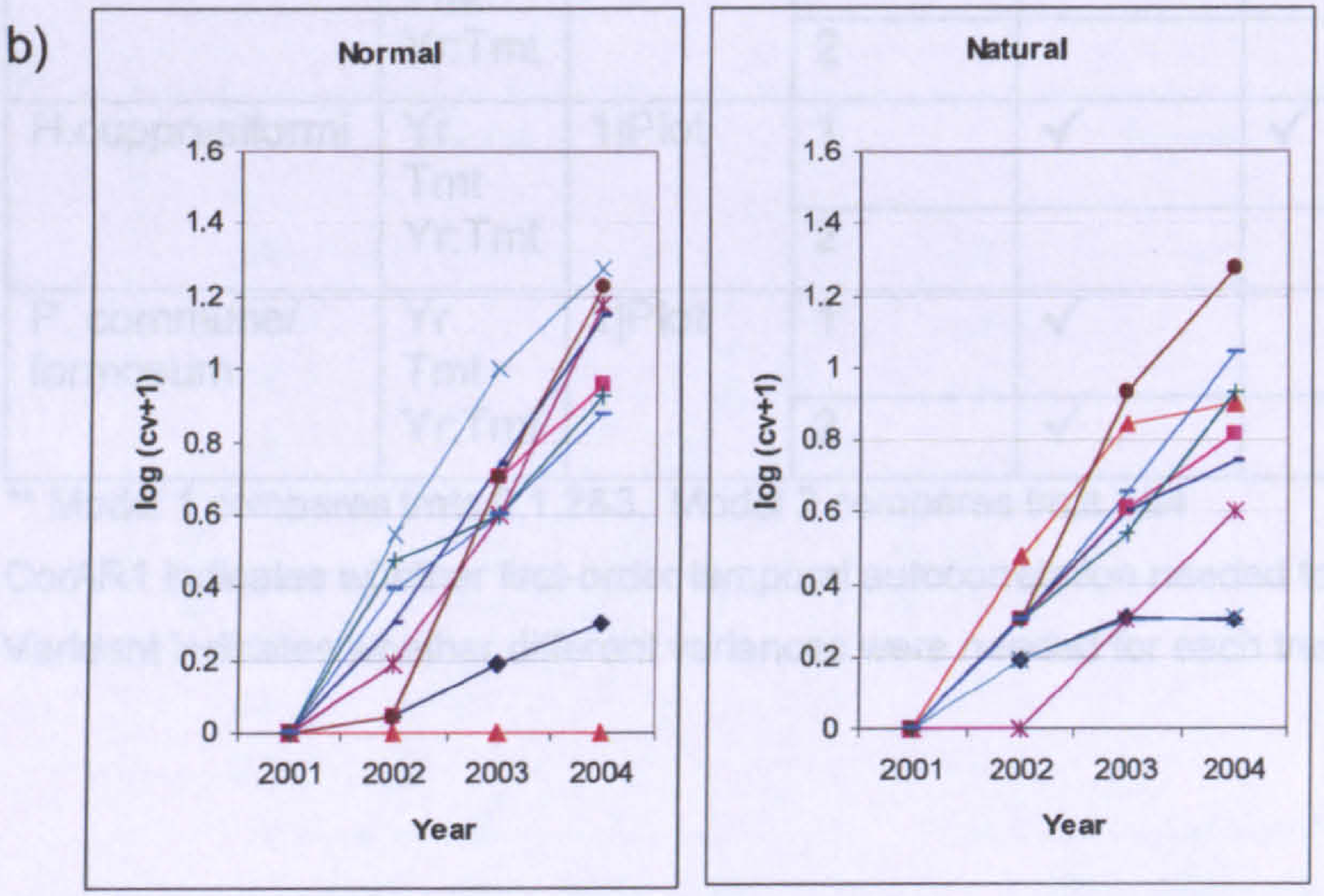


Figure 4.2: Change in cover of *Calluna.vulgaris* (log (cv+1)) on individual plots for different treatments a) Treatments 0, 1, 2 & 3
b) Treatment 1 & Control 4

Table 4.2: Composition and results of linear mixed effects models for different species (Treatments:- 0 - All chip removed, 1 - Normal weight of chip, 2 - Double weight of chip, 3 - Triple weight of chip, 4 – 'natural' control, no chip removed or replaced).

Species	Fixed effects	Random effects	Model No.**	CorAR1	VarIdent	Tmt P-value	Tmt*Year P-value	P-values for orthogonal contrasts		
								0 : 1,2&3	2 : 3	1 : 2&3
C.vulgaris	Yr Tmt Yr:Tmt	1|Plot	1	✓	✓	<0.0001	<0.0001	0.0008	0.0722	0.0170
			2	✓		0.8363	0.3539			
Campylopus sp.	Yr Tmt Yr:Tmt Yr^2	1|Plot	1	✓	✓	0.0002	0.0096	0.3535	0.3149	0.0048
			2	✓		0.8140	0.3051			
D.flexuosa	Yr Tmt Yr:Tmt	1|Plot	1	✓		0.4922	0.0933			
			2			0.6961	0.6604			
E.vaginatum	Yr Tmt Yr:Tmt	1|Plot	1	✓		0.0356	0.0166	0.6416	0.0671	0.0132
			2			0.0245	0.2437			
H.cuppresiformi	Yr Tmt Yr:Tmt	1|Plot	1	✓	✓	0.6543	0.5890			
			2			0.5364	0.4118			
P. commune/ formosum	Yr Tmt Yr:Tmt	1|Plot	1	✓		<0.0001	<0.0001	0.0008	0.0146	0.0009
			2	✓		0.3870	0.2597			

** Model 1 compares tmts 0,1,2&3. Model 2 compares tmts 1&4

CorAR1 indicates whether first-order temporal autocorrelation needed to be included in the model

VarIdent indicates whether different variances were needed for each treatment in the model

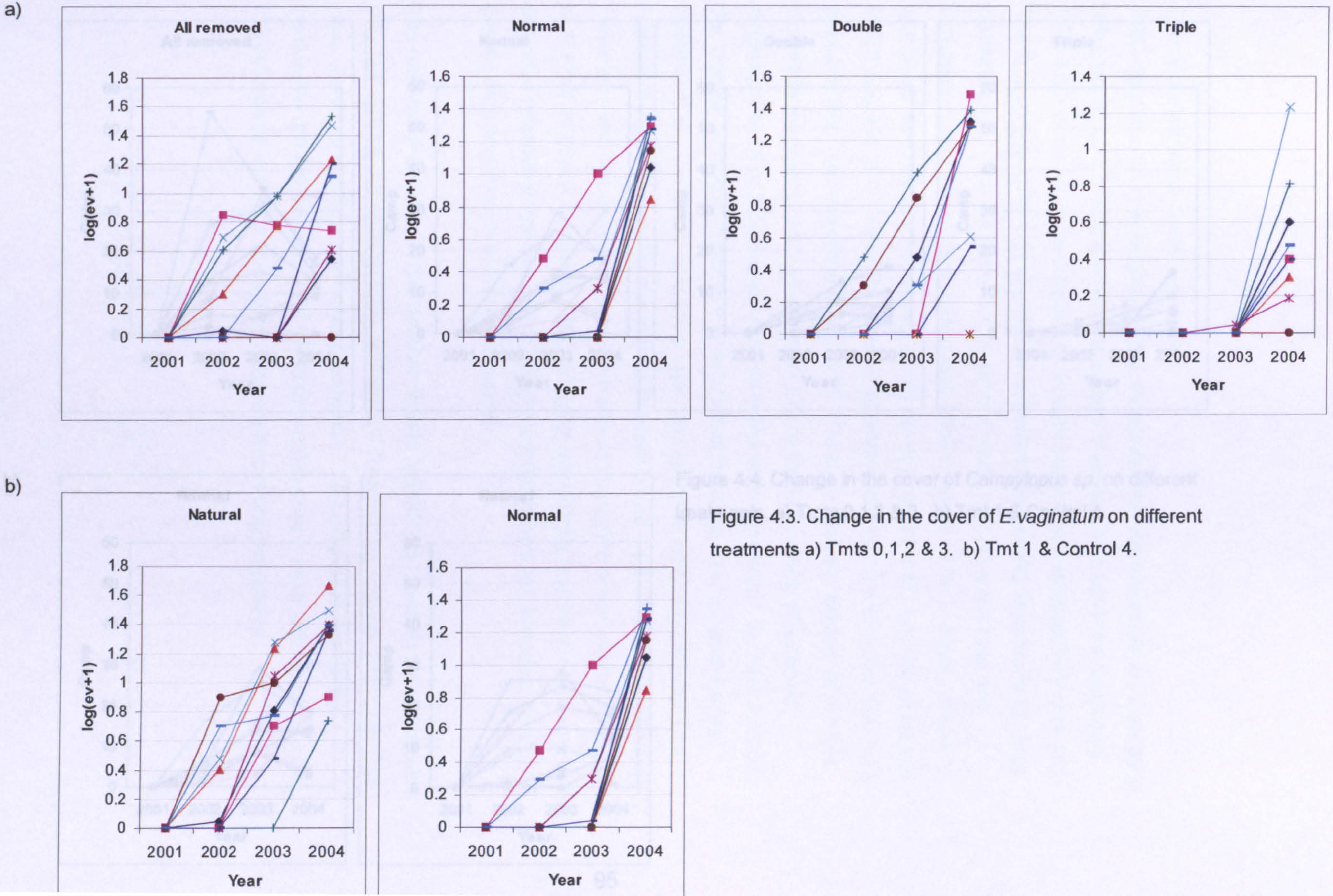
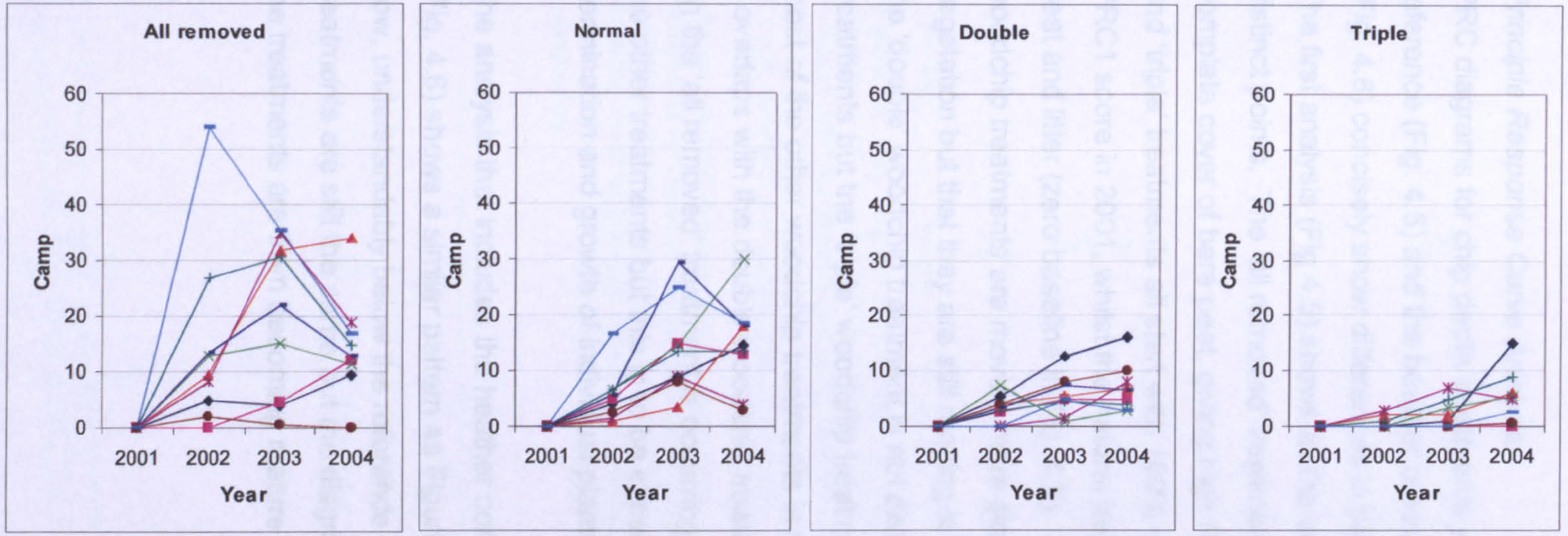


Figure 4.3. Change in the cover of *E.vaginatum* on different treatments a) Tmts 0,1,2 & 3. b) Tmt 1 & Control 4.

a)



b)

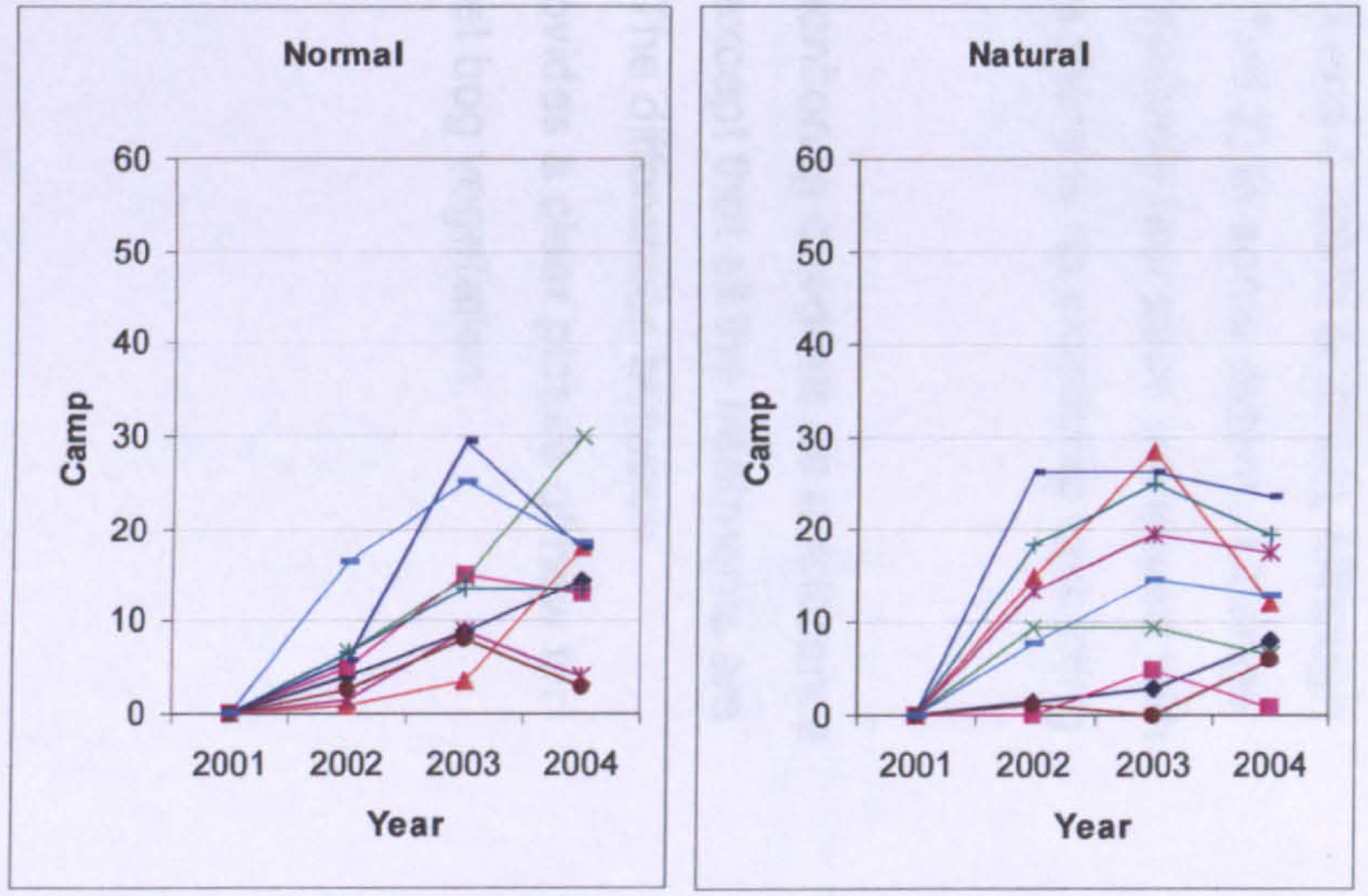
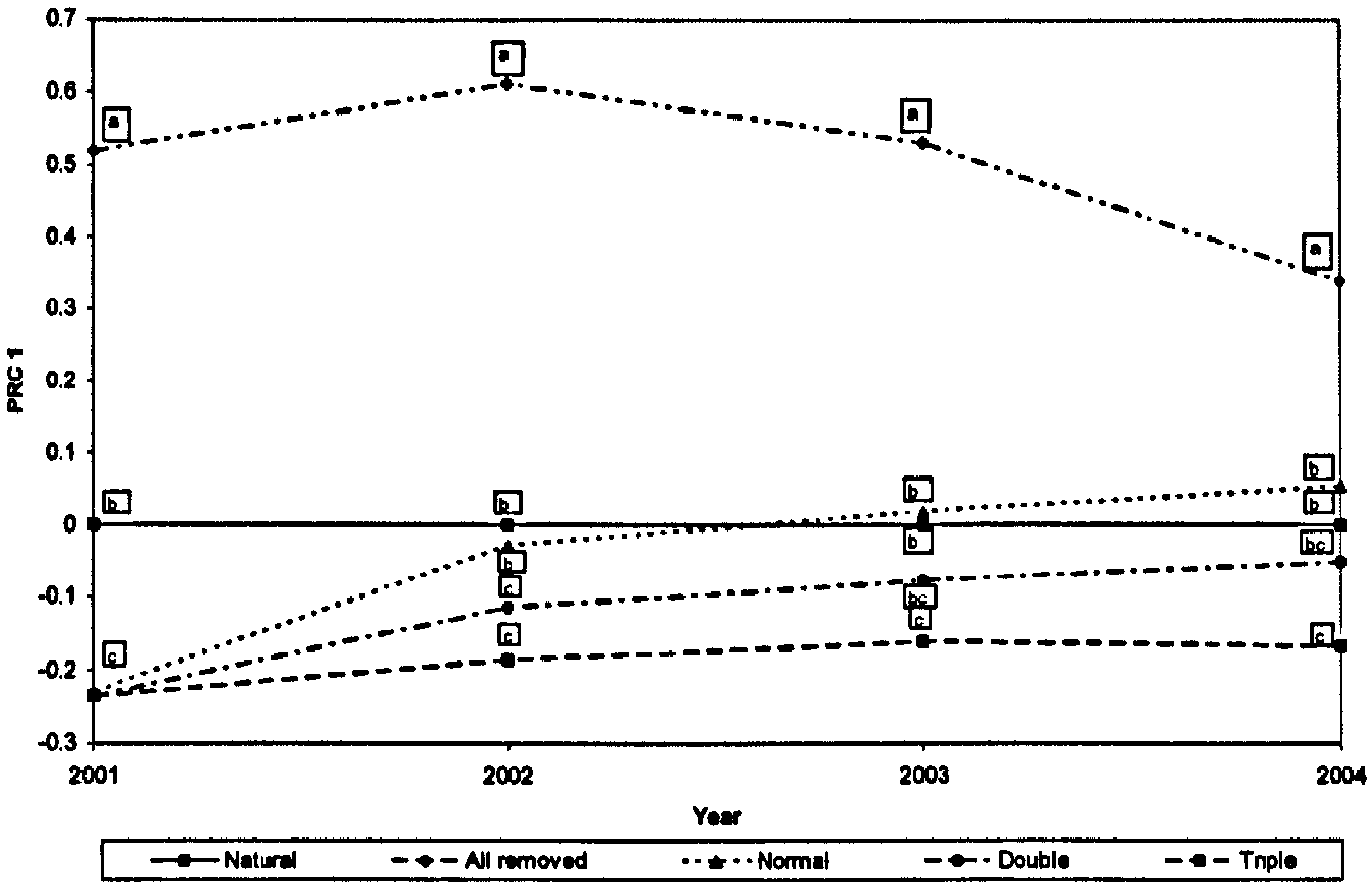


Figure 4.4. Change in the cover of *Campylopus sp.* on different treatments. a) Tmts 0,1,2 & 3. b) Tmt 1 & Control 4.

Principle Response Curve Analysis

PRC diagrams for chip depth treatments with the natural treatment as a baseline reference (Fig. 4.5) and the heather control quadrats as a baseline reference (Fig. 4.6) concisely show differences in plant community development over time. The first analysis (Fig 4.5) shows all the treatments moving together from three distinct points. The 'all removed' treatment starts with no wood chip and complete cover of bare peat, giving high PRC1 scores. The 'normal', 'double' and 'triple' treatments all start with 100% cover of wood chip, and the same low PRC1 score in 2001, whilst the natural treatment is a mixture of woodchip, bare peat and litter (zero baseline in Fig. 4.5). It is clear that the 'double' and 'triple' woodchip treatments are moving more slowly towards a fully developed vegetation but that they are still moving in the same direction. By year 3 (2003) the 'double' woodchip treatment is not distinct from the 'normal' and 'natural' treatments but the 'triple' woodchip treatment is still significantly different from most of the other woodchip treatments in years 3 and 4 (2003 & 2004), although it overlaps with the double woodchip treatment (Tmt 2) to some extent. Change on the 'all removed' treatment is occurring at a relatively fast pace compared with the other treatments but this is to be expected as there is no woodchip restricting germination and growth of individual plants.

The analysis that includes the heather control monitoring quadrats as a reference (Fig. 4.6) shows a similar pattern as Figure 4.5 except that all the treatments are now, understandably below the reference line. The differences between treatments are still the same but the diagram provides a clear picture of how far the treatments are from becoming mature blanket bog vegetation.



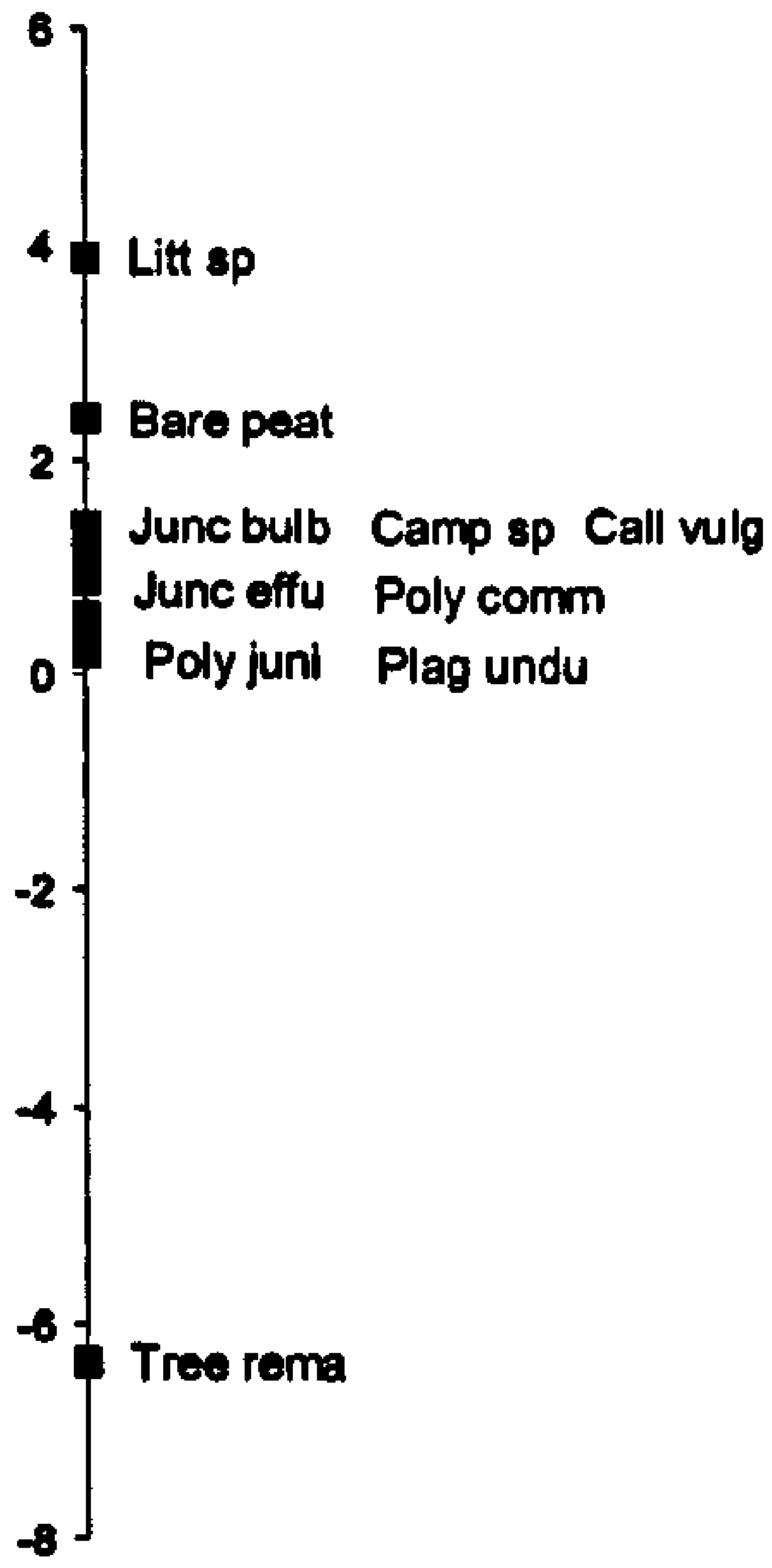
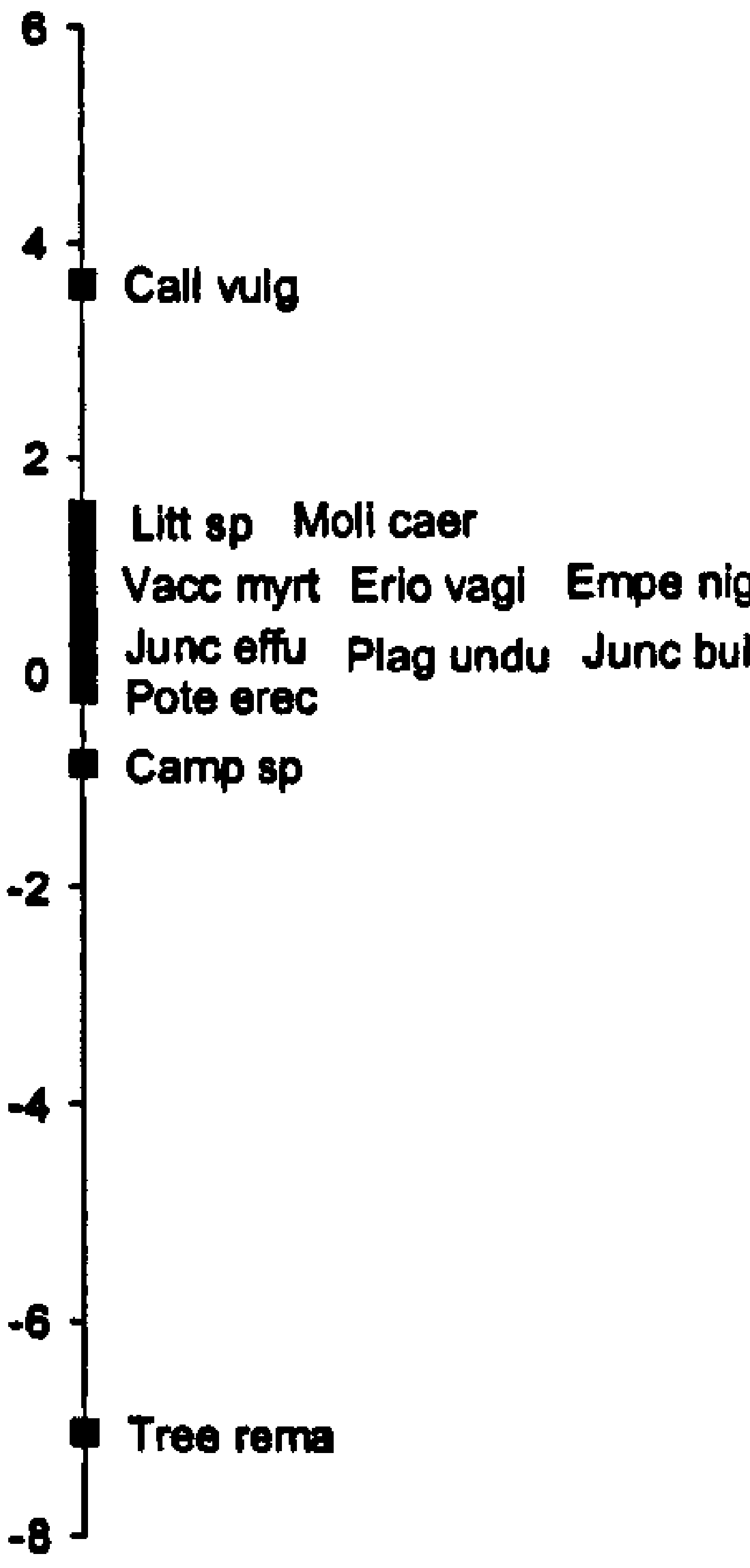
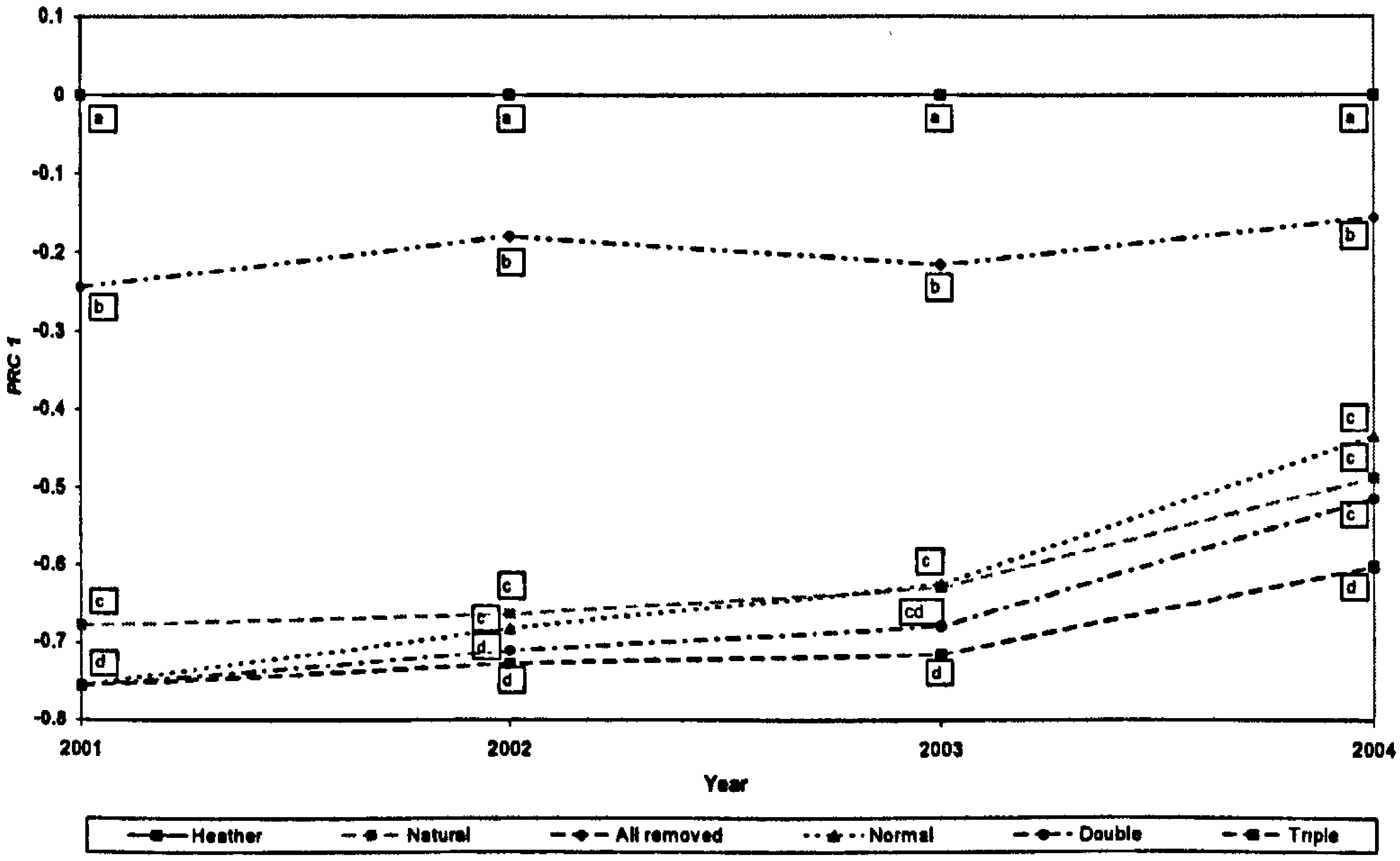


Figure 4.5: PRC diagram and species weights for all chip depth treatments with 'natural' included as the reference. At each year PRC 1 values differ significantly (p<0.008) between treatments that do not share the same letter code (a-c). Shared or omitted letter codes denote contrasts that do not differ significantly.

Figure 4.6: PRC diagram and species weights for all chip depth treatments with heather control monitoring quadrats included as the reference. At each year PRC 1 values differ significantly (p<0.008) between treatments that do not share the same letter code (a-d). Shared or omitted letter codes denote contrasts that do not differ significantly.





4.3.2 Wood chip decomposition

There was no significant difference (p=0.3177) in chip decomposition rate between the four different chip depth treatments; all removed, normal, double and triple. Similarly there was no significant difference (p=0.3213) between the normal and natural control treatment. The similarity in chip decomposition rate between the different treatments is highlighted in figure 4.7 below.

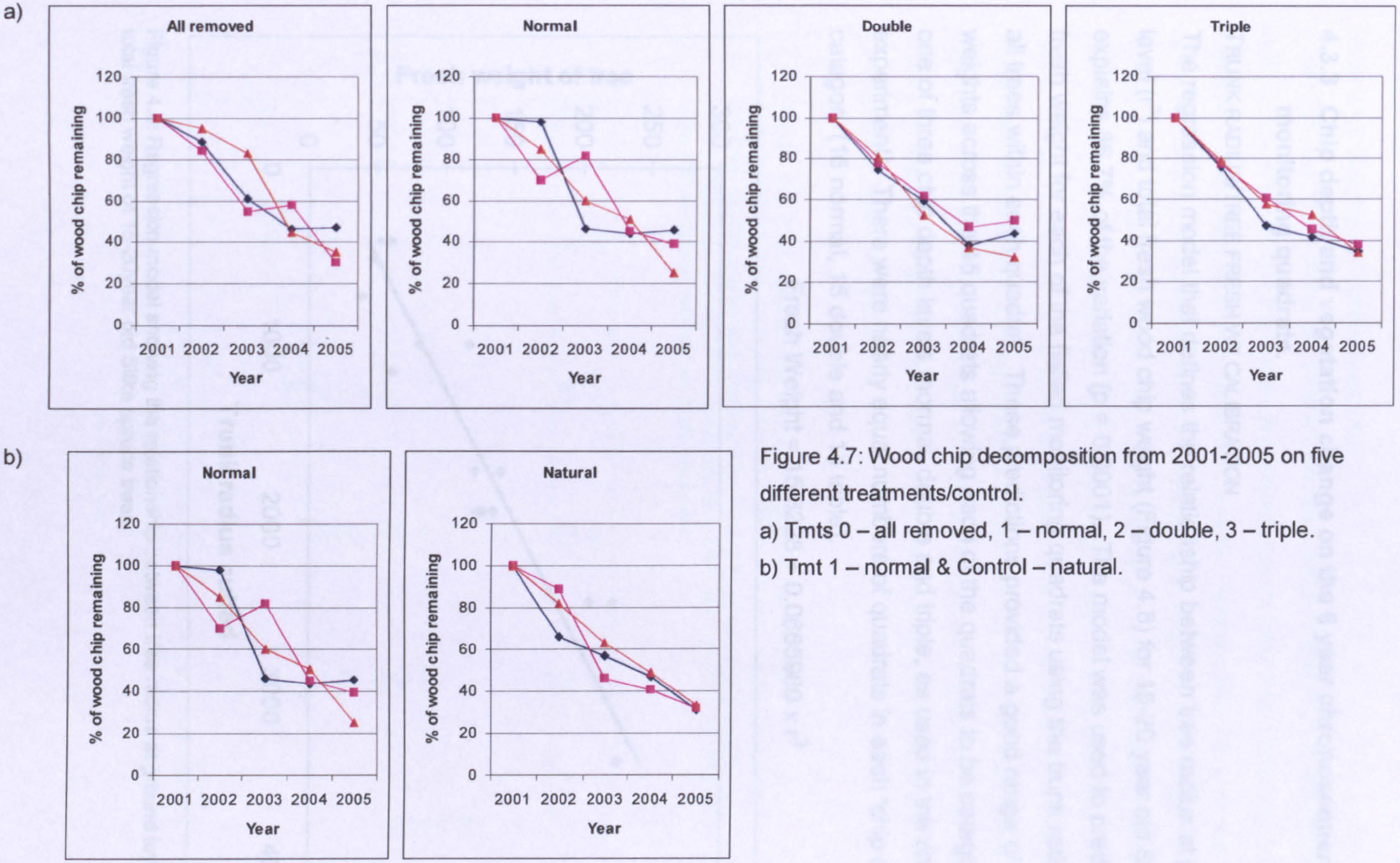


Figure 4.7: Wood chip decomposition from 2001-2005 on five different treatments/control.

a) Tmts 0 – all removed, 1 – normal, 2 – double, 3 – triple.

b) Tmt 1 – normal & Control – natural.

4.3.3 Chip depth and vegetation change on the 6 year chronosequence of monitoring quadrats.

TRUNK RADIUS/TREE FRESH WT CALIBRATION

The regression model that defines the relationship between tree radius at ground level (r^3) and total fresh wood chip weight (Figure 4.8) for 15-20 year old Sitka spruce explains 86.7% of the variation ($p = 0.0001$). The model was used to predict chip fresh weight for each of the flailed monitoring quadrats using the trunk radii figures for all trees within each quadrat. These predictions provided a good range of chip fresh weights across the 45 quadrats allowing each of the quadrats to be categorised into one of three chip depth levels (normal, double and triple, as used in the chip depth experiment). There were nearly equal numbers of quadrats in each 'chip depth' category (16 normal, 15 double and 14 triple).

$$\text{Fresh Weight} = 15.6228 + 0.0665980 \times r^3$$

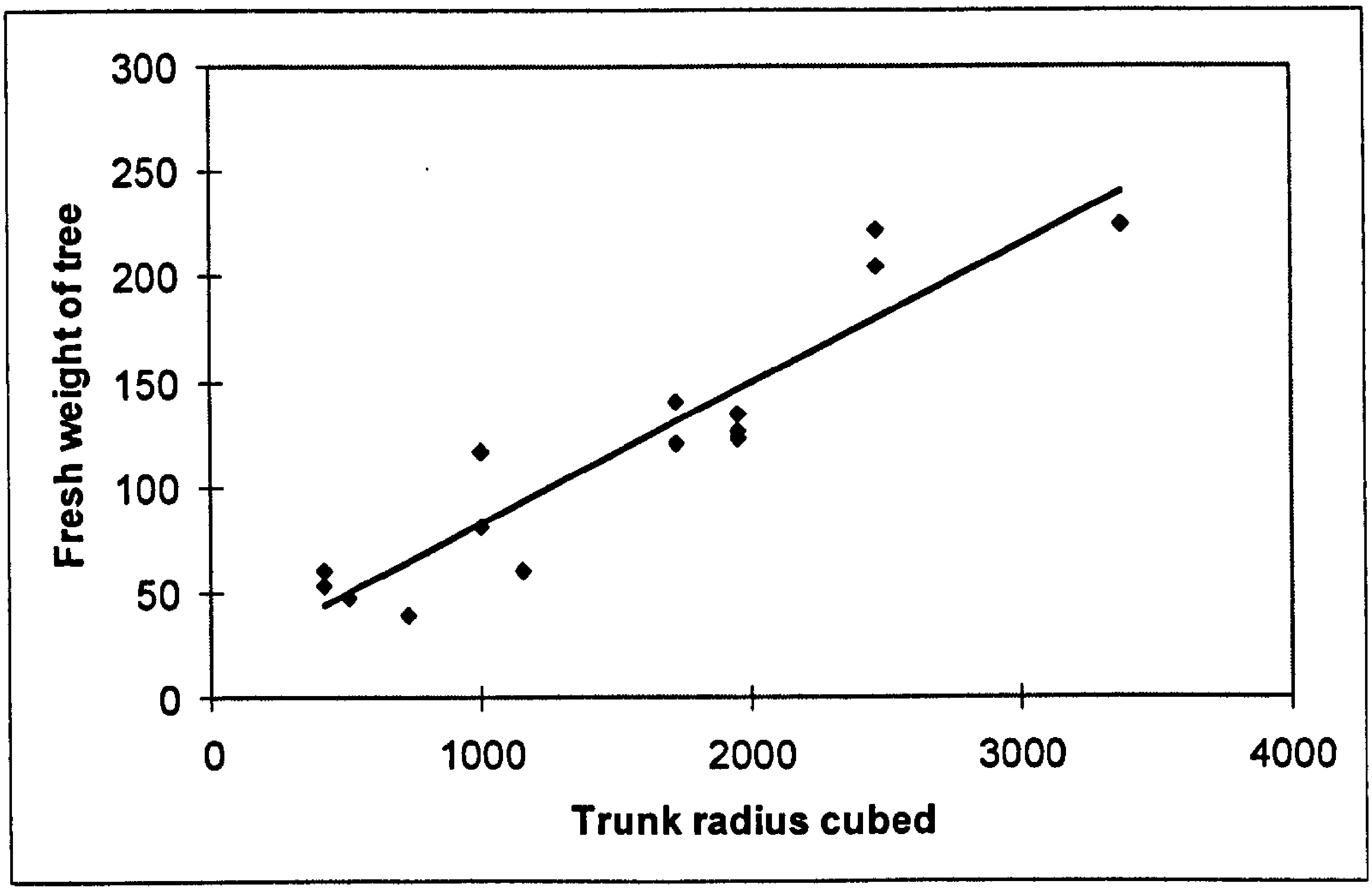
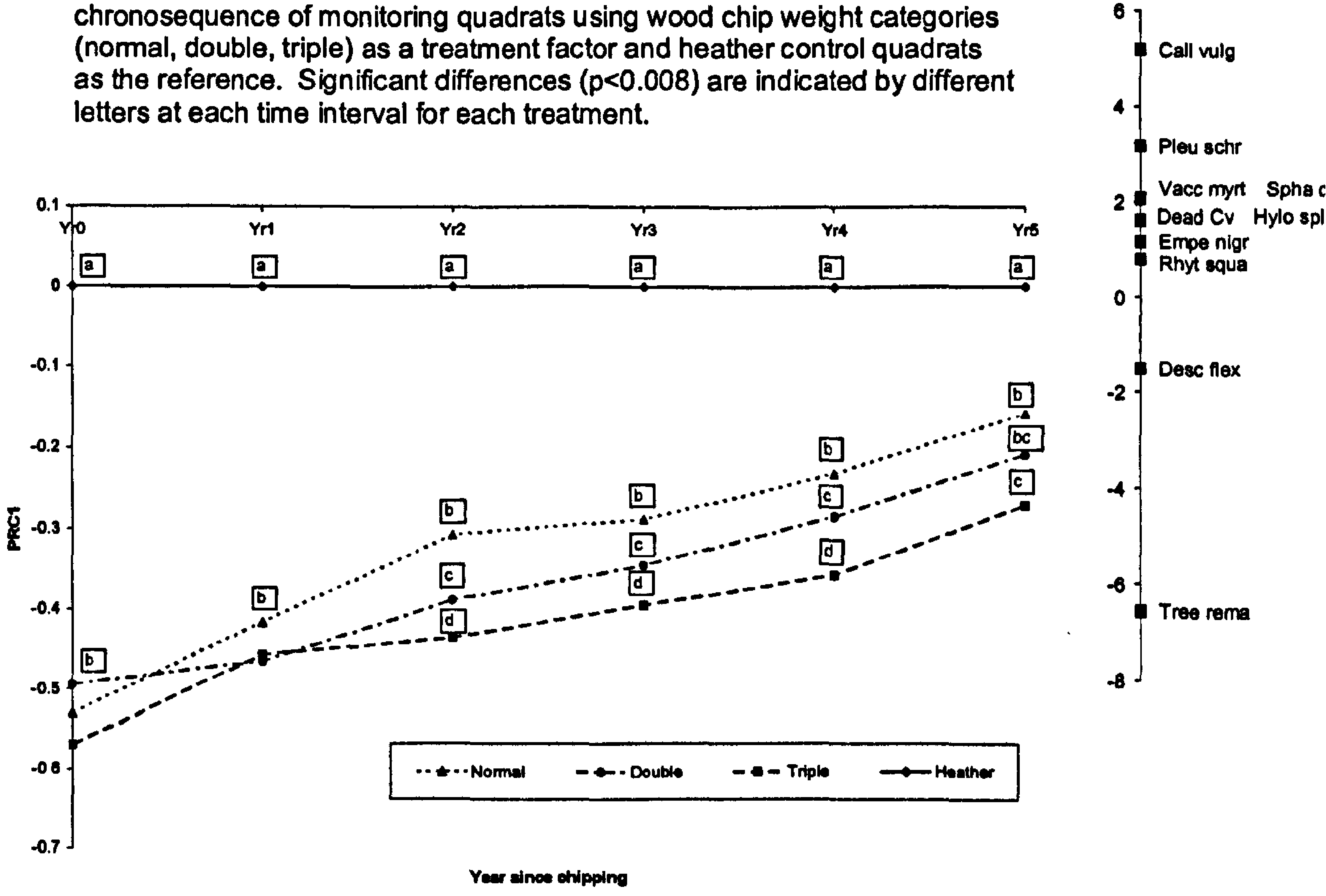


Figure 4.8: Regression model showing the relationship between tree radius at ground level (r^3) and total fresh weight of 15-20year old Sitka spruce trees.

PRINCIPLE RESPONSE CURVE ANALYSIS

The PRC diagram for the six year chronosequence of monitoring quadrats (Figure 4.9) clearly shows how the vegetation development after tree chipping is moving towards the existing heather vegetation on site. Species that are dominant in an M19 plant community (Rodwell et al. 1991) including *C.vulgaris, Pleurozium schreberi* and *Sphagmum capilifolium* have high PRC weightings, near the heather baseline reference, and all three of the wood chip weight/depth categories are moving in the same direction. Apart from a small discrepancy at the beginning (before year 2) the movement toward heather vegetation is consistent for all three treatments and in the expected order with 'normal' most similar to the mature vegetation then 'double' and 'triple'. A significant difference between the treatments emerges in year 2 but starts to disappear again in year 5.

Figure 4.9: PRC diagram and species weights for the six year chronosequence of monitoring quadrats using wood chip weight categories (normal, double, triple) as a treatment factor and heather control quadrats as the reference. Significant differences (p<0.008) are indicated by different letters at each time interval for each treatment.



By fitting a linear regression model to each of the PRC curves in figure 4.9 (Figure 4.10) it is possible to predict the number of years that it might take for the normal, double and triple treatments to reach a state of mature blanket bog vegetation, assuming that rates of change remain constant. These predictions are detailed in Table 4.3 along with the R-squared value for each regression model.

Figure 4.10: Predicted time for blanket bog vegetation to develop under three different chip depths

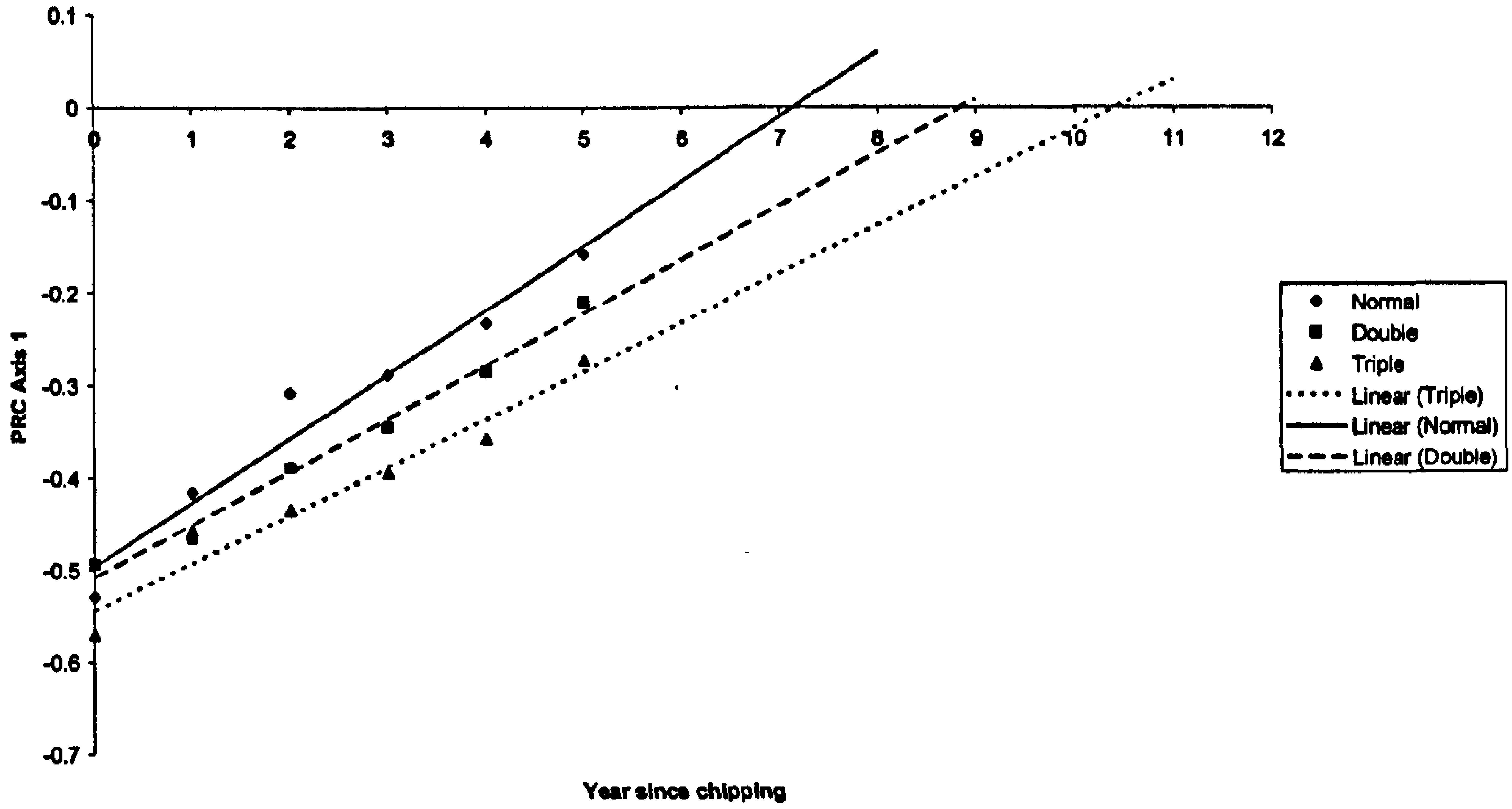


Table 4.3. Predicted number of years, with 95% CI, for mature vegetation to develop under the normal (<12kg/m2), double (12 – 20 kg/m2) and triple (>20kg/m2) wood chip quantities.

Woodchip quantity	R-squared value	Predicted no of years to mature veg.	95% CI	Shortest time to mature vegetation	Longest time to mature vegetation
Normal	98.6%	7.17	0.93	6.25	8.10
Double	99.7%	8.86	0.43	8.43	9.29
Triple	99.3%	10.44	0.77	9.66	11.21

4.4 Discussion

VEGETATION DEVELOPMENT

The restoration of blanket bog vegetation, following 'in situ' chipping of Sitka spruce, planted on former blanket bog habitat, appears to be achievable based on these findings. However the size of the trees, pre clearance, will affect the time taken for the vegetation to reach the target state. As the size of the trees increase, the volume of wood chip left on site after chipping increases and this almost certainly has an inhibitory affect on vegetation development. After four years the plant community on the all chip removed treatment was considerably closer to existing mature blanket bog vegetation than any of the chip treatments. The three chip treatments; normal, double and triple had a predictable effect on plant community development with all treatments moving in the same direction but at different rates. The predicted time to the target plant community under treatments normal, double and triple is 7, 9 and 10.5 years respectively although these are estimates based on rates of change being constant in the extrapolated area. It is possible that rates of change become slower the closer the vegetation succession gets to the blanket bog climax, as with other plant communities (Myster and Pickett 1994; Foster and Tilman 2000), so these estimates should be considered as estimates at the lower end of the potential timescale. 95% confidence limits indicate that these predicted times to target vegetation are significantly different between different chip depths.

The other factor to consider in the restoration of blanket bog vegetation following tree clearance is time since the plantation achieved full canopy cover. When Sitka spruce plantations achieve canopy cover light is totally excluded from the ground and as a result ground vegetation disappears (Taylor 1991). The length of time that vegetation has been absent is likely to affect the composition and size of the propagule bank and this may have implications for the development of the plant community.

There have been a number of studies done on seed banks beneath conifer plantations of different ages (Hill and Stevens 1981; Granstrom 1988; Pywell et al.

2002) although only one of these was done on a blanket bog site (Hill and Stevens 1981). There was undoubtedly a decline in the size of the seed bank with age of plantation, although there were still viable seeds (*C.vulgaris, E.tetralix* and *Carex sp.*) after 43 years. The other two studies were done on heathland sites and the results are conflicting, with studies in the south of England indicating a significant exponential decline in the log transformed number of viable *C.vulgaris* and *Erica sp.* seeds (Pywell et al. 2002). Despite this there were still a small number of viable seeds in the seed bank 70 years after the site was planted. In Sweden a similar study showed no trend in the decline of seed densities with forest stand age (Granstrom 1988) although site conditions may have differed significantly from the previous study. Dominance of *C.vulgaris* seed in the seed bank was a result common to all of the studies and in addition the seed banks were relatively species poor, even under the younger forest stands. Apart from *C.vulgaris* the species that seemed to have some longevity within the seed bank included *Molinia* caerulea, *Erica tetralix, Erica cinerea, Juncus effusus, Juncus squarrosus, Rumex acetosella, Vaccinium myrtillus* and *Potentilla erecta* (Chippindale and Milton 1934; Hill and Stevens 1981; Pywell et al. 2002).

Many bryophyte species have the capacity to form a persistent spore bank (Sundberg and Rydin 2000; Ghorbani et al. 2007) and some species, notably species from the genus *Sphagnum*, can regenerate vegetatively from fragments of leaf or stalk as well as from spores (Clymo and Duckett 1986; Rochefort et al. 1995). Vegetative regeneration has occurred from sphagnum bog peat cores taken up to 30cm below the surface vegetation and representing an age range from 25-60 years (Clymo and Duckett 1986). Some species of leafy liverwort also grew from these peat cores although it was not clear whether they grew from spores or vegetative propagules. It is also suggested that some vascular plants including *E.vaginatum* and *Vaccinium myrtillus* regenerate from vegetative parts found in mires and that this may be the most important method of plant regeneration following disturbance (Jauhiainen 1998). Van der Valk and Davis (1979) suggest that a more appropriate term for a wetland seed bank would be a 'propagule bank' and it is thought that the cool, dark and anaerobic conditions, coupled with the sterility of very acid sphagnum peat may account for seed, spore and vegetative propagule longevity (Clymo 1965; Leck 1989).

Quantity of woodchip on the ground and time since the plantation achieved canopy closure is closely linked but it appears that the depth of woodchip is probably more significant in determining how quickly a blanket bog community develops. Some species never become part of the propagule bank despite being common in the above vegetation (Chippindale and Milton 1934; Miller and Cummins 2003). As soon as canopy cover is achieved and the ground vegetation disappears a number of species are rapidly lost from the propagule bank (Chippindale and Milton 1934; Hill and Stevens 1981; Pywell et al. 2002; Ghorbani et al. 2007) . Those species that have any long term viability in the propagule bank are likely to remain viable, at some level, for a number of decades and at least for the first rotation (as is the case on the tree clearance area), which is 45-55 years for Sitka spruce (Anonymous 1981). Provided conditions are conducive to germination and growth after the trees have been removed, these species will be the first plants to grow and influence plant community development. Seeds and spores will undoubtedly move into a newly cleared area from neighbouring mature vegetation, either through wind or animal dispersal, but this will depend on the dispersal mechanism which may not be immediate. It is likely, therefore, that ingression of seeds will increase species diversity of the developing plant community over a reasonably long period of time.

On the experimental plots the average number of species found on each of the treatments; natural, all removed, normal, double and triple, one year after the treatments were applied, were 9.7, 13.4, 10, 8.4 & 3.6 respectively. Given that the propagule bank and distance to existing seed sources would have been roughly the same for all the plots it is clear that increasing wood chip depth had an inhibitory affect on plant germination and establishment. *Potentilla erecta, Hypnum cupressiforme, Campylopus sp.* and *Rhytidiadelphus loreus* were found on all of the treatments one year after the treatments were applied. All these species have demonstrated persistence in a peat propagule bank (Hill and Stevens 1981; Ghorbani et al. 2007) and it appears that they do not require much, if any, sunlight to stimulate germination and growth. *C. vulgaris* is well known for requiring sunlight to stimulate seed germination (Pons 1989) but this species was certainly present on some of the deepest chip depth treatment plots in year one. It can only be assumed that seed had worked its way into the chip layer during the raking and re-distribution of chip as experimental treatments.

There were four plant species, *Molinia caerulea, Vaccinium myrtillus, Juncus bulbosus* and *E.vaginatum,* that only occurred consistently in year one on the all chip removed treatment. The first three species could have germinated from seed although if this was the case then it should have appeared on the other treatments which it did not. *E.vaginatum* shows no persistence in the seed bank (Miller and Cummins 2003) so either seed was brought in by wind or the plants grew from vegetative propagules as described by Jauhiainen (1998). Raking of chip from the experimental plots did involve a considerable amount of disturbance to the peat surface and this may have exposed vegetative propagules. Since no wood chip was returned to the 'all removed' treatments all vegetative propagules at the peat surface would have been exposed to a high level of light and peat surface warming. These are the conditions that triggered immediate growth from vegetative propagules in degraded mire peat samples and this method of propagation was thought to be the most important for restoration of degraded mire (Jauhiainen 1998).

WOOD CHIP TREATMENTS AND FOREST AGE/SIZE

The chip depth treatments, normal (8kg/m^2), double (16kg/m^2) and triple (24kg/m^2) roughly equate to a Sitka spruce plantation that is 20 years old, with a yield class of 10, 12 & 14 respectively. The UK average yield class for Sitka spruce is 12 with a range between 6 and 24 (Hibberd 1991) and the range on the tree clearance area was thought to be 6-14. An alternative way of looking at what the chip depth treatments represent would be to fix the yield class at 10 and the normal, double and triple chip treatments would represent trees at 20, 25 & 30 years old.

Yield class, the maximum mean annual increment of one hectare of forest plantation (m^3/ha/yr), is determined from top height/age curves published by the Forestry Commission (Anonymous 1981). The top height in a stand of trees is a very specifically defined measurement that is calculated by selecting a defined number (depending on stand area) of trees that have the largest diameter at breast height. The average height of these trees is the top height of the stand. Top height data were obviously not available for the different chip depth treatments but height data was collected for the trees used in the trunk radius/tree fresh weight calibration exercise. These data were used to determine an approximate yield class for 20 year old trees that would have produced the three chip depth treatments. The majority of the trees on the tree clearance area were 20 years old when they were cleared.

It was not considered necessary to have a chip depth treatment that represented older trees because by this time it would probably be economically viable to extract the timber for paper pulp, particle board or biomass heat/electricity generation (Sheridan *pers. comm.*). This would be a more cost effective way of clearing forest to restore blanket bog as some of the costs would be covered by selling the timber. Similarly, a chip depth treatment to represent younger trees or lower yield classes was not included as the trees are unlikely to have achieved canopy cover. As a result a certain amount of ground vegetation would still be present. In this situation chip depth and distribution would be patchy and unlikely to inhibit growth or germination to a great extent.

SPECIES RESPONSE

At a plant community level the vegetation on the experimental plots appear to be moving in the same general direction, irrespective of treatment. A DCA ordination was done using only 2004 data to explore the possibility that different treatments might lead to the development of different plant communities. This ordination produced no distinct groups of vegetation on either the first or second axis and this is not too surprising given that all the plots were in the same location and likely to develop into a similar plant community.

Given that the plant community is moving in the same direction on all the treatments, albeit at different rates, one might expect the same sort of response from individual species within the plant community. To a large extent this was the case with the cover of *C. vulgaris, P. commune/formosa, E. vaginatum, D. flexuosa* and *H. cupressiforme* all increasing over the four year experiment. There were treatment differences for the first three species, particularly *C. vulgaris* and *P.commune/formosa,* with the increase in cover occurring more slowly as the wood chip became deeper. This was also the case with *E. vaginatum* but the treatment differences were not so obvious. It seems highly likely that these three species appeared from the propagule bank and that they all require some level of light to initiate germination and growth. As the chip depth increases, levels of light reaching the peat surface decrease having an inhibitory effect on growth and establishment.

Deschampsia flexuosa and *Hypnum cupressiforme* showed no treatment differences and cover increased at exactly the same rate on all treatments. Interestingly enough neither of these species appeared on any of the plots until year two suggesting perhaps that they did not originate from the propagule bank but were introduced through wind dispersal from nearby mature blanket bog vegetation. *D.flexuosa* seed is noted for its transient nature within a seed bank, rarely persisting for longer than one year (Hodgson et al. 1995) so introduction through wind dispersal seems the most obvious explanation. There is no information available relating to dispersal of *H. cupressiforme* spores but it is an extremely common moss (Watson 1981) so it is highly likely that the species produces and disperses spores very effectively. If seeds and spores of *D. flexuosa* and *H.cupressiforme* were introduced during the first year then the chip depth treatment may be irrelevant if the seeds/spores could germinate in the woodchip. This is certainly possible as the chipping process projected wood chip down towards the ground at high speed so there would inevitably be some mixing of peat and woodchip and this would provide a substrate for seed and spore germination.

The response of *Campylopus sp* was slightly different to the other species investigated although it was in keeping with reports that this genus is a primary coloniser of bare peat (Watson 1981; Equihua and Usher 1993). On the shallower chip depth treatments (all removed, normal and natural) *Campylopus sp.* showed a unimodal response, increasing in cover exponentially during the first two years and then starting to decrease in years three or four. On the deeper chip depth treatments (double and triple) the species increased more slowly and did not start to decrease in cover during the four year experiment. Given the response curves for the other five species it seems likely that Campylopus sp. colonised areas of bare peat very quickly and then started to die out as other species began to compete for resources. On the deeper chip treatments the colonisation potential was limited and other species did not increase in cover as quickly so there was less competition for resources.

WOOD CHIP DECOMPOSITION

The rate of wood chip decomposition did not appear to be influenced by chip depth in any way. This is surprising given that microclimatic factors, such as moisture and temperature have been shown to have a high level of influence on the decay rate of wood (Abbott and Crossley 1982) and forest litter (McClaugherty et al. 1985). Although the TinyTag temperature loggers were unreliable and did not provide a data set that was suitable for statistical analysis, they did provide an indication of the temperature fluctuations on the all chip removed and shallow chip treatments compared to the deeper chip treatments. For example on a warm summer day surface temperatures frequently reached 35-40°C on the all chip removed treatment but never exceeded 15°C on the triple chip treatment. In addition, wood chip (in the chip decomposition bags) on the all chip removed treatment was found to be completely dry on several occasions in the summer but on the triple chip treatment it never dried out. However, it appears that the most important factor affecting decomposition of wood and woody litter is the level of microbial abundance and activity (Abbott and Crossley 1982; McClaugherty et al. 1985). Other factors such as temperature and moisture influence decomposition because they affect microbial activity. This suggests that the temperature and moisture fluctuations on the different chip depth treatments were not for sufficiently long periods to significantly affect microbial activity. Weather conditions on the tree clearance area were generally wet and cool for most of the year which is typical for the west of Britain (Lindsay 1995) so the extreme temperatures recorded on the Tiny Tag loggers were only on hot sunny days, which are relatively infrequent in Kintyre. If the climatic conditions were different with lower summer rainfall then perhaps the wood chip decomposition rates would differ between treatments.

Although decomposition of woodchip occurred at the same rate the impact of this on the different treatments may have been different. Romero et al (2005) found that the first two month period following deposition of coarse woody debris in mangrove forest was characterized by rapid loss of mass as labile components were leached out of the wood. After this initial period and for a few years the wood served as a sink for nitrogen and phosphorus (Romero et al. 2005) with microbial activity fuelled by nutrients from substrates surrounding the wood. If there had been a similar decay response for wood chip on the experimental plots the all chip removed treatment would not have received the initial pulse of nutrients leached from the wood chip but similarly a higher level of nutrients would be available for plant growth throughout the first few years following tree clearance. As the amount of wood chip increased on chip depth treatments double and triple this may well have increased the size of the nitrogen and phosphorus sink. Further research would be required to determine what ecological processes occur when Sitka spruce wood chip decomposes on blanket bog but if nutrients are tied up in the decay process then growth of vegetation may be inhibited by nutrient supply as well as the physical obstruction posed by a layer of wood chip. This may help to promote the development of an ombrotrophic vegetation community which is known to have a very low nutrient requirement (Anderson 2001).

Restoration of forested blanket bog sites through 'in situ' chipping of trees is certainly affected by tree size. This is mainly due to the quantity of wood chip that is left on site rather than the impact that tree size has on ground vegetation and the associated propagule bank. The physical barrier that is created by the wood chip inhibits many species although different species respond differently to chip depth and this is thought to be due to their individual requirements for light to stimulate growth. As a result tree size affects the time taken for a blanket bog plant community to establish but it appears to have no effect on plant community composition.

CHAPTER 5

MICROSITE VARIATION AND THE EFFECT ON GERMINATION AND GROWTH OF CALLUNA VULGARIS

5.1 Introduction

Factors affecting species distribution at a small scale (1x1metres) have been described in terms of seed availability / dispersal and the presence of suitable micro-sites for germination and growth (Munzbergova and Herben 2005; Calvino-Cancela 2007). There is a gradient from full seed limitation to full micro-site limitation, with each species population lying somewhere in between (Munzbergova and Herben 2005). *C. vulgaris* is known to produce copious amounts of seed (Legg et al. 1992; Barclay-Estrup and Gimingham 1994) which accumulates in the soil to form a long-lived seed bank (Granstrom 1988; Miller and Cummins 2003). Cummins and Legg (1995) estimated a lifespan for *C.vulgaris* seed of 150 years in blanket peat. Although no work has been done to investigate the spatial distribution of *C.vulgaris* seed in blanket peat it seems highly likely that it will be ubiquitous where the species has been a dominant component of the vegetation cover within the recent history of the site.

The term micro-site has been used to describe the local growing environment for seeds and seedlings (Dalling and Hubbell 2002; Calvino-Cancela 2007; Balogh Benard and Toft 2008) and it includes several different aspects of the environment, ground substrate conditions, the influence of other plant species and the fine scale topography, or micro-topography of the ground surface. Micro-topography describes soil surface variation encompassing both vertical relief (variation in absolute elevation) and surface roughness (Moser et al. 2007). Micro-topography can influence hydrology, physiochemistry and other aspects of micro-site variability and it is therefore important in determining vegetation patterns (Moser et al. 2007). The germination requirements of species vary widely and consequently, the array of micro-sites offered on any natural surface will favour some species more than others (Harper et al. 1965). In addition it is important to remember that the nature of micro-sites will change throughout the year as weather conditions vary (Sheldon 1974).

A number of researchers have investigated the effect of micro-topography on seed germination and seedling growth of a wide range of species (Harper et al. 1965; Sheldon 1974; Calvino-Cancela 2007; Balogh Benard and Toft 2008) and small changes in seed placement, in relation to micro-topography, can have dramatic effects on germination and establishment (Harper et al. 1965; Sheldon 1974). It is particularly important for surface lying seeds (Sheldon 1974) which are constantly subjected to weathering processes such as drying, wetting and frost. *C.vulgaris* requires some sunlight to stimulate germination (Gimingham 1972) so seeds will only germinate if they are on or close to the peat surface. It also depends on an adequate and maintained water supply (Gimingham 1960) so a ground substrate that reduces the chances of extreme drying is likely to improve survival for germinating seeds and new seedlings. This was shown by Equiha and Usher (1993) when investigating the effect of carpets of *Campylopus introflexus* on germination and growth of *C.vulgaris.* Presence of the moss had a significant negative impact on germination but a positive effect on post germination performance of seedlings. The depressive effect of the moss on germination was because a large number of seeds slipped into the moss carpet and thus were deprived of light. This indicates that although moss carpets of *C.introflexus* offer a potential water supply buffer for seedlings they do not provide good micro-sites for germination (Equihua and Usher 1993) and this is likely to be the case for a number of other moss species.

Increased species diversity is often associated with greater environmental heterogeneity (MacArthur and MacArthur 1961; Tilman 1982) and micro-topographic variation has been strongly correlated with plant distribution, performance of individual plant species and floristic diversity (Harper et al. 1965; Sheldon 1974; Eldridge et al. 1991; Vivian-Smith 1997). Small scale (1-3cm) variability in micro-topography on experimental wetlands produced highly significant differences in plant community structure with diversity, richness and evenness consistently greater in communities with more heterogeneous micro-topography (Vivian-Smith 1997).

No specific research has been done to explore the effect of micro-topography on germination and growth of *C.vulgaris* although work has been done on a variety of other plant species either to investigate the behaviour of seeds (in general) in relation micro-topography (Harper et al. 1965; Sheldon 1974) or to investigate the establishment of specific species, usually in arid environments (Eldridge et al. 1991; Nash et al. 2004; Calvino-Cancela 2007; Balogh Benard and Toft 2008). There is also a considerable body of research relating to wetland micro-topography in restored wetlands both in relation to wetland function (Bruland and Richardson 2005) and species richness or diversity (Vivian-Smith 1997; Moser et al. 2007). In many ecological studies micro-topography is described qualitatively with descriptors such as hummock, hollow and flat (Bruland and Richardson 2005), windward and lee aspects of interspaces between shrubs, under shrub canopies and under snag canopies, respectively (Balogh Benard and Toft 2008) and 'open ground', 'underneath female shrub', 'underneath male shrub' (Calvino-Cancela 2007). Alternatively, micro-sites have been simulated at a relatively large scale by applying treatments such as litter addition or removal and ground disturbance (Edwards and Crawley 1999; Dalling and Hubbell 2002). Relatively few ecological studies have measured micro-topography quantitatively (Werner and Zedler 2002; Nash et al. 2004; Moser et al. 2007) although these investigators have used a variety of techniques that were originally developed for use in tillage and water erosion research where it is important to measure soil surface variation at a very small scale. The most appropriate method for calculating surface roughness at the scale of a 1x1m quadrat on blanket peat is a method used by Moser (2007) where the spatial distance (up and down slopes) between two points is divided by the planar distance (from one point to another assuming they are at the same relative height).

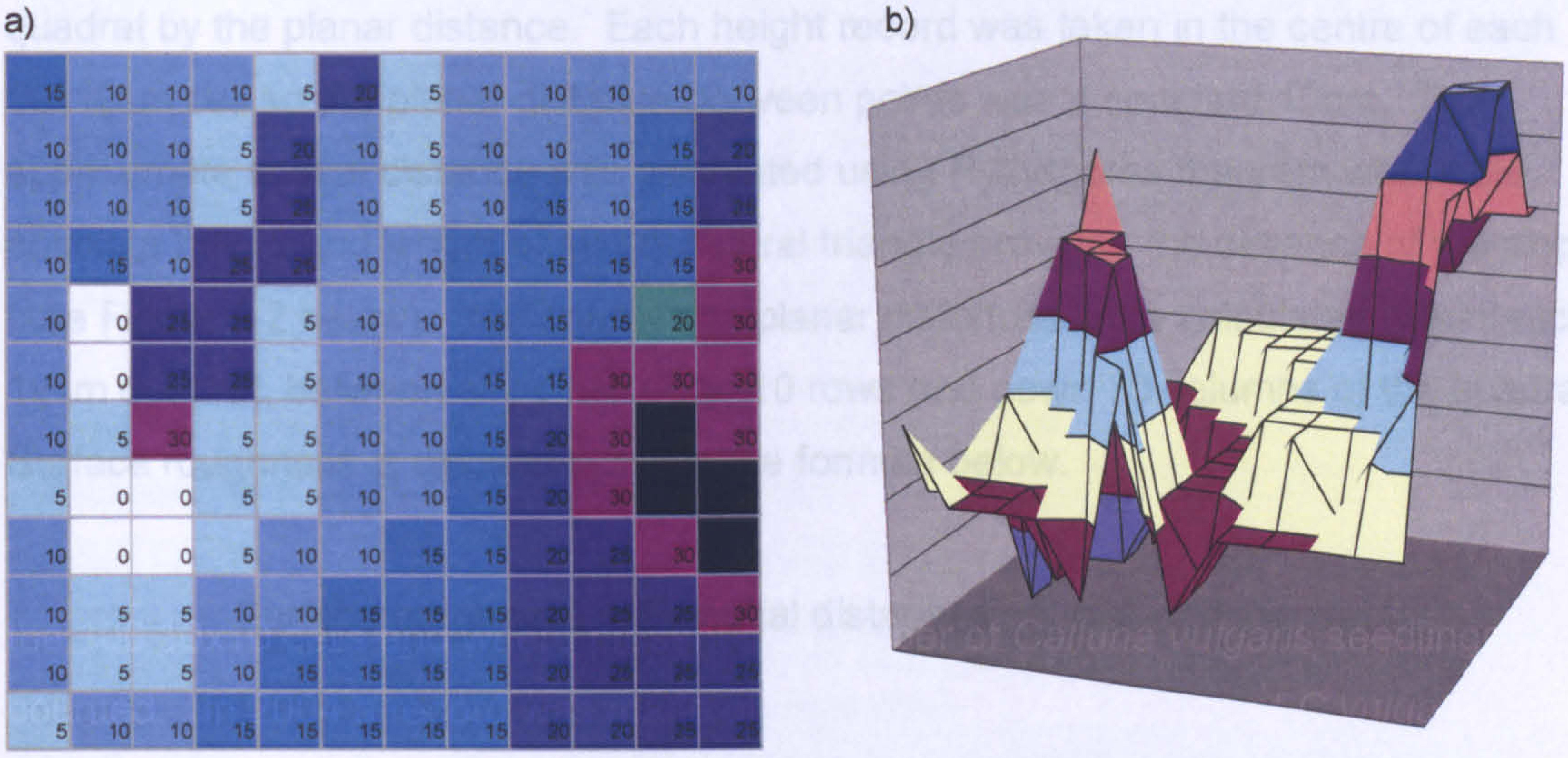
The aim of this investigation was two fold, firstly to determine how differences in micro-site influence germination, growth and survival of *C.vulgaris* seedlings. The description 'micro site' is used to define small scale topographical variations in the peat surface (micro-topography) as well as the dominant vegetation type which will influence resource availability for developing seedlings. Micro-topography and dominant vegetation was assessed at the cell level (10x10cm) and analysed at both the cell and quadrat level (1x1m). Since micro-topography, at the quadrat level, is a relatively complex thing to measure five different methods for quantifying the soil surface height diversity are compared. The assumption that *C.vulgraris* seed is ubiquitous across the tree clearance area forms the basis of this work.

The second aspect of this investigation was to explore the hypothesis that coexistence is facilitated in heterogeneous environments (Tilman 1982; Keddy 1984; Sterling et al. 1984) by investigating the relationship between species richness or diversity of plant communities and the mico-topography of the peat surface. Again the five measures of soil surface height diversity were used to explore the relationship between micro-topography and species diversity.

5.2 Materials and Methods

DATA COLLECTION

Sampling design, quadrat set up and relocation is described in detail in Section 2.3.1. In 2002 a series of micro-site assessments were made in each of the middle mini-quadrats on flailed and harvested ground (48 mini-quadrats). A 1x1m quadrat with 100 10x10cm cells, on adjustable legs, was placed over the mini-quadrat location and a spirit level used to adjust the legs so that the quadrat was level above the miniquadrat. A 1m measuring stick was used to measure the vertical distance from the level quadrat to the ground. 144 measurements were taken, one in the middle of each of the 100 10x10cm cells of the quadrat with an additional measurement creating a buffer around the quadrat, essentially making the quadrat 120x120cm in size. The measured distances were adjusted so that the lowest point of each quadrat, within the 120 x 120 area, was recorded as zero. Measurements were recorded in height bands with each band representing a 5cm range so 0=0, 5=1-5cm, 10=6-10cm and so on providing a micro-topographical map of each quadrat, as shown in Figure 6.1 below. In addition to the micro-topography data the dominant plant species or ground type (bare peat, litter, tree remains) was recorded for each of the 100 10x10 cells and where present the number of *Calluna vulgaris* seedlings was counted. In 2004 a record was made of the presence or absence of *C.vulgaris* plants in each of the 100 10x10cm.



15	10	10	10	5	20	5	10	10	10	10	10
10	10	10	5	20	10	5	10	10	10	15	20
10	10	10	5	25	10	5	10	15	10	15	25
10	15	10	25	25	10	10	15	15	15	15	30
10	0	25	25	5	10	10	15	15	15	20	30
10	0	25	25	5	10	10	15	15	30	30	30
10	5	30	5	5	10	10	15	20	30		30
5	0	0	5	5	10	10	15	20	30		
10	0	0	5	10	10	15	15	20	25	30	
10	5	5	10	10	15	15	15	20	25	25	30
10	5	5	10	15	15	15	15	20	25	25	25
5	10	10	15	15	15	15	15	20	20	25	25

Figure 6.1a & b: Microtopographical map of a quadrat a) Two dimensional diagram 'looking down' on to the quadrat, including heights relative to the lowest point (zero)

b) Three dimensional diagram showing variation in heights relative to lowest point.

DATA ANALYSIS

The data were analysed at two different scales, first at the quadrat level and then at the individual cell (10x10cm) level.

Quadrat level

A series of analyses or calculations were performed in order to 'characterise' the micro-site profile of each quadrat. Firstly, ordination was employed as a data reduction tool to provide a predictor variable for regression analysis (Beals 2006; Watts et al. 2008). In general ordination is used descriptively to explore continuity of species change within a plant community but here the categorical height data for each 10x10cm cell was incorporated into a DCA analysis with height categories treated as species and quadrats as samples. A similar analysis was done using the dominant species/ground cover data and the DCA Axis 1 and 2 scores for each analysis were used as 'quadrat characters' of micro-topography and dominant species composition respectively. Secondly, the 'roughness' (Moser et al. 2007) of each quadrat was calculated by dividing the spatial distance between all points in the quadrat by the planar distance. Each height record was taken in the centre of each 10x10cm cell so the planar distance between points was a constant 10cm. The approximate spatial distance was calculated using Pythagoras theorem where the absolute height and length of an equilateral triangle provides the distance of the slope (see Figure 6.2 below). 180 spatial and planar distances were calculated within each 1x1m quadrat, between all points along 10 rows and down 10 columns of the quadrat. Surface roughness is calculated using the formula below.

$$\text{Surface roughness} = \sum \text{spatial distances} \, / \sum \text{planar distances}$$

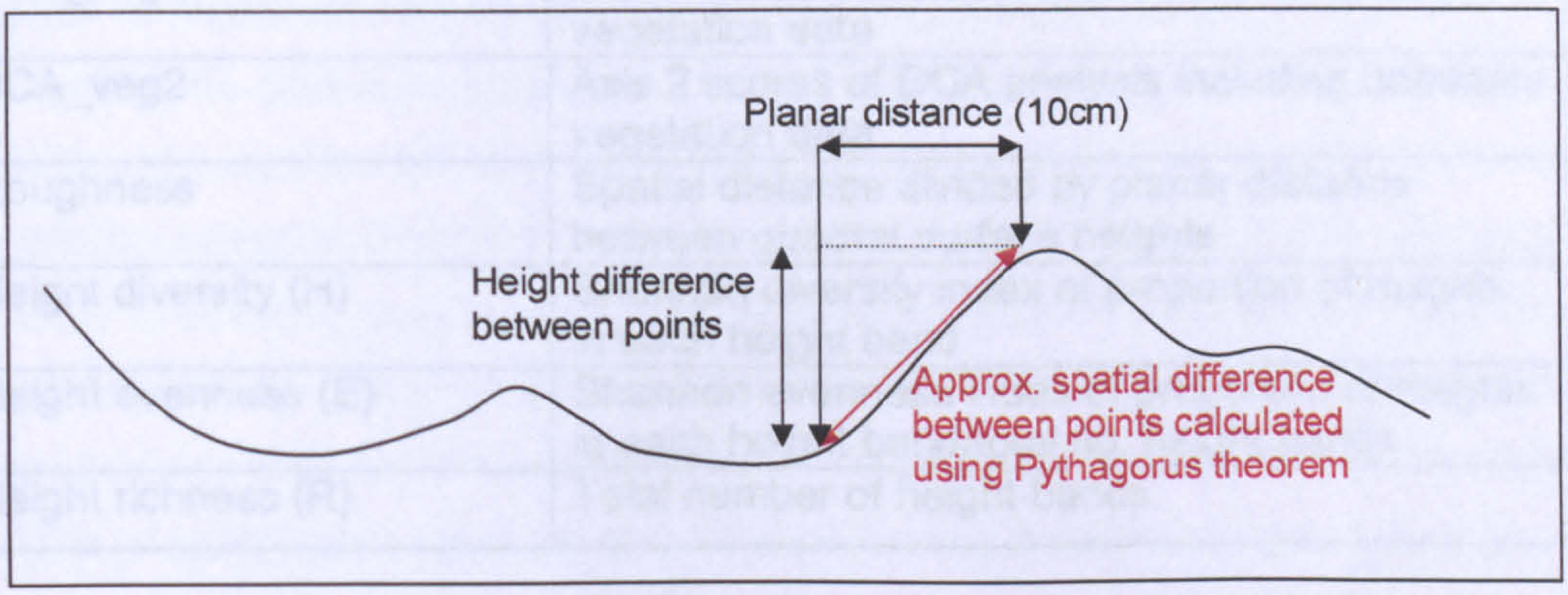


Figure 6.2: A schematic diagram showing the measurements required for the calculation of surface roughness.

Lastly, height diversity, evenness and richness of each quadrat was calculated using the Shannon diversity Index and Shannon evenness index shown below. Height richness equates to the total number of height bands in each quadrat.

$H' = -\sum p_i \ln p_i$ $\quad$ $E = (-\sum p_i \ln p_i)/n$ height bands

Where p_i is the proportion of heights in each i'th height band

The micro-site profile characters are summarised in Table 6.1 and different combinations of these characters were included within a series of multiple regression analyses to explore the effect of micro-site on total number of *C.vulgaris* seedlings in 2002 (cv seed), *C.vulgaris* presence in 2004 (cv present) and species diversity/richness of the plant community in 2004 (species H and species R respectively). The species diversity and richness indices were calculated using the percentage cover data for all species present in the quadrat in 2004.

Table 6.1: Summary of the quadrat-level microsite profile characters

Microsite profile character	**Description**
DCA_ht1	Axis 1 scores of DCA analysis including quadrat surface height data
DCA_ht2	Axis 2 scores of DCA analysis including quadrat surface height data
DCA_veg1	Axis 1 scores of DCA analysis including dominant vegetation data
DCA_veg2	Axis 2 scores of DCA analysis including dominant vegetation data
Roughness	Spatial distance divided by planar distance between quadrat surface heights
Height diversity (H)	Shannon diversity index of proportion of heights in each height band
Height evenness (E)	Shannon evenness index of proportion of heights in each height band/total no. height bands
Height richness (R)	Total number of height bands

Cell level

A mean weighted height figure was calculated for each cell. This was done by subtracting the heights in each of the 8 neighbouring cells around a cell from the height in the cell. The mean weighted height was calculated from the 8 individual subtraction calculations. The dominant vegetation types in each cell were categorized into 11 different categories: 1.bare peat, 2.*Campylopus sp,* 3.*C.vulgaris,* 4. *Eriophorum vaginatum,* 5. fine leaved grasses, 6. herbs, 7. litter, 8. moss, 9. tall sedges/grasses, 10. *Sphagnum sp,* 11. tree remains.

Initially the number of *C.vulgaris* seedlings in each cell in 2002 was subjected to a series of generalised linear models with negative binomial or poission distribution in order to control for the large number of zeros in the response data. Of the 4800 cells only 536 cells contained *C.vulgaris* seedlings. However, an appropriate residual error distribution could not be found due to zero inflation of the data which caused serious over dispersion in the residuals. As an alternative the data set was reduced to the 536 cells that contain the *C.vulgaris* seedlings. These data were subjected to linear mixed effects modelling (Pinheiro and Bates 2000) to test the effect of weighted height and dominant vegetation category (micro-site) on the extent of *C.vulgaris* germination where germination had occurred in 2002. The number of seedling data were log transformed (log(seedling no +1)) and the LME model fitted included fixed and random effects. The model included weighted height and 11 levels of dominant vegetation category as fixed effects and quadrat as the grouping variable for estimating random effects.

In order to explore the presence/absence of *C.vulgaris* (cv seedlings) in 2004 three versions of the data were subjected to binary regression analysis. The predictor variables included in each of the initial models were cv seedlings in 2002, dominant vegetation category, weighted height index and cv patch. Cv patch was calculated from the cv seedling data based on the assumption that if *C.vulgaris* seedlings exist in a cell they are more likely to grow in neighbouring cells because the micro-site characteristics are more likely to be similar. To calculate a cv patch index the total number of seedlings in each cell and the surrounding 8 cells were summed and divided by the total number of seedlings that could have been found in those 9 cells, which was 144. The largest number of seedlings found in any of the cells was 16 so the maximum potential number of seedlings in 9 cells was assumed to be 144. Cells that contained no seedlings could have a cv patch index if one or more of the 8 surrounding cells contained seedlings. As a result the number of cells with a record of cv increased from 536 cells containing cv seedlings to 1542 cells that were within a 'cv patch'.

The first data set used in the binary regression analysis included those samples where *C.vulgaris* seedlings were present in 2002 (536 samples). Therefore this analysis looked specifically at survival of seedlings between 2002 and 2004. The second data set included those samples with a cv patch index in 2002 (1542 samples) so this analysis explored the relationship between micro-sites that are most likely to support *C.vulgaris* germination and those that continue to provide a good environment for establishment and growth of *C.vulgaris* seedlings. The final analysis included all cells (4800 samples) and provides a detailed picture of the types of micro-sites where *C.vulgaris* will become and will not become successfully established. The final analysis included data with approximately five times as many zeros as ones in the response variable and a large number of zeros in two of the predictor variables, cv seed and cv patch. However, this is not considered to be a problem as zero inflation of the residual error distribution and associated over dispersion of residuals does not exist with binary regression (Crawley 2002).

5.3 Results

5.3.1 Quadrat level

Figure 6.4 shows results for the cell height DCA analysis where Axis 1 represents an increasing range of variation in height across the quadrat as axis scores increase. Axis 2 distinguishes between quadrats that have high height diversity but the height bands do not exceed 45cm and quadrats of high height diversity including some heights between 50-75cm i.e. Axis 2 score decreases when height extremes (>50cm) are included in the quadrat. The ordination diagrams in Figure 6.5 shows results for the dominant vegetation DCA analysis where Axis 1 is related to cover of woodchip and scores are highest when most of the cells have tree remains as the dominant ground cover. Axis 2 defines a wet to dry wet gradient as scores increase.

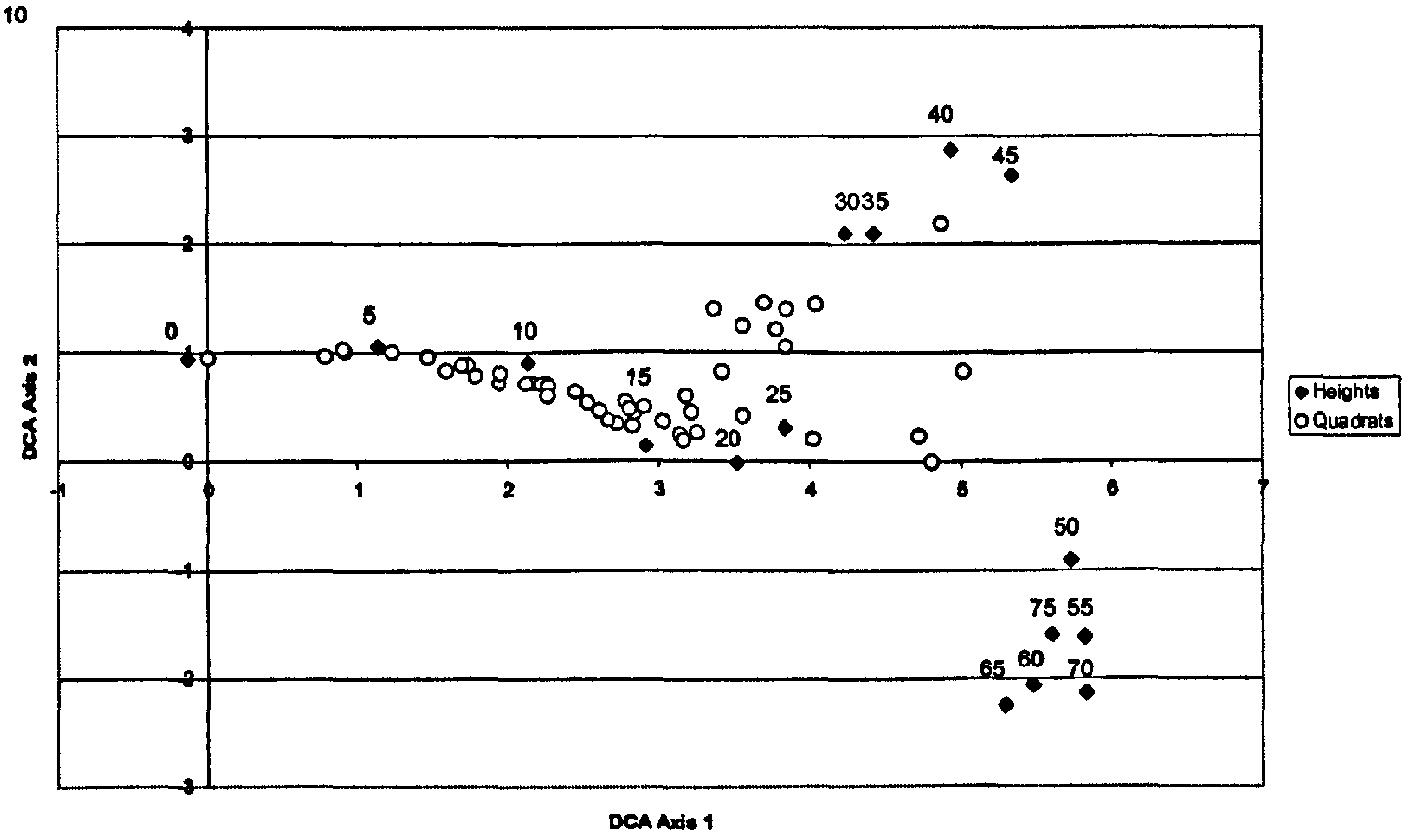


Figure 6.4: Height x quadrat (species x sample) ordination biplot of DCA Axis 1 and 2 scores.

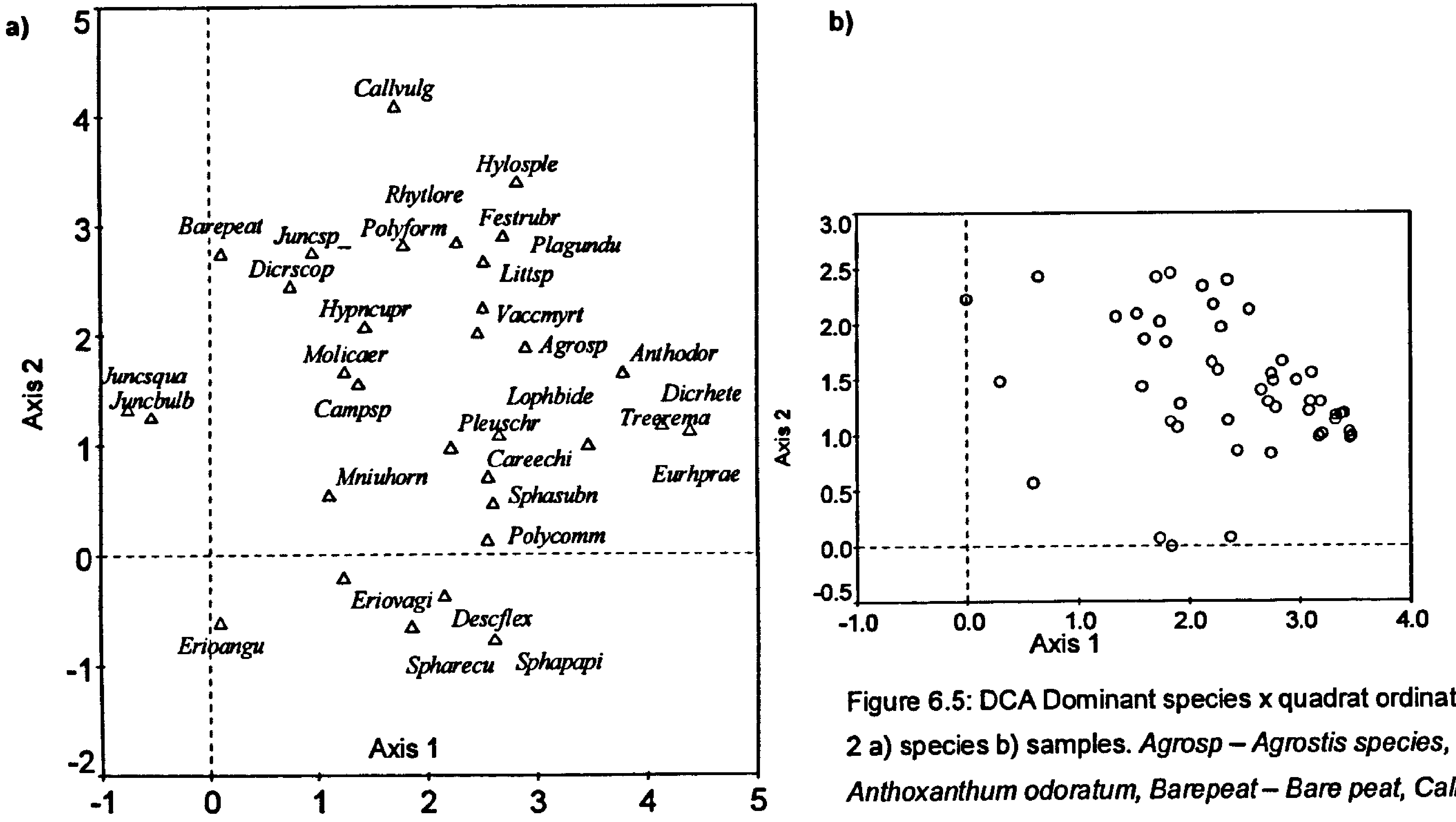


Figure 6.5: DCA Dominant species x quadrat ordination plots for Axis 1 & 2 a) species b) samples. *Agrosp – Agrostis species, Anthodor – Anthoxanthum odoratum, Barepeat – Bare peat, Callvulg – Calluna vulgaris, Campsp – Campylopus species, Careechi – Carex echinata, Descflex – Deschampsia flexuosa, Dicrhete – Dicranella heteromalla, Dicrscop – Dicranum scoparium, Erioangu – Eriophorum angustifolium, Eriovagi - Eriophorum vaginatum, Eurhprae – Eurhynchium praelongum, Festrubr – Festuca rubra, Hylosple – Hylocomium splendens, Hypncupr – Hypnum cupressiforme, Juncbulb – Juncus bulbosus, Juncsp – Juncus sp, Juncsqua – Juncus squarrosus, Littsp – Litter, Lophbide – Lophocolea bidentata, Molicaer – Molinia caerulea, Mniuhorn – Mnium hornum, Plagundu – Plagiothecium undulatum, Pleuschr – Pleurozium schreberi, Polycomm, Polytrichum commune, Polyform – Polytrichum formosum, Rhytlore – Rhytidiadelphus loreus, Sphapapi, Sphagnum papillosum, Spharecu – Sphagnum recurvum, Spagsubn – Sphagnum subnitens, Treerema – Tree remains, Vaccmyrt – Vaccinium myrtillus.*

Results from the series of linear regression analyses (Table 6.2) indicate that germination and growth of *C.vulgaris* is influenced by micro-site both in terms of the micro-topography and dominant vegetation. Axis 1 of the cell heights DCA analysis provides a good predictor of cv presence in 2004 (model 2a) and is almost significant (P<0.057) as a predictor for cv seed (model 1a). Axis 1 represents increase in height variation and both cv seed and cv present are negatively correlated with increasing axis score. This indicates that quadrats with most height variation have fewer *C.vulgaris* seedlings in 2002 and less *C.vulgaris* in 2004. Axis 1 of the dominant vegetation DCA analysis (Fig. 6.5b) is a significant predictor of cv seed and cv presence (model 1a & 2a). The picture is similar for Axis 2, particularly for cv present (model 2a) and although it is non-significant as a predictor for cv seed there is some indication of an effect (P<0.1; model 1a). Axis 1 represents increasing cover of tree remains and both cv seed and cv present are negatively correlated with increasing Axis 1 scores indicating that as cover of wood chip increases the likelihood of *C.vulgaris* seedlings growing and becoming established plants is reduced. Axis 2 represents a wet to dry gradient with increasing scores and both cv seed and cv present show a positive correlation with increasing dryness.

Table 6.2: Details of linear regression analyses including model structure and results

Model No.	Response variable	Predictors	Significance of predictor		Regression ANOVA	
			p-value	R-Sq	F	P
1a	Log (cv seed +1)	DCA_ht1	0.057	44.0	8.46	<0.001
		DCA_ht2	0.375			
		DCA_veg1	<0.001			
		DCA_veg2	0.095			
1b	Log (cv seed +1)	H	0.224	3.2	1.52	0.224
1c	Log (cv seed +1)	E	0.294	2.4	1.13	0.294
		R	0.156	3.4	2.08	0.156
1d	Log (cv seed +1)	Roughness	0.427	5.7	1.35	0.269
2a	Cv present	DCA_ht1	0.006	46.5	9.34	<0.001
		DCA_ht2	0.451			
		DCA_veg1	0.002			
		DCA_veg2	0.002			
2b	Cv present	H	0.106	5.6	2.72	0.106
2c	Cv present	E	0.086	6.3	3.08	0.086
2d	Cv present	R	0.075	6.7	3.31	0.075
2e	Cv present	Roughness	0.568	5.0	1.19	0.315
2f	Cv present	Log (cv seed+1)	<0.001	66.3	90.694	<0.001
3a	Species H	DCA_ht1	0.467	1.3	0.31	0.738
		DCA_ht2	0.793			
4a	Species R	DCA_ht1	0.997	0	0	0.997
		DCA_ht2				
4b	Species R	Cv present	0.011	13.3	32.24	0.011

Height diversity, evenness, richness and roughness showed no significant correlations with either cv seed or cv present. However, there is some weak indication (p = 0.086) that cv present is positively correlated with height evenness (model 2c) and negatively correlated (p = 0.075) with height richness (model 2d) in linear regression analyses with only one predictor in each case. There is a highly significant and very clear positive correlation between cv seed and cv present but it appears that species richness of the plant community declines as the cover of *C.vulgaris* increases. This is not a particularly strong correlation but it is significant (p = 0.011). Species richness and diversity does not appear to be correlated in any way with micro-topography (models 3 and 4). Only the results for regression analyses with the height and dominant vegetation DCA Axis scores are reported in table 6.4 but the results were very similar for regression analyses with height diversity, evenness, richness and roughness.

5.3.2 Cell level

Results from the lme model, to determine the effect of weighted height and dominant vegetation category on extent of *C.vulgaris* germination where germination had occurred in 2002 are shown in Table 6.3. Weighted height was not significant and of the eleven different dominant vegetation categories *C.vulgaris* germination was less likely to occur with litter, moss or tree remains compared with bare peat and equally likely to occur with *Campylopus, C.vulgaris, E.vaginatum,* fine leaved grasses, herbs, sedges & tall grass and *Sphagnum* sp as with bare peat.

Table 6.3: Results from the lme model to determine the effect of different factors on the extent of *C. vulgaris* germination where germination had occurred in 2002.

Factor	T - value	P - value
Weighted height of cell	0.609	0.542
Campylopus	-1.301	0.194
C. vulgaris	-1.043	0.298
E. vaginatum	-1.512	0.131
Fine leaved grasses	-0.294	0.770
Herbs	-2.219	0.400
Litter	-2.219	0.027
Moss	-2.422	0.016
Tall sedges and grasses	-1.397	0.163
Sphagnum	-1.050	0.294
Tree remains	-3.104	0.002

Results from the three binary regression analyses are presented in Table 6.4 with significant predictors highlighted in red. The first model, where only cells that contained *C.vulgaris* seedlings in 2002 were included in the analysis, shows that cv seedling is not significant in predicting the presence of *C.vulgaris* plants in 2004. Cv patch was a significant predictor which suggests that although there was a high level of mortality amongst *C.vulgaris* seedlings between 2002-2004 new seedlings did emerge in cells that were immediate neighbours to the cells that originally contained *C.vulgaris* seedlings and that these seedlings subsequently grew into heather plants. Most of the dominant vegetation types had the same impact on seedling survival/mortality as bare peat although there was significantly more mortality where *Eriophorum vaginatum* was the dominant vegetation type.

Table 6.4: T-values and p- values for predictors in each of the three binary regression models. Response variable = *C.vulgaris* plants in 2004, Predictors= cv patch, cv seed, dominant vegetation category (11 categories with bare peat used as reference level for comparisons + = more *C.vulgaris* plants than bare peat, - = fewer than bare peat).

Predictors	Model 1 (cv seed cells)		Model 2 (cv patch cells)		Model 3 (all cells)	
	t-value	p-value	t-value	p-value	t-value	p-value
Cv seed	-1.184	0.236	0.030	0.976	-1.719	0.086
Cv patch	2.427	0.015	5.434	<0.001	13.840	<0.001
Campylopus	-1.098	0.272 (-)	-0.999	0.318 (-)	-1.360	0.174 (-)
C. vulgaris	0.770	0.441 (+)	3.491	<0.001(+)	7.109	<0.001(+)
E. vaginatum	-2.677	0.007 (-)	-3.580	<0.001(-)	-4.495	<0.001(-)
Fine leaved grasses	0.274	0.784 (-)	-2.093	0.036 (-)	-4.950	<0.001(-)
Herbs	-0.098	0.922 (-)	-0.133	0.894 (-)	0.078	0.938 (-)
Litter	-0.226	0.821 (-)	1.066	0.286 (-)	-0.808	0.419 (-)
Moss	1.045	0.296 (-)	2.705	0.007 (-)	0.457	0.648 (-)
Tall sedges and grasses	-1.844	0.065 (-)	-1.048	0.295 (-)	-2.665	0.008 (-)
Sphagnum	0.025	0.980 (-)	-0.016	0.987 (-)	-2.056	0.040 (-)
Tree remains	-0.198	0.843 (-)	0.526	0.599 (-)	-4.504	<0.001(-)

The second model, where only cells that had a cv patch index were included, shows a similar picture to model 1 except that cv patch index is a highly significant predictor and more of the dominant vegetation types had a significant impact on the survival of *C.vulgaris* seedlings. *C.vulgaris* plants were more likely to be present in cells in 2004 where either *C.vulgaris* vegetation or moss had been the dominant vegetation type in 2002 compared with bare peat and less likely to be present in cells where either *E.vaginatum* or fine leaved grass had been the dominant vegetation type in 2002 compared with bare peat.

In the final analysis where all cells are included cv seed is not a significant predictor of cv present in 2004 although there is some indication of a relationship (p=0.086) and cv patch is highly significant. Again *C.vulgaris* was more likely to be present in cells where *C.vulgaris* had been the dominant vegetation type in 2002 compared with bare peat and less likely to be present in cells where *E.vaginatum*, fine leaved grasses, tall sedges and grasses, sphagnum or tree remains were the dominant vegetation type in 2002. In this analysis *C.vulgaris* seedlings were as likely to survive on moss as they were on bare peat and this was the same for litter, herbs and *Campylopus* species.

5.4 Discussion

Micro-site characteristics, both micro-topography and ground cover / dominant vegetation, have a clear influence on germination and growth of *C.vulgaris*. It appears that micro-topography is important at the scale of the quadrat but not at the cell level and that flatter ground is more suitable for *C.vulgaris* germination and subsequent survival. A wide range of different methods were used for calculating a figure to represent the micro-topography of quadrats and although these figures are all significantly correlated with one another they describe different aspects of the micro-topography.

The DCA analysis of height data with height categories considered as species appears to capture more of the elements of micro-topography that are important for *C.vulgaris* growth than the other methods. The key aspects of micro-topography, that increase the likelihood of *C.vulgaris* growth, appear to be the number of height categories (fewer the better for *C.vulgaris*) as well as the particular height categories that are included. So the best combination is a few height categories at the lower end of the scale (0-20cm). The Shannon diversity and evenness index and height richness figures do not identify which height categories are included within a sample so quadrats with equal amounts of height categories 0, 5, 10 & 15 would be the same as quadrats with equal amounts of height categories 0, 20, 35, 60 and these quadrats clearly have a different micro-topography. In reality the chances of the second quadrat occurring are very small because ground height is unlikely to go straight from 35cm to 60cm without a slope in between. As a result the height evenness and richness figures, which take into account the number of height categories in a sample, do appear to provide some indication of ground suitability for *C.vulgaris*, although it is non significant. Roughness would certainly distinguish between the two quadrats described above but it would not identify a quadrat with lots of small changes in height from one with a few large changes in height and this difference appears to be important for *C.vulgaris* growth. These results suggest that using ordination as a data reduction tool is an effective method to capture the essence of a multi dimensional data set which appears to make more biological sense than the single dimension diversity, evenness, richness and roughness indices.

The dominant vegetation type or ground cover is also important at both the scale of the whole quadrat and the individual cell. At the quadrat scale, Axis 1 and 2 of the DCA analysis of dominant vegetation types provides good predictors of *C.vulgaris* germination, survival and establishment of plants with *C.vulgaris* being more likely to grow where there is less wood chip on the ground and the ground conditions are generally drier. This response would be expected as *C.vulgaris* requires some light for germination (Gimingham 1972) and although it will grow successfully on soil with a wide range of water contents the best growth occurs when the soil is at least moderately well drained (Pearsall 1938; Poel 1948; Gimingham 1960). Optimal development of *C.vulgaris* occurs when soils are able to oxidise, and even in the wettest soils some level of oxidation must occur at some time during the year (Poel 1948).

The cell level analysis provides more specific information relating to the preferred micro-site characteristics of *C.vulgaris*. Germination tends to occur in patches which are generally greater in size than a 10x10cm cell and although this may be related to seed availability it is more likely to be a result of the ground conditions and existing ground cover. Compared with bare peat, germination is less likely to occur when the ground is covered with litter, moss or tree remains and these results are supported by the findings of Mallik *et al* (1984b) who reported that significantly more seedlings established where litter and moss (*P.schreberi* or *Hypnum* sp.) were absent. The other seven vegetation types, *Campylopus, C.vulgaris, E.vaginatum,* fine leaved grass, herbs, sedges/ tall grass (*M.caerulea*) and *Sphagnum* species were just as likely to support *C.vulgaris* germination as bare peat. These results indicate that *C.vulgaris* is less likely to germinate where a dense layer of litter, moss or wood chip is already covering the ground but will readily germinate within the vicinity of other vegetation irrespective of plant morphology. One might expect that *Campylopus* and *Sphagnum* species would have a similar ground covering effect as other mosses but these species did not cover the ground as quickly as other moss species and this is one of the reasons why they were considered separately in the analysis.

Survival of *C.vulgaris* seedlings between 2002 and 2004 was generally poor as cv seed was not a significant predictor of *C.vulgaris* presence in 2004. High mortality of *C.vulgaris* seedlings has been reported after heather burning (Mallik et al. 1984a) probably as a result of dry conditions. *C.vulgaris* is susceptible to drought (Rosen 1984) so germination and survival is increased considerably if the seedbed substrate has good water retention properties such as a dense layer of organic matter (Mallik et al. 1984a; Mallik et al. 1988). Drought conditions are not something one would expect on the west coast of Scotland but the surface layer of peat is prone to drying especially if there is little or no vegetation cover. The summer of 2003 was relatively dry so it is highly likely that localised drying of the peat surface could have caused some seedling mortality during the summer. Other causes of mortality could be competition from other plant species for light, water and nutrients or water logging of the peat during the winter. Where *E.vaginatum* was recorded as the dominant vegetation type *C.vulgaris* seedling mortality was significantly higher than on bare peat. 'Tall sedges and grasses' had a similar effect, although the result was not quite significant. This effect is thought to be a result of plant competition for resources although it is possible that *C.vulgaris* did poorly in the vicinity of *E.vaginatum* due to water-logging of the peat. *E.vaginatum* will tolerate prolonged water logging (Wein 1973) but *C.vulgaris* seedlings are less tolerant (Poel 1948).

C.vulgaris plants became established in quite specific locations relative to other plants that were colonising the peat surface. Apart from cells where mature *C.vulgaris* plants already existed the most likely locations for *C.vulgaris* establishment were bare peat, *Campylopus* sp., herbs, litter or moss. The 'herbs' category includes mainly *Potentilla erecta* and *Galium saxatile* which are both ground covering species so with the exception of bare peat the most suitable micro-sites for *C.vulgaris* establishment offered good ground cover but minimal competition for light. The water holding capacity of the peat was almost certainly enhanced by these 'vegetation' categories as it would be protected from the drying affects of sun and wind and the *Campylopus*, moss and litter categories may have also provided a potential water supply buffer for the growing plants. It is interesting that although moss and litter cover appeared to inhibit germination of *C.vulgaris*, once the seedlings were established their chances of survival increased significantly in these micro-sites. These results are supported by work done on the impact of *Campylopus introflexus* on *C.vulgaris* establishment where presence of the moss had a significant negative impact on germination but a positive effect on post germination performance of seedlings (Equihua and Usher 1993). Other moss species where *C.vulgaris* seelings have been found growing in close association include *Hylocomium splendens, Pleurozium schreberi,*(in a water saturated atmosphere only, as hypnacious mosses are prone to drying) *Aulacomnium palustre, Dicranum scoparium* and *Sphagnum* sp (Gimingham 1960). All of these species were included within the 'moss' category, except for *Sphagnum* which was a category in its own right.

Despite considerable evidence that micro-topographic variation is correlated with floristic diversity (Harper et al. 1965; Sheldon 1974; Eldridge et al. 1991; Vivian-Smith 1997) this was not found to be the case for developing blanket bog vegetation on the tree clearance area. This may be a result of the immaturity of the plant community which was only 4 - 6 years since tree clearance. Alternatively the variation in micro-topography may not have been sufficient to provide the range of micro-sites required for enhanced diversity. However, on experimental wetlands small scale variability in micro-topography, in the order of 1-3cm, produced highly significant differences in species diversity (Vivian-Smith 1997). It is therefore unlikely that the height variation between 0 – 75cm recorded in quadrats on the tree clearance area did not provide sufficient variability. The only correlation with species richness that was found was a negative relationship with the presence of *C.vulgaris* suggesting that where *C.vulgaris* is present species richness of the plant community is reduced. As the likelihood of *C.vulgaris* being present in a quadrat increased as the ground became flatter perhaps there is a weak link between species richness and micro-topography but this is unlikely.

In general wood chip and litter have an inhibitory effect on germination and growth of *C.vulgaris.* If colonisation of a site by this plant species is the desired objective then it would be sensible to minimise the amount of woodchip deposited on the drier patches of ground within the vicinity of tree stumps. A certain amount of ground disturbance should be beneficial as this will create breaks in the litter layer, exposing peat for colonisation by *C. vulgaris* or other species that may improve micro-site conditions for *C. vulgaris*. However, excessive disturbance is likely to increase surface roughness of the peat which may reduce the suitability of the site for colonisation by *C. vulgaris.*

CHAPTER 6

THE DEVELOPMENT OF VEGETATION STRUCTURE ON BLANKET BOG FOLLOWING DEFORESTATION, WITH PARTICULAR REFERENCE TO RED GROUSE

6.1 Introduction

Habitat heterogeneity or the structural diversity of vegetation has long been recognized as a fundamental variable indicative of species diversity (MacArthur and MacArthur 1961; Southwood et al. 1979; Goetz et al. 2007). The habitat heterogeneity hypothesis proposed by Tewes *et al.* (2004) states that the more complex the habitat, in terms of structure, the more niches are available, and therefore the higher the animal species richness. A literature survey found that 85% of all studies on the relationship between habitat heterogeneity and animal species diversity found a positive correlation (Tews et al. 2004). In general, invertebrate (Lassau et al. 2005; Poyry et al. 2006; Reid and Hochuli 2007), bird (MacArthur and MacArthur 1961; Moss 1978; Goetz et al. 2007) and small mammal (Williams et al. 2002) species diversity increases with increasing structural diversity or vegetation complexity.

Population density of red grouse (*Lagopus lagopus scoticus*) has been positively correlated with the structural diversity of moorland vegetation where diversity at a landscape scale is increased by heather burning (Picozzi 1968; Hudson 1992; Tharme et al. 2001). Red grouse require heather at different growth stages and they particularly like shorter more nutritious heather immediately adjacent to tall vegetation so they can feed but quickly hide from predators (Bains et al. 1999). Although *C.vulgaris* forms a significant proportion of the diet of red grouse (Jenkins et al. 1963; Lance and Mahon 1975) there is evidence to suggest that invertebrates (Butterfield and Coulson 1975) provide an important source of nitrogen and phosphorus at certain times during the year, particularly in the spring. Invertebrates are also a very important food source for red grouse chicks during the first few weeks after hatching (Park et al. 2001). Although a considerable amount of work has been done investigating the invertebrate populations of upland vegetation (Butterfield and Coulson 1975; Coulson and Butterfield 1986; Coulson et al. 1990; Coulson et al. 1995; Downie et al. 1995) there is no clear indication that species diversity increases with structural diversity of the vegetation. Coulson and Butterfield (1986) indicate that there are other factors, such as a high and exposed water table, which may influence the invertebrate diversity to a greater extent than the plant architecture. However, large invertebrate populations on moorland tend to be limited to cool and wet climates, where most blanket bog exists (Butterfield and Coulson 1975), and vegetation complexity certainly affects invertebrate distribution (Downie et al. 1995) even if a direct relationship between invertebrate diversity and vegetation complexity has not been shown.

Vegetation structural diversity is likely to be important for red grouse at two different scales. Firstly, small scale plant community architecture, within a 10x10cm area, where taller and more complex vegetation may yield a higher number and diversity of invertebrates. Secondly, large scale patch structure, over distances greater than 10m, providing edges between different types of vegetation where grouse can feed, shelter and hide from predators, within the same patch. A number of different workers have assessed structure in grassland or heathland habitats at the small scale (Southwood et al. 1979; Downie et al. 1995; Borges and Brown 2001; Poyry et al. 2006) and the large scale (Tharme et al. 2001; Pearce-Higgins and Grant 2006) and various different approaches to measurement have been taken. At the small scale mean vegetation height has been used as a surrogate for vegetation structure (Poyry et al. 2006) but more detailed assessments have used the pin intercept method (Southwood et al. 1979; Downie et al. 1995; Borges and Brown 2001) where vertical pins, usually in a pin frame, are passed through the vegetation with the number of vegetation touches recorded in various height categories, from 2 - 20cm intervals depending on the vegetation type. The number of pins/sample varied from 20-45 but the diameter of the pin and distance between each pin was not always specified. Estimation of percentage cover or biomass for different species using the pin intercept method are sensitive to pin diameter (Goodall 1952; Frank and McNaughton 1990) and this is likely to be the case for measuring vegetation density, so it is important to ensure that pin diameter is consistent for repeat assessments (Hill 2005).

Whilst planning vegetation monitoring on the tree clearance area a number of tests were done using a 10 pin frame and it took between 10 – 15 minutes to complete each sample. The weather was particularly poor whilst these tests were being done (high winds and rain), which is common in Kintyre, making the sampling particularly difficult. It was decided that a quick method, where relatively consistent results would be obtained in different weather conditions, needed to be developed. The Game Conservancy Trust use a technique to assess heather height and condition on moorland (Bains et al. 1999) and this involves using a narrow cane, 1m in length and approximately 1 cm in diameter, which is placed vertically into the vegetation to be sampled. The maximum heather height is measured to the nearest 5cm and the number of heather contacts on the cane is recorded. This technique has been used on a large number of moorland estates in Scotland so it was decided that a modification of the technique would be used to assess small scale vegetation structure on the tree clearance area.

On a large scale various techniques have been used that involve the use of vegetation height or vegetation density over a relatively large area i.e. 1-2km^2 (Tharme et al. 2001; Pearce-Higgins and Grant 2006). Tharme *et al* (2001) collected 40 vegetation height records in a 1km^2 area and used these data to calculate the Shannon evenness index of the vegetation where values close to zero indicated an even stand and higher values represented a more complex vegetation structure such as tussocky grass or the presence of muirburn. Pearce-Higgins and Grant (2006) used a more complex approach measuring vegetation height and assessing vegetation density using a bamboo cane with 10cm height intervals marked on it. They recorded heights in three different height categories (0-15cm, 15-30cm, >30cm) for three different vegetation types (dwarf shrubs, graminoids and all vegetation) and assessed the density by taking a mean of the number of height intervals that were visible through the vegetation across all sampling points. Essentially the three methods described above all produced one figure to describe vegetation height variability for a specified area which was then used to give an index of structural diversity.

One of the main aims of the Central Kintyre Habitat Management Plan is to restore blanket bog habitat for red grouse through the clearance of immature Sitka spruce forest by 'in situ' chipping. Prior to setting up the monitoring quadrats on the tree clearance area the mean number of red grouse on the rest of the management area was 8.78 pairs/km^2. This figure is a three year mean (1999 – 2001) and is relatively low compared with managed grouse moors in the north east of England and Scotland (Hudson 1992). However, it represents a good sized population for unkeepered moorland on the west coast of Scotland (Moss *pers. comm.*). It was assumed, therefore, that the structure of the existing blanket bog vegetation on site could be used as a 'target' for the purposes of monitoring vegetation structure development on the tree clearance area, against the aims of the management plan.

The aim of this study was to investigate development of vegetation structure on the tree clearance area at two different scales, a small scale that would be relevant to invertebrate populations and a larger scale that is likely to influence red grouse territory size and therefore red grouse numbers. Structural diversity of the developing vegetation, post tree clearance, was compared with that of existing mature blanket bog vegetation. In addition the structural diversity of vegetation developing on ground with different depths of wood chip was also studied. Conventional methods of assessing structural richness and diversity are compared with a multivariate approach using Principle Components Analysis to investigate the relationship between plant species and structure.

6.2 Materials and Methods

6.2.1 Vegetation structure – large scale

DATA COLLECTION

As part of the grouse monitoring work for the Central Kintyre Habitat Management Plan a series of vegetation transects were established over the whole management area in 2001. Five transects were located on the tree clearance area and four transects on the two management units immediately adjacent to the tree clearance area (see Appendix 3). Transects were located on vegetation that was considered to be representative of the whole management area, although as there was very little vegetation on the tree clearance area the transect route was selected to include the full range of peat depths, slopes, aspects and wetness. The transects were also routed to ensure that the start, any midpoints and the end were easily relocated i.e. fence posts, large and recognisable rocks or hill summits.

Once the transects were located, records were taken annually every 10 paces along the transect. The maximum vertical height of the leaf or shoot, touching the end of the observer's boot after the tenth pace, was measured at the end of the tenth pace. The measurement was made at the highest point of the leaf or shoot, above ground level, to the nearest cm, using a one metre measuring stick where the scale starts at 0. No attempt was made to keep paces even, so each pace varied in length depending on the slope. As a result the total number of measurements per transect varied by a small amount (<5%) each year.

DATA ANALYSIS

The vegetation height data were categorised into 5cm height bands. The range of vegetation heights was 0-98cm giving a total of 20 height bands. The

Shannon Diversity Index was calculated for the 'target' vegetation and the tree clearance vegetation in four sample years 2001 – 2004, using Eqn. 1 below. In order to compare values of H for different vegetation in different years the variance and t-values were calculated as detailed by Magurran (1988) using equations 2-4 below.

$$H = -\sum_{i=1}^{h} p_i \ln p_i \qquad \text{Eqn, 1}$$

where p_i is the proportion of the total number of hits, *h*, in each i'th height category

$$VarH = \frac{\sum p_i(\ln p_i)^2 - (\sum p_i \ln p_i)^2}{N} - \frac{S-1}{2N^2} \qquad \text{Eqn. 2}$$

$$t = \frac{H_1 - H_2}{(VarH_1 + VarH_2)^{1/2}} \qquad \text{Eqn. 3}$$

$$df = \frac{(VarH_1 + VarH_2)^2}{[(VarH_1)^2 / N_1] + [(VarH_2)^2 / N_2]} \qquad \text{Eqn. 5}$$

Where p_i is the proportion of heights in each i'th height band, VarH is Shannon variance, S is number of height bands and N is number of individuals. Differences were only recorded as significant where the p-value was lower than 0.005 (Bonferroni correction to avoid Type I statistical error).

6.2.2 Vegetation structure - small scale

DATA COLLECTION

Quadrat location, establishment and the annual re-location procedure is described in detail in Section 2.3.1. In each assessment year (2001-2004) a vegetation structure measurement was made in each of the five mini-quadrats within the flailed and heather control main quadrats. A cane (1 meter long x 7mm diameter with height intervals marked every 10cm) was used as a 'pin' and this was placed vertically in the centre of each mini quadrat (see figure 5.1). All vegetation touching the pin was recorded including the species and height interval at which the touch occurred. One pin was assessed for each mini-quadrat giving five replicates within each main quadrat.

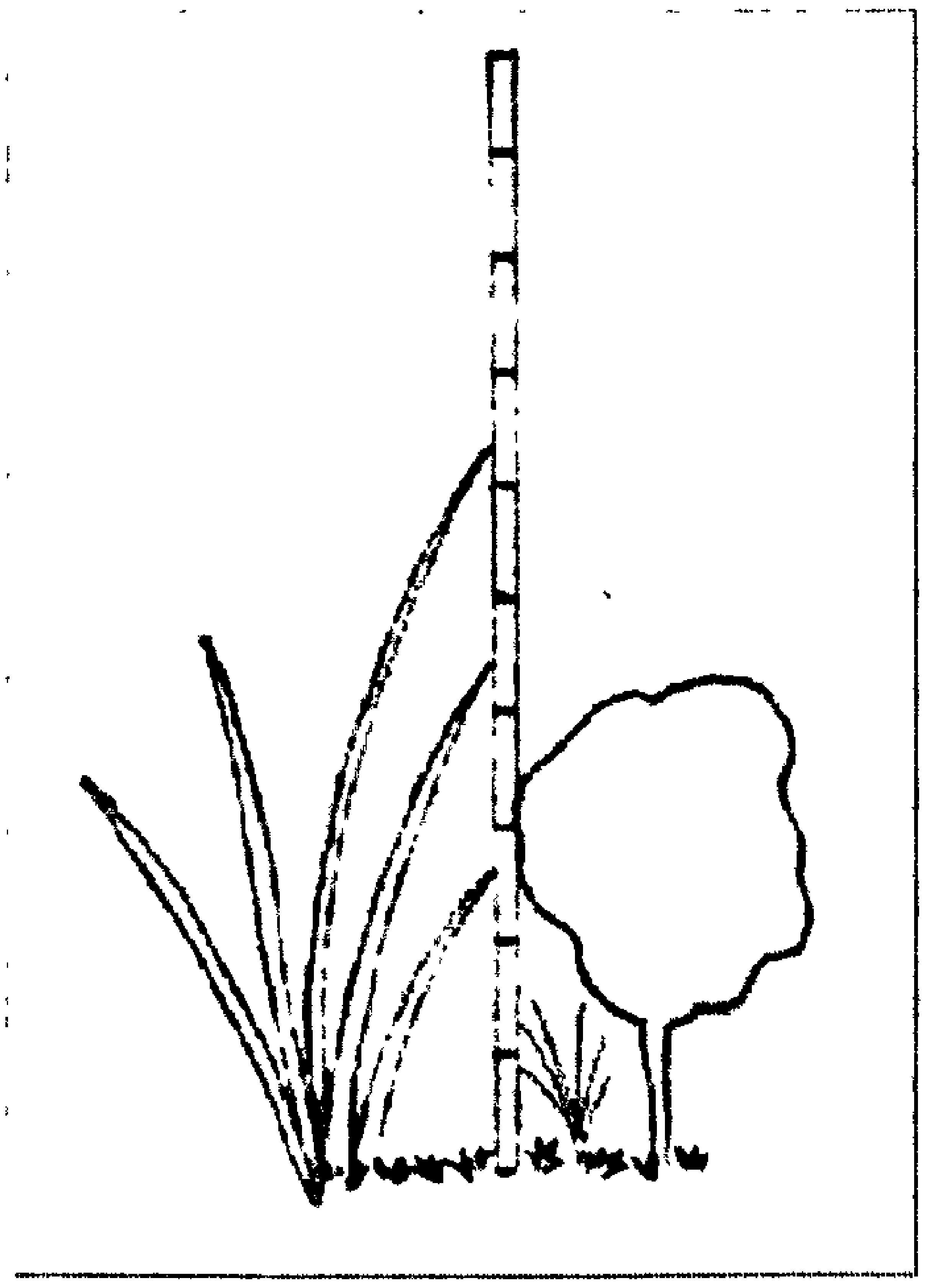


Figure 5.1: Diagram of the 'pin' used to assess vegetation structure.

DATA ANALYSIS

Structural diversity and richness was explored in a number of different ways using conventional indices as well as two multivariate techniques. Two different interpretations of structural richness and the Shannon Diversity Index were used to compare the developing vegetation on the tree clearance area with 'target' blanket bog vegetation on adjacent management units. The influence of chip depth on development of small scale vegetation structure over time was investigated using the two structural richness indices and Shannon Diversity index but also through a PRC analysis. Lastly, Principle Components Analysis

(Ter Braak and Smilauer 1998) was used to explore the full small scale vegetation structure data set which includes species, height category and sample and is essentially a three dimensional data set.

Structural richness and diversity

For the small scale structure assessment two variations of structural richness were calculated for each sample. The first richness index (R1) was mean number of vegetation hits (or mean number of individuals) on the 5 pins/sample and the second (R2) was mean number of height categories on the 5 pins/sample, which is equivalent to species richness (Magurran 1988). Shannon Diversity Index was calculated for each sample using equation 1 above.

The figures calculated for R1, R2 and H' were subjected to linear mixed effects (LME) modelling (Pinheiro and Bates 2000) to test the effect of time, treatment (target or tree clearance) and chip depth (tree clearance only) on structural richness and diversity. Three designs of LME models were fitted for each richness/diversity index and all models included fixed and random effects. The first model included only the 'target' vegetation quadrats to check for differences between sample year, including sample year (2001-2004) as a fixed effect. The second model included only tree clearance quadrats to check for differences between year since clearance and chip depth, where year since clearance (0-5) and chip depth treatment (three levels: Tmt 1 – normal, Tmt 2 – double and Tmt 3 – triple) were included as fixed effects. The third model included 'target' and tree clearance vegetation to check for differences between treatment and treatment over time, where sample year (2001-2004), treatment and the year*treatment interaction were included as fixed effects. The random effects were year nested within individual quadrats.

Where necessary temporal autocorrelation was accounted for within models using a first-order autoregressive function (Pinheiro and Bates 2000; Crawley 2002), this was done by specifying residual correlation that decays exponentially with distance between years. Differences between treatment variances, either chip depth or vegetation type depending on the model, were checked and in one case separate error terms were specified for the two different vegetation types. Other models were improved by including separate error terms for treatment but it was not possible to include the autoregressive function and the treatment variance function in the same model. In all cases, the simplest possible model that gave the best fit to the data, and most appropriate residual error distribution was sought. Different models were compared by likelihood ratio tests and if models were significantly different ($p<0.05$), the model with the lower Akaike's information criterion, as shown in equation 5, was selected (Burnham and Anderson 2002):

$$AIC = -2 logLik + 2n \qquad \text{Eqn. 5}$$

where n is the number of parameters in the model, and is effectively a 'penalty term' related to the complexity of the model.

Ideally a series of multiple comparison tests would have given some indication of whether or not structural richness and diversity on the tree clearance area was moving towards the target vegetation. However, there is no specific method for doing a multi comparison test within an lme model and the technique is not particularly well suited to the theory of lme models (Bates 2003). In order to visualize the change in small scale structural diversity on the tree clearance area, relative to the target vegetation, mean values and the standard errors for R1, R2 and H were calculated and shown graphically in three separate figures.

Principal Response Curve Analysis

The multivariate technique Principal Response Curve (PRC) analysis (Frampton et al. 2001) is described in detail in section 4.2.1, Data analysis, multivariate analysis. PRC was used to display temporal changes in structural diversity between 'target' vegetation and tree clearance vegetation under three chip depth treatments. Sample year was used as the time variable rather than year since chipping as 'target' vegetation data were only available for sample year. The same method was followed as that described in section 4.2.1 including multiple comparison testing of each treatment at each time point on the PRC (Frampton et al. 2001). To avoid a Type 1 statistical error a Bonferroni correction was applied to the significance level for p-values based on doing three comparisons/year. As a result differences were only recorded as significant where the p-value was lower than 0.017. It was not possible to undertake a single Monte Carlo permutation test for the PRC analysis as this requires equal numbers of samples for each treatment and control.

Three dimensional Principal Components Analysis

For each pin sampled all vegetation touching the pin was recorded both in terms of species and the height category at which it was touching the pin. Conventional richness and diversity indices can only use one aspect of a potentially three dimensional data set (as shown in Figure 5.2), for example either the height categories where vegetation touches the pin, the species touching the pin or the species in different height categories. As a result two dimensions of these data are lost when studying structural richness or diversity and these may be important components of vegetation structure.

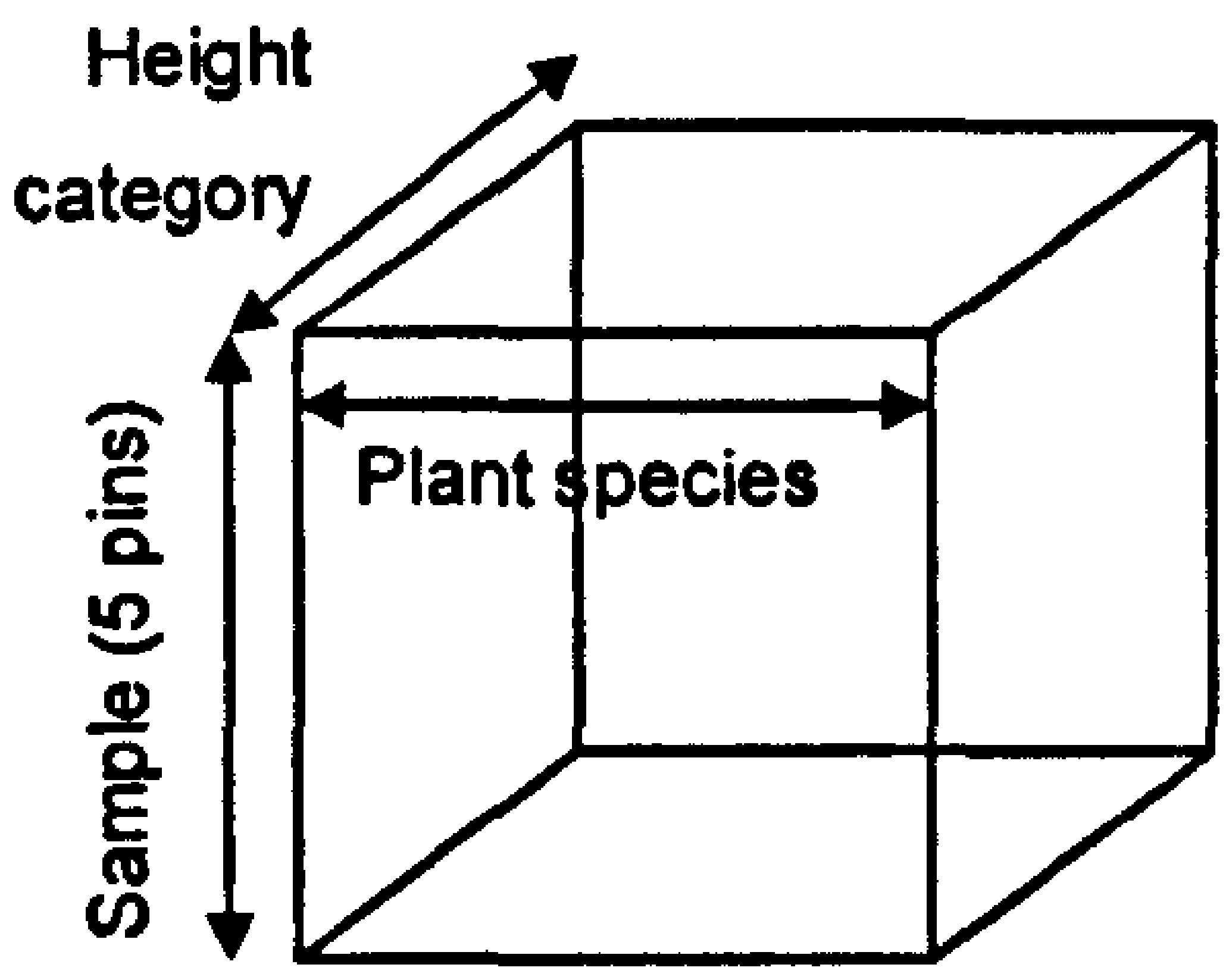


Figure 5.2: Schematic diagram demonstrating the 3-Dimensional nature of the small scale vegetation structure data

In order to explore all three dimensions of these data Principle Components Analysis (PCA) (Ter Braak and Smilauer 1998) was employed. Detrended

Correspondance Analysis gave relatively short gradients (< 3.00) therefore PCA was selected for these analyses. Aggregate values across any two dimensions were calculated to create three separate 2D matrices, which were subject to PCA:

1. Sample x Height category
2. Sample x Plant species
3. Plant species x Height category

In each case the aggregate values were calculated as a sum of the vegetation touches. For sample x height category the data were total number of vegetation touches, in each height category, across the five mini-quadrat replicates and therefore gives a measure of vegetation height density. For sample x plant species the data were total number of vegetation touches, for each species, across the five mini-quadrat replicates and therefore gives a measure of species composition. For plant species x height category the data were total number of vegetation touches for each species in each height category giving a measure of species height diversity. In all analyses both the plant species and height category data were log transformed.

'Target' vegetation for four sample years (2001-2004) and tree clearance vegetation for six years since chipping (0-5) were included in all PCA analyses. Target and tree clearance vegetation, as well as sample or year since chipping year can be identified in ordination diagrams from the first two PCA analyses but this is not possible in the last PCA analysis. For this analysis (plant species x height category analysis) data are used from across all years and both vegetation types.

6.3 Results

6.3.1 Vegetation structure – large scale

Large scale structural diversity (Shannon Diversity Index) of target and tree clearance vegetation is compared over a four year period (2001 – 2004) in Table 5.1. The multiple comparison tests, also shown in Table 5.1, indicate that in 2001, which is when the tree clearance work was completed, large scale structural diversity of the vegetation was significantly higher on the target vegetation compared to the tree clearance vegetation (F=-8.70, P=<0.001). This difference was also significant in 2002 (F=-8.26, P=<0.001) and apparent, although not significant, in 2003 (F=-2.94, P=0.005). By 2004 there was no difference between the two vegetation types indicating that the diversity of vegetation height on the tree clearance area had become similar to that on the target vegetation. Diversity (Table 5.1, column 3) of the target vegetation shows some unexpected variation between years with 2002 being lower than 2001 and 2003. This can be partly explained because the diversity and variance appears to be unusually high in 2001 and this is thought to be due to sampling date. In 2001 the transects were assessed during May when vegetation growth had started but in all other years the work was completed by the end of April. Growth of the vegetation is likely to have increased vegetation height variation across the site, increasing diversity compared with other years. This sampling difference may have affected the results for the tree clearance vegetation aswell which would explain why there is not an obvious increase in structural diversity between 2001 and 2002.

Table 5.1: Shannon Diversity for target and tree clearance vegetation between 2001-2004. Multi comparison tests are recorded as significant and shown in red where the p-value is lower than 0.005 (Bonferroni correction to avoid a Type I statistical error).

Vegetation Type	Year	Shannon Diversity (H)	Var H	n	Multi Comparison t – Tests (p-value)							
					T2001	T2002	T2003	T2004	C2001	C2002	C2003	C2004
Target vegetation	2001	-2.08346	0.001087	620								
	2002	-1.96946	0.000397	642	-2.96 (0.005)							
	2003	-2.041	0.000283	653	-1.15 (0.2)	2.74 (0.01)						
	2004	-2.03538	0.000321	637	-1.28 (0.2)	2.46 (0.02)	-0.23					
Tree Clearance	2001	-1.61365	0.001831	818	-8.70 (<0.001)							
	2002	-1.61662	0.001427	855		-8.26 (<0.001)			0.05 (0.5)			
	2003	-1.95357	0.000603	851			-2.94 (0.005)		6.89 (<0.001)	6.82 (<0.001)		
	2004	-2.01209	0.000412	825				-0.86 (0.5)	8.41 (<0.001)	8.33 (<0.001)	1.84 (0.1)	

6.3.2 Vegetation structure – small scale

6.3.2.1 Structural richness and diversity

The number of vegetation hits on each pin ranged from 1-13, for both the target and tree clearance quadrats. There were a total of 8 height categories (0-80cm) recorded across all samples although hits in the 7th (60-70cm) and 8th (70-80cm) height categories were limited to three quadrats that had *Juncus effusus* or flowering *Deschampsia flexuosa* growing in the centre of the quadrat. Lastly the Shannon Diveristy Indices ranged from 0 -1.97.

The composition and results from each lme model are summarised in Table 5.2. The necessity of accounting for first-order temporal correlation and/or differences in treatment variances in the model is also detailed. Firstly, the lme model to investigate change over time of the target vegetation clearly indicates that there were no changes in either of the richness indices or the diversity index. Change over time of the tree clearance vegetation showed a different picture with year since tree clearance showing a highly significant effect on richness and diversity. However, chip depth had no effect on either of the richness indices or the diversity index. Differences in richness and diversity between the target and tree clearance vegetation were highly significant with a highly significant interaction with sample year (time). The three richness/ diversity indices are very similar and all demonstrate a movement of the tree clearance vegetation towards the target vegetation, as shown in Figure 5.3 below. Structural richness and diversity is relatively low following tree clearance but with time it increases and becomes more similar to the structural richness and diversity of the target vegetation.

Table 5.2: Composition and results of linear mixed effects models for different structural richness/diversity indices

Model purpose	Fixed effects	Random effects	Response variable	Cor AR1	varIdent	Time p-value	Veg type p-value	V type*time p-value	Chip depth relative to 'normal' (8kg/m^2)	
									double	triple
Are there any changes in target vegetation over time?	samp yr	samp yr|quad	R1			0.609				
			R2			0.231				
			H	✓		0.234				
Are there any changes in tree clear veg over time relative to chip depth?	yr since chip dpth	yr since|quad	R1	✓		0.000			0.919	0.594
			R2			0.000			0.726	0.713
			H	✓		0.000			0.986	0.583
Is there a difference between target and tree clear veg over time?	samp yr veg type	samp yr|quad	R1	✓		0.000	0.000	0.000		
			R2			0.000	0.000	0.000		
			H		✓	0.000	0.000	0.000		

CorAR1 indicates whether first-order temporal autocorrelation needed to be included in the model

VarIdent indicates whether different variances were needed for each treatment in the model

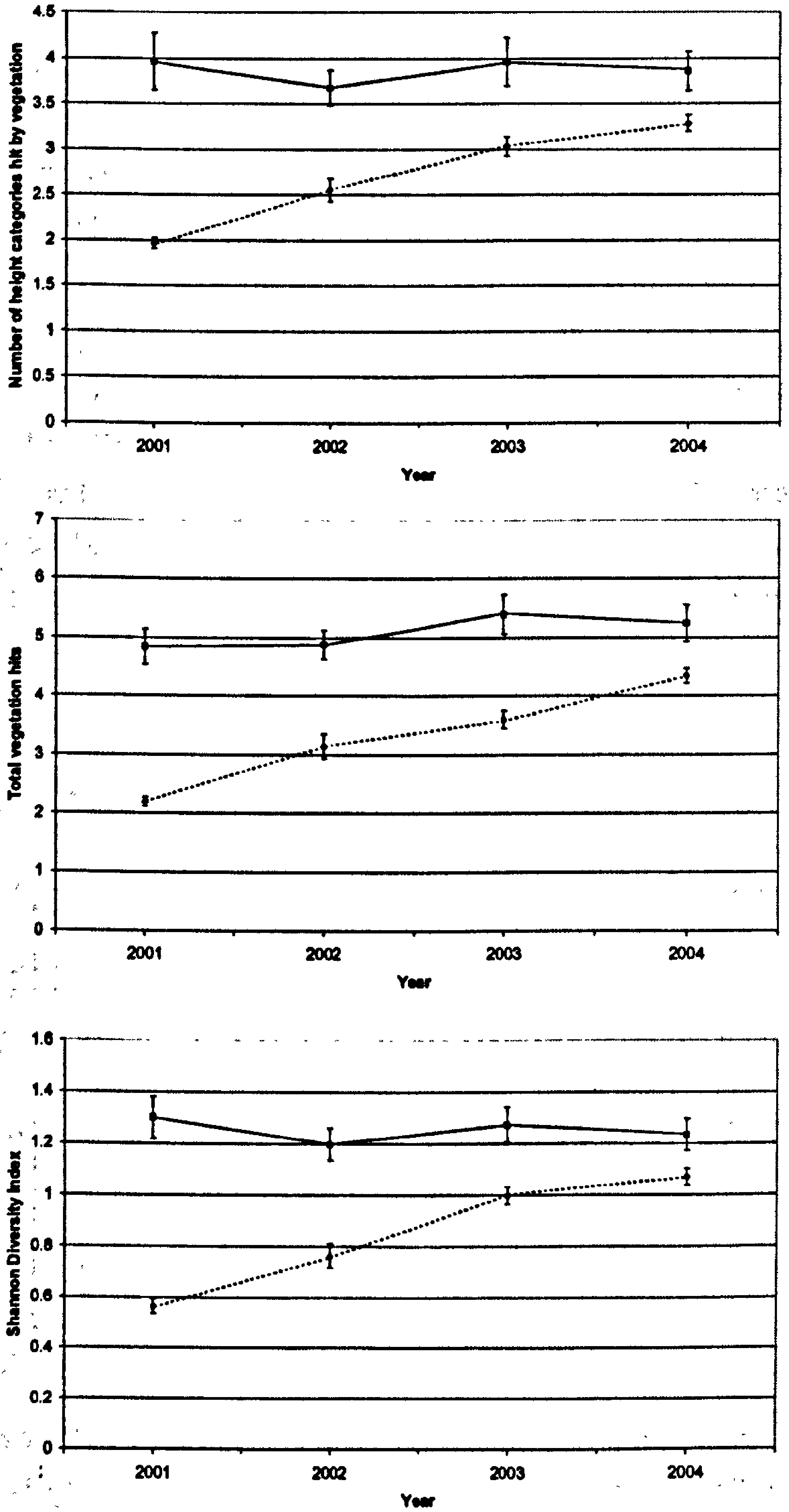


Figure. 5.3 Mean (+\- SD) of a) R1 (mean no. height categories), b) R2 (total vegetation hits) and c) H (Shannon diversity index) respectively, in years 2001-2004. Black line represents target vegetation, dashed line represents flailed quadrats.

6.3.2.2 Principal Response Curve

The PRC diagram for three different chip depth treatments (normal = < 12kg/m^2, double = 12-20kg/m^2, triple = >20kg/m^2) and the target vegetation as a baseline reference (Fig. 5.4) show differences in vegetation structure over time. Vegetation structural diversity is increasing with time on the tree clearance area and moving towards the target vegetation. By 2004 the normal and double chip depth treatments are not significantly different from the target vegetation although the Triple treatment is still different. Between 2001 – 2003 there was no significant difference between chip depth treatments but a small difference between the normal and triple treatment becomes apparent in 2004.

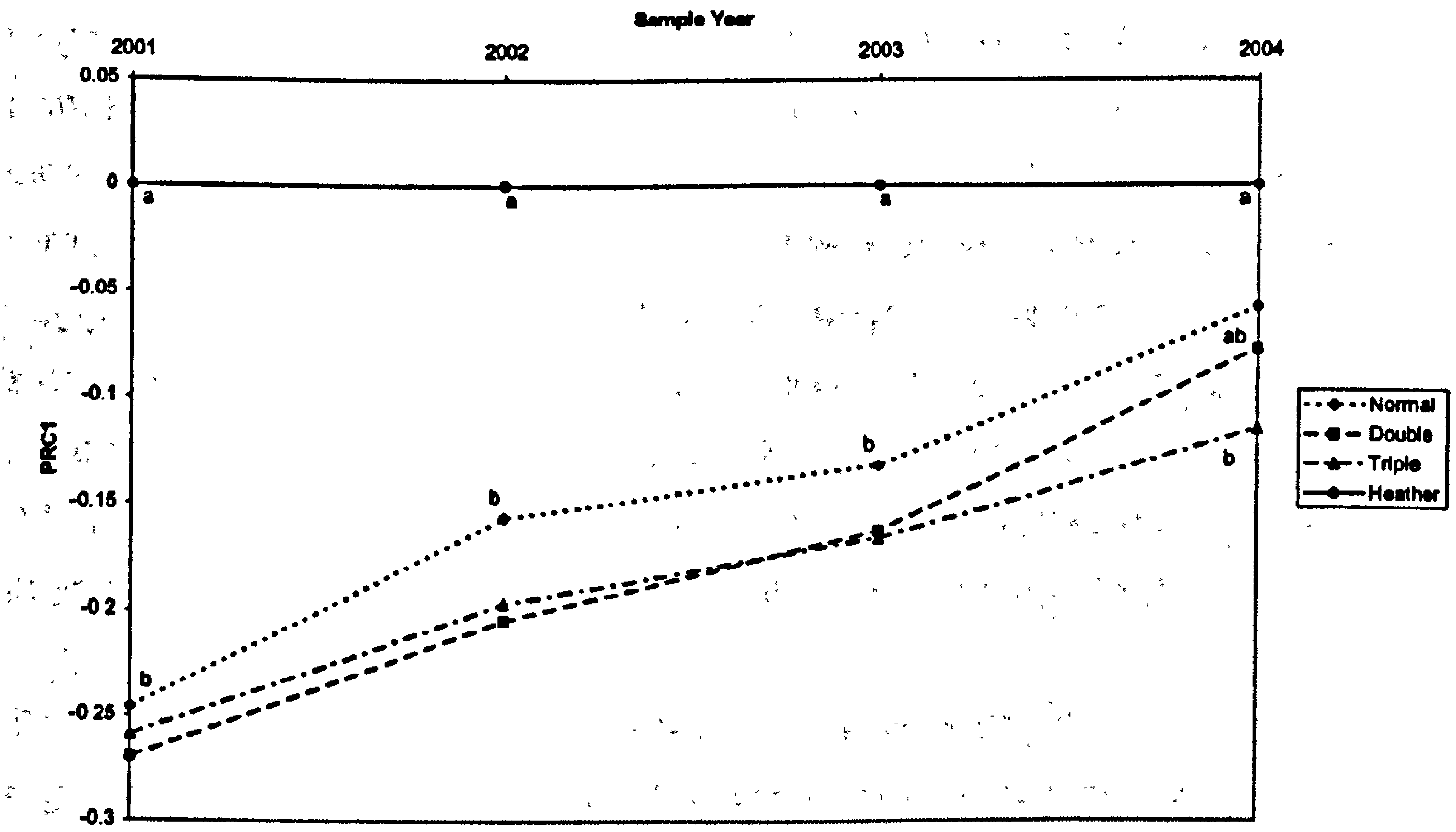


Figure 5.4: PRC diagram of 'vegetation structure' development over time since chipping at three different chip depths compared with mature heather vegetation. At each year, PRC 1 values differ significantly ($p<0.017$ for individual contrasts) between treatments that do not share the same letter code (a or b). Shared or omitted letter codes denote contrasts that do not differ significantly.

6.3.2.3 Three dimensional Principal Components Analysis

Ordination diagrams from the three separate Principal Components Analyses are shown in figures 5.5-5.7 below.

SAMPLE BY HEIGHT CATEGORY ANALYSIS - SHOWING VEGETATION HEIGHT DENSITY

Figures 5.5 a & b show results from the analysis of a matrix of total number of hits (on 5 pins/sample) in each height category. Axis 1 reflects the total number of hits in the sample which increases with year since chipping on the tree clearance area and remains constant on the target vegetation in each sample year. Axis 2 is more difficult to interpret but it may represent the most prevalent height categories in different vegetation samples. For example the target vegetation is dominated by height categories 20 - 40cm, with a greater number of hits in these height categories than the tree cleared samples. Despite this there is a large amount of variation indicating that there is a reasonable amount of vegetation in all of the height categories so the vegetation is probably more dense throughout the profile than the tree clearance vegetation. The tree clearance vegetation shows a clear movement towards the target vegetation in terms of total number of hits (Fig. 5.5a) but the relatively small variation on axis 2 suggests that only a narrow band of height categories are important in each year since chipping. The location of height category vectors in Figure 5.5b considered in conjunction with the sample ordination (Fig 5.5a) suggest that in years 0, 1 and 2 the '1' height category (ground level) is the most important height category and in years 3-5 height categories 10 and 20 become more important.

SAMPLE BY SPECIES ANALYSIS – SHOWING SPECIES COMPOSITION

Figures 5.6 a & b show results from the analysis of a matrix of total number of hits (on 5 pins/sample) for each plant species. Axis 1 probably represents an increase in number of species per sample and Axis 2 appears to reflect the range of species (plant community) found in each sample. The target vegetation in the bottom right hand corner of the ordination has the largest number of species per sample (highest Axis 1 score) with *C.vulgaris* and *M. caerulea* being the most important species in these samples. The tree clearance vegetation has an increasing number of species recorded in each sample with year since chipping but the dominant species in year 5 are *E. vaginatum* and *D. flexuosa.* Both these species were much quicker to colonise and grow on the tree clearance area than *C.vulgaris* and *M. caerulea.* From examination of only axis 1, it is apparent that the tree clearance vegetation has almost reached the target vegetation by year 5 since chipping. However, axis 2 demonstrates how different the vegetation actually is and that growth of some of the slower growing species, typically *C.vulgaris,* is necessary before the 'target' is achieved.

SPECIES BY HEIGHT CATEGORY ANALYSIS – SHOWING SPECIES HEIGHT DIVERSITY

Figures 5.7 a & b show results from the analysis of a matrix of total number of hits for each plant species in each height category.

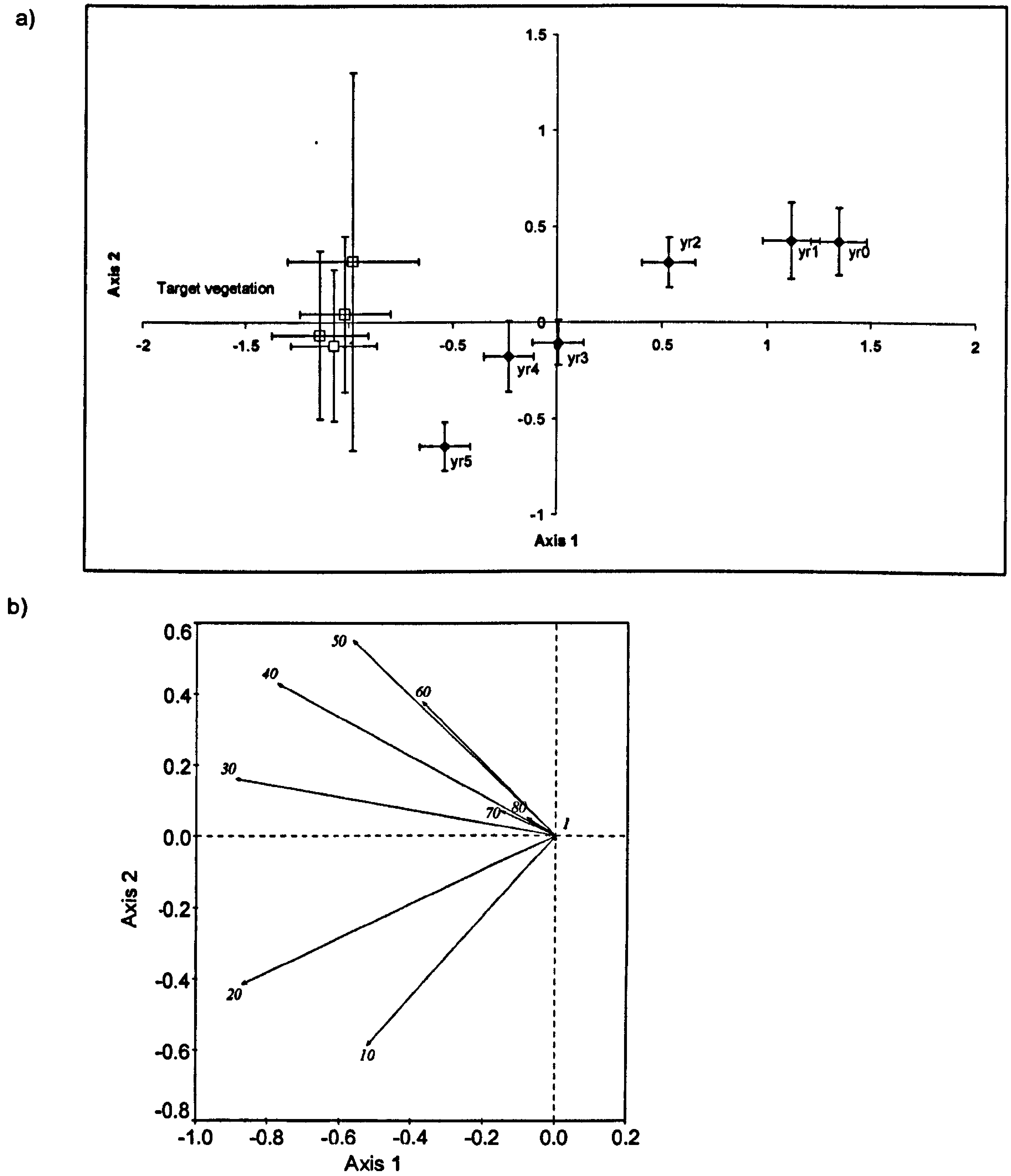


Figure 5.5: Sample by height category PCA ordination plots a) sample plot including tree clearance vegetation (diamond symbol) each year since chipping and target vegetation (square symbol) for sample years b) height category plot showing influence of height categories on the ordination.

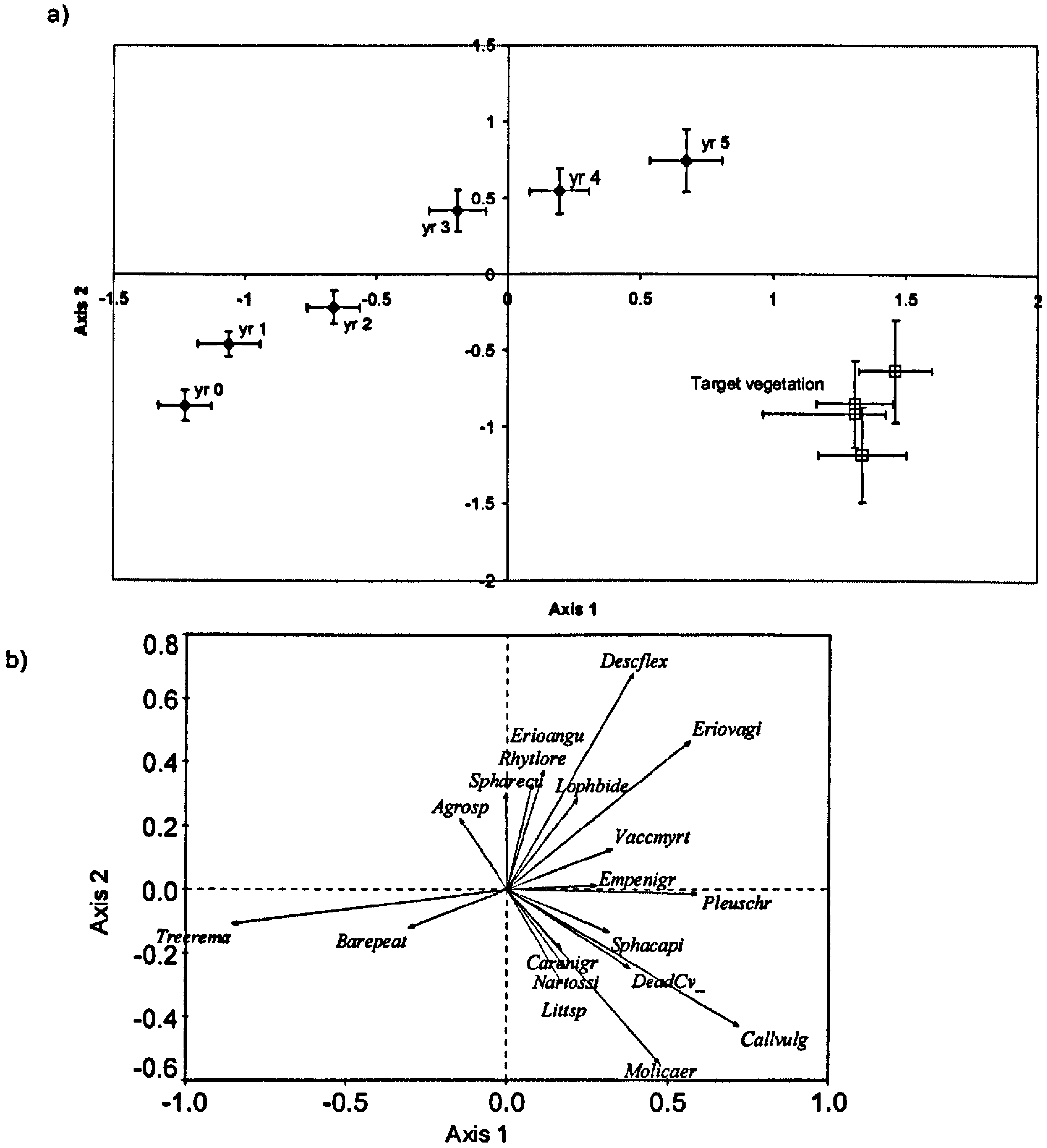
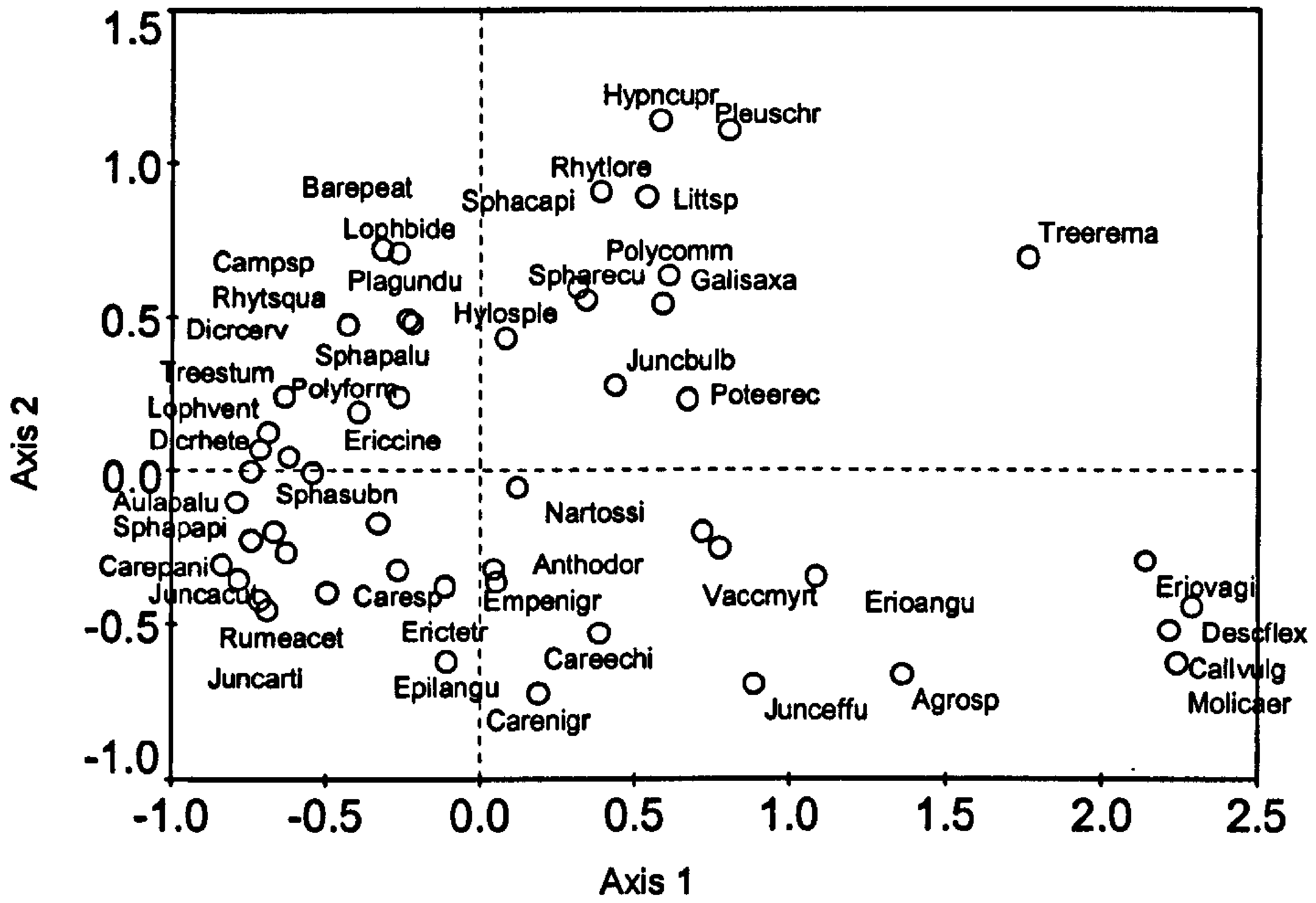


Figure 5.6: Sample / species PCA ordination plots a) sample plot including tree clearance vegetation (diamond symbol) each year since chipping and target vegetation (square symbol) for sample years b) species plot showing the influence of species on the ordination. Spha recu = Sphagnum recurvum; Spha capi = Sphagnum capillifolium; Call vulg = Calluna vulgaris; Erio angu = Eriophorum angustifolium; Moli caer = Molinia caerulea; Tree rems = Tree remains; Litt sp. = Litter; Erio vagi = Eriophorum vaginatum; Rhyt lore = Rhytidiadelphus loreus; Desc flex = Deschampsia flexuosa; Barepeat = Bare peat; Agrosp = Agrostis species; Lophbide = Lophocolea bidentata; Vaccmyrt = Vaccinium myrtillus; Empenigr = Empetrum nigra; Pleuschr = Pleurozium schriebri; DeadCv_ = Dead Calluna vulgaris; Carenigr = Carex nigra; Nartossi = Narthecium ossifragum.

Axis 1 represents frequency of species in all height categories. Tree remains (wood chip), *E.vaginatum*, *D. flexuosa*, *C. vulgaris* and *M.caerulea* are the 'species' to be hit most frequently by all pins. Axis 2 defines vegetation height and is inversely proportional to dominant height category. Tree remains are the most frequently hit 'species' at height category 1 with a high axis 2 score and *E.vaginatum*, *D. flexuosa*, *C. vulgaris* and *M.caerulea* are the most frequently hit species at height categories 20, 30 and 40 with a low axis 2 score. Figure 5.9a clearly shows groupings of species that have similar structures for example most of the species above 0.5 on Axis 2 are all short mosses; between 0 and 0.5 the species are all relatively short in stature or are creepers that cover the ground; from 0 to -0.5 the species include the smaller dwarf shrubs i.e. *V. myrtillus* and *E. nigrum* and more substantial grass species; finally the taller sedge, grass species and *C. vulgaris* are found between -0.5 and -1.0



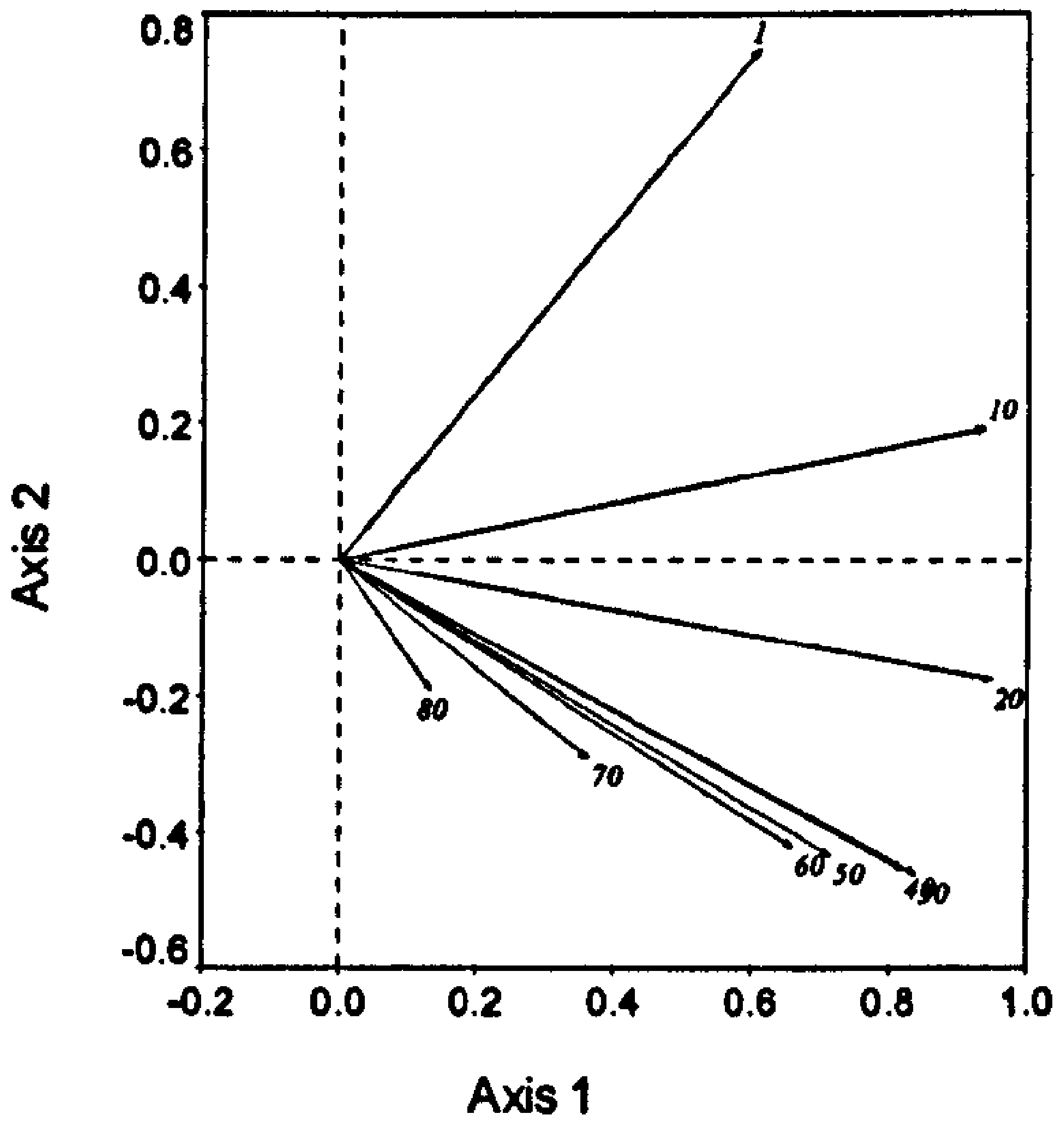


Figure 5.7: Species/height category PCA ordination plots a) species plot. Agrosp = Agrostis species; Anthodor = Anthoxanthum odoratum; Aulapalu = Aulacomnim palustre; Barepeat = Bare peat; Call vulg = Calluna vulgaris; Campsp = Campylopus species; Careechi = Carex echinata; Carenigr = Carex nigra; Carepani = Carex panicea; Caresp = Carex species; Descflex = Deschampsia flexuosa; Dicrcerv = Dicranum cerviculata; Dicrhete = Dicranella heteromala; Empenigr = Empetrum nigra; Epilangu = Chamaenerion angustifolium; Ericcine = Erica cinerea; Erictetr = Erica tetralix; Erio angu = Eriophorum angustifolium; Erio vagi = Eriophorum vaginatum; Galisaxa = Galium saxatile; Hypncupr = Hypnum cupressiforme; Hylosple = Hylocomnium splendens; Juncacut = Juncus acutiflora; Juncarti = Juncus articulatus; Juncbulb = Juncus bulbosus; Junceffu = Juncus effusus; Littsp = Litter; Lophbide = Lophocolea bidentata; Lophvent = Lophozia ventricosa; Moli caer = Molinia caerulea; Nartossi = Narthecium ossifragum; Plagundu = Plagiothecium undulatum; Pleuschr = Pleurozium schriebri; Polycomm = Polytrichum commune; Polyform = Polytrichum formosa; Poteerec = Potentilla erecta; Rhyt lore = Rhytidiadelphus loreus; Rhytsqua = Rhytidiadelphus squarrosus; Rumeacet = Rumex acetosella; Spha capi = Sphagnum capillifolium; Sphapalu = Sphagnum palustre; Sphapapi = Sphagnum papillosum; Spha recu = Sphagnum recurvum; Sphasubn = Sphagnum subnitens; Tree rems = Tree remains; Treestum = Tree Stump; Vaccmyrt = Vaccinium myrtillus.

b) height category plot showing the influence of different height categories on the ordination.

6.4 Discussion

Conventional indices that seek to describe diversity and richness provide a useful means of comparing structural differences between similar vegetation types and describing structural development of vegetation over time. The selected indices clearly indicate that vegetation structure on the tree clearance area, at both a small and large scale, was becoming increasingly diverse with time since tree clearance and that it was approaching the levels of diversity seen in the target vegetation. On the assumption that changes in structural diversity of vegetation affects the distribution of invertebrate populations and that increased structural diversity may increase invertebrate diversity it is probable that the tree clearance vegetation is supporting a greater diversity of invertebrates with time since chipping.

There appeared to be no significant difference in richness or diversity between chip depth treatments which is similar to the results of the PRC analysis. Here there was no difference in structural diversity between the three different chip depth treatments until 2004 when the triple chip treatment is significantly different from the normal treatment. This response is rather difficult to interpret as one would expect the effect of the chip depth treatments to diminish with time but perhaps slower growing species, such as *C. vulgaris,* started to appear on the normal and double treatments in 2004 but not on the triple treatment creating this difference. The lack of differences between the chip depth treatments was a little surprising as one might expect to find less dense vegetation where the chip depth is greatest, especially in the earlier years since chipping. Perhaps the species that do well when the ground is covered in a dense layer of wood chip, i.e. species that do not require light to germinate, are generally good at covering the ground. For example *Potentilla erecta* was present on all of the chip depth experimental plots one year after the treatments were applied, irrespective of treatment. This species was very quick to cover the ground and was common on all the flailed quadrats. It is possible that this species and other colonisers created similar structural profiles irrespective of chip depth. Alternatively it is possible that there are differences in vegetation structure between chip depth categories but that five vertical pins per sample provides insufficient data to detect these differences. Other researchers have certainly used more pins per sample to measure structure with anything from 20 - 45 pins/sample (Southwood et al. 1979; Downie et al. 1995; Borges and Brown 2001; Hartley et al. 2003) but the initial objective for collecting these data was to compare vegetation structure year on year following tree clearance. It was thought that the differences between years would be so great that 5 samples would be adequate to measure change and indeed this is the case.

The many diversity indices available seek to characterise the diversity of a sample or community with a single number (Magurran 1988) and as a result a considerable amount of information about the sample or community is lost. In addition the various techniques completely ignore species identity which may be critical when describing the structural diversity of vegetation. By using multivariate techniques, such as PCA, it is possible to incorporate all the different dimensions of the data set and in this case it has been used to explore the following relationships.

1. **Vegetation height diversity** or total number of vegetation hits (all species) in each height category for each sample.
2. **Species composition** or number of hits for each species in each sample.
3. **Species height diversity** or total number of hits in each height category for each species.

Vegetation height diversity and species diversity on the tree clearance area showed an obvious movement towards the target vegetation with year since tree clearance. However, in both cases the movement appears to be in one dimension only i.e. in terms of total number of hits either in each height category or for each species. The multi dimensional view of each measure of diversity indicates that the tree clearance vegetation does not have the full complement of height categories or species that are found in the target vegetation. Interestingly enough the PCA multi dimensional approach gives roughly the same end result as the conventional diversity and richness indices i.e. that the tree clearance vegetation has not reached the target by the end of the monitoring period. This suggests that the conventional approach is reasonably accurate but does not provide any insight as to why differences in diversity or richness exist.

The species height diversity analysis elegantly demonstrates the relationship between vegetation structural diversity and the taxonomic identity of species. Vegetation structure of blanket bog vegetation is clearly linked to plant species although rather than being closely associated with individual species it is dictated by types of species that have the same sort of growth form. For example *Juncus bulbosus, Potentilla erecta* and *Galium saxatile* have a similar growth form, all fairly low growing with lots of side branches or leaves. They are unlikely to be in the same sort of plant community because *J. bulbosus* grows in very wet locations (Chabbi 1999), *P. erecta* in slightly drier locations and *G. saxatile* in locations that are slightly drier still. However, they all have roughly the same structural profile. The species height diversity ordination shows a number of similar groupings where the species are unlikely to be found in the same plant community but share similar structural profiles which suggests that vegetation structure is only loosely related to plant community, at least during the first five years of plant community development on blanket bog.

The multi dimensional approach to assessing the structural diversity and species composition of vegetation is particularly useful for comparing similar samples and for investigating time series data especially where a control or 'target' is available that acts as a point of reference for the other samples. It would not be suitable for comparing the diversity/composition of totally unrelated and completely different samples because ordination relies on the assumption that there is continuity of change (Leps and Smilauer 2003). Conventional diversity indices would be more appropriate for comparing unrelated samples (Magurran 1988).

The PCA species composition analysis indicates that *C. vulgaris* cover is considerably lower on the tree clearance area, five years after the trees were cleared, compared with the target vegetation. *C. vulgaris* makes up at least 90% of the diet of a red grouse (Jenkins et al. 1963) so the presence of this plant species is essential if the habitat is going to support red grouse. Research on feeding preferences of red grouse indicate that they select *C.vulgaris* that is greater than 2 years old and less than 8 years old (Savory 1978). It is thought that this is linked to both the nutrient content of the shoots, which is higher in younger plants, as well as the height of the plant and therefore the potential to provide cover from predators and shelter from bad weather (Moss et al. 1972; Savory 1978). The preferred age range of *C.vulgaris* equates to a height range between 10 and 37cm (Savory 1978). The height of a squatting adult red grouse is approximately 15cm so *C.vulgaris* at 10cm would not provide effective cover but is almost certainly more nutritious than older and taller heather (Thomas 1956). The full height of an adult red grouse is about 30cm so it is thought that vegetation greater than 37cm would restrict visibility and movement and hence become less attractive (Moss et al. 1972).

The PCA vegetation diversity results indicate that height categories 20 and 30 are the most important categories defining the target vegetation and the PCA species composition results show that *C.vulgaris* is the most influential species for the target vegetation. This suggests that the target vegetation on site is highly suitable for red grouse with plenty of *C.vulgaris* between 20 and 30cm high. Data on *C.vulgaris* height on the tree clearance area in 2004 indicates that for the height bands 10, 20, 30 & 40 *C.vulgaris* is present in 58, 42, 4 & 0 percent of quadrats. It seems reasonable to assume, therefore, that by year 5 the tree clearance ground is providing good quality heather shoots for grouse food but the cover provided by *C.vulgaris* is limited. Grouse numbers on the tree clearance area did increase over the period of the project (Sheridan 2005) so presumably the birds were using other plant species or patches of mature heather adjacent to tree clearance ground to provide cover and shelter.

It is clear that vegetation structure on the tree clearance area is moving towards the 'target' both at a small and large scale. Although the vegetation height diversity target was achieved by the last year of the investigation this assessment does not take into account species composition which is of importance for red grouse. It seems likely that the *C. vulgaris* component of the vegetation needs to increase, both in terms of cover and height, before the vegetation will provide habitat that meets all the needs of red grouse.

CHAPTER 7

GENERAL DISCUSSION

7.1 Can blanket bog vegetation be restored when immature Sitka spruce plantation is removed from blanket peat?

7.1.1 Tree clearance method

'In situ' chipping of trees using an excavator mounted flail is an effective method to clear large areas of conifer forest, between 3-8 m high, from blanket bog sites. The resultant wood chip layer does not appear to hinder vegetation regeneration in the long term or affect the plant community that is predicted to develop. It would not be worth chipping trees smaller than 3m high because the blanket bog vegetation beneath the trees would be relatively intact and may be damaged by the machinery. For trees that are taller than 8m high extraction for paper pulp, paper board or biomass fuel is likely to be cost effective (Sheridan *pers. comm.*).

Manual felling of trees using a chainsaw is not a suitable method for clearing trees, between 3-8m high, from blanket bog if blanket bog vegetation restoration is the key objective. The process creates a deep brash layer (0.5-1m deep) that inhibits vegetation establishment. It may be suitable for felling trees that are smaller than 3m high especially if the brash and trunk can be used to block up plough furrows (Wilkie 2005).

Whole tree removal using a conventional harvesting machine can be used effectively although the costs will be substantially greater (£3,000 - £4,000/ha[2]) than 'in situ' chipping of trees with an excavator mounted flail (£1,200 - £1,800/ha[2]). Initial vegetation response to whole tree removal is quicker than with in situ chipping but the differences in vegetation development are negligible after 6 years.

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[2] These figures were estimated by Tilhill Economic Forestry as part of the project planning process

7.1.2 Size of trees

The size of trees and hence the amount of wood chip has a significant affect on the time taken for blanket bog vegetation to develop. It is estimated that it will take 7, 9 & 10.5 years for the blanket bog vegetation to develop following in situ chipping of Sitka spruce trees (yield class 10) that are 20, 25 and 30 years old respectively. The physical barrier to light that a layer of wood chip creates appears to be the main reason why vegetation development is delayed as wood chip depth increases. Increasing depth of wood chip certainly delays the appearance of many plant species including some of the most common blanket bog species, *C.vulgaris, E.vaginatum, Campylopus sp.* and *H. cupressiforme.* It is also very clear that wood chip on the peat surface inhibits germination and growth of *C.vulgaris* seedlings.

In reality chipping trees with an excavator mounted flail does not deposit wood chip evenly over the ground. To a certain extent the flail can be angled to influence the direction of wood chip and this was done in some parts of the tree clearance area in order to fill plough furrows. As a result the higher ground near the tree stumps received only small amounts of chip even when the trees were relatively tall. This creates a highly heterogeneous situation where patches of deep wood chip are within one metre of patches of shallow wood chip leading to differential vegetation development at a scale of a few metres. The monitoring quadrat design with five mini quadrats (1x1m) nested within the main quadrat (10x10m) provided a useful data set that allowed the differential vegetation development to be detected very clearly.

Directing wood chip is a feature of the excavator mounted flail that is not necessarily common to all flail equipment. Some machinery operates at ground level, knocking the trees down and chipping them on the ground surface (see Appendix 4 for a picture of this type of flail machinery). The excavator mounted machinery offers considerable flexibility which may facilitate blanket bog restoration in two ways. Firstly, by blocking plough furrows to encourage re-wetting of the peat and secondly by minimising wood chip cover on higher areas of ground allowing vegetation to develop more quickly.

There is considerable evidence to suggest that the propagule bank of forested blanket bog sites is likely to decrease with increase in size of the trees and the associated time since canopy closure (Hill and Stevens 1981). However, those species that have any longevity within the seed bank appear to remain viable for at least 45-55 years (Hill and Stevens 1981) which is the length of time that a Sitka spruce crop takes to mature (Taylor 1991). So it seems likely that, provided the forest plantation is in its first rotation, there will still be some viable propagules in the surface peat. The propagule bank certainly appears to be important during the first year of plant colonisation following tree clearance but in subsequent years seed dispersal from nearby mature blanket bog vegetation starts to influence vegetation development. If there was no existing blanket bog vegetation within the vicinity of a tree clearance site then the propagule bank may be more important although it will not supply anything like the full complement of blanket bog species as many species are only transitory within the seed bank (Grime et al. 1988). In this situation seed introduction may be necessary to create the desired plant community.

7.1.3 Development of blanket bog vegetation

Development of the plant community, following in situ chipping of the trees, showed a clear movement towards the target vegetation. Subtle changes in the plant community over the 6 years since chipping indicate that the peat was becoming increasingly wet with time since clearance. A tree crop planted on blanket bog has a significant drying effect on the peat by year 20 (Pyatt et al. 1989) so removal of the crop should start to reverse this effect (Anderson 2001) provided that significant cracking of the Catotelm has not occurred (Anderson et al. 1995). Many of the plough furrows and drainage channels on site had become partially blocked with moss or general forest detritus before tree clearance began and no attempt had been made to maintain the forest drainage system. For this reason, coupled with the high rainfall levels in Kintyre, it was decided that no additional effort should be made to re-wet the site following tree clearance except using wood chips to block plough furrows. On drier sites where forest drainage has been more effective it may be necessary to put additional effort into blocking plough furrows and forest drainage systems in order to ensure that the desired blanket bog plant communities develop.

There was a good range of peat depths found on the tree clearance area varying from 10cm on steep slopes to over 2m on some of the flatter areas. As expected there was a clear difference in plant community development depending on peat depth and slope with the true mire communities (M19 and M15) (Rodwell et al. 1991) developing on the areas of deep peat. pH had some influence on the plant community but as the pH range was only relatively small and all areas were below pH 4 it was not possible to see a clear differentiation of plant community type in relation to pH.

7.1.4 Ground disturbance

Whilst setting up the chip depth experimental plots the ground was raked to remove all the wood chip which was then re-applied as different treatments. This was not done on the 'natural' control as it was left untouched and although there were patches of chip on these control plots there were also patches of bare ground. Plant growth on these plots differed from that on the 'all removed' treatment suggesting that the raking disturbance on the 'all removed' treatment stimulated the vegetative, seed and spore propagules in the peat. On second rotation sites or sites where the trees are older the propagule bank may be limited and it is possible that a level of surface disturbance may stimulate propagules that would not develop if undisturbed. This is only really relevant if there is relatively little wood chip on the surface because light availability is also thought to be important (Jauhiainen 1998) and not necessary where mature blanket bog vegetation exists within the vicinity.

7.2 Does blanket bog vegetation, which has been restored through tree removal, provide suitable habitat for red grouse?

7.2.1 Manual felling of trees

Manual felling of trees using a chainsaw is a completely unsuitable method for clearing forested ground if red grouse habitat creation is the desired objective. The brash layer that is created by felling trees between 3-8m high is too deep to provide sensible cover for the birds and it hinders development of the vegetation. It is thought that vegetation taller than 37cm would be unattractive to red grouse as it restricts visibility and movement (Moss et al. 1972) so a brash layer of 50cm or more is unlikely to be used by red grouse. During spring 2001 a red grouse nest was found under a pile of Sitka spruce brash on the tree clearance area but the brash pile was relatively small with very good visibility in all directions. Extensive areas of brash would severely inhibit visibility and movement to a much greater extent than the tall vegetation described by Moss et al. (1972). 'In situ' chipping or complete removal of trees are far more appropriate methods to clear forest to create habitat for red grouse.

7.2.2 Calluna vulgaris on blanket bog

Calluna vulgaris is an essential component of the vegetation if a blanket bog habitat is going to support a red grouse population. This is largely to do with the diet of red grouse with at least 90% of their diet made up of *C.vulgaris* shoots (Jenkins et al. 1963). *C.vulgaris* is a 'constant' species in all but one of the NVC blanket bog plant communities (M20) where it is found in 21-40% of examples of the plant community (Rodwell et al. 1991). This is perhaps surprising given that the species grows best when the soil is at least moderately well drained (Pearsall

1938; Poel 1948; Gimingham 1960) but it will grow where some level of oxidation occurs for some time during the year (Poel 1948). *C.vulgaris* is unlikely to exist at high percentage covers in blanket bog communities, although this depends on management (Rodwell et al. 1991) but it is thought that a percentage cover above 30% is sufficient to support red grouse (Moss *pers. comm.*).

Vegetation on the tree clearance area had not reached the 'target' by 2004 and this was largely to do with the dwarf shrub component of the plant community which had not become fully established. The mean percentage cover of *C.vulgaris* in the monitoring quadrats on flailed ground in 2004 was 10.82% compared with 45% in the 'target' vegetation control quadrats. The maximum predicted time to achieving the 'target' vegetation on flailed ground was 10.5 years so one would assume that the percentage cover of *C.vulgaris* will have continued to increase after 2004. Indeed data from vegetation monitoring along a series of transects on the tree clearance site indicates that the percentage cover of *C.vulgaris* was 11% in 2001, 15% in 2004 and is now 33% in 2008 (Sheridan 2008).

E. vaginatum became established across much of the tree clearance area in a relatively short space of time (during the first year after tree clearance) indicating that the species is good at colonising bare peatland sites. Indeed the species has been used in the restoration of mined peatlands which are usually completely devoid of vegetation. Initially it was thought that *E.vaginatum* may provide a 'nurse crop' for *C.vulgaris* seedlings as suggested by Lavoie *et al.* (2005). However, the reverse was found to be true with *C. vulgaris* doing significantly less well where *E. vaginatum* was present. This may be due to competition for light and nutrients but may also be related to wetness of the site as *C.vulgaris* tends to prefer reasonably dry conditions (Poel 1948) and although *E. vaginatum* can tolerate drought it will also grow on waterlogged peat (Wein 1973). Re-wetting of a site through drain blocking is certainly a pre-requisite for the restoration of mined peat bogs using *E. vaginatum* (Tuittila et al. 2000a). The

M19 NVC plant community (Rodwell et al. 1991) is the pre-dominant vegetation type on and around the tree clearance area and this community is suitably named the *Calluna vulgaris* – *Eriophorum vaginatum* blanket mire community with these two species being the most abundant within the community (Rodwell et al. 1991). This suggests that although the two species may have slightly different micro-site requirements they do co-exist well at the plant community level. In any case *E. vaginatum* is an important food item for red grouse as the flowers or 'cotton buds' are a rich source of protein during early spring when hen grouse need to be in good condition for egg laying (Moss *pers. comm.*).

7.2.3 Vegetation structure

Development of the vegetation structure, following in situ chipping of the trees, showed a clear movement towards the target vegetation. At a large scale (> 10m) structural diversity or vegetation height diversity was the same on flailed ground 4-6 years after chipping as it was on the target blanket bog vegetation. However, at a small scale (10x10cm – 1x1m) the vegetation structure and plant community composition indicated that the cover of *C. vulgaris* was not anywhere near as high on the flailed ground as the target vegetation. Since red grouse rely so heavily on *C. vulgaris* (Jenkins et al. 1963) the vegetation structure/ composition combination is unlikely to have provided ideal habitat for the birds 4-6 years after tree removal. *C. vulgaris* was present on the flailed ground but the plants were relatively young and therefore short, providing a good source of food but only limited shelter and cover from predators (Thomas 1956). It is possible that other plant species could provide the necessary cover for red grouse but all the taller species were grasses, sedges or rushes and the growth habit of these species is considerably different to *C. vulgaris*. It seems likely that although the vegetation on the tree clearance area offered some potential as a habitat for red grouse 4-6 years after tree clearance the potential would improve as the cover and height of *C. vulgaris* increased. It is predicted that it may take 10 years before the 'target' plant community is reached so perhaps this is a realistic estimate for achieving the 'target' vegetation structural diversity that is required to support a red grouse population at its maximum capacity.

Red grouse numbers have been monitored on the tree clearance area every year since 2000. An initial increase was seen between 2000 and 2004 of 3.1 grouse pairs/km^2. However, since then numbers have declined back down to the levels seen in 2000. Although this suggests that the developing habitat is not ideal for red grouse there are a number of other factors that affect grouse numbers including predators and weather conditions, particularly during the spring and early summer (Moss *pers. comm.*). One of the main reasons for this blanket bog restoration project was to create habitat for red grouse and ultimately to provide live prey for a pair of golden eagles. The golden eagle monitoring indicates the birds have increased their use of the tree clearance area since 2000 (Walker et al. 2005) so it is possible that the small declines in grouse numbers since 2004 are a result of increased numbers of grouse are being taken by the eagles.

7.3 What scale is the most appropriate for monitoring blanket bog vegetation?

The questions explored in this thesis were studied at a range of scales and the results varied considerably depending on the scale of study. Plant community development of the blanket bog vegetation appeared to reach the 'target' in some quadrats, within 5 years of tree removal when working at a scale of 1x1m. However, at the larger scale of 10x10m the vegetation was some way off the 'target' 5 years after the trees were removed. This difference in results was largely due to heterogeneity in wood chip depth, which varied considerably from one metre to the next, but was also influenced by vegetation cover that existed prior to tree clearance. At the 1x1m scale some patches of vegetation did develop quickly or existed prior to tree clearance but the larger scale assessments indicated that this was not sufficiently widespread to assume that the target vegetation composition had been reached over the whole tree clearance area.

The vegetation structure assessments that were done at a large scale with transects that cover the whole tree clearance area, showed that the vegetation height diversity at the end of the study was the same as the 'target' vegetation. However, at the small scale of 10x10cm the data showed a completely different picture where the structure of the vegetation, 5 years after the trees were removed, was not as diverse as the target vegetation. This was in part due to the assessment techniques used with the small scale measurements being more sensitive to species composition which had an influence on vegetation structure.

The influence of micro-site characteristics on *C.vulgaris* germination and growth was also considered at a range of scales from 10x10cm to 1x1m and although there were similarities in the results there were some clear differences. For example it appears that micro-topography is important for *C.vulgaris* germination and growth at the 1x1m quadrat scale but the relative height of 10x10cm cells around a 10x10cm patch does not influence the suitability of that micro-site for *C.vulgaris* germination.

Initially it was thought that a multi-scale approach would allow the most appropriate scale of study to be identified in each situation. However, study at each scale provided complimentary data that improved understanding of the different processes under investigation and aided interpretation of all the results. Different species respond to their environment at a unique range of scales (Levin 1992) so there is no single correct spatial scale at which to describe species habitat relationships (Wiens 1989; Saunders et al. 1998). Indeed many ecological relationships between species pattern and process may occur along a continuum of scale (Saunders et al. 1998). The results from small scale ecological experiments cannot always be extrapolated directly to larger scales (Carpenter et al. 1995; Schneider et al. 1997). Similarly it is unusual that fine scale predictions can be obtained from coarse scale data (Hartley et al. 2004). As a result multi-scale approaches, similar to that taken in this thesis, are necessary in the study of species habitat relationships (Graham and Knight 2004; Graf et al. 2005).

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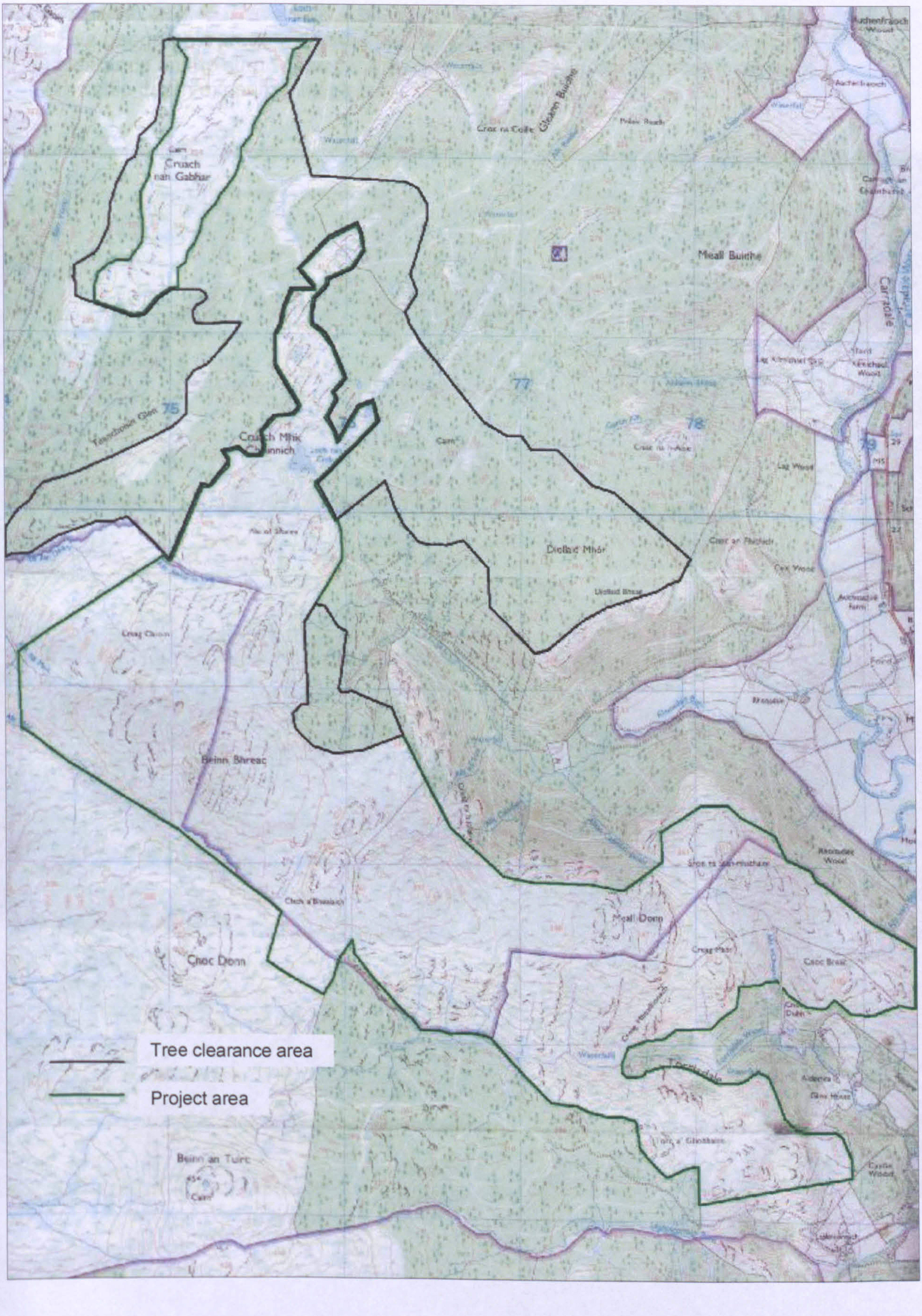
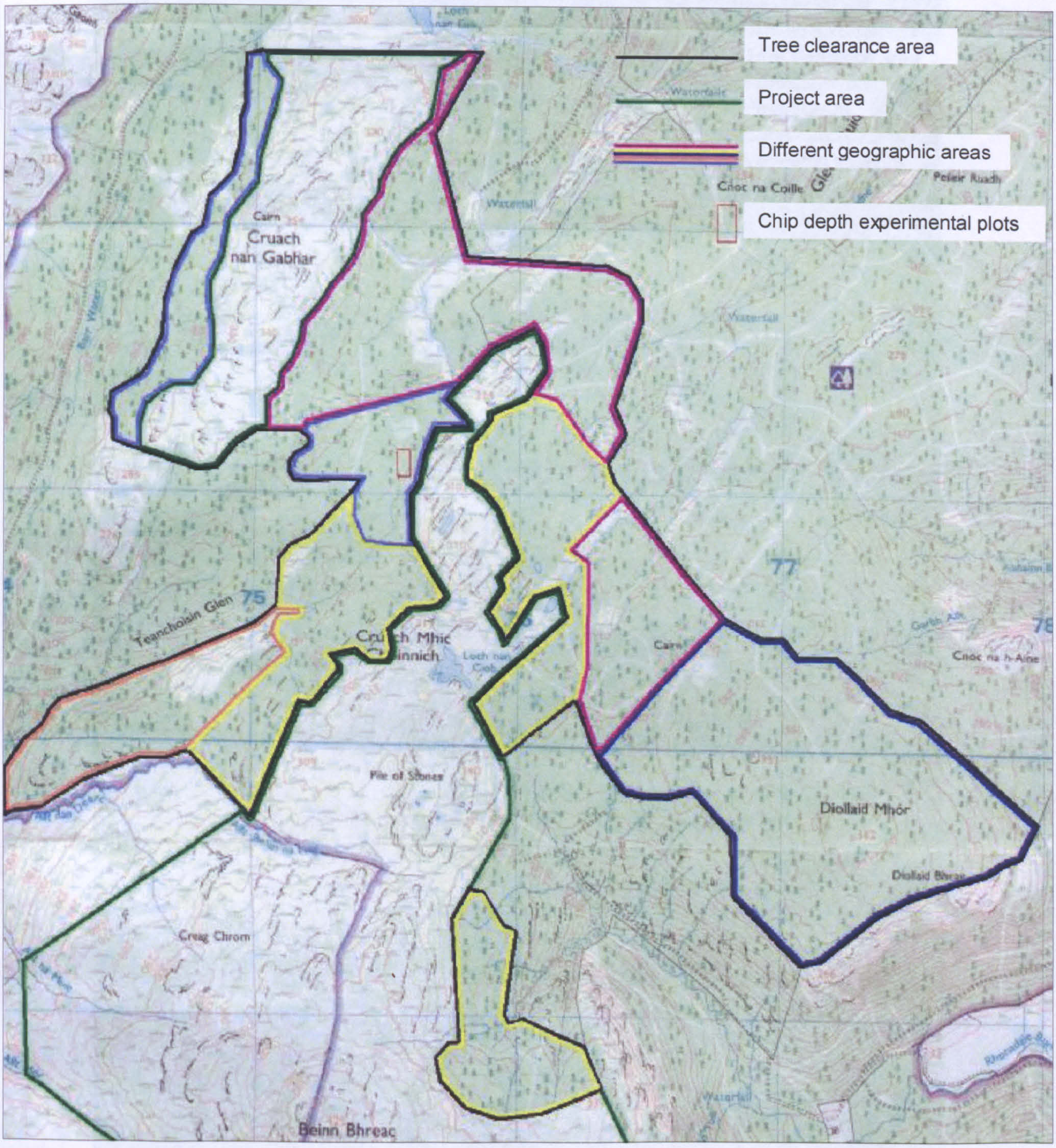
9 APPENDICES

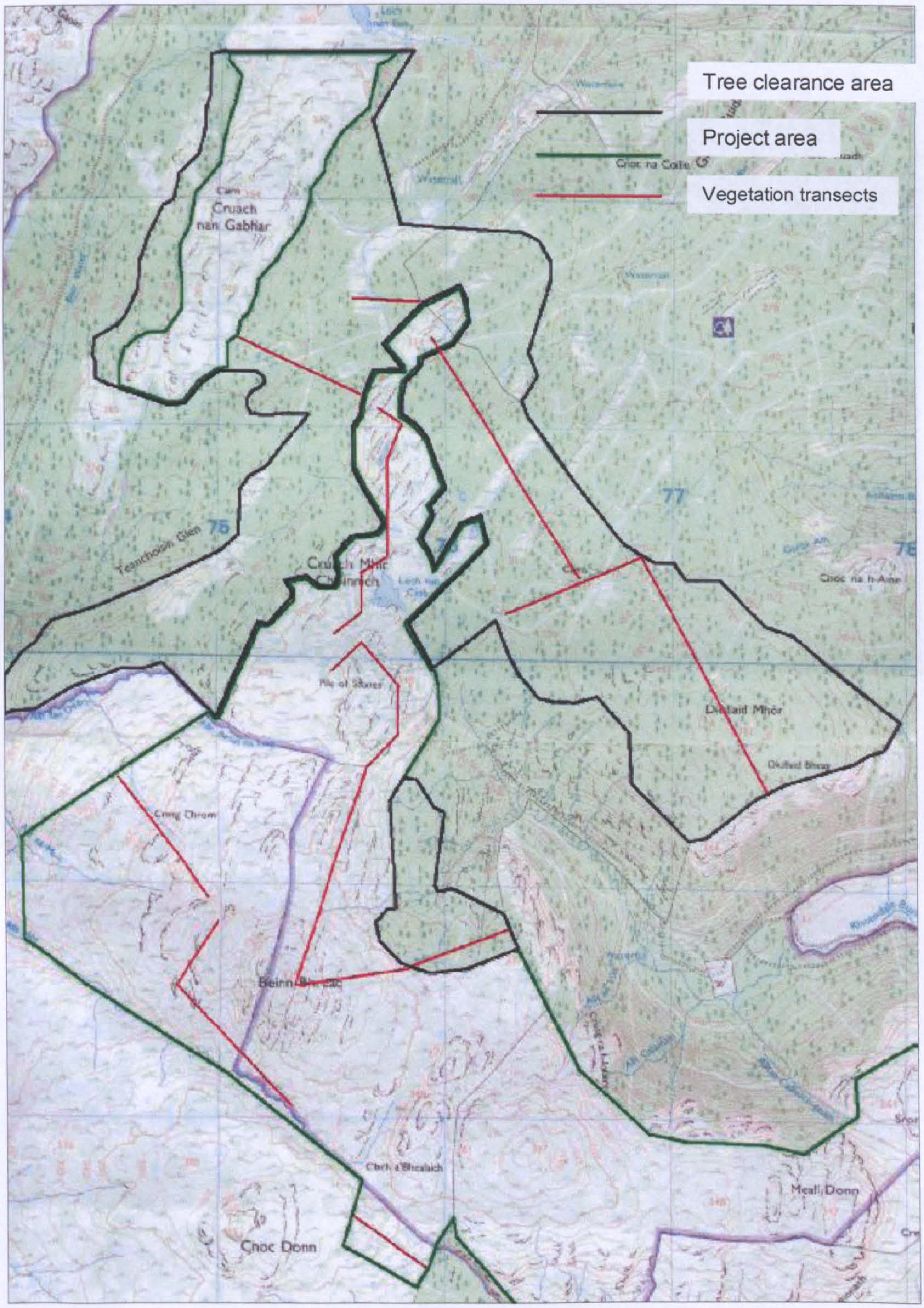
Appendix 1
Project and tree clearance area



Appendix 2
Five geographic areas within the tree clearance area used to managed tree clearance and to stratify sampling for monitoring quadrats. Includes location of the chip depth experimental plots



Appendix 3
Location of vegetation transects on the tree clearance area and on the two management units immediately adjacent to the tree clearance area.



Appendix 4

Ground level flail machine