STUDIES OF SUCCESSION ON DORSET HEATHS

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

by

Ruth Joy Mitchell

November 1997

Abstract

STUDIES OF SUCCESSION ON DORSET HEATHS

Ruth Joy Mitchell

Lowland heaths are high-profile ecosystems for conservation action in Europe. The Dorset heaths are an important component of the European heathland resource and they have been considerably reduced and greatly fragmented over the last century. Today they are under threat from invasion by *Betula* spp., *Pinus sylvestris, Pteridium aquilinum, Rhododendron ponticum* and *Ulex europaeus.*

A series of hypotheses to explain (i) vegetation successional trajectories and (ii) soil chemical properties associated with vegetation change, were tested using multivariate models (DECORANA - vegetation; CANOCO - vegetation and soil). A range of pathways was found along which heathland communities move during succession, with some successional pathways remaining closer to heathland than others. The *Betula* spp. succession caused the greatest changes in terms of the vegetation present. The *Ulex europaeus* and *Pinus sylvestris* trajectories retained some typical heathland species. Different soil nutrients were found to increase along different successional pathways, which were associated with the different successional species invading. *Pinus sylvestris* had similar soil nutrient concentrations to those of heathland. Sodium concentrations increased during the *Rhododendron ponticum* succession. Concentrations of ammonium-nitrogen and nitrate/nitrite-nitrogen increased during the *Pteridium aquilinum* and *Ulex europaeus* succession. The *Betula* spp. had the greatest effect on the soil nutrients with increased pH, extractable phosphorus and exchangeable calcium.

An array of managed sites (managed successional sites) was studied to assess the efficacy of conservation management to restore heathland. The management allowed many heathland species to establish and the majority of sites to become similar to the neighbouring heathland. The reversion of increased soil nutrients was found to be more problematic with levels of ammonium-nitrogen, phosphorus, pH, calcium and magnesium remaining significantly different from those of heathland soils. The vegetation and soil data was analysed by CANOCO and used to produce a model by which the success of management might be assessed. Restoration of heathland was generally found to be most successful on *Pinus sylvestris* sites.

The seedbanks of the successional sites were also compared with those of nearby heathland sites. The seedbanks of all successional sites contained some heathland species, although densities varied, with *Pinus sylvestris* and *Pteridium aquilinum* sites having higher densities than the other successional communities. *Betula* spp. and *Ulex europaeus* successional sites contained more seeds of invasive/successional species than the other sites and the *Rhododendron ponticum* sites had a poor seedbank flora.

The results are related to practical conservation management and the restoration of heathland after succession. Specifically, that restoration of heathland is likely to be more successful on sites where *Pinus sylvestris* successions have occurred, than where *Betula* spp. successions have occurred.

The potential of CANOCO models for measuring ecosystem resilience and stability is discussed. A model is proposed which would allow ecosystem resilience to be measured against two fixed points, two ecosystems at notional equilibrium along a successional trajectory. However, the model is designed to include any variability or movement over time caused by these ecosystems not being at equilibrium. It provides a measure of change not only of the ecosystem structure but also of the important driving variables of the ecosystem.

To my Parents

With many thanks for all their help and support,
in so many ways, throughout all my education.

CONTENTS

ACKNOWLEDGEMENTS

This work was funded by the Royal Society for the Protection of Birds (RSPB), and I am grateful to them for this financial support and for their generous contribution towards field work expenses.

I wish to thank my supervisor Professor Rob Marrs for all his help and encouragement throughout my Ph.D. I would also like to express my gratitude to Dr Phil Putwain (SOBS, The University of Liverpool), Dr Martin Auld and Dr Ceri Evans (both RSPB) for advice throughout, Dr Mike Le Duc (SOBS, The University of Liverpool) for statistical advice and Dr Hugh McAllister (SOBS, The University of Liverpool) for taxonomic support. This work would not have been possible without the help of the all the RSPB staff involved in the conservation of Dorset heaths, especially Mr Neil Gartshore, Mr Bryan Pickess and Mr Nigel Symes.

Professor Nigel Webb (ITE Furzebrook) made helpful comments on earlier drafts of this thesis and provided laboratory facilities during fieldwork. I am also grateful for technical support from the horticultural staff at Ness Botanic Gardens, University of Liverpool and from Miss Joy Harrison during analytical work. Dorset County Council kindly allowed access to their aerial photograph collection.

I am also grateful to the following landowners and conservation bodies for allowing me access to their heathlands: Atomic Energy, Bournemouth International Airport, Mr A Chamberlain, Christchurch Borough Council, Dorset County Council, Dorset Trust for Nature Conservation, Herpetological Conservation Trust, Holton Lee (East Holton Charity), Poole Borough Council, RSPB and Mr G Sturdy.

Finally I would like to thank my parents, sister and friends for all their support, help and encouragement during the last three years.

Chapter 1

INTRODUCTION

1.1 INTRODUCTION

Heathlands are dwarf ericaceous shrub communities, usually dominated by *Calluna vulgaris*, where growth of trees is prevented either by climatic factors or by man's influence (Gimingham 1972). Communities dominated by *Calluna vulgaris* within the UK are often considered as two types: lowland heaths, studied here, which occur on nutrient poor acidic mineral soils at low altitudes (below 250m) and the heaths of upland areas of Britain, commonly called moorlands, which occur at higher altitudes on peat soils (Webb 1986).

Britain contains a significant proportion of European lowland heaths (Farrell 1989) and therefore the conservation of British lowland heaths is of international importance. In 1977 the UK was signatory to the Council of Europe's resolution on the conservation and management of heathland, which advises member governments to protect the last fragments of heathland (Cadbury 1989). The Berne Convention signed by the UK government in 1979 provides protection to several species associated with lowland heaths whose populations are declining. The EC directive on the conservation of wild birds includes several heathland species and obliges members to take special measures to conserve the habitat of these birds, designating the most suitable areas as Special Protection Areas (SPA's) (Cadbury 1989). Britain is therefore under an international obligation to conserve lowland heathlands (Department of the Environment 1995 a&b).

1.2 THE ORIGINS OF HEATHLANDS

The podzolic soils and ericaceous shrub community common to lowland heaths (Groves 1981) have largely developed due to anthropogenic influences (Gimingham 1972). Most lowland areas that have heath on them today would naturally be oak or beech woodland (Webb 1986).

The development of heathlands probably started in Atlantic times (4000 years BC), most of Britain was then forest covered and the soils were predominantly a brown forest soil. During this time heathland plants are thought to have survived beneath gaps in tree cover in the forest (Webb 1986). At the end of the Atlantic period (2000 years BC) the soils began to deteriorate and the forest started to decline. Whether the deterioration of the soils and the increased trend towards podzolization caused the forest to decline or whether the removal of trees caused the start of podzolization is unknown; however it seems likely that the leaching of the soils and consequent deterioration of the soils was already in progress before the tree cover significantly decreased (Dimbleby 1962; Haskins 1978).

The clearance of the forest by Mesolithic man accelerated if not initiated the development of podzolic soils. In Atlantic times soil nutrients would have been tightly cycled between the vegetation and the soil (Webb 1986). When the trees were cleared the soils were unable to retain the nutrients leading to leaching and the start of podzolization. Because of the inherently poor nature of the parent material that forms the Dorset heathland soils, the soils here would have been particularly susceptible to man's activities and podzols may have been widespread before the Bronze Age (1600 years BC) (Haskins 1978). Pollen analysis from Wareham, Dorset, (Seagrief 1959) shows that forest clearance by prehistoric man started to occur in the Boreal/Atlantic (4-3000 years BC) times, much earlier than elsewhere in Britain. As the forests were cleared so heathland species began to spread. In most areas the treeless landscape and poor soils were maintained by man's activities. However on some sites the soil profile and nutrients may naturally be in a steady state (Chapman 1979) and tree growth inhibited by nutrient-poor, phosphorus-limiting, soils (Chapman, Rose & Basanta 1989).

1.3 HISTORICAL USES OF THE HEATHS

For many centuries heaths were an important part of the farming life style of rural communities (Taylor 1970; Armstrong 1971; Gimingham 1972; Traynor 1995), they are mentioned in the Domesday book (Hutchins 1861) and were extensively and intensively used by the local people. The heaths provided grazing for the livestock and *Ulex* spp. were cut for fodder. *Pteridium aquilinum* was cut to provide bedding for the animals. *Ulex* spp. was sometimes used for thatching to provide a structure equivalent to the rafter of a cottage over which thatch was woven (Webb 1986). Turfs or sods of the surface humus were cut either for fuel or after being mixed with manure were used as a fertiliser for arable fields (Gimingham 1972; Diemont 1996). Shepherds regularly burnt the heaths to encourage the growth of young *Calluna vulgaris* shoots which was the principle source of food for the sheep (Gimingham 1972). All these activities helped to prevent succession by trees and to maintain the dwarf ericaceous shrub communities.

1.4 THE DORSET HEATHS

1.4.1 Geology and soils

The Dorset heaths are on the western extension of the syncline that forms the Hampshire Basin, this has traditionally been called the Poole Basin (Good 1948). The heaths occur on the Bagshot sands, Tertiary deposits, which overlie the chalk that forms the margin of the Poole Basin (Good 1948; Perkins 1977). In a few places the younger Bracklesham beds overlie the Bagshot sands. The soils formed on the Bagshot sands are well developed humus iron podzols (Pywell 1993) with phosphorus being the major limiting nutrient (Chapman 1967).

1.4.2 Flora

The flora of Dorset is in a transitional zone between the oceanic heaths of the south-west and the more continental heaths of eastern England (Webb 1986). The flora therefore has great variety as it reflects this transition and also a number of species that occur in Dorset are at the northern limit of their distribution. The dry heaths are dominated by *Calluna vulgaris* with *Erica cinerea* and *Ulex minor* or *Ulex gallii.* The most common grass is *Agrostis curtisii;* on the wetter heaths *Erica ciliaris* and *Erica tetralix* occur together with *Molinia caerulea* (Webb 1986).

1.4.3 Conservation value

The Dorset heaths comprise 10% of British lowland heaths (British Gas 1988), 96% of them are designated as SSSI's and they are candidates to become Special Areas of Conservation (SAC's) under the 1992 EEC habitats directive.

The Dorset heaths contain significant proportions of the UK populations of species which are confined to heathland habitats (Woodrow, Symes & Auld 1996), including 41%

of the Dartford Warbler (*Sylvia undata*) population, 13% of the Woodlark (*Lullula arborea*) population and 12% of the Nightjar (*Caprimulgus europaeus*) population, all of which are Red data book species (Battern *et al* 1990); (nomenclature follows Jonsson 1993 for birds). The Dorset heaths contain 90% and 80% respectively of the UK population of Sand Lizard (*Lacerta agilis*) and Smooth Snake (*Cornonella austriaea*) and all six of Britain's native reptiles are found in Dorset (Webb & Haskins 1980); (nomenclature follows Morrison 1994 for reptiles). The insect life of the heaths is very rich including a number of *odonata*, *orthoptera*, *lepidoptera*, *hymenoptera* and *arachnida*, many of which are continental in their distribution and reach the northern limits of their European range in Dorset (Webb 1986; Webb & Haskins 1990). The flora of Dorset is important for its mixture of continental and oceanic heath species, it also contains species such as *Erica ciliaris* and *Gentiana pneumonanthe* which reach the northern limit of their range in southern England and whose population is concentrated in Dorset (Webb 1986). The Dorset heaths are therefore of high conservation value both nationally and internationally.

1.4.4 Decline and fragmentation

In common with most European heaths the Dorset heaths have decreased in area by about 80% since the mid 18th century (Webb & Haskins 1980; Chapman, Clarke & Webb 1989). Haskins (1978) calculated from Isaac Taylor's maps of Hampshire and Dorset that 39960 ha of heathland existed in the Poole Basin between 1759 and 1765. The 18th century saw the start of heathland enclosures and the loss of heathland to agriculture (Taylor 1970) and at the time of the first Ordnance Survey maps in 1811 about 30000 ha is shown as rough and unenclosed land and was undoubtedly heath (Moore 1962); by 1896 this had declined to about 22672 ha (Haskins 1978). During the last century there has been a rapid decline in the area of the Dorset heaths (Table 1.1), with only 5141 ha remaining by 1987 (Webb 1990).

Table 1.1. Estimates of the area of heathland in Dorset (adapted from Webb & Haskins 1980)

The definition of heathland changed between these surveys and therefore these figures should be treated as estimates only and are not directly comparable.

Year	Area	Source
1750	39960 ha	Taylor (Haskins 1978)
1811/1817	30400 ha	1st edn. Ordnance Survey (Haskins 1978)
1896	22672 ha	2nd edn. Ordnance Survey (Haskins 1978)
1931/1934	18200 ha	Land Utilisation Survey (Haskins 1978)
1960	10000 ha	Moore (1962)
1978	5832 ha	Webb & Haskins (1980)
1987	5141 ha	Webb (1990)

The rates of loss of heathland in the mid 18th century were about 0.37% a year (Webb & Haskins 1980). This increased to 0.52% between 1896 and 1934 and reached a peak between 1960 and 1973 of 3% a year (Webb & Haskins 1980). By 1978 this had slowed to 0.89% a year, but even at this rate most of the heaths would be lost in 80 years (Webb & Haskins 1980).

As the area of the heaths has declined they have also been fragmented. Isaac Taylor's maps show that the heathlands of the Poole Basin consisted of about 10 large blocks which were separated only by the major rivers (Haskins 1978). By 1960 the heathlands had become fragmented, with over 100 pieces with an area of 4 ha or more (Moore 1962). By 1978 fragmentation had increased to 768 pieces of which only 14 were greater than 100 ha, 146 sites had an area between 100 and 4 ha and the remaining 608 sites were less than 4 ha, of which 476 were less than 1 ha (Webb & Haskins 1980).

The fragmentation of the Dorset heaths as well as its decline poses serious problems for the conservation of heathland species (Moore 1962; Webb & Haskins 1980; Chapman, Clarke & Webb 1989). On small and more isolated fragments it is more difficult to conserve the whole heathland species assemblage and when species are lost from isolated areas it may be difficult or impossible for them to recolonise (Webb 1990). The size, shape and area of the fragments also affects the risk of that site to invasion by successional species (Webb & Vermaat 1990; Nolan, Atkinson & Bullock 1997).

1.4.5 Causes of decline

The improvement in agricultural techniques and increased fertiliser use made it possible to farm the infertile heath soils. By 1960 28% of the original 30000 ha of heath in 1811 had been converted to agricultural land (Moore 1962). Losses due to agriculture continue to be the greatest cause of loss, accounting for 46% (183 ha) of the losses of heathland between 1978 and 1987 (Webb & Haskins 1990). Urban development, the second greatest cause of decline, occupied nearly a quarter of the original 1811 heathland in 1960 and has continued to expand since then with a further 148 ha lost in 9 years between 1978 and 1987 (Webb 1990). After World War I extensive areas of the Dorset heaths were planted with conifers by the Forestry Commission so that by 1960 7700 ha of trees had been planted on former heathland (Moore 1962). The losses due to forestry have now slowed, accounting for only 7 ha (2%) of the losses between 1978 and 1987 (Webb 1990). Mineral extraction which started after the Second World War and the loss of heathland to woodland through successional change are the other two main factors causing loss of heathland (Webb 1990).

Webb (1990) noted that the most significant change in vegetation between his two extensive surveys of the Dorset heaths in 1978 and 1987 was the invasion of the heathlands by *Ulex* spp., *Betula* spp. and *Pinus* spp (nomenclature follows Stace 1991). The area of these species increased by 15% suggesting that invasion and succession to scrub and woodland is now proceeding at a rapid rate. This is a disturbing trend, assuming the rate of succession to be exponential it is equivalent to 1% annually (Webb 1990). Preliminary results from a recent repeat of this survey in 1996 show that this rate of scrub increase has continued (Webb pers com.). This increase in scrub and woodland is due to the cessation of traditional management of the heathland which previously halted succession, in particular grazing and controlled burning (Webb 1990).

1.5 CHANGES CAUSED BY SUCCESSIONAL PROCESSES

1.5.1 Vegetation changes

Webb (1990) recorded *Betula* spp., *Pinus* spp. and *Ulex* spp. as the most noticeable invasive species found on the Dorset heaths. Colonisation of heathland by *Betula* spp. and *Pinus sylvestris* occurs on many heaths in Britain (Summerhayes, Cole & Williams 1924; Harrison 1976; Marrs, Hicks & Fuller 1986). *Pteridium aquilinum* is also invasive on heathlands (Marrs, Hicks & Fuller 1986) and the naturalised species *Rhododendron ponticum* has invaded some Dorset heaths (Pickess, Burgess & Evans 1989). Thus the five species, *Betula* spp., *Pinus sylvestris*, *Pteridium aquilinum*, *Rhododendron ponticum* and *Ulex europaeus* are the most frequent invaders of heathland.

While heathland is known to be lost to these species, little work has been done on the changes that occur in species composition during succession. Miles (1981a) noted that the moorland flora changed to a flora more typical of a scrub/woodland flora following invasion by *Betula* spp, but there is little known about the successional process on lowland heaths. Moreover, it is possible some heathland species are able to survive during succession.

1.5.2 Do soil nutrient levels change during succession?

Heathlands are generally found on soils which are extremely infertile (Gimingham 1992). Any change in nutrient status will affect the vegetation composition and succession (Heil & Diemont 1983; Aerts & Berendse 1988; Van Der Eerden *et al* 1991). It is well known that the soil has a major effect on the species composition (Tilman 1984; Pastor *et al.* 1984), but the influence of vegetation on the soil is less well understood (Miles 1985). Some studies have shown species altering the soil (Mackney 1961; Ernst 1978, Pigott 1970, Wedin & Tilman 1990) and Miles (1985) in his study of the pedogenic effects of some trees commented that "the neglect of this topic was puzzling". Changes in the soil due to the vegetation should be expected as a) the litter from species varies markedly in chemical composition and rates of decomposition, directly affecting the acidity of the soil and accelerating eluviation and b) different species vary in the extent to which they modify the chemical composition of the rain dripping off their leaves (Miles 1981b).

Betula spp. have always had a reputation as a soil improver and have been recommended by forest scientists for restoring degraded soils in many European countries (Gardeniner 1968). In Britain, Dimbleby (1952) investigated the use of *Betula* to change heathland podzols to forest brown earths. He concluded that naturally regenerating *Betula* stands on former heather moors caused a gradual increase in pH, the formation of a mull horizon in the mineral soil and the slow disintegration of the iron pan. Dimbleby (1952) estimated that it would take 60-100 years for the raw humus to be converted to a mull. These conclusions were based on a chronosequence of sites, making an assumption that the soils under the *Betula* stands were initially alike. Long term experiments were set up to test this assumption and thirty years later Satchell (1980a) found that the soil profile under the *Betula* remained a fully differentiated podzol.

In contrast, Miles (1981a) concluded that while soil nutrient change may be minimal under *Betula* on very nutrient poor mineral soils, such as those studied by Satchell (1980a), *Betula* invasion did cause richer soils to start to change from a podzol to a more fertile brown forest earth soil. Increases in pH, exchangeable calcium and total phosphorus and decreases in the ratios of carbon/nitrogen, carbon/phosphorus and to a lesser extent carbon/potassium were found on moorland soils colonised by *Betula* (Miles 1981a; Miles & Young 1980). As the podzol soil is changed the soil profile is changed too, with the bleached Ea horizon in the podzol gradually being obliterated by the incorporation of organic matter and the boundary between the B and Ea or A horizons becomes less sharp (Miles & Young 1980). Thus there is a growing amount of evidence that as *Betula* colonises moorland, changes in the soil nutrient levels do occur.

Miles (1988) suggests that the soil may change regularly during the course of succession depending on the podzolizing effects of the species present (Miles 1981b). The change from a mor to mull humus and the depodzolizing that occurs may be a cyclic effect with podzolization occurring again if the *Betula* degenerates (Miles 1981b).

Soil nutrient levels also change when other tree species colonise heathland. Leuschner (1993) studied three presumed successional stages of heathland succession in Germany. Phosphate, potassium and magnesium were found to be markedly higher in late successional oak-beech forest than in both the *Calluna* heathland and the pioneer birch-pine forest. Total stocks of calcium, magnesium, potassium, phosphorus and nitrogen in the organic layer increased from the *Calluna* heathland to the pioneer birch-pine forest to the oak-beech woodland. Nielsen, Dalsgaard and Nørnberg (1987a,b) also observed differences in the morphology, chemistry and organic matter of soils beneath stages of a heathland to oak woodland succession in Denmark.

The effect of invasion by *Pinus sylvestris, Pteridium aquilinum, Rhododendron ponticum* and *Ulex europaeus* on the soil has received less attention than that of *Betula.* Soil profiles under a *Calluna vulgaris* to *Pteridium aquilinum* transect indicated a less advanced stage of leaching under the *Pteridium aquilinum* than under the *Calluna vulgaris* and there is evidence that *Pteridium aquilinum* may have a depodzolizing effect on the soil, turning it from a mor to a mull humus (Jarvis & Duncan 1976). *Rhododendron ponticum* is known to have a deleterious effect upon the soil mobilising cations directly or indirectly by the production of polyphenols (Cross 1975).

1.6 MANAGEMENT PROBLEMS ARISING FROM THE SUCCESSIONAL PROCESS

1.6.1 Problems of invasive species

The scale of a successional sequence on heathlands depends on the change in species composition. The invasion of a single species such as *Betula* may be relatively easy to control (Marrs 1984, 1985a), but if the entire heathland flora is converted to a woodland one then the problems are more difficult. Most sites where succession has occurred will be on a gradation from a heathland to a woodland flora, the fewer woodland species relative to the remaining heathland species present will result in easier restoration. However, other factors such as the length of time woodland species have been on the site, the content of the viable seedbank and the proximity of open heathland may also influence the success of restoration.

1.6.2 Problems caused by raised nutrient levels

Soil nutrient levels on heathlands are usually low (Gimingham 1992) and nutrient levels play an important role in determining the species composition and production of an area (Pastor *et al.* 1984; Tilman 1984). Phosphorus has been suggested as a limiting factor on the Dorset heaths (Chapman, Rose & Clarke 1989) and the level of phosphorus availability may be related to the risk of invasion by *Betula* and *Ulex* (Chapman Rose & Basanta 1989). Raised nutrient levels on heathland in the Netherlands have been shown to alter the plant community with grasses and other more competitive species invading and dominating the heather (Heil & Diemont 1983; Aerts & Berendse 1988; Van der Eerden *et al.* 1991). Manipulation of organic matter levels and litter levels in heathland successions has been shown to influence the species present, the plant productivity and the rate of species replacement during succession (Berendse 1990; Berendse, Schmitz & Visser 1994; Diemont 1994).

Soil nutrient levels, therefore, play a critical role in determining the species composition of an area and if soil nutrients are raised during succession this will have important implications for the successful restoration of heathland (Marrs 1993a; Marrs & Gough 1989). Higher fertility would favour the growth of more competitive species than the heathland species, it would also favour the growth of late successional species over early successional species (Marrs & Gough 1989). This may mean that successional stages cleared to restore heathlands may quickly return to the successional community, the raised nutrient levels allowing an accelerated initial floristics composition succession (Egler 1954).

Management practices such as litter stripping, top soil removal or vegetation cropping may therefore be needed to lower nutrient levels before restoration of heathland may be successful (Marrs 1993a). These techniques have been tried on the restoration of heathland on arable land (Marrs 1985b; Snow 1995; Snow & Marrs 1996). However, little work has been done on the reversal of soil nutrients on successional sites, or, indeed, whether such measures are even needed if the soil nutrient levels naturally decline following management.

1.7 THE CONSERVATION OF THE DORSET HEATHS

The loss of heathlands due to farming, urbanisation, forestry and mineral extraction is a planning issue, the loss of heathland through succession to woodland is a conservation problem. There is now an urgent need to manage the heaths to maintain the dwarf ericaceous shrub community (Webb 1990), and the reintroduction of grazing and burning of heaths may help this (Harrison 1976; Bakker *et* al 1983; Webb 1990; Byfield & Pearman 1995; Bullock & Pakeman 1997).

However, on some sites successional species have already invaded and drastic management measures are now required to reverse these successional changes and to restore heathland. With this aim the RSPB established the "Dorset Heathland Project" in 1989. The project had the following aims:

" i) To halt further losses of existing heathland by a programme of reserve acquisitions and conservation policy promotions to statutory authorities

ii) To offset continuing losses of southern heathland by a programme of habitat restoration" Woodrow, Symes & Auld (1996). In the five years between 1989 and 1995 the project had restored around 433 ha of open heath (Woodrow, Symes & Auld 1996).

Much of the work conducted in this study has been carried out on sites at which the RSPB heathland team has worked. To help target this work we need a knowledge of the changes that have occurred during succession so that changes in both vegetation and soil can be successfully reversed and heathland restored. If some changes are easier to reverse than others, or if some successional communities are more similar to heathland than others, this needs to be known so that the most cost effective management measures are implemented. Factors that influence the success of management such as management techniques and the viable content of the seedbank also need to be evaluated. This project was established with the aim of working with the RSPB heathland team, and as well as providing an opportunity for some theoretical considerations of heathland succession to be studied, it was also hoped to relate the results to some of the above practical management issues.

1.8 AIMS

The aims of this project were:

- To study successional trajectories on Dorset heaths and assess changes in species composition,
- To test whether soil nutrient levels increase during succession on lowland heaths in Dorset, and, if so, which nutrients are associated with which invasive species,
- To study the efficacy of conservation management to reverse successional changes both in terms of the vegetation and the soil nutrients,
- To compare the viable soil seedbank of heathland and successional communities,
- To relate the results of the above to practical conservation management and the targeting of resources to restore heathland on successional stages,
- To relate the results to wider ecological issues: the resistance and resilience of ecosystems.

Chapter 2

A STUDY OF SUCCESSION ON LOWLAND HEATHS IN DORSET, SOUTHERN ENGLAND: VEGETATION CHANGE

2.1 INTRODUCTION

The majority of the Dorset heaths are an ancient man-made biotope dating back to forest clearances in the early Atlantic times (4000 years BP; Seagrief 1959). The heaths were managed as an important part of the rural economy of the area; heaths provided grazing for cattle, gorse (furze) was cut for fodder, bracken was cut to provide animal bedding, and peats, turves and gorse were all cut for fuel (Webb 1986). These activities maintained the dwarf ericaceous shrub communities common to lowland heaths and prevented natural succession to scrub and woodland. Heathlands are a high priority ecosystem for conservation because they have been considerably reduced and greatly fragmented over the last 200 years by land use changes (Moore 1962; Webb 1980; Webb & Haskins 1980; Chapman, Clarke & Webb 1989; Webb 1990).

Today the heaths are no longer managed in traditional ways, and succession to other communities has occurred leading to a further decline in heathland quality and quantity. Webb (1990) documented a 15% increase in the area of scrub and woody vegetation in the nine years between his two surveys of the Dorset heaths in 1978 and 1987. This suggests that succession is a major challenge to the conservation of these Dorset heathlands.

Webb (1990) recorded *Betula* spp., *Pinus* spp. and *Ulex* spp. as causing the most noticeable invasion on the Dorset heathlands. Colonisation of heathland by *Betula* spp. and *Pinus sylvestris* has been shown to be a major threat to heathland in other areas of Britain

(Harrison 1976; Marrs, Hicks & Fuller 1986). Moreover, *Pteridium aquilinum* is also invasive on heathlands (Marrs, Hicks & Fuller 1986), and the naturalised species *Rhododendron ponticum* has invaded some Dorset heaths, and can be very difficult to eradicate (Andrews 1990; Squires 1991).

Throughout this study the term heathland is used to describe the dwarf ericaceous shrub community and the term successional stage is used to describe areas that were once heathland but are now dominated by other non-heathland species.

The aims of this study were to describe vegetation change on Dorset Heaths, specifically on sites where succession was known to have taken place in the recent past in order to:

i) test the hypothesis that succession is simply the addition of one dominant species to the heathland flora and to test a series of more complex hypotheses which could explain heathland succession,

ii) help target the best use of conservation management resources aimed at reversing these successions.

2.2 HYPOTHESES

2.2.1 Succession is the addition of one dominant species

A useful starting point is to consider the minimum successional change possible; the addition of one species to the existing heathland flora. Thus the successional stages (hereafter called stages) would be the addition of one of the following invasive species; *Betula* spp. (+B), *Pinus sylvestris* (+PS), *Pteridium aquilinum* (+PA), *Rhododendron ponticum* (+R) or *Ulex europaeus* (+U). If this hypothesis is accepted then addition of these species would leave all other heathland species unaffected. If heathland species are lost and others gained, this hypothesis is rejected. If the hypothesis is accepted then reversion of the succession back to heathland would simply be the removal of the invader.

2.2.2 Models of heathland succession

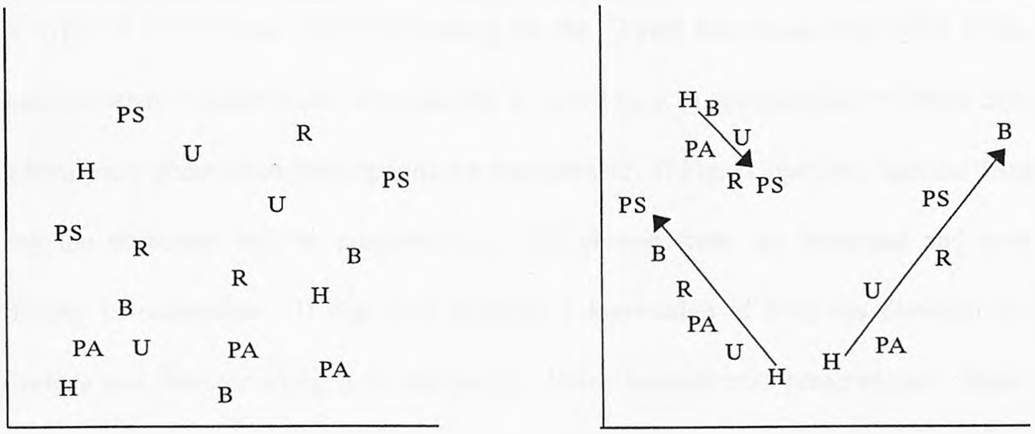
Four possible models for describing succession on heathland are shown in Figure 1:

a) No obvious successional trajectory (Fig. 2.1a); where each individual heathland site moves at random to any one of the successional stages at varying distances from that heathland.

b) Site-dominated successional trajectories (Fig. 2.1b), where the trajectory changes at different sites.

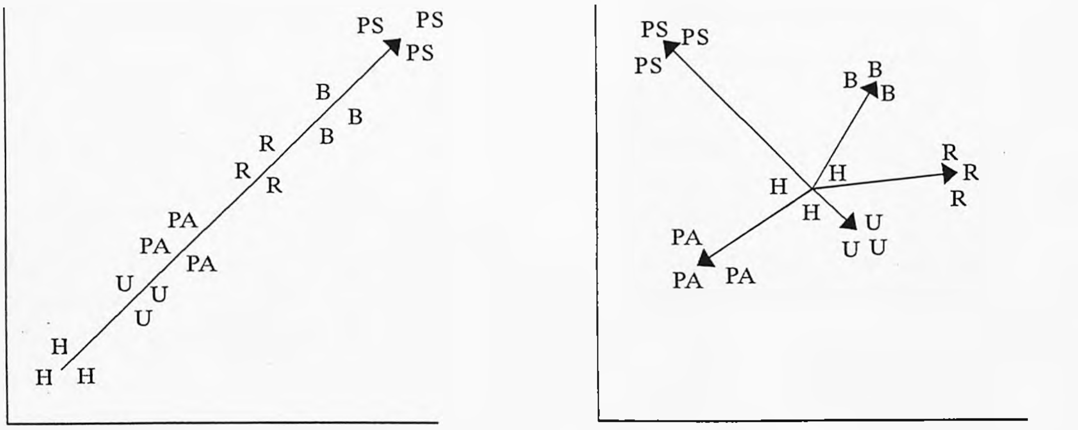
c) A single overall successional trajectory (Fig. 2.1c), where all sites trend along the same line either being early-successional or late-successional depending on the amount of change that has occurred.

d) A multi-trajectory model of succession (Fig. 2.1d), where succession moves along a different trajectory depending on the different species invading.



a) No successional trajectory from the heath to successional stages; a random distribution of quadrats from the different successional stages and sites.

b) Site effect. The major influence over the successional trajectories is the site.



c) Only one successional trajectory along which a heathland site moves. In this example open heath goes to +U to +PA to +R to +B and finally to +PS.

d) Several different successional trajectories along which a heathland site may move, depending on the species which invades. In this case the +U stage is closest to the heathland, the +PS stage is furthest from the heathland and the +PA, +R and +B stages are all similar in their distance from the heathland.

Fig. 2.1. Hypothetical ordination diagrams illustrating results which might be obtained from DECORANA analysis of quadrat data obtained from successional stages on heathland, assuming different possible successional trajectories. H = open heathland; B = +B (*Betula* spp.) successional stage; PS = +PS (*Pinus sylvestris*) successional stage; PA = +PA (*Pteridium aquilinum*) successional stage; R = +R (*Rhododendron ponticum*) successional stage; U = +U (*Ulex europaeus*) successional stage.

2.2.3 Targeting conservation resources

The type of successional model operating on the Dorset heathlands will have profound consequences for conservation. If model Fig. 2.1a or Fig. 2.1b operates then it will be difficult to provide any generalised prescriptions for management. If Fig. 1c operates, then the distance along the trajectory will be proportional to the change from the heathland and perhaps difficulty in restoration. If Fig. 2.1d operates a knowledge of both the direction of the trajectory and distance along it is required to derive management prescriptions. Once the correct model is identified, it should be possible to start targeting the most profitable stages and sites to manage for heathland restoration programmes.

2.3 MATERIALS AND METHODS

2.3.1 Areas

Ten heathland areas within the Poole Basin of Dorset were selected (Table 1). All are in the syncline of the Poole Basin and as they are in close proximity (within a 20 km radius), should experience a similar climate; they lie either on the Bracklesham or Bagshot beds and thus the geology is also similar. Within this relatively small geographical area the areas represent as broad a geographical spread as possible, ranging from the south (Arne and Trigon), westwards (Blackhill, Higher Hyde and Winfrith Common) and northwards along the Avon Valley (Sopley & Ramsdown, St Catherines Hill & Town Common, Avon Heath Country Park and Cranborne Common).

Table 2.1. The heathland areas in Dorset, their location, successional stages noted as the approximate time (years before 1995) over which these stages have occurred (x); data derived from aerial photographs.

Site	Grid Reference	Successional Stage Heath	+B	+PS	+PA	+R	+U
Arne	SY973882	H	$30 > x > 23$	$43 > x > 23$	$49 > x > 43$	$49 > x > 43$	$49 > x > 30$
Avon Heath County Park (AHCP)	SU128035	H	$x > 23$	$x > 23$	$23 > x$	?	$23 > x$
Blackhill	SY840940	H	$23 > x > 9$	$23 > x > 9$	$48 > x > 23$	$48 > x > 23$	$48 > x > 23$
Canford Heath	SZ030950	H	$23 > x$	$x > 49$	$48 > x > 23$	$48 > x > 23$	$23 > x$
Cranborne Common	SU104112	H			$x > 49$		$x > 49$
Higher Hyde Heath	SY851907	H	$48 > x > 23$		$23 > x > 9$	$48 > x > 23$	$48 > x > 23$
St Catherines Hill & Town Common	SZ142955	H	$48 > x$	$48 > x$		$48 > x$	
Sopley & Ramsdown	SZ133974	H	$x > 48$	$x > 48$		$x > 48$	
Trigon	SY884908	H		$48 > x > 23$	$48 > x > 23$	$48 > x > 23$	
Winfrith Heath	SY805865	H			$23 > x > 9$		$x > 23$
Total number of quadrats		100	70	70	80	80	70

H = Open Heath site
? = stage sampled but time over which successional stage occurred unknown
$>$ = greater than sign used to indicate the range of years over which the successional stage (x) has occurred, for some stages the data was incomplete and only the maximum or minimum of the range is shown

2.3.2 Successional stages

Within each area a range of successional stages, each dominated by a different species was selected and compared to the open heathland, which had not been invaded by any of the major successional species.

Five stages in which major species had invaded recently were chosen:

+B - major invader is *Betula* spp.,

+PS - major invader is *Pinus sylvestris*,

+PA - major invader is *Pteridium aquilinum*,

+R - major invader is *Rhododendron ponticum*,

+U - major invader is *Ulex europaeus*.

The sites were selected so that the major invader was the dominant species present, mixed sites were rarely encountered and therefore avoided with the exception of *Pteridium aquilinum* which often formed a dense understorey in the +B and +PS stage.

The successional stages were all heathland 20 - 50 years ago but in the intervening period had been invaded by one or other of the above species. The sites selected for sampling were as close as possible to the open heath sites to make comparisons as valid as possible. An assumption was made that the successional sites were similar to the open heath sites until the invasion had occurred. Each area had sites where some or all of the above successional stages occurred (Table 2.1). Estimates of the time over which the successional stages had developed were made using aerial photographs of the areas taken in 1946/47, 1972/73 and 1986 (Table 2.1).

2.3.3 Sampling strategy

At each site (an area about 50m by 50m) ten 1m^2 quadrats were placed using random numbers, and the percentage cover of each plant species estimated. The basal area of the trees was estimated in the +B and the +PS stages using a relascope (Manx Marker relascope factor x2, Stanton Hope Ltd). A total of 470 quadrats were recorded; 100 quadrats from open heath sites and 370 from successional stages (Table 2.1). Nomenclature follows Stace (1991) for higher plants, Duncan (1970) for lichens and Smith (1978) for mosses.

2.3.4 Statistical analysis

The vegetation results were analysed using DECORANA (Hill 1979) to test the hypotheses outlined above. A range of analyses was done using untransformed and transformed data, with and without downweighting of rare species. All analyses gave broadly similar results. In this paper the analyses are based on percentage cover transformed using the octave scale (Hill 1979), essentially a $\log_2$ transformation, and rare species were downweighted.

2.4 RESULTS

2.4.1 Community descriptions

The open heathland sites were all dominated by *Calluna vulgaris* (Table 2.2). *Erica tetralix* or *Erica cinerea* were present on many of the sites. *Molinia caerulea* was the only grass found in significant amounts; this occurred at Cranborne which was slightly wetter than the other sites, here the *Calluna vulgaris* cover was lower and *Erica tetralix* cover greater than at the other sites. *Agrostis curtisii* was the other grass that occurred on the heaths, but at low cover. *Ulex gallii* and *Ulex minor* were found on some sites at greater than 5% cover. Other higher plant species found on the heaths included *Cuscuta epithymum* (one site), a few *Pinus sylvestris* seedlings and a few *Pteridium aquilinum* fronds. The heath vegetation contained a large number of bryophytes and lichens. *Brachythecium rutabulum, Hypnum cupressiforme* and *Hypnum jutlandicum* were the most common mosses and *Cladonia portentosa* the most common lichen. *Cladonia portentosa* was the most dominant species after *Calluna vulgaris* on some sites (Sopley & Ramsdown and Trigon). Other bryophytes and lichens especially *Cladonia* species usually occurred at low cover.

The +B stage (*Betula* spp) (Table 2.3) had a larger number of species present than the +PS stage, the majority of which were additional invaders, these invaders included *Agrostis capillaris, Pteridium aquilinum, Pseudoscleropodium purum, Rubus glandulosus, Carex nigra, Chamerion angustifolium, Digitalis purpurea, Galium saxatile, Hedera helix, Holcus lanatus, Ilex aquifolium, Juncus effusus, Lonicera periclymenum, Luzula campestris, Pinus sylvestris, Quercus robur, Rhododendron ponticum, Rumex acetosella, Senecio erucifolius, Sorbus aucuparia, Teucrium scorodonia, Ulex europaeus, Hypnum mammillatum* and *Mnium hornum.* The first four species listed above were present at some sites at an average cover greater than 5%. The heathland species which occurred in this stage included *Agrostis curtisii, Calluna*

Table 2.2. Mean % cover (n = 10) of species found in heathland (H) sites in Dorset; only species with an average cover of 5% or more on any of the sites are shown in detail.

Species	Arne^1	AHCP^2	Blackhill^3	Canford^4	Cranborne^5	Higher^6 Hyde	St^7 Catherines Hill	Sopley^8 & Ramsdown	Trigon^9	Winfrith^{10}
Calluna vulgaris	62.0	70.5	66.1	84.8	44.2	88.2	96.9	62.6	71.6	79.5
Cuscuta epithymum	0.0	0.0	5.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Erica cinerea	22.4	8.0	25.7	3.6	6.1	2.6	1.0	0.0	14.0	6.7
Erica tetralix	9.9	0.0	2.6	1.0	24.6	6.9	0.0	12.9	1.6	3.2
Molinia caerulea	0.0	0.0	0.0	<0.1	16.3	0.3	0.0	2.4	0.5	0.3
Ulex gallii	0.0	0.0	0.0	12.0	0.0	0.0	0.0	0.0	0.0	0.0
Ulex minor	0.0	5.2	4.8	0.0	4.6	1.3	0.2	0.0	1.4	10.7
Brachythecium rutabulum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.4	0.0
Hypnum cupressiforme	0.0	15.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hypnum jutlandicum	3.8	1.4	1.3	0.3	0.2	0.9	5.1	1.4	0.0	<0.1
Pleurozium schreberi	0.0	15.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cladonia portentosa	8.5	0.3	0.0	0.0	12.3	0.5	0.2	56.9	34.4	0.8

The following species were also recorded: *Agrostis curtisii* $^{1\ 5}$ *Pinus sylvestris* $^{2\ 7\ 9}$ *Pteridium aquilinum* $^{4\ 6\ 7\ 8\ 9}$ *Campylopus introflexus* $^{1\ 2\ 3\ 5\ 7\ 8\ 9\ 10}$ *Dicranum scoparium* $^{1\ 2\ 3\ 4\ 6\ 7\ 8\ 9}$ *Eurhynchium praelongum* $^{3\ 7}$ *Leucobryum glaucum* $^{1\ 6}$ *Polytrichum juniperinum* ^{2} *Cladonia spp* ^{2} *Cladonia cf bacillaris* ^{3} *Cladonia cf coccifera* ^{7} *Cladonia crispata* $^{9\ 10}$ *Cladonia floerkeana* ^{8} *Cladonia cf furcata* $^{1\ 7}$ *Cladonia pyxidata* $^{2\ 3\ 4\ 10}$ *Hypogymnia physodes* $^{9\ 10}$. The superscripts relate to the sites shown in the table heading above, and indicate the sites at which the species occurred.

Table 2.3. Mean % cover (n = 10) of species found in +B sites in Dorset; only species with an average cover of 5% or more on any of the sites are shown in detail.

Species	Arne^{1}	AHCP^{2}	Blackhill^{3}	Canford^{4}	Higher^{6} Hyde	St^{7} Catherines Hill	Sopley^{8} & Ramsdown
Betula spp	10.3	5.4	8.0	9.2	18.2	8.1	6.2
Betula spp (relascope)	18.9	11.6	11.7	16.4	16.5	11.0	13.9
Agrostis capillaris	0.0	0.0	0.0	0.0	1.0	1.4	5.3
Agrostis curtisii	0.0	0.0	53.6	0.0	0.0	0.0	0.1
Calluna vulgaris	0.0	5.1	0.0	0.0	0.4	0.0	0.0
Molinia caerulea	0.0	23.1	0.0	9.2	1.2	2.9	2.0
Pteridium aquilinum	25.2	14.6	7.5	6.1	1.6	0.0	6.2
Rubus glandulosus	0.0	2.2	0.9	1.8	3.2	5.3	6.2
Hypnum jutlandicum	12.1	0.0	0.6	0.4	1.9	5.9	0.4
Pseudoscleropodium purum	0.0	0.0	0.0	0.0	0.0	0.0	8.0

The following species were also recorded: *Carex nigra* $^{3 8}$ *Chamerion angustifolium* ^{7} *Digitalis purpurea* $^{1 7}$ *Erica cinerea* ^{8} *Erica tetralix* $^{2 7}$ *Galium saxatile* ^{3} *Hedera helix* $^{2 3 4 6}$ *Holcus lanatus* $^{6 7}$ *Ilex aquifolium* $^{1 2}$ *Juncus effusus* $^{2 7}$ *Lonicera periclymenum* $^{1 3 8}$ *Luzula campestris* ^{1} *Pinus sylvestris* ^{2} *Quercus robur* $^{2 3 4 6 7 8}$ *Rhododendron ponticum* ^{4} *Rumex acetosella* ^{1} *Senecio erucifolius* ^{7} *Sorbus aucuparia* $^{1 2}$ *Teucrium scorodonia* $^{3 6}$ *Ulex europaeus* $^{1 6}$ *Campylopus introflexus* $^{2 4 7}$ *Campylopus pyriformis* ^{4} *Dicranum scoparium* $^{1 2 5}$ *Eurhynchium praelongum* ^{2} *Hypnum mammillatum* ^{3} *Mnium hornum* $^{3\ 6}$ *Polytrichum juniperinum* $^{6 7}$. The superscripts relate to the sites in the table heading above, and indicate the sites at which the species occurred.

Table 2.4. Mean % cover (n = 10) of species found in +PS sites in Dorset; only species with an average cover of 5% or more on any of the sites are shown in detail.

Species	Arne^{1}	AHCP^{2}	Blackhill^{3}	Canford^{4}	St^{7} Catherines Hill	Sopley^{8} & Ramsdown	Trigon^{9}
Pinus sylvestris	4.8	3.6	6.7	11.0	4.5	5.3	3.3
Pinus sylvestris (relascope)	36.2	21.4	38.2	22.8	19.0	41.8	27.6
Erica cinerea	0.0	0.0	0.0	0.0	0.0	0.7	9.2
Pteridium aquilinum	0.3	7.7	24.7	8.4	10.8	1.7	6.4
Pinus pinaster (relascope)	0.0	2.2	0.0	1.8	8.4	0.0	1.2

The following species were also recorded: *Betula spp* $^{3\,4}$ *Calluna vulgaris* $^{2\,8\,9}$ *Castanea sativa* ^{4} *Hedera helix* ^{1} *Ilex aquifolium* $^{1\,3}$ *Holcus lanatus* ^{8} *Lonicera periclymenum* ^{1} *Molinia caerulea* $^{2\,9}$ *Quercus robur* $^{1\,9}$ *Rhododendron ponticum* ^{4} *Rubus glandulosus* ^{3} *Sorbus aucuparia* ^{1} *Campylopus introflexus* $^{1\,9}$ *Dicranum scoparium* $^{2\,7\,8\,9}$ *Eurhynchium praelongum* ^{3} *Hypnum jutlandicum* $^{1\,2\,3\,4\,7\,8\,9}$. The superscripts relate to the sites shown in the table heading above, and indicate the sites at which the species occurred.

Table 2.5. Mean % cover (n = 10) of species found in +PA sites in Dorset; only species with an average cover of 5% or more on any of the sites are shown in detail.

Species	Arne^{1}	AHCP^{2}	Blackhill^{3}	Canford^{4}	Cranborne^{5}	Higher ^{6} Hyde	Trigon^{9}	Winfrith^{10}
Pteridium aquilinum	88.9	90.0	98.9	84.4	94.6	98.0	93.9	71.2
Erica cinerea	0.3	5.6	1.4	5.4	0.0	0.0	0.3	9.8
Molinia caerulea	1.1	0.0	0.0	0.3	19.3	37.2	0.2	2.8
Campylopus introflexus	16.8	0.1	0.8	0.2	0.0	0.0	0.3	<0.1

The following specie were also recorded: *Agrostis capillaris* ^{10} *Agrostis curtisii* $^{1\ 3\ 5\ 6\ 9}$ *Agrostis gigantea* ^{9} *Aira praecox* ^{1} *Anthoxanthum odoratum* ^{9} *Betula spp* $^{1\ 3\ 4\ 6}$ *Calluna vulgaris* $^{1\ 2\ 3\ 4\ 6\ 9\ 10}$ *Carex pilulifera* $^{1\ 3\ 4\ 6\ 10}$ *Crataegus monogyna* ^{9} *Erica tetralix* $^{1\ 9\ 10}$ *Lonicera periclymenum* $^{3\ 4\ 6\ 9}$ *Luzula campestris* $^{1\ 9}$ *Pinus pinaster* ^{9} *Pinus sylvestris* $^{1\ 2\ 4}$ *Potentilla erecta* ^{9} *Prunus spinosa* ^{9} *Quercus robur* ^{2} *Rubus glandulosus* $^{3\ 4\ 6\ 9\ 10}$ *Rumex acetosella* $^{1\ 10}$ *Serratula tinctoria* ^{9} *Teucrium scorodonia* $^{2\ 9}$ *Ulex europaeus* $^{1\ 6}$ *Ulex minor* $^{2\ 3\ 9}$ *Vaccinium myrtillus* ^{3} *Campylopus pyriformis* $^{5\ 6\ 10}$ *Dicranum scoparium* $^{2\ 4\ 9\ 10}$ *Eurhynchium praelongum* ^{6} *Hypnum jutlandicum* $^{2\ 3\ 4\ 9\ 10}$ *Polytrichum juniperinum* $^{1\ 2\ 4\ 9}$ *Cladonia chlorophaea* ^{1} *Cladonia portentosa* $^{1\ 10}$ *Cladonia pyxidata* $^{2\ 10}$. The superscripts relate to the sites shown in the table heading above, and indicate the sites at which the species occurred.

Table 2.6. Mean % cover (n = 10) of species found in +R sites in Dorset; only species with an average cover of 5% or more on any of the sites are shown in detail.

Species	Arne^{1}	AHCP^{2}	Blackhill^{3}	Canford^{4}	Higher Hyde^{6}	St^{7} Catherines Hill	Sopley^{8} & Ramsdown	Trigon^{9}
Rhododendron ponticum	68.5	47.5	23.2	88.0	72.3	29.6	53.7	73.1

The following species were also recorded: *Calluna vulgaris* ^{9} *Erica tetralix* ^{9} *Hedera helix* ^{1} *Pinus pinaster* ^{9} *Luzula campestris* ^{1} *Molinia caerulea* ^{9} *Pinus sylvestris* ^{1} *Pteridium aquilinum* $^{1\,3\,4\,6\,8}$ ^{9} *Rubus glandulosus* ^{6} *Sorbus aucuparia* ^{1} *Ulex europaeus* ^{1} *Campylopus introflexus* $^{1\,4\,9}$ *Dicranum scoparium* ^{9} *Eurhynchium praelongum* ^{6} *Hypnum jutlandicum* $^{1\,2\,3\,8\,9}$ *Cladonia pyxidata* ^{9}. The superscripts relate to the sites shown in the table heading above, and indicate the sites at which the species occurred.

Table 2.7. Mean % cover (n = 10) of species found in +U sites in Dorset; only species with an average cover of 5% or more on any of the sites are shown in detail.

Species	Arne^{1}	AHCP^{2}	Blackhill^{3}	Canford^{4}	Cranborne^{5}	Higher^{6} Hyde	Winfrith^{10}
Ulex europaeus	87.0	89.8	75.3	75.2	80.7	79.0	86.3
Agrostis curtisii	0.0	0.0	0.0	12.0	0.0	2.0	2.5
Calluna vulgaris	14.7	12.8	5.8	4.8	0.0	7.2	1.7
Erica cinerea	1.5	25.5	11.3	18.6	0.0	4.3	12.1
Erica tetralix	0.0	0.0	0.3	0.0	0.0	0.3	8.9
Molinia caerulea	0.0	0.0	0.0	0.2	34.2	32.1	26.5
Pteridium aquilinum	0.0	2.2	1.7	1.6	9.5	7.8	3.0
Ulex gallii	0.0	0.0	0.0	18.0	2.8	0.0	0.0
Ulex minor	0.0	15.5	1.0	0.0	0.0	0.0	0.0
Vaccinium myrtillus	0.0	0.0	8.1	0.0	0.0	0.0	0.0

The following species were also recorded: *Agrostis gigantea* ^{2} *Betula spp* $^{1\,3\,4}$ *Cuscuta epithymum* ^{3} *Hedera helix* ^{2} *Pinus sylvestris* $^{2\,4}$ *Potentilla erecta* ^{10} *Quercus robur* ^{10} *Rubus glandulosus* ^{1} *Brachythecium rutabulum* $^{2\,5}$ *Campylopus introflexus* $^{1\,3\,10}$ *Campylopus paradoxus* ^{4} *Dicranum scoparium* $^{3\,10}$ *Eurhynchium praelongum* $^{3\,5}$ *Hypnum cupressiforme* ^{2} *Hypnum jutlandicum* $^{1\,2\,3\,6\,10}$ *Mnium hornum* ^{6} *Polytrichum juniperinum* ^{4}. The superscripts relate to the sites shown in the table above, and indicate the sites at which the species occurred.

vulgaris and *Molinia caerulea* at greater than 5% cover and *Erica cinerea* and *Erica tetralix* at less than 5% cover.

Erica cinerea, Pinus pinaster and *Pteridium aquilinum* were the only species to occur at more than 5% cover in the +PS stages, which were dominated by *Pinus sylvestris* (Table 2.4). *Calluna vulgaris* and *Molinia caerulea* were the only other higher heathland species to occur, but at low cover. The heathland bryophytes *Campylopus introflexus, Dicranum scoparium, Eurhynchium praelongum,* and *Hypnum jutlandicum* were found at low cover, and no lichens were present. Additional invaders included *Betula* spp., *Castanea sativa, Hedera helix, Holcus lanatus, Ilex aquifolium, Lonicera periclymenum, Quercus robur, Rhododendron ponticum, Rubus glandulosus* and *Sorbus aucuparia,* all of which occurred at low cover.

The +PA stage (*Pteridium aquilinum*) (Table 2.5) had a large number of species. It had retained many of the heathland species, but only *Erica cinerea, Molinia caerulea* and *Campylopus introflexus* (other than *Pteridium aquilinum*) occurred at greater than 5% cover. However other heathland bryophytes, lichens and the higher plants *Agrostis curtisii, Calluna vulgaris, Erica tetralix, Ulex gallii* and *Ulex minor* were also recorded, usually at low cover. The number of species present was further increased by the presence of some additional invaders recorded infrequently and at low cover, including *Agrostis capillaris, Agrostis gigantea, Aira praecox, Anthoxanthum odoratum, Betula* spp., *Carex pilulifera, Crataegus monogyna, Lonicera periclymenum, Luzula campestris, Quercus robur, Rubus glandulosus, Rumex acetosella, Serratula tinctoria, Teucrium scorodonia, Ulex europaeus* and *Vaccinium myrtillus.*

In the +R stage the only species occurring at greater than 5% was the dominant *Rhododendron ponticum* (Table 2.6). The few other species present were recorded infrequently and at low cover and were a mixture of heathland species (*Calluna vulgaris, Erica tetralix, Molinia caerulea, Campylopus introflexus, Dicranum scoparium, Eurhynchium praelongum, Hypnum jutlandicum and Cladonia pyxidata*) and invaders (*Hedera helix, Luzula campestris, Pinus pinaster, Pinus sylvestris, Pteridium aquilinum, Rubus glandulosus, Sorbus aucuparia* and *Ulex europaeus*). In this stage the species present were few in number and had low cover values.

The +U stage (*Ulex europaeus*) (Table 2.7) is the one most similar to the heathland. This stage is almost the same as heathland, with the addition of the major invader *Ulex europaeus*. Many of the heathland species were present at more than 5% cover; *Agrostis curtisii, Calluna vulgaris, Erica cinerea, Erica tetralix, Molinia caerulea, Ulex gallii* and *Ulex minor*. Some of the heathland bryophytes were also present at low cover, but none of the lichens were present. However despite this mainly heathland flora there were some additional invaders, *Agrostis gigantea, Betula* spp., *Hedera helix, Pinus sylvestris, Pteridium aquilinum, Quercus robur* and *Rubus glandulosus*.

The species recorded in this study were divided into three groups for each stage (Table 2.8); these were (1) heathland species found in the successional stage, (2) heathland species recorded on the heathland sites but not found in the successional stage and (3) additional species which had invaded. Heathland species were defined as those occurring in heathland quadrats in this study with the exception of *Pinus sylvestris* and *Pteridium aquilinum* which were classified as invaders. Each successional stage contained some heathland species,

Table 2.8. The heathland species present or absent, and the invaders (additional to the invading dominant) at each successional stage.

Successional Stage	Heathland species found	Heathland species not found	Additional invaders
+PS *Pinus sylvestris*	*Calluna vulgaris* *Erica cinerea* *Molinia caerulea* *Campylopus introflexus* *Dicranum scoparium* *Eurhynchium praelongum* *Hypnum jutlandicum* *Leucobryum glaucum* *Pleurozium schreberi* *Polytrichum juniperinum* *Cladonia* spp. *Cladonia cf coccifera* *Cladonia crispata* *Cladonia floerkeana* *Cladonia portentosa* *Cladonia pyxidata* *Hypogymnia physodes*	*Agrostis curtisii* *Cuscuta epithymum* *Erica tetralix* *Ulex gallii* *Ulex minor* *Brachythecium rutabulum* *Hypnum cupressiforme* *Quercus robur* *Rhododendron ponticum* *Rubus glandulosus* *Sorbus aucuparia*	*Betula* spp. *Castanea sativa* *Hedera helix* *Holcus lanatus* *Lonicera periclymenum* *Pinus pinaster* *Pteridium aquilinum*
+B *Betula* spp.	*Agrostis curtisii* *Calluna vulgaris* *Erica cinerea* *Erica tetralix* *Molinia caerulea* *Campylopus introflexus* *Dicranum scoparium* *Eurhynchium praelongum* *Hypnum jutlandicum* *Polytrichum juniperinum* *Cladonia crispata* *Cladonia floerkeana* *Cladonia portentosa* *Cladonia pyxidata* *Hypogymnia physodes*	*Cuscuta epithymum* *Ulex gallii* *Ulex minor* *Brachythecium rutabulum* *Hypnum cupressiforme* *Leucobryum glaucum* *Pleurozium schreberi* *Cladonia* spp. *Cladonia cf bacillaris* *Cladonia cf coccifera* *Luzula campestris* *Pinus sylvestris* *Pteridium aquilinum* *Quercus robur* *Rhododendron ponticum*	*Agrostis capillaris* *Carex nigra* *Chamerion angustifolium* *Digitalis purpurea* *Galium saxatile* *Hedera helix* *Holcus lanatus* *Ilex aquifolium* *Juncus effusus* *Lonicera periclymenum* *Rubus glandulosus* *Rumex acetosella* *Senecio erucifolius* *Sorbus aucuparia* *Teucrium scorodonia* *Ulex europaeus* *Campylopus pyriformis* *Hypnum mammillatum* *Mnium hornum* *Pseudoscleropodium purum*

Table 2.8 cont.

Successional Stage	Heathland species found	Heathland species not found	Additional invaders
+PA *Pteridium aquilinum*	*Agrostis curtisii* *Calluna vulgaris* *Erica cinerea* *Erica tetralix* *Molinia caerulea* *Ulex gallii* *Ulex minor* *Campylopus introflexus* *Dicranum scoparium* *Eurhynchium praelongum* *Hypnum jutlandicum* *Polytrichum juniperinum* *Cladonia chlorophaea* *Cladonia portentosa* *Cladonia pyxidata*	*Cuscuta epithymum* *Brachythecium rutabulum* *Hypnum cupressiforme* *Leucobryum glaucum* *Pleurozium schreberi* *Cladonia* spp. *Cladonia cf bacillaris* *Cladonia cf coccifera* *Cladonia crispata* *Cladonia floerkeana* *Cladonia cf furcata* *Hypogymnia physodes* *Prunus spinosa* *Quercus robur* *Rubus glandulosus*	*Agrostis capillaris* *Agrostis gigantea* *Aira praecox* *Anthoxanthum odoratum* *Betula* spp. *Carex pilulifera* *Crataegus monogyna* *Lonicera periclymenum* *Luzula campestris* *Pinus pinaster* *Pinus sylvestris* *Potentilla erecta* *Rumex acetosella* *Serratula tinctoria* *Teucrium scorodonia* *Ulex europaeus* *Vaccinium myrtillus* *Campylopus pyriformis*
+R *Rhododendron ponticum*	*Calluna vulgaris* *Erica tetralix* *Molinia caerulea* *Campylopus introflexus* *Dicranum scoparium* *Eurhynchium praelongum* *Hypnum jutlandicum* *Cladonia pyxidata* *Cladonia floerkeana* *Cladonia cf furcata* *Cladonia portentosa* *Hypogymnia physodes* *Cladonia crispata*	*Agrostis curtisii* *Cuscuta epithymum* *Ulex gallii* *Ulex minor* *Brachythecium rutabulum* *Hypnum cupressiforme* *Leucobryum glaucum* *Pleurozium schreberi* *Polytrichum juniperinum* *Cladonia* spp. *Cladonia cf bacillaris* *Cladonia cf coccifera*	*Luzula campestris* *Hedera helix* *Pinus pinaster* *Pinus sylvestris* *Pteridium aquilinum* *Rubus glandulosus* *Sorbus aucuparia* *Ulex europaeus*
+U *Ulex europaeus*	*Agrostis curtisii* *Calluna vulgaris* *Cuscuta epithymum* *Erica cinerea* *Erica tetralix* *Molinia caerulea* *Ulex gallii* *Ulex minor* *Brachythecium rutabulum* *Campylopus introflexus* *Dicranum scoparium* *Eurhynchium praelongum* *Hypnum cupressiforme* *Hypnum jutlandicum* *Polytrichum juniperinum*	*Leucobryum glaucum* *Pleurozium schreberi* *Cladonia* spp. *Cladonia cf bacillaris* *Cladonia cf coccifera* *Cladonia crispata* *Cladonia floerkeana* *Cladonia portentosa* *Cladonia pyxidata* *Hypogymnia physodes*	*Agrostis gigantea* *Betula* spp. *Hedera helix* *Pinus sylvestris* *Pteridium aquilinum* *Potentilla erecta* *Quercus robur* *Rubus glandulosus* *Vaccinium myrtillus* *Campylopus paradoxus* *Mnium hornum*

although usually at reduced cover. Some typical heathland species were not recorded and it is possible that they had disappeared during the succession.

2.4.2 Community descriptions: analysis of change

The DECORANA analysis provided eigenvalues for the first four axes of 0.832, 0.598, 0.374 and 0.232, but only the first two axes are presented here (Fig. 2.2). This analysis shows that quadrats from the same stage all group together, irrespective of sampling area. The open heath quadrats appear in a cluster in the lower left of the diagram with the other successional communities radiating out from them.

The +U and +PS quadrats are nearest to the heath samples, with +PA more in the centre of the graph. The +R samples do not merge with the other samples in any way and are separated out to one extreme on the graph as a distinct group. The +B quadrats are also more separated than the heath, +PS, +U and +PA are from each other. It is of interest that each succession radiates out from the heathland in a different direction, with the exception of +B which is separated from the heathland by either +PA or +U, perhaps indicating that the +PA and +U are intermediates on the trajectory to +B.

The species ordination (Fig. 2.3) shows two main clusters; those from the heath sites in the lower left corner of the diagram and those from the +B sites higher up on Axis 1.

In a separate analysis, the major species from each stage were removed to test their effects on the ordination. This eliminated 6 out of 70 +PS samples, 6 out of 80 +PA samples and 46 out of 80 +R samples from the analysis, because the major species was the only one in these quadrats. The results of this second analysis were similar to those of the first. However quadrats from the same stage were not clustered as closely together, with the exception of the heathland quadrats which were still tightly clustered, and quadrats from different stages were more intermixed.

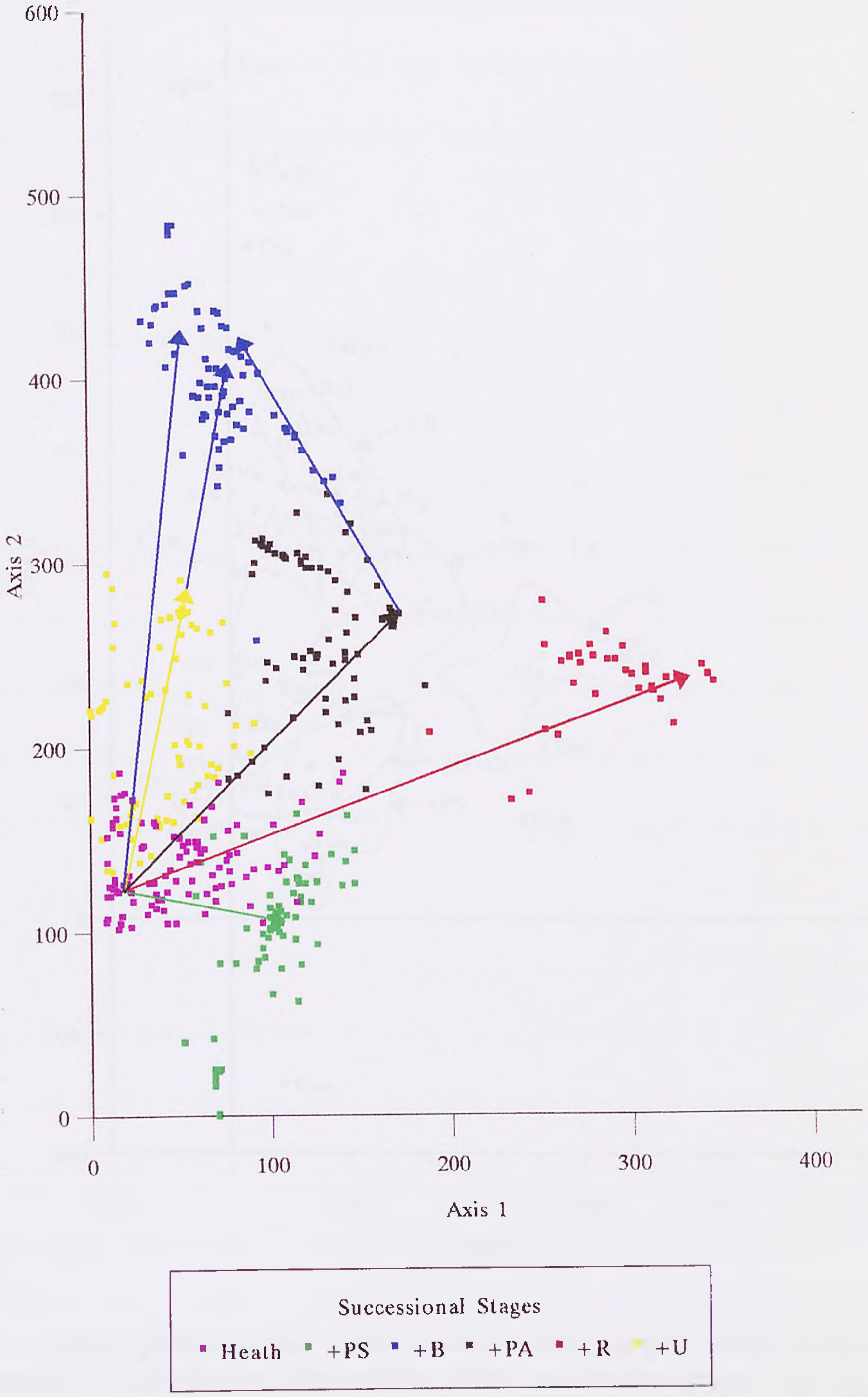


Fig. 2.2. Quadrats plotted by their scores on the first two axes from the DECORANA analysis, showing how quadrats from the same successional stages cluster together and the relationships between the different successional stages. The postulated successional trajectories are marked with arrows. Heath = Open heathland; +PS = *Pinus sylvestris* is the major invader; +B = *Betula spp* is the major invader; +PA = *Pteridium aquilinum* is the major invader; +R = *Rhododendron ponticum* is the major invader; +U = *Ulex europaeus* is the major invader.

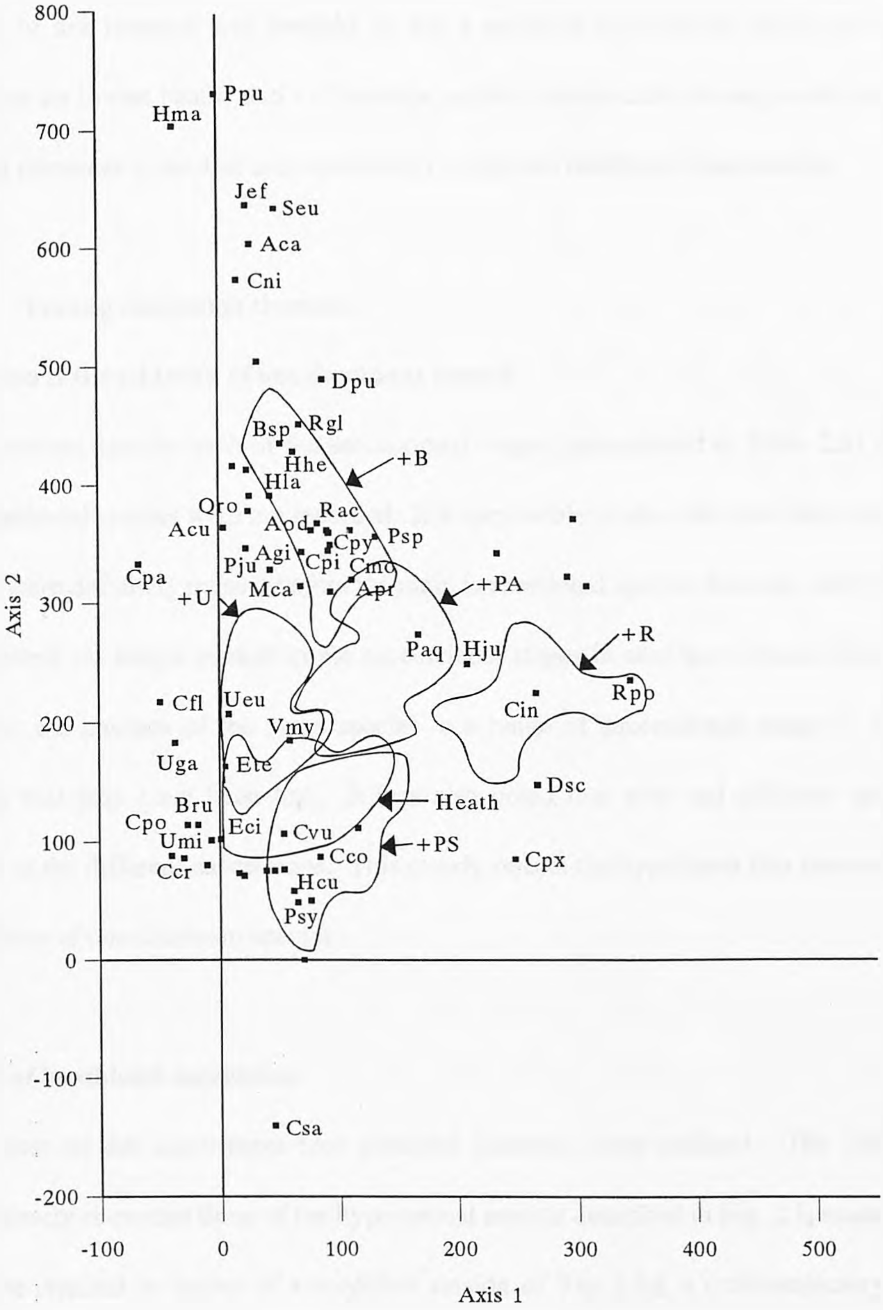


Fig. 2.3. Species plotted by their scores on the first two axes from the DECORANA analysis; key species are labelled and the position of the successional stages from Fig. 2 are also labelled.

Species codes: Aca *Agrostis capillaris*; Acu *Agrostis curtisii*; Agi *Agrostis gigantea*; Apr *Aira praecox*; Aod *Anthoxanthum odoratum*; Bsp *Betula spp;* Cvu *Calluna vulgaris*; Cni *Carex nigra*; Cpi *Carex pilulifera*; Csa *Castanea sativa*; Cmo *Crataegus monogyna*; Dpu *Digitalis purpurea*; Eci *Erica cinerea*; Ete *Erica tetralix*; Hhe *Hedera helix*; Hla *Holcus lanatus*; Jef *Juncus effusus*; Mca *Molinia caerulea*; Psy *Pinus sylvestris*; Psp *Prunus spinosa*; Paq *Pteridium aquilinum*; Qro *Quercus robur*; Rpo *Rhododendron ponticum*; Rgl *Rubus glandulosus*; Rac *Rumex acetosella*; Seu *Senecio erucifolius*; Ueu *Ulex europaeus*; Uga *Ulex gallii*; Umi *Ulex minor*; Vmy *Vaccinium myrtillus*; Bru *Brachythecium rutabulum*; Cin *Campylopus introflexus*; Cpa *Campylopus paradoxus*; Cpy *Campylopus pyriformis*; Dsc *Dicranum scoparium*; Hcu *Hypnum cupressiforme*; Hju *Hypnum jutlandicum*; Hma *Hypnum mammillatum*; Pju *Polytrichum juniperinum;* Ppu *Pseudoscleropodium purum*; Cco *Cladonia cf coccifera;* Ccr *Cladonia cf crispata*; Cfl *Cladonia floerkeana*; Cpo *Cladonia portentosa*; Cpx *Cladonia pyxidata.*

2.5 DISCUSSION

The aim of this research was twofold, to test a series of hypothetical models of vegetation succession on Dorset heaths and to formulate applied conservation management strategies for targeting resources to reverse succession and re-establish heathland communities.

2.5.1 Testing succession theories

Succession is the addition of one dominant species

The vegetation data for each of the successional stages (summarised in Table 2.8) shows that some heathland species were not recorded. It is impossible to show for sites such as these that; (a) they were definitely present before the main successional species invaded, and (b) that they are definitely no longer present in the successional stages in seed/spore banks (Miles 1979). However, the absence of the same species in a range of successional stages in many sites suggests that they have been lost. It was also noted that new and different species have invaded in the different successions. This clearly rejects the hypothesis that succession is just the addition of one dominant species.

Models of heathland succession

At the start of this experiment four potential scenarios were outlined. The DECORANA results clearly show that three of the hypothetical models described in Fig. 2.1, models a, b and c, can be rejected in favour of a modified version of Fig. 2.1d, a multi-trajectory model of succession. The successional stages are grouped around the heath quadrats, implying that there are many successional trajectories along which the heath may move. However the model must be modified as the +B stage may be on a trajectory with +PA or +U which gives a suggestion of model Figure 2.1c. The +B succession may therefore be either a dual succession, heath to +PA or +U, to +B or a straight succession to +B. *Betula* spp frequently colonise and eventually replace degenerating *Ulex europaeus* bushes, (Grime, Hodgson &

Hunt 1988) and will also invade *Pteridium aquilinum*/grass communities, (Marrs, Hicks & Fuller 1986). Whether the +B succession is a single succession or one that occurs via other stages remains to be tested.

Which trajectory a heath moves along depends on many factors. Closeness to a seed source of the successional species influences which species invade. Early aerial photographs of the sites often showed single plants of the invasive species in open heath areas, and spread presumably occurred from these individuals. Variation in soil nutrients has also been postulated to make one area more susceptible to invasion than another (Chapman, Rose & Basanta 1989). Other possible factors which may be important include disturbance and the occurrence of bare ground. These factors are necessary to trigger germination for some invading species (Grime, Hodgson & Hunt 1988). The health and age of *Calluna vulgaris* will also be important (Khoon & Gimingham 1984).

The successional stages can be ranked in order of "proximity to heath", +U and +PS < +PA < +R and +B, (where < refers to distance in the ordination). The +U stage appears closest to the heathland, shown by the way the +U quadrats merge in with the heaths, mainly because many of the heathland species survive in the +U stage. The reasons for the +U succession keeping some of the heathland species may be two fold. First, *Ulex europaeus* does not form such a dense canopy as *Pteridium aquilinum* or *Pinus sylvestris*. The heathland species are therefore less likely to be shaded out and may survive close to or alongside *Ulex europaeus*. Second *Ulex europaeus* is the only one of the successional species with a shorter life span than that of *Calluna vulgaris*. After about 15 years *Ulex europaeus* bushes begin to degenerate and break apart (Grime, Hodgson & Hunt 1988), thus other species can colonise. Heathland species may therefore survive. Thus the +U stage rarely dominates the heathland completely so its plant community is not altered as much as the other successional stages. As *Ulex* *europaeus* degenerates, heathland species may be able to re-establish in the gaps. However the richer soil around the *Ulex europaeus* bushes, caused by its nitrogen fixing ability (Green 1972), may allow other successional species such as *Betula* spp. (Grime, Hodgson & Hunt 1988), and possibly also *Pteridium aquilinum* to invade. New *Ulex europaeus* plants may also establish as the older plants degenerate thus maintaining the successional stage.

In the ordination, +PS (*Pinus sylvestris*) stage quadrats fall close to the open heath sites. Due to the long life-span of *Pinus sylvestris* and the low light intensity under the mature canopy there was a minimal ground flora. The species present were either heathland species, or invaders (Table 2.8). Examples of both categories were often present, but heathland species were found more frequently and at greater cover than most invaders, the exception being *Pteridium aquilinum.*

The +PA quadrats are intermediate in their position between those stages closest to the heath, +U and +PS, and those furthest from the heath, +R and +B. There is some intermixing between the +PA and +U quadrats possibly showing that *Pteridium aquilinum* may invade old +U sites as well as directly on heathland. *Pteridium aquilinum* itself appears to have few species regularly associated with it (Fig. 2.3), because it tends to shade out the majority of other species. The species that were found in the +PA quadrats occurred at very low cover and infrequently, although there was a great variety of species which did invade.

The +R quadrats were separated at some distance from the other successional stages. This is because the +R quadrats generally only have *Rhododendron ponticum* growing there, most of the other species being shaded out except for a few bryophytes.

The +B stages were also separated from the other successional stages. Unlike the *Pinus sylvestris*, the +B stages altered the whole plant community present. The species which invaded included *Agrostis capillaris, Holcus lanatus, Carex nigra, Juncus effusus, Chamerion angustifolium, Digitalis purpurea, Hedera helix, Ilex aquifolium* and *Teucrium scorodonia* and are more typical of a scrub/woodland flora; this is typical of *Betula* spp. succession (Miles 1981a). *Quercus robur* was also included in this cluster of +B invaders. Although this species only occurred occasionally as small seedlings or plants, it may indicate that the ultimate direction of the succession is towards oak woodland (Nielsen, Dalsgaard & Nørnberg 1987a,b). There are two reasons for these changes in ground flora. First the inability of the *Calluna vulgaris* and other heathland species to tolerate the shading of the *Betula* spp., (Gimingham 1960; Miles 1981a; Hester 1987; Hester, Miles & Gimingham 1991). Second, the *Betula* spp. may change the soil from a podsol to a brown earth, altering the soil nutrient supply, (Miles & Young 1980; Miles 1981a) so that more competitive species can establish on hitherto poorer heath soils.

2.5.2 Management strategies for conservation

The vegetation changes and the direction of change that occur during succession have important management implications if these successional communities are to be restored to heathland. As heathland restoration is an important part of Britain's response to Agenda 21 and Natura 2000 (Department of the Environment 1995a,b) and as there are financial pressures on heathland restoration it is important to:

a) use the money available for conservation cost-effectively or

b) at least to be aware that additional costs are involved if the more difficult options are chosen.

Cost effective restoration strategies

Sites which have undergone succession to +U or +PS should be easier to restore to heathland than the others as they still generally contain many of the heathland species, with a source of seed/propagules for recolonization. The removal of *Ulex europaeus* may be difficult as it can resprout from cut young stems and also has a large and persistent seed bank (Grime, Hodgson & Hunt 1988). The removal of *Pinus sylvestris* is relatively easy as it does not resprout from the stumps and can therefore be removed at low cost.

The reversion of the +B stage to heathland is likely to prove more difficult, because *Betula* spp. resprout from cut stumps, and the stumps or regrowth have to be treated with herbicide (Marrs 1985a; Marrs 1987). Removal of the ground flora under *Betula* spp. may also be difficult as these species are more competitive on the modified soil than the heathland species (Grime, Hodgson & Hunt 1988) and may, therefore, inhibit the recolonization of the site by heathland species.

The removal of *Pteridium aquilinum* and the restoration of heathland is problematic because of the large underground rhizome reserves (Lowday & Marrs 1992; Marrs, Pakeman & Lowday 1993) and the control of *Rhododendron ponticum* is also difficult as cut stumps have to be treated with herbicide, and the root mat may inhibit heathland restoration (Squires 1991).

The success of reversion depends not only on the heath vegetation that remains but on other factors such as the contents and viability of the propagules in the soil as well as any soil nutrient changes that may have occurred during succession (Miles & Young 1980; Marrs *et al.* 1992).

2.6 CONCLUSION

Although successional stages on the Dorset heaths may be categorised by the presence of a single dominant invasive species, succession is not the simple addition of one species to the existing heathland flora. As succession occurs species are lost and gained, specifically the *Cladonia* lichen species appear to be quickly lost from all successional stages. The loss of other heathland species depends upon the successional stages with +PS and +U stages retaining more heathland species than the other stages. The +B stage caused the greatest change in terms of the vegetation present with a range of additional species invading.

A range of pathways along which heathland communities move during succession has been found with some successional pathways remaining closer to the heathland than others. These results may be related to practical heathland management and the restoration of heathland after succession. Specifically it is more sensible and cost effective to restore heathlands on sites where *Ulex europaeus* or *Pinus sylvestris* successions have occurred, then *Betula* spp.

This study shows that research on successional pathways in a habitat is of great value for the development of models which may show how cost-effective management options can be selected.

Chapter 3

A STUDY OF SUCCESSION ON LOWLAND HEATHS IN DORSET, SOUTHERN ENGLAND: CHANGES IN SOIL CHEMICAL PROPERTIES

3.1 INTRODUCTION

Dorset heaths, along with many other British lowland heaths, are declining because of scrub invasion and other successional changes (Marrs, Hicks & Fuller 1986; Webb 1990; Gimingham 1992). There are many successional pathways along which a heath may move (Chapter 2), with *Betula* spp., *Pinus sylvestris, Pteridium aquilinum, Rhododendron ponticum* and *Ulex europaeus* being the most common. As these successions take place the species complement changes to differing degrees (Chapter 2).

Generally heathlands occur on very infertile soils (Gimingham 1992), and any increase in soil resources is likely to lead to a different community, as has been shown in the Netherlands (Heil & Diemont 1983; Aerts & Berendse 1988; Van Der Eerden *et al.* 1991). The effect of soil on the plant species present is fairly well known, but possible effects of the plants and plant communities on soil properties have received less attention.

The Dorset heaths occur on soils derived from the Bagshot and Bracklesham beds and are strongly podzolized (Chapman 1967). These soils are very nutrient poor, with phosphorus being a major limiting factor (Chapman, Rose & Clarke 1989). These nutrient poor podzol soils have been maintained over the years by the podzolizing effects of *Calluna vulgaris*, exploitation of the heaths by man (Webb 1986) and grazing or fire, both of which prevent the establishment of trees (Chapman 1967).

Succession is accompanied by changes in these nutrient poor podzol soils. Miles (1981a) demonstrated that as *Betula* spp. invaded moorland the soil changed from a podzol (mor) to a brown earth (mull) soil, resulting in increased pH, exchangeable calcium, and total phosphorus, while the ratios of carbon/nitrogen, carbon/phosphorus and to a lesser extent carbon/potassium decreased. However *Betula* spp. are not the only species to invade heathland. Are the successional trends found for *Betula* spp. similar for all species invading heathlands or do others have different effects, or none at all, upon the soil nutrients?

There were two aims in this work. The first was to test four hypothetical models of succession and associated soil nutrient chemical status on Dorset heathlands, and to answer the following questions:

- Do soil nutrients change with succession?
- If so, which nutrients change?
- Are different successional species associated with different soil nutrients?

The second aim was to apply the results from the above models in targeting the best use of conservation management resources towards reversing these successions.

The problem with this type of study is that there is a circularity of argument. Are the changes in soil nutrients levels caused by the invasive species (Miles 1981a), or are intrinsic site differences in soil nutrient status the driving variables that cause some sites to be invaded by late-successional species (Chapman, Rose & Clarke 1989). While current theory suggests that the former argument is correct, even if the latter one is proven this study is still valid as it identifies sites at greatest risk of succession, and any changes in the soil factors needed to be tackled in restoration schemes.

3.2 HYPOTHETICAL SUCCESSIONAL MODELS

The possible types of successional pathways and soil nutrient changes occurring on heathland can be depicted in multivariate space by CANOCO (Canonical Correspondence Analysis - CCA, Ter Braak 1988). Four hypothetical ordination diagrams which could describe the results obtained from CCA analysis of vegetation and soil data taken from open heath and successional stages are shown in Fig. 3.1:

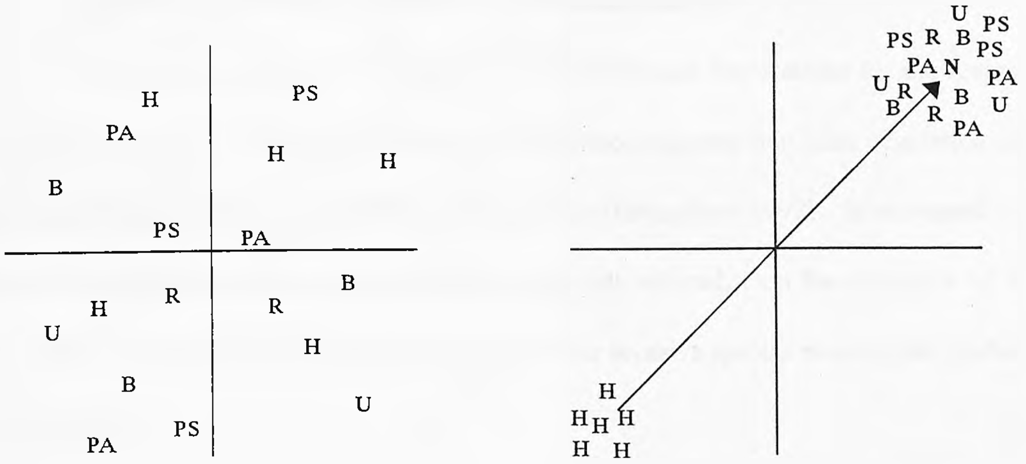
(i) A random distribution of the open heath sites and the successional stages, with no relationship to soil nutrients (Fig. 3.1a).

(ii) A successional trajectory with soil nutrients increasing but no influence of species (Fig. 3.1b). Samples are either low-nutrient heath samples or high-nutrient late-successional samples. All soil nutrients increase, independent of which successional species is invading.

(iii) All soil nutrients increase although by different amounts depending on which successional species is invading (Fig. 3.1c). The successional stages are positioned along a similar trajectory with distance along it being related to increasing soil nutrient concentrations.

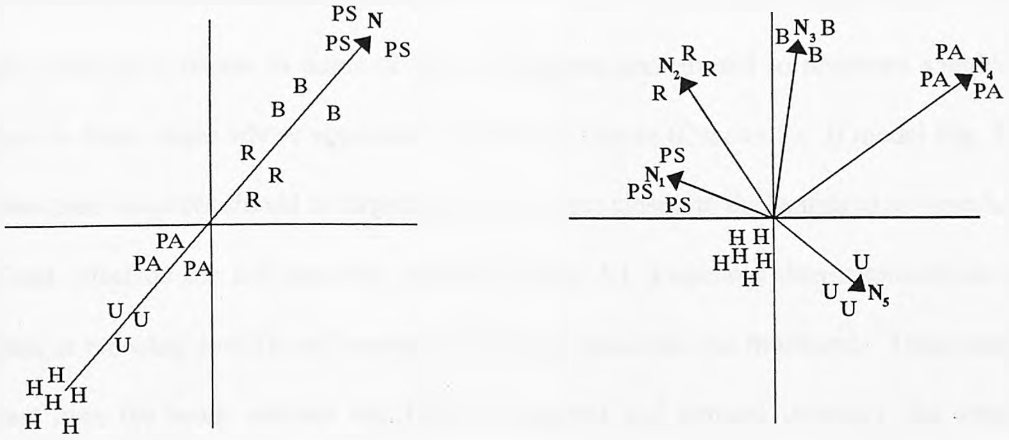
(iv) A multi-trajectory model of succession (Fig. 3.1d). Each succession radiates from the heathland sites on different trajectories, each associated with different soil nutrients. The different soil nutrients and their relative importance are represented by the different directions and lengths of the arrows.

The ordination of vegetation samples reported in Chapter 2, when no account was taken of soil nutrients, has suggested that a multi-trajectory model of succession was appropriate. The aim here was to assess whether the inclusion of soil data altered this conclusion.



a)Random distribution of open heath and successional sites, no relationship to soil nutrients.

b)Successional trajectory, with soil nutrients increasing, but no influence of species.



c) All soil nutrients increase although by different amounts depending on which successional stage is occurring.

d)A multi-trajectory model of succession with different soil nutrients increasing along different trajectories.

Fig. 3.1. Hypothetical ordination diagrams illustrating results which might be obtained from CCA analysis of vegetation and soil data taken from samples taken in open heath and various successional stages. The arrows indicate increasing soil nutrients. H = open heathland; B = +B (*Betula* spp.) successional stage; PS = +PS (*Pinus sylvestris*) successional stage; PA = +PA (*Pteridium aquilinum*) successional stage; R = +R (*Rhododendron ponticum*) successional stage; U = +U (*Ulex europaeus*) successional stage; N = soil nutrient.

3.2.1 Targeting conservation resources to reverse succession.

The processes at work on the Dorset heathlands have significant implications for the reversal of succession and the restoration of heathland; experience suggests that both vegetation and soil changes be considered in heathland management (Gimingham 1992). If increased soil nutrient concentrations accompanying succession are not reduced, then the clearance of the stage dominant species may just allow the same or other invasive species to establish (Bullock & Webb 1995).

If the processes described by Fig. 3.1a operate then restoration of heathland will be easy as there is no influence of soil nutrients, so heathland managers need only to concern themselves with the restoration of the vegetation. If Fig. 3.1b is operates then all stages will be equally difficult to restore in terms of the soil nutrients present and so resources should be targeted to those stages whose vegetation is easiest to restore (Chapter 2). If model Fig. 3.1c operates then resources should be targeted at those stages closest to the heathland as these have had least effect on the soil nutrients present. If Fig. 3.1 d operates then resources can be targeted at reducing specific soil nutrients in stages closest to the heathland. Those stages furthest from the heath samples will have the greatest soil nutrient increases (the longest vectors) and may be the most difficult to reverse.

3.3 MATERIALS AND METHODS

Ten heathland areas in the Poole Basin of Dorset (Table 2.1) where succession had occurred in the last 20 - 50 years were surveyed. Five successional stages (hereafter called stages) where major species had invaded recently were chosen:

+B - major invader is *Betula* spp,

+PS - major invader is *Pinus sylvestris*,

+PA - major invader is *Pteridium aquilinum*,

+R - major invader is *Rhododendron ponticum*,

+U - major invader is *Ulex europaeus*.

Detailed descriptions of sites and techniques for vegetation description are provided in chapter 2, here only methods for sampling soils are given. Nomenclature follows Stace (1991) for higher plants, Duncan (1970) for lichens and Smith (1978) for mosses.

At the time of vegetation sampling a soil sample to a depth of 21 cm was taken from the centre of each quadrat using a Bi-partite Edelman auger (Eijelkamp Agrisearch Equipment, Giesbeek, The Netherlands). Soil samples were stored in a cold room (4 °C) until analysis.

3.3.1 Analysis of soil samples

Fresh soil (5 g) was removed from each sample and shaken with 30 ml 1M potassium chloride for analysis of extractable nitrogen. The extract was analysed for ammonium-nitrogen and nitrate/nitrite-nitrogen colorimetrically following the method in Allen *et al.* (1974).

The remainder of the soil samples were air dried and sieved through a 2 mm sieve. A 2.5 g sub-sample was extracted in 2.5% v/v acetic acid. The extractable phosphorus present in this extract was measured using the stannous chloride method in Allen (1989). The same extractant was used to measure exchangeable cations (calcium, magnesium, sodium and potassium). Ca and Mg were measured using absorption spectrometery and Na and K by emission spectrometery (Unicam 1991). A measure of the organic matter present was made by loss-on-ignition following the method in Allen (1989). The soil pH was recorded in a 1:2.5 slurry of soil and deionised water (Allen *et al.* 1974).

The above soil nutrients were chosen for analysis as they include those nutrients known to be growth limiting and those shown to increase during *Betula* succession on moorland (Miles 1981a).

3.3.2 Statistical analysis

The vegetation and soil results were analysed using CANOCO (Canonical correspondence analysis - CCA, Ter Braak 1988). CCA is a direct ordination technique in which species abundance is directly and immediately related to the measured environmental variables (soil data in this case). The axes in the ordination are constrained to optimise their linear relationships to the environmental variables. The relationships can be shown in an ordination diagram by vectors for the environmental variables with lengths proportional to their importance and directions showing their correlations with each axes. In this paper the vectors are displayed at x10 their actual length as the scores for the environmental variables and species/samples are of a different order of magnitude (Ter Braak 1988). The samples and/or species are then plotted in the ordination so that major relationships are easy to see. The statistical validity of the resulting ordination was evaluated by an unrestricted Monte Carlo permutation test (Ter Braak 1990).

In the analysis the vegetation data were transformed by a log transformation and rare species were downweighted. Comparisons of the analysis with and without downweighting revealed that two groups of species were affected: (i) a few species of lichen, which only occurred occasionally and at a low cover on the heaths, and (ii) species that occurred infrequently and at low cover mainly in the +B stages. It therefore seemed reasonable to use downweighting of rare species in the analysis. Covariables were also used in the analysis for each area, this aimed to take account of any differences between the sites in geology and climate. Detrending was also used to minimise any influence that the first axis may have had over the positioning of the second, ie the arch effect (Ter Braak 1990). All analyses were done in all possible combinations of these modifications and the results throughout were similar.

3.4 RESULTS

3.4.1 Soil analysis results

The heath soils (Table 3.1) were very acidic, generally in the range pH 3.5 to 4.0 with Sopley & Ramsdown being the most acidic at pH 3.4 and Winfrith the least acidic at pH 4.4. These are typical figures for heathland soils; Pywell, Webb & Putwain (1994) recorded 3.7 at Arne, 4.0 at Stoborough and 3.8 at Hartland, (Stoborough and Hartland are both Dorset Heathlands close to many of the areas used in this study). The +PS stage had pH values that were usually similar to the corresponding heathland values for that site, eg at Blackhill the pH of both heath and +PS stage was 3.6. On some areas the +PS stage was more acidic than the heath. The +PA, +R and +U stages had values in the range of 3.5 to 4.5. The +B stages often had higher values than the heath samples, with those at Higher Hyde, and Sopley & Ramsdown having values greater than pH 5.

Loss-on-ignition for heath samples ranged from 4.3% to 17.2% (Table 3.1) and are typical of heathland soils; Pywell, Webb & Putwain (1994) recorded 7.8%, 11.2% and 10.6% at Hartland, Stoborough and Arne respectively. The stages ranged from 4.3% (Sopley & Ramsdown, +PS) to 27.1% (Higher Hyde, +PA), and showed no obvious trends.

Extractable ammonium-nitrogen values were lowest for the heath samples (1.0 to 3.1 $\mu g\ N\ g^{-1}$) (Table 3.1), which were similar to Pywell, Webb & Putwain (1994). The successional stages all showed higher concentrations of ammonium-nitrogen than the heath samples. The +R stage was most similar to the heath with values of 2.4 to 6.7 $\mu g\ N\ g^{-1}$. The +PS stage had values of 5.1 to 11.7 $\mu g\ N\ g^{-1}$, while the +B stages were slightly higher (6.1 to 16.1 $\mu g\ N\ g^{-1}$). The +PA stage (range 1.6 to 55.3 $\mu g\ N\ g^{-1}$) and the +U stage (range 6.3 to 48.5 $\mu g\ N\ g^{-1}$) had the highest ammonium-nitrogen concentrations.

Table 3.1. Chemical properties of soil samples from heath and successional sites in Dorset, mean values ± SE (n = 10) are presented.

Soil chemical property	Site	Successional stage					
		Heath	+B	+PS	+PA	+R	+U
pH	Arne	3.74 ± 0.11	3.65 ± 0.06	3.55 ± 0.05	3.55 ± 0.08	3.63 ± 0.07	3.68 ± 0.05
	Avon Heath Country Park	4.33 ± 0.25	3.95 ± 0.08	3.47 ± 0.04	3.95 ± 0.14	3.31 ± 0.07	4.03 ± 0.17
	Blackhill	3.56 ± 0.04	3.62 ± 0.04	3.55 ± 0.07	3.46 ± 0.07	3.35 ± 0.07	3.60 ± 0.06
	Canford Heath	3.51 ± 0.07	3.46 ± 0.06	3.41 ± 0.06	3.39 ± 0.05	3.37 ± 0.08	3.87 ± 0.05
	Cranborne Common	3.60 ± 0.05			4.07 ± 0.07		4.04 ± 0.06
	Higher Hyde Heath	3.58 ± 0.05	5.27 ± 0.21		3.60 ± 0.08	4.66 ± 0.20	3.55 ± 0.07
	St Catherines Hill & Town Common	3.41 ± 0.05	4.08 ± 0.13	3.09 ± 0.03		3.22 ± 0.07	
	Sopley & Ramsdown	3.37 ± 0.07	5.24 ± 0.21	3.57 ± 0.08		3.80 ± 0.06	
	Trigon	3.99 ± 0.04		4.03 ± 0.06	4.08 ± 0.07	4.49 ± 0.39	
	Winfrith Heath	4.35 ± 0.05			3.97 ± 0.05		4.19 ± 0.04
Loss-on-ignition (%)	Arne	9.95 ± 2.67	8.02 ± 0.62	9.96 ± 1.08	7.85 ± 0.82	9.01 ± 1.32	5.31 ± 0.21
	Avon Heath Country Park	10.05 ± 1.03	8.95 ± 1.15	7.87 ± 0.74	9.76 ± 1.41	14.10 ± 2.41	8.11 ± 0.82
	Blackhill	11.56 ± 1.12	10.40 ± 0.56	13.86 ± 1.65	14.90 ± 3.00	11.89 ± 2.31	19.14 ± 3.16
	Canford Heath	9.31 ± 0.78	15.08 ± 3.35	8.76 ± 0.95	9.44 ± 1.59	9.10 ± 1.42	8.80 ± 1.28
	Cranborne Common	8.70 ± 1.21			9.95 ± 0.67		7.82 ± 0.86
	Higher Hyde Heath	17.16 ± 1.57	4.62 ± 0.63		27.07 ± 3.59	5.00 ± 0.58	23.95 ± 1.41
	St Catherines Hill & Town Common	13.46 ± 1.28	3.20 ± 0.34	8.97 ± 1.45		17.98 ± 4.31	
	Sopley & Ramsdown	4.30 ± 0.68	4.12 ± 0.54	4.26 ± 0.71		11.97 ± 2.17	
	Trigon	13.18 ± 1.03		10.23 ± 1.61	9.24 ± 1.22	9.90 ± 1.08	
	Winfrith Heath	8.91 ± 1.18			14.78 ± 1.92		11.84 ± 1.27
Extractable ammonium-nitrogen (µg N g^{-1})	Arne	3.08 ± 0.18	8.87 ± 1.51	5.11 ± 0.51	5.70 ± 1.89	5.66 ± 0.78	14.60 ± 1.19
	Avon Heath Country Park	3.66 ± 0.52	7.27 ± 2.91	5.18 ± 0.69	5.03 ± 0.50	6.18 ± 0.88	6.27 ± 1.35
	Blackhill	2.95 ± 0.98	16.05 ± 4.85	11.71 ± 1.62	19.16 ± 3.12	6.74 ± 0.94	18.85 ± 2.94
	Canford Heath	2.07 ± 0.57	10.71 ± 4.92	6.22 ± 1.69	1.68 ± 0.34	2.37 ± 0.35	6.27 ± 0.75
	Cranborne Common	2.89 ± 1.09			55.32 ± 12.50		30.96 ± 5.60
	Higher Hyde Heath	1.22 ± 0.17	6.11 ± 1.50		15.58 ± 3.88	6.42 ± 1.62	48.51 ± 15.80
	St Catherines Hill & Town Common	1.48 ± 0.25	4.85 ± 0.93	5.35 ± 1.96		5.18 ± 1.06	
	Sopley & Ramsdown	1.14 ± 0.19	6.52 ± 1.04	6.21 ± 1.21		3.43 ± 0.67	
	Trigon	1.03 ± 0.11		5.88 ± 0.97	18.62 ± 7.29	2.44 ± 0.33	
	Winfrith Heath	2.37 ± 0.57			9.76 ± 1.82		19.05 ± 3.51

Table 3.1 cont.

Soil chemical property	Site	Successional stage					
		Heath	+B	+PS	+PA	+R	+U
Extractable nitrate/nitrite-nitrogen (µg N g^{-1})	Arne	0.50 ± 0.01	0.62 ± 0.03	0.53 ± 0.06	0.76 ± 0.09	0.58 ± 0.06	0.97 ± 0.19
	Avon Heath Country Park	0.59 ± 0.05	0.57 ± 0.03	0.72 ± 0.03	0.71 ± 0.08	0.65 ± 0.08	0.95 ± 0.11
	Blackhill	0.84 ± 0.29	0.88 ± 0.14	0.97 ± 0.15	1.17 ± 0.37	0.51 ± 0.05	2.31 ± 0.59
	Canford Heath	0.65 ± 0.04	0.53 ± 0.03	0.66 ± 0.10	0.60 ± 0.06	0.41 ± 0.05	0.74 ± 0.10
	Cranborne Common	0.56 ± 0.07			5.89 ± 1.61		2.23 ± 0.37
	Higher Hyde Heath	0.69 ± 0.12	0.98 ± 0.09		1.75 ± 0.50	0.73 ± 0.05	3.64 ± 1.21
	St Catherines Hill & Town Common	0.45 ± 0.03	0.71 ± 0.22	0.37 ± 0.03		0.45 ± 0.08	
	Sopley & Ramsdown	0.46 ± 0.04	0.49 ± 0.05	0.30 ± 0.04		0.37 ± 0.05	
	Trigon	0.42 ± 0.03		0.62 ± 0.06	1.34 ± 0.87	0.87 ± 0.14	
	Winfrith Heath	0.42 ± 0.06			0.63 ± 0.09		1.57 ± 0.36
Extractable phosphorus (µg P g^{-1})	Arne	2.41 ± 0.27	3.54 ± 0.31	2.69 ± 0.41	3.24 ± 0.43	3.34 ± 0.48	3.16 ± 0.33
	Avon Heath Country Park	4.91 ± 0.61	6.98 ± 1.01	3.44 ± 0.36	4.41 ± 0.58	6.43 ± 0.60	4.41 ± 0.46
	Blackhill	4.15 ± 0.29	1.91 ± 0.12	2.79 ± 0.32	5.02 ± 0.84	3.83 ± 0.58	7.55 ± 1.25
	Canford Heath	1.97 ± 0.16	2.87 ± 0.64	1.49 ± 0.21	4.43 ± 0.57	2.78 ± 0.22	2.47 ± 0.50
	Cranborne Common	3.44 ± 0.28			1.10 ± 0.09		1.15 ± 0.10
	Higher Hyde Heath	5.08 ± 0.54	1.35 ± 0.22		8.92 ± 1.81	1.27 ± 0.13	7.76 ± 0.60
	St Catherines Hill & Town Common	6.13 ± 0.56	17.60 ± 2.65	3.73 ± 1.09		6.67 ± 1.28	
	Sopley & Ramsdown	1.98 ± 0.25	10.22 ± 4.42	2.24 ± 0.44		4.46 ± 0.53	
	Trigon	4.54 ± 0.55		3.78 ± 0.35	4.27 ± 0.25	4.13 ± 0.68	
	Winfrith Heath	2.77 ± 0.52			7.36 ± 1.19		1.24 ± 0.12
Exchangeable potassium (µg K g^{-1})	Arne	30.77 ± 7.07	63.00 ± 10.10	43.78 ± 5.91	90.00 ± 18.60	79.50 ± 20.50	39.46 ± 4.79
	Avon Heath Country Park	31.00 ± 4.89	41.30 ± 6.77	27.59 ± 6.43	17.48 ± 4.98	60.40 ± 13.20	24.87 ± 3.15
	Blackhill	68.64 ± 6.35	61.03 ± 7.91	65.57 ± 8.28	113.90 ± 22.70	73.18 ± 8.97	107.90 ± 25.30
	Canford Heath	47.43 ± 8.42	51.04 ± 7.35	49.83 ± 7.43	69.70 ± 7.33	46.84 ± 7.66	50.89 ± 5.81
	Cranborne Common	56.43 ± 5.87			224.70 ± 23.00		72.05 ± 8.97
	Higher Hyde Heath	80.78 ± 9.22	75.60 ± 10.50		234.40 ± 38.40	66.30 ± 9.35	190.00 ± 44.30
	St Catherines Hill & Town Common	85.51 ± 9.26	28.75 ± 4.68	37.10 ± 11.60		99.40 ± 23.90	
	Sopley & Ramsdown	15.12 ± 3.98	34.09 ± 6.12	16.89 ± 3.76		54.38 ± 7.20	
	Trigon	47.49 ± 5.86		27.23 ± 4.67	76.80 ± 18.50	32.32 ± 7.07	
	Winfrith Heath	29.78 ± 9.58			81.45 ± 8.67		36.44 ± 4.60

Table 3.1 cont.

Soil chemical property	Site	Successional stage					
		Heath	+B	+PS	+PA	+R	+U
Exchangeable sodium (µg Na g^{-1})	Arne	17.10 ± 4.41	43.60 ± 6.00	81.92 ± 9.65	22.50 ± 4.77	33.80 ± 12.10	15.48 ± 3.32
	Avon Heath Country Park	16.87 ± 4.25	32.58 ± 8.53	17.37 ± 4.07	12.54 ± 2.35	31.44 ± 6.41	30.65 ± 4.37
	Blackhill	29.89 ± 4.43	51.15 ± 5.88	84.90 ± 14.30	86.80 ± 23.70	23.15 ± 5.15	55.34 ± 9.51
	Canford Heath	26.48 ± 7.22	50.00 ± 15.50	57.07 ± 9.50	42.20 ± 11.50	35.00 ± 10.60	13.82 ± 3.07
	Cranborne Common	11.76 ± 1.72			65.30 ± 11.80		21.72 ± 6.00
	Higher Hyde Heath	50.06 ± 6.73	30.07 ± 6.25		87.74 ± 9.35	42.25 ± 8.07	118.30 ± 16.80
	St Catherines Hill & Town Common	42.30 ± 6.36	17.19 ± 3.41	53.60 ± 13.30		168.40 ± 29.20	
	Sopley & Ramsdown	6.17 ± 1.25	21.53 ± 3.18	11.27 ± 3.36		69.60 ± 20.70	
	Trigon	30.02 ± 6.00		41.67 ± 8.50	71.70 ± 20.30	49.80 ± 10.60	
	Winfrith Heath	18.65 ± 4.44			69.60 ± 10.80		18.20 ± 4.17
Exchangeable magnesium (µg Mg g^{-1})	Arne	35.48 ± 5.13	43.43 ± 4.05	55.10 ± 5.27	50.50 ± 9.63	27.18 ± 5.38	33.63 ± 3.20
	Avon Heath Country Park	54.30 ± 10.20	59.00 ± 11.10	38.52 ± 4.50	50.17 ± 8.00	33.38 ± 8.97	58.05 ± 4.92
	Blackhill	61.82 ± 5.44	53.33 ± 4.65	67.55 ± 7.70	49.89 ± 9.19	44.08 ± 7.44	83.50 ± 12.50
	Canford Heath	38.73 ± 5.32	31.84 ± 6.45	37.25 ± 5.17	47.67 ± 8.15	24.97 ± 2.68	26.66 ± 2.88
	Cranborne Common	28.41 ± 2.70			26.36 ± 2.57		14.99 ± 1.81
	Higher Hyde Heath	74.12 ± 6.94	78.10 ± 10.50		134.40 ± 12.70	60.31 ± 6.67	133.30 ± 19.50
	St Catherines Hill & Town Common	74.53 ± 5.18	35.33 ± 4.52	46.03 ± 5.40		82.70 ± 18.30	
	Sopley & Ramsdown	12.32 ± 2.18	56.92 ± 9.98	15.72 ± 2.87		30.83 ± 4.12	
	Trigon	87.26 ± 7.94		55.36 ± 9.05	75.30 ± 12.40	61.80 ± 11.80	
	Winfrith Heath	49.96 ± 7.91			85.60 ± 8.78		28.19 ± 4.32
Exchangeable calcium (µg Ca g^{-1})	Arne	65.21 ± 9.63	121.64 ± 8.32	110.60 ± 16.30	127.00 ± 18.90	90.89 ± 5.78	67.97 ± 7.11
	Avon Heath Country Park	1020.00 ± 419.00	338.60 ± 35.70	167.50 ± 23.50	345.70 ± 58.80	181.60 ± 68.30	518.00 ± 170.00
	Blackhill	123.21 ± 9.38	74.23 ± 6.93	127.60 ± 10.80	109.10 ± 18.40	47.20 ± 15.40	176.20 ± 18.80
	Canford Heath	95.00 ± 10.90	121.80 ± 36.50	98.20 ± 12.40	124.20 ± 13.80	37.02 ± 4.83	54.94 ± 7.26
	Cranborne Common	52.59 ± 4.55			34.01 ± 2.73		41.67 ± 6.05
	Higher Hyde Heath	171.90 ± 13.90	697.00 ± 101.00		326.70 ± 35.70	659.00 ± 200.00	272.70 ± 22.80
	St Catherines Hill & Town Common	157.60 ± 12.90	217.90 ± 50.00	79.14 ± 8.85		168.30 ± 32.90	
	Sopley & Ramsdown	31.58 ± 6.71	557.00 ± 118.00	50.46 ± 8.98		74.30 ± 15.20	
	Trigon	177.64 ± 9.92		110.60 ± 15.50	301.80 ± 58.00	1354.00 ± 1237.00	
	Winfrith Heath	97.60 ± 15.70			153.40 ± 15.90		61.50 ± 10.30

Extractable nitrate/nitrite-nitrogen concentrations were generally less than 1 μg N g^{-1} at all stages and all sites (Table 3.1). However a similar pattern to that for ammonium-nitrogen was observed; with the heath samples having the lowest values, the +B, +PS, +R stages had slightly higher values while the +PA and +U stages had the highest concentrations, greater than 1 μg N g^{-1} in some cases.

Extractable phosphorus concentrations from the heath ranged from 2.0 to 6.1 μg P g^{-1} (Table 3.1). The geological outlier, Blackhill, and some of the northern areas in the Avon Valley had greater concentrations than those at Arne, Canford and Winfrith. Pywell, Webb & Putwain (1994) recorded values of 1-2 μg P g^{-1} which come from samples taken from the nutrient poor southern sites and these values are similar to the lower values here. The +PS stages often had phosphorus values lower than those for the corresponding heathland site. In all but two of the +B stages the phosphorus concentrations were considerably higher than those found on the heaths. Sopley & Ramsdown showed a 500% increase, St Catherine's Hill a 250% increase and the others about a 150% increase. The other stages usually had higher concentrations than the heath sites but lower than the +B stages, the exception being the values at the +PA and +U stages at Higher Hyde which were greater than those in the +B stage.

Exchangeable potassium results showed a large range of values within the heath sites (Table 3.1), with the lowest values of 15.1 μg K g^{-1} at Sopley & Ramsdown and values greater than 80 μg K g^{-1} at Higher Hyde and St Catherine's Hill & Town Common. The rest of the sites had concentrations in the range 29-68 μg K g^{-1}, which are more typical of heathland (Pywell, Webb & Putwain 1994). The successional stages generally had higher concentrations than the corresponding heath site, two +PA stages had greater than 200 μg K g^{-1} (Cranborne and Higher Hyde) and two +U stages had greater than 100 μg K g^{-1} (Higher Hyde and Blackhill).

Exchangeable sodium concentrations in the heath sites ranged from 6.2 μg Na g^{-1} at Sopley & Ramsdown to 50.1 μg Na g^{-1} at Higher Hyde (Table 3.1). They were higher for 29 out of 36 of the successional stages; however no stage consistently showed higher concentrations than any other stages. Both the highest and lowest concentrations were recorded in the +U stage, 15.5 μg Na g^{-1} at Arne and 118.3 μg Na g^{-1} at Higher Hyde.

The heath at Sopley & Ramsdown had the lowest concentrations of magnesium, 12.3 μg Mg g^{-1} and Trigon had the greatest, 87.3 μg Mg g^{-1} (Table 3.1). Most other sites ranged between 28.4 to 74.5 μg Mg g^{-1}. All these are typical heathland values; Pywell, Webb & Putwain (1994) recorded 40, 50 and 80 μg Mg g^{-1} at Hartland, Stoborough and Arne. The successional stages showed little pattern, with sites having both higher and lower values than those of comparable heathlands. The +R stages generally had lower values than the heath samples, the +PA and +U stages had the highest values; the greatest being 130 μg Mg g^{-1} at Higher Hyde.

The heath sites showed large variability in the exchangeable calcium concentrations with most sites ranging between 50 and 180 μg Ca g^{-1}, the exceptions being Sopley & Ramsdown at 31 μg Ca g^{-1} and AHCP at 1020 μg Ca g^{-1} (Table 3.1). All but two of the +B stages had higher calcium concentrations than the corresponding heath sites. The exceptionally high concentrations recorded in the +R stage at Trigon was due to one outlier which had an extremely high value; this result was checked and it was not an analytical error.

3.4.2 CCA analysis

As expected with a large ecological dataset the data showed large variation with the CCA results having low eigenvalues and regression coefficients for the first two axes (summarised in Table 3.2).

Table 3.2. Eigenvalues and intra-set correlations of soil variables for the first two CCA axes

Axis	1		2	
Eigenvalue	0.202		0.150	
Species-environment correlations	0.597		0.481	
Percentage variance				
of species data	3.9		3.0	(6.9)
of species-environment relation	44.3		32.6	(76.9)
Intra-set correlations				
pH	-0.816	(1)	-0.056	
Loss on ignition	0.253	(3)	-0.037	
NH_4-N	-0.161		-0.470	(2)
NO_3-N	-0.053		-0.249	
P	-0.534	(2)	0.052	
Ca	-0.199		-0.050	
Mg	-0.099		0.064	
K	-0.003		-0.360	(3)
Na	0.180		-0.644	(1)

Cumulative percentage variances are shown in parentheses.
On the intra-set correlation, the first three leading variables are shown in parentheses.

For the species data, 3.9% of the variation is explained by axis 1 which has a 0.597 correlation between the species and the soil data. This accounts for 44.3% of the explained species-environment relationships. Axis 2 explains a further 3.0% of the species variation and has a species-environment correlation of 0.48. This accounts for a further 32.6% of the species-environment relationship. Of the variation accounted for in the model the first two axes account for 76.9% of the species-environment relationship. The intraset correlations show the relative importance of the different soil variables. On the first axes pH, extractable phosphorus, and loss-on-ignition are most important, on the second axes sodium, ammonium-nitrogen and potassium are important.

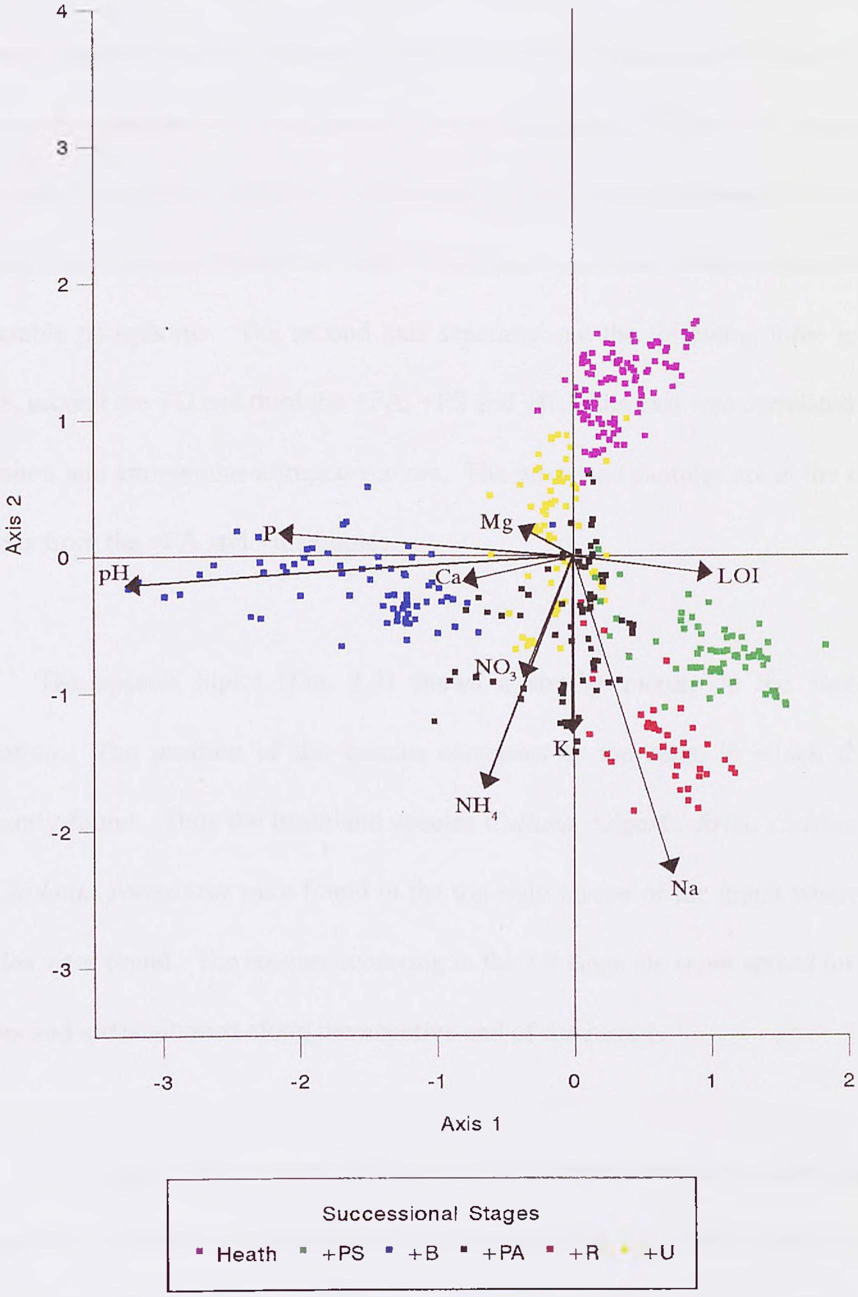


Fig. 3.2. Ordination diagram from CANOCO for the first two axes, showing the relationship between the different successional stages and the soil nutrients. The soil nutrient vectors are shown by arrows and their length is multiplied by a factor of ten. Heath = Open heathland; +PS = *Pinus sylvestris* is the major invader; +B = *Betula spp* is the major invader; +PA = *Pteridium aquilinum* is the major invader; +R = *Rhododendron ponticum* is the major invader; +U = *Ulex europaeus* is the major invader; Ca = exchangeable calcium; K = exchangeable potassium; LOI = loss-on-ignition; Mg = exchangeable magnesium; Na = exchangeable sodium; NH_4 = extractable ammonium-nitrogen; NO_3 = extractable nitrite/nitrate-nitrogen; P = extractable phosphorus; pH = pH

The ordination diagram (Fig. 3.2) shows that samples from the same stage are clustered together and the different stages are separated out along the axes. The first axis separates the samples into three groups; first the heathland, +PS and +R samples, second the +PA, and +U samples and third the +B samples. The +B stage is shown at one extreme of this first axis and separate from the rest. This axis was most closely correlated to pH and extractable phosphorus. The second axis separated out the following three groups; first the heaths, second the +U and third the +PA, +PS and +R. This axis was correlated to the sodium, potassium and ammonium-nitrogen vectors. The heathland samples are at the opposite end of this axis from the +PA and +R samples.

The species biplot (Fig. 3.3) shows a similar picture to the successional stage ordination. The position of the species correlates to the stage in which they were most frequently found. Thus the heathland species *Calluna vulgaris, Erica cinerea, Erica tetralix* and *Cladonia portentosa* were found in the top right corner of the graph where the heathland samples were found. The species occurring in the +B stage are more spread out than the other species and are positioned along the negative end of the Axis 1.

The length of the vectors in Figs 3.2 & 3.3 represent their relative importance; thus pH, sodium, phosphorus and ammonium-nitrogen are the four most important soil factors in the ordination. The positioning of the samples relative to the vectors in Fig. 3.2 relates the different stages to changes in different soil properties. Thus, phosphorus, pH and calcium increase towards the +B stages, ammonium-nitrogen, nitrate/nitrite-nitrogen and potassium increase towards the +PA and +U , sodium increases during the +R and +PA stages and loss-on-ignition increases in the +PS stages.

An unrestricted Monte Carlo test was carried out on both the axes and the result was significant at $P = 0.001$, showing that the relationships between the soil and vegetation data is not random and that this analysis gives the best possible description of these data.

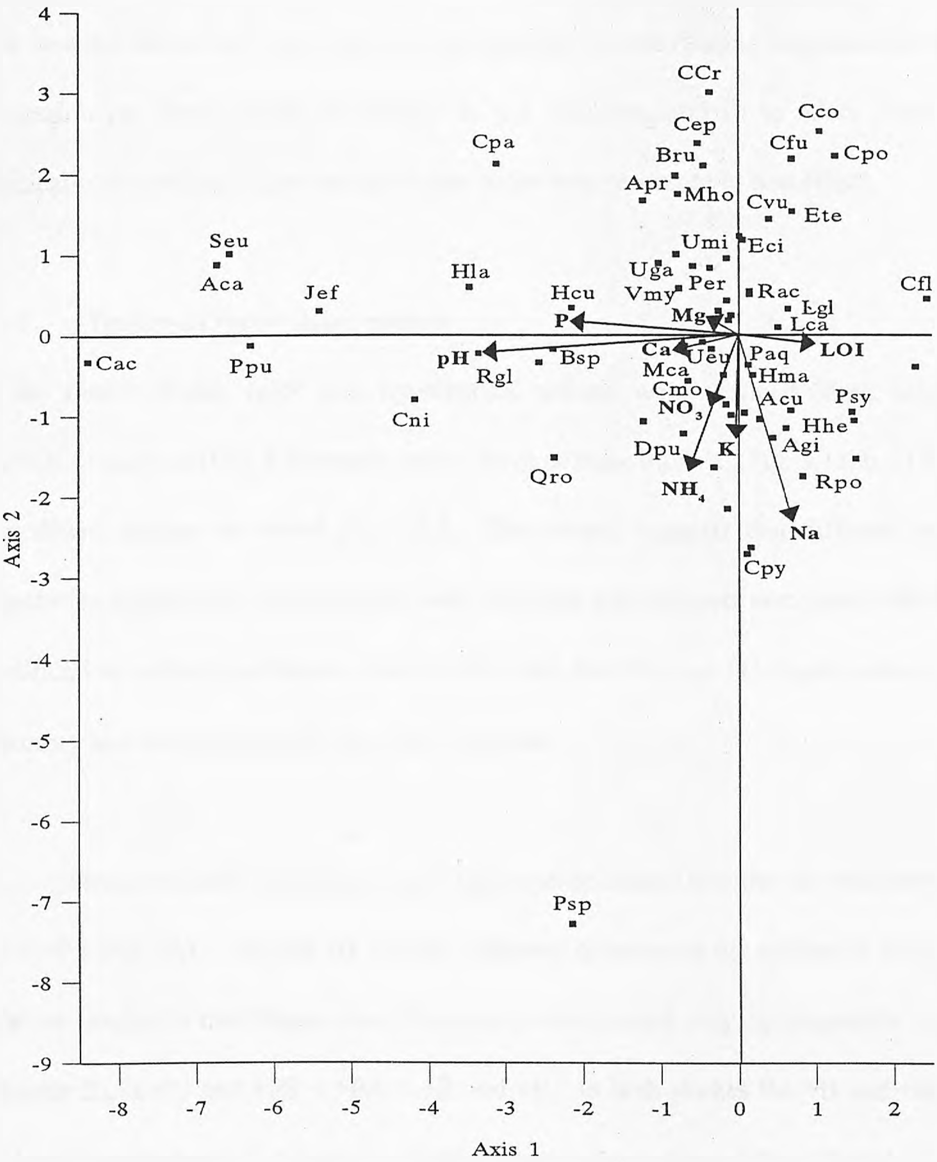


Fig. 3.3. Biplot diagram from the first two axes from the CANOCO analysis; key species are labelled. Soil nutrient vectors are shown by arrows and their length is multiplied by a factor of ten.

Ca = exchangeable calcium; K = exchangeable potassium; LOI = loss-on-ignition; Mg = exchangeable magnesium; Na = exchangeable sodium; NH4 = extractable ammonium-nitrogen; NO3 = extractable nitrite/nitrate-nitrogen; P = extractable phosphorus; pH = pH. Species codes: Aca *Agrostis capillaris*; Acu *Agrostis curtisii*; Agi *Agrostis gigantea*; Apr *Aira praecox*; Bsp *Betula spp;* Cvu *Calluna vulgaris*; Cni *Carex nigra*; Can *Chamerion angustifolium*; Cep *Cuscuta epithymum*; Cmo *Crataegus monogyna*; Dpu *Digitalis purpurea*; Eci *Erica cinerea*; Ete *Erica tetralix*; Hhe *Hedera helix*; Hla *Holcus lanatus*; Jef *Juncus effusus*; Lca *Luzula campestris*; Mca *Molinia caerulea*; Psy *Pinus sylvestris*; Per *Potentilla erecta*; Psp *Prunus spinosa*; Paq *Pteridium aquilinum*; Qro *Quercus robur*; Rpo *Rhododendron ponticum*; Rgl *Rubus glandulosus*; Rac *Rumex acetosella*; Seu *Senecio erucifolius*; Ueu *Ulex europaeus*; Uga *Ulex gallii*; Umi *Ulex minor*; Vmy *Vaccinium myrtillus*; Bru *Brachythecium rutabulum*; Cpa *Campylopus paradoxus*; Cpy *Campylopus pyriformis*; Hcu *Hypnum cupressiforme*; Hma *Hypnum mammillatum*; Lgl *Leucobryum glaucum*; Mho *Mnium hornum*; Ppu *Pseudoscleropodium purum*; Cba *Cladonia cf bacillaris*; Cco *Cladonia cf coccifera;* Ccr *Cladonia cf crispata*; Cfl *Cladonia floerkeana*; Cfu *Cladonia cf furcata*; Cpo *Cladonia portentosa*

3.5 DISCUSSION

This research aimed to i) test a series of hypothetical models relating vegetation change during succession on Dorset heaths to change in soil nutrients; and ii) to relate these results to practical conservation so that managers can target their resources to best effect.

3.5.1 Testing of successional models

At the outset of this work four hypothetical models were outlined (Figs. 3.1a-d). The CANOCO analysis (Fig. 3.2) clearly rejects three of these models, (Fig. 3.1a, b, c) in favour of a modified version of model Fig. 3.1d. This model suggests that different successional trajectories radiate from the heathland with different soil nutrients associated with each. The modification to the hypothetical model is that both the +PA and +U stages occur on a similar trajectory and have similar effects on soil nutrients.

From this study the successional stages can be ranked in order of "proximity to heath", +U < +PS and +PA < +R and +B, (where < denotes distance on the ordination diagram). This order is similar to that found when the stages were ranked only by vegetation composition (Chapter 2), ie +U and +PS < +PA < +R and +B. In both studies the +B and +R stages are furthest from the heath, but there is a slight change in the ranking of the +PS and +U stages.

Successional stages and soil nutrient changes.

That soil nutrient concentrations can increase during succession is now generally accepted, (Miles 1981b; Leushner 1993; Miles 1985). However the fact that different soil nutrients increase with different successional pathways is only poorly understood. The results here suggest that such differences occur on successions on Dorset Heaths.

The heathland samples occur at the low end of all the nutrient vectors, confirming that heathland soils have a low fertility, low pH and low nitrogen values (Gimingham 1992).

The closest samples to the heaths were from the +U stages. Samples from the +U stages are spread out along the two nitrogen vectors and intermix with the +PA samples. The +PA intergrade into the +B, +PA and +R samples. The two nitrogen vectors are the fourth and seventh most important vectors in the ordination and are shown to increase in both the +PA and +U stages. The increase in nitrogen along the +U succession was expected as *Ulex europaeus* fixes atmospheric nitrogen (Skeffington & Bradshaw 1980). The +PA stage also showed increased nitrogen concentrations; presumably this is part of the process of *Pteridium aquilinum* turning a mor soil to a mull soil, (Miles 1985). The cations sodium and potassium also increased in these successions. These were the second and fifth most important vectors in the ordination. Magnesium showed a slight increase along the +U succession but this is the least significant vector in the ordination. The increases in these cations may be due to one or a combination of three reasons. First, the different chemical composition of the plant litter affects the rates of organic matter decomposition and nutrient cycling (Miles 1985). Second, leaching of chemicals from the plants by rain may increase cation concentrations in the soil (Miles 1985). Third, the deep tap roots of *Ulex europaeus* may enable it to draw up nutrients from lower down the soil profile thus enriching the soil higher up the profile. *Ulex europaeus* has an acidifying effect upon the soil (Grime, Hodgson & Hunt 1988; Grubb, Green & Merrifield 1969; Miles 1985), and this stage was found in a similar position along the pH vector to the heath quadrats.

The +PS stage is further along the nitrogen vector than the heath quadrats, but the major difference between the heaths and the +PS stage soils is increased loss-on-ignition, ie. organic matter. This may be due to the large litter fall of *Pinus sylvestris*, which with its slow rate of break down (Carlisle and Brown 1968), may have increased the soil organic matter. This vector was only the sixth longest out of the nine present and is therefore of limited significance.

The +R stage lies along the sodium vector. The reason for this increase in sodium is not known but *Rhododendron ponticum* is thought to have a deleterious effect on the soil, mobilising cations directly or indirectly by the production of polyphenols (Cross 1975). Like the heath samples the +R stage is found at the low end of the pH and phosphorus vectors. This may be expected because *Rhododendron ponticum* is an ericaceous species like *Calluna vulgaris* and grows best on acidic sands (Cross 1975).

The +B stage shows the greatest change in soil nutrients with increasing pH, phosphorus and calcium occurring during the succession, the pH vector being the most important in the analysis. *Betula* spp. have always had a reputation as soil improvers on moorland, and have been shown to increase soil pH in some situations (Miles & Young 1980; Miles 1981a). This also appears to be true for *Betula* spp. succession on these Dorset heathlands. Exchangeable calcium concentrations also increased. This factor is involved in the change of the soil from a mor to a mull humus which occurs during *Betula* spp. succession (Miles 1981a&b). Increased calcium concentrations may be due to a temporarily enhanced rate of inputs from the lower branches shed after canopy closure, deeper *Betula* roots bringing up the calcium from further down the soil profile, or accelerated weathering, (Miles & Young 1980).

Extractable phosphorus concentrations also increased in the +B stage; phosphorus was the third most important vector in the ordination. Soil phosphorus is a key element in heathland dynamics (Chapman, Rose & Clarke 1989) as it is present in low levels and is important in limiting plant growth. Chapman, Rose & Basanta (1989) showed a clear correlation between phosphorus and vegetation change on heathland, especially in relation to the risk of the heathland being invaded by *Betula* spp. Soils with low phosphorus adsorption capacities are likely to remain as open heathland. Those sites with slightly higher phosphorus adsorption capacity are likely to be invaded by *Ulex europaeus* (Chapman, Rose & Basanta 1989). Fig. 3.2 shows the +U stage slightly further along the phosphorus vector than open heath sites indicating that these sites may have slightly greater phosphorus levels. Succession to *Betula* spp. woodland is most likely to occur on those soils with the highest phosphorus adsorption capacity (Chapman, Rose & Basanta 1989).

Whilst it is impossible from a study such as this to prove that the soil nutrient concentrations of the successional stages were similar to those of the heath before succession occurred, and that invasion of the major species has caused these changes, the results do show similar trends for each successional species at different sites. This result implies that these differences are because of the effects of vegetation on the site rather than intrinsic site differences. If this is correct an attempt can be made to answer the three questions posed at the beginning of this work; (1) soil nutrients and pH increase during succession; (2) pH, sodium, phosphorus and ammonium-nitrogen show the greatest increase; (3) different successional pathways alter different nutrients, with *Betula* spp. increasing the phosphorus and pH levels, *Pteridium aquilinum* and *Ulex europaeus* increasing the nitrogen concentrations and *Rhododendron ponticum* increasing the sodium levels.

Species composition and soil nutrient changes.

It has already been established that species are "lost" and "gained" during these heathland successions (Chapter 2). While many of the "losses" may be due to physical factors such as increased shading, many of the "gains" may be because of an increased soil nutrient supply allowing additional invaders to establish on the previously nutrient poor soil. Increases in pH may make available some of the nutrients that were previously deficient (Miles and Young 1980), and there is a strong positive correlation between soil pH and species richness (Grime 1979; Miles 1988). This was especially noticeable in the +B stage in this study where the nutrient changes permit edaphically more demanding species to establish. Fig. 3.3 shows *Betula* spp. isolated from the heathland species and surrounded by a wide spread of species more typical of a field/scrub flora such as *Rubus glandulosus, Holcus lanatus, Carex nigra, Juncus effusus, Chamerion angustifolium* and *Agrostis capillaris*. Whether these additional invaders are only present because of the changes in soil nutrients brought about by the major invasive species (ie *Betula* spp.) or whether these additional invaders themselves have an influence on the soil remains to be tested (Grime 1987; Wedin & Tilman 1990).

3.5.2 Reversal of succession and the restoration of heathland: targeting conservation resources.

The UK is committed to the restoration of lowland heathlands as part of its response to its Biodiversity Action Plans (Department of Environment 1995a,b). However as financial and manpower resources are limited they must be targeted towards those stages that will be most cost-effective to restore to heathland, ie those with the least requirement for soil nutrient and vegetation change. If more difficult successions are tackled then the reversion may not be as successful and the costs will be greater.

As succession proceeds both vegetation and soil nutrients change. When considering the reversal of succession and the restoration of heathland both of these factors should be taken into account. If only the vegetation is considered then the higher nutrient concentrations on a site where the invasive species is controlled will quickly allow the reinvasion of late-successional species to occur. Obviously stages with vegetation and soil nutrient concentrations similar to those of heathland will be the easiest to restore. In terms of both the soil and the vegetation the +PS and +U stages appear closest to the heathland vegetation and the +R and +B the most different, (Chapter 2).

The +U stages are closest to the heathland both in terms of soils and vegetation and may therefore be the easiest to restore to heathland as they have a ready seed source for recolonization. Reversion of the changes in soil nutrient concentrations that have occurred may be more problematic. If the *Ulex europaeus* is cleared and the increased nitrogen concentrations are not reversed heathland managers run the risk of more competitive, higher nutrient demanding, non heathland species invading (Green 1972).

The +PS stage retains some heathland species (Chapter 2). While this stage is not as close to the heath sites as the +U stage the increase in organic matter may be easier to halt or reverse than the reversal of increased nitrogen levels in the +U stage. The removal of the litter layer after clearing the trees may help to halt if not reverse the increase in the organic matter content of the soil. The reversal of +PS stages to heathland may, therefore, prove to be the easiest and most successful.

As sodium is not an essential nutrient like phosphorus, nitrogen or calcium the raised levels in the +R stages are unlikely to cause problems in the reversal of the +R stage to heathland. However, there are three main problems with *Rhododendron ponticum*, first the cut stumps resprout and must be treated with herbicide or removed (Squires 1991); second, *Rhododendron ponticum* forms a large mat of roots and humus on the soil surface, which inhibits germination (Cross 1975); third, *Rhododendron ponticum* leaves may contain toxins which can inhibit other plants from growing (Cross 1975). Hence the removal of the root mat may be needed before reversion to heathland is possible.

Control of *Pteridium aquilinum* is difficult (Marrs 1987; Lowday & Marrs 1992; Marrs, Pakeman & Lowday 1993) because of its extensive rhizome system. This coupled with the difficulty of reversing any increase in nitrogen and cation concentrations, may make the restoration of heathland from the +PA stage a difficult proposition.

The +B stage caused the greatest changes in both the vegetation and the soil nutrients present. This coupled with the problem of *Betula* spp. resprouting from cut stumps and therefore needing some form of herbicide treatment (Marrs 1985a, 1987) makes restoration of heathland from this stage the most difficult to achieve successfully. Some form of litter or nutrient stripping may be required to reduce the nutrient levels before successful restoration is possible.

The management of an area will influence the success of the reversal of succession and the restoration of heathland. Grazing will affect the speed of recolonization of both heathland species and invasive species. Fires, still a common form of heathland management, will influence the vegetation and soil nutrients (Bullock & Webb 1995). Abiotic factors such as differences in climate may influence the success and speed of colonisation of the site by both heathland and invasive species, while geological differences may effect the speed with which any soil nutrient changes may be reversed.

3.6 CONCLUSION

On the Dorset heaths there is a range of pathways along which heathland succession may move. Each successional trajectory is associated with a different major invasive species and increases in different soil nutrients. *Pinus sylvestris* had similar soil nutrient concentrations to those of the heathland. Sodium concentrations increased during the *Rhododendron ponticum* succession. Concentrations of ammonium-nitrogen and nitrate/nitrite-nitrogen increased during the *Pteridium aquilinum* and *Ulex europaeus* succession. The *Betula* spp. had the greatest effect on the soil nutrients with increased pH, extractable phosphorus and exchangeable calcium.

When related to practical conservation these results show that the restoration of heathland on +B sites is likely to be problematic due to the increases in soil nutrient levels. The +U and +PS sites were closest to the heath, the soil nutrient levels of the +U stage are closer to the heath than the those of the +PS, however the changes occurring in the +PS stage may be easier to reverse and hence the restoration of heathland on +PS sites is likely to be most successful

The studies reported in Chapter 2 and here have attempted to separate the vegetation and soil nutrient changes that occur during heathland succession. It has been shown that some successional stages are closer to the heathland than others depending on whether the stages are ordinated by vegetation or both vegetation and soil nutrient content. When management plans are being produced and resources allocated, both of these factors must be combined to target the easiest and most cost-effective stages to restore to heathland.

Chapter 4

A STUDY OF THE RESTORATION OF HEATHLAND ON SUCCESSIONAL SITES IN DORSET, SOUTHERN ENGLAND; CHANGES IN VEGETATION AND SOIL CHEMICAL PROPERTIES.

4.1 INTRODUCTION

Dorset heaths have declined dramatically in area, diversity and structure over the last century (Moore 1962; Webb 1980; Webb & Haskins 1980; Chapman, Clarke & Webb 1989; Webb 1990). One cause of these losses has been an increase in scrub invasion and succession to woodland (Webb 1990), because of a decline in farming and other management practices, in particular fires, which inhibit the succession of heath to woodland.

Management to reverse succession is usually targeted at the major invasive species which on the Dorset heaths include *Betula* spp., *Pinus sylvestris, Pteridium aquilinum* and *Rhododendron ponticum*. However, succession is not just the simple addition of one major species (Mitchell *et al.* 1997; Chapter 2); as the succession occurs the ground flora changes, with *Calluna vulgaris* being shaded out (Hester 1987) and a range of other species invading. In the case of *Betula* spp. a range of more competitive species may also invade (Miles 1981a; Mitchell *et al.* 1997), many of which are more typical of a scrub/woodland field layer (Miles 1981a). The ability of the invaders to recover or persist after management, i.e. the resilience of the successional stage, will influence the success of conservation management to restore heathland.

Heathlands are generally found on nutrient poor and infertile soils (Gimingham 1992). As succession occurs soil chemical properties change (Miles & Young 1980; Miles 1981a&b, 1985; Nielsen, Dalsgaard & Nørnberg 1987a&b; Miles 1988; Leuschner 1993;

Mitchell *et al.* 1997; Chapter 3). The greatest changes occur when *Betula* spp. invades with the soil slowly changing from a podzol (mor) to a brown earth (mull) soil, resulting in increased pH, exchangeable calcium and extractable phosphorus (Miles 1981a, Mitchell *et al.* 1997; Chapter 3). Increased concentrations of other soil nutrients are associated with different successional trajectories; extractable ammonium-nitrogen, nitrate/nitrite-nitrogen and exchangeable potassium increased with *Pteridium aquilinum* and *Ulex europaeus* successions, sodium increased with *Rhododendron ponticum* succession and organic matter increased with *Pinus sylvestris* succession on Dorset Heaths (Mitchell *et al.* 1997; Chapter 3).

If restoration is to be successful then management to restore heathland must reverse both the changes in vegetation and soil nutrients. The soil is particularly problematic; if the soil nutrient changes are not reversed, then enriched soil may either allow the more competitive species to establish to the detriment of slower growing ones or favour the establishment of late successional species (Marrs 1985b; Marrs & Gough 1989; Marrs 1993a).

This paper studies the efficacy of restoring heathland communities on land where succession has occurred and the 'starting' communities were dominated by one of the following species: *Betula* spp, *Pinus sylvestris, Pteridium aquilinum* and *Rhododendron ponticum*. The aims were to answer the following questions:

1) Was management effective in restoring heathland communities and preventing the recovery of the late-successional communities?

2) Was management effective in reducing any soil properties which were known to be greater in the late-successional communities?

3) Was it possible to measure the success of management and the resilience of the managed site?

4) Does the invasive species present before management, type of management applied or the length of time since management affect the success of the restoration?

An attempt was made to answer these questions by contrasting a range of sites where late-successional communities were managed by the RSPB to restore heathland (managed sites), with areas where heathland communities were still present ('target' communities) and where the successional species are still present ('start' communities). An assumption was made that the 'start' community and the managed communities were similar before management was applied. Multivariate analysis was used to test four hypothetical models of ecosystem response to management and a method devised to measure the success of management to restore heathland on successional sites.

4.2 HYPOTHETICAL MODELS

I have already established that the succession associated with each of the four species involved in Dorset Heathland succession moves along a different trajectory from heathland in multivariate space using CANOCO (Canonical Correspondence Analysis - CCA, Ter Braak 1988) and that these are associated with changes in biotic factors (species composition) and abiotic factors (soil nutrients) (Mitchell *et al* 1997; Chapter 3). If we consider just one of these successions there are four hypothetical models which can be used to describe the relationship between 'start', managed and 'target' sites during restoration (Fig. 4.1).

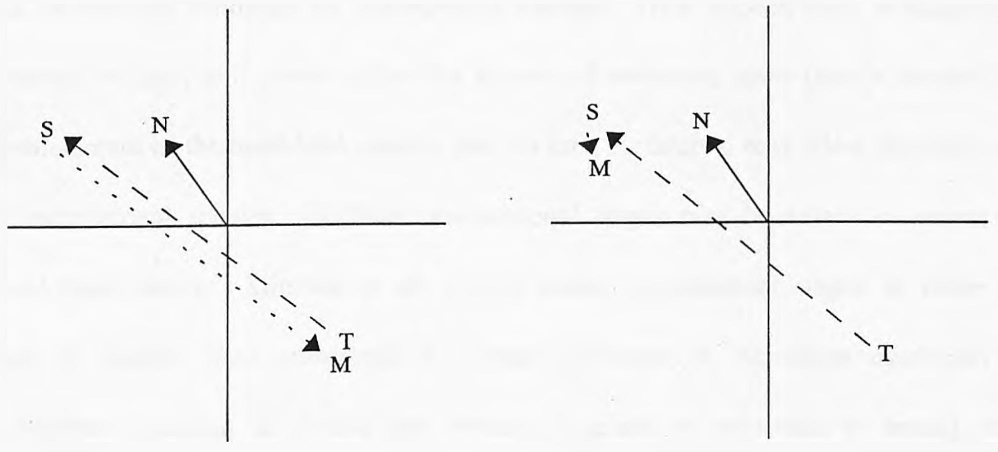
i) Good restoration (Fig. 4.1.a), where managed sites are indistinguishable from the 'target'. This is the ideal scenario with both vegetation and soil reverting back to those typical of heathland.

ii) Very poor restoration (Fig. 4.1b), where managed sites remain close to the 'start' site in terms of the soil and the vegetation.

iii) Partial restoration (Fig. 4.1c), where managed sites start to move towards the 'target' but have not yet reached the 'target'; given time the site may reach the 'target' or start to move back towards the 'start' if there is high resilience.

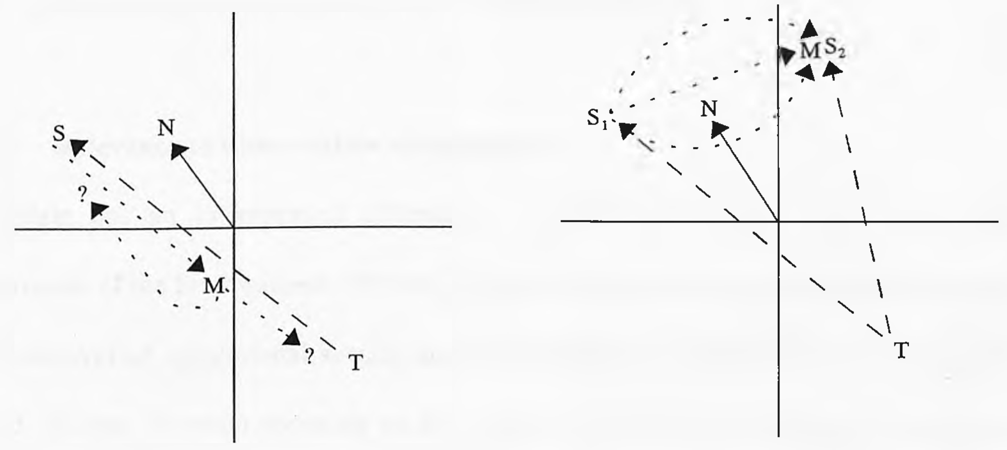
iv) Move to a different 'target' (Fig 4.1d), where the managed site moves to a different successional stage rather than towards the 'target' or returning to its 'start'. Different patterns are clearly possible for this model.

In this paper we aimed to test these models and then to explore the relationships between the 'start', managed and 'target' sites so that we can use the distances between sites as a measure of both management success and ecosystem resistance.



a) Good reversion, the managed site is indistinguishable from the heath.

b) Very poor reversion, the managed site remains close to the successional site.



c) Partial restoration, managed sites start to move back towards the heath, given time the site may either continue to move towards the target or return towards the starting point.

d) Management causes the site to move towards a different successional stage; different routes are possible.

Fig. 4.1. Hypothetical ordination diagrams illustrating results which might be obtained from CCA analysis of vegetation and soil data taken from samples in open heath, successional and managed sites. T = Target (heathland), S = Start (successional stage), M = managed site, ——▶ N = increasing soil nutrients, ------▶ = Successional pathway from heath, - - - -▶= Trajectory of managed site.

4.2.1 The effect of age, stage and management on the success of reversion

Various factors will influence the management success. Time elapsed since management implementation (age) will clearly affect the success of reversion; some time is needed for the establishment of the heathland species, but too long an interval may allow the recovery of the successional species. Different successional stages may be easier to restore to heathland than others. Mitchell *et al.* (1997) ranked successional stages in order of closeness to heath; *Ulex europaeus* < *Pinus sylvestris* & *Pteridium aquilinum* < *Rhododendron ponticum* & *Betula* spp. (where < relates to closeness to heath), and suggested that this might indicate the ease with which stages may be restored. In addition different management treatments will have differing degrees of intensity of effect on restoration and in Dorset a range of practices have been implemented. It was hoped to be able to gain some information on all of these factors in this study.

4.2.2 Relevance to conservation management

As Britain has an international obligation to restore and mange its lowland heaths (Department of the Environment 1995a,b), conservation bodies are targeting their resources at the removal of successional species and the restoration of heathland. As resources are limited, the type of model operating on the managed sites and the influence of management on the success of restoration will be relevant to conservation bodies. A knowledge of the processes operating will allow efficient targeting of resources on sites with a high probability of success.

4.3 MATERIALS AND METHODS

4.3.1 Sampling strategy

In 1996 a structured sampling strategy was set up in the Poole Basin area of Dorset; nine heathland areas within the syncline of the Poole Basin were chosen (Table 4.1.). The areas were all in close proximity to each other (within a 20 km radius) and should experience similar climate, they all lie on a similar parent material, the Bagshot beds.

Table 4.1. The stages present at each area and the number of sites within each stage. National Grid References for the areas are also shown.

Area	Grid Ref.	Heath	+B	mB	+PS	mPS	+PA	mPA	+R	mR
Arne	SY973882	1			1	5	1	1	1	1
Avon Heath Country Park (AHCP)	SU128035	1	1	1	1	2				
Blackhill	SY840940	1			1	1	1	2	1	1
Cranborne Common	SU104112	1					1	1		
East Holton Heath	SY958917	1			1	2				
Grange Heath	SY909835	1			1	1				
Merritown Heath	SZ113991	1	1	1	1	1				
Sopley & Ramsdown	SZ133974	1	1	1	1	1			1	2
Trigon Heath	SY884908	1	1	1	1	1	1	1	1	1
Total number of sites		9	4	4	8	14	4	5	4	5
Total number of samples		90	40	40	80	140	40	50	40	50

Most of these areas were included in the earlier 1995 study of heaths and their successions (Mitchell *et al.* 1997; Chapters 2 & 3), and the 1996 study included a subset of heath and successional stages ('start' and 'target') which could be used to validate the conclusions from their study.

Within each area there were examples of heathland, successional and managed sites (Table 4.1). The successional and heath sites provided reference points denoting the 'start' and desired 'target' for the trajectory of the managed site. The heathland sites were open heath dominated by dwarf ericaceous shrubs. The successional sites were heath until 20-50 years ago when they were invaded by one of four major successional species. The successional species had been removed on the managed sites by RSPB as part of management to restore heathland. The successional, managed and heath sites were in close proximity so that comparisons would be as valid as possible.

Four successional stages were sampled:

+B - major invader *Betula* spp.

+PS - major invader is *Pinus sylvestris*

+PA - major invader is *Pteridium aquilinum*

+R - major invader is *Rhododendron ponticum.*

For each of these stages there were corresponding managed sites where the succession had been managed in an attempt to restore heathland, namely: mB = managed +B; mPS = managed +PS; mPA = managed +PA; and mR = managed +R.

The managed sites

For each managed site three variables were known: the stage (the major invader that was present before management occurred), the age (time elapsed (years) since management) and the type of management applied (Table 4.2). Comprehensive management information was supplied by the RSPB.

At the mB stage the *Betula* spp. was cut and removed and then managed in two ways. At three sites, Merritown, Sopley & Ramsdown and Trigon the cut stumps were treated with herbicide to stop *Betula* spp. regrowth (Marrs 1985a). At a fourth site (AHCP) the cut stumps were not treated but the site was fenced and grazed during the summer for three years, before grazing was discontinued. At the mPS sites two treatments were applied after felling and tree removal: litter-stripping and no litter-stripping. At the litter-stripped sites the litter and decaying pine needles were removed, although the depth of litter-stripping varied. At Arne, for example, the litter was removed to expose the mineral soil,

Table 4.2. Managed sites details, showing stages present at each area, the date of management and hence the age of the site at the time of the survey and the type of management carried out

Stage	Area	Date of Management	Age (years)	Vegetation before management	Details of management
mB	AHCP	Feb- Apr 91	5	Scrub *Betula* spp. not managed since fire in 1979.	Clear felling of trees, wood removed, brash chipped and removed, the stumps were not treated. The site was fenced and then grazed during the summer for 3 years.
	Merritown	Nov 91	5	c45+ *Betula* spp. trees in the 2 ha area managed.	Trees felled, brash chipped and stumps treated with Garlon 4 in diesel.
	Sopley & Ramsdown	Jan - Feb 93	3	Dense *Betula* spp.	Trees were felled and brash chipped. The cut stumps were treated with a 5% mixture of Garlon 4 in diesel.
	Trigon	Winter 92	4	Dense *Betula* spp.	The trees were clear felled and the stumps treated with Garlon 4 in diesel.
mPS	Arne(a)	Winter 90/91	5	40 year old plus *Pinus sylvestris*, 100% cover.	Trees clear felled, litter removed down to mineral soil using a brush and vacuum and *Pteridium aquilinum* sprayed out.
	Arne(b)	Winter 90/91	5	40 year old plus *Pinus sylvestris*, 100% cover.	As above but only partially litter stripped, a covering of 2-3 cm of litter was left on the surface.
	Arne(c)	Winter 90/91	5	Dense *Pinus sylvestris*.	Trees clear felled but not litter stripped. *Pteridium aquilinum* was sprayed.
	Arne(d)	Winter 90/91 & early spring 96	0.5	Dense *Pinus sylvestris*.	As above but then litter stripped using a small digger in March 96.
	Arne(e)	Early 80's	c13	*Pinus sylvestris* trees 20-25 years old with a few remaining *Calluna vulgaris* plants underneath.	Trees clear felled, litter not removed.
	Avon Heath Country Park(a)	Winter 94	2	Dense *Pinus sylvestris*.	Trees felled, brash chipped and removed, not litter stripped.
	Avon Heath Country Park(b)	March 90	6	About 120 *Pinus sylvestris* trees mostly 15-30 cm in diameter with c 15 to 20 trees 60+ cm in diameter.	Trees felled, brash chipped and removed, not litter stripped.
	Blackhill	92	4	Big dense *Pinus sylvestris* trees.	Trees felled, not litter stripped.
	East Holton(a)	95	1	Dense *Pinus sylvestris*.	Trees felled in 94 and then litter stripped in 95, 2-3 cm of litter was left on top of the mineral soil.
	East Holton(b)	Winter 92/93	3	Dense 60 year old *Pinus sylvestris*.	Trees were clear felled, no litter stripping.
	Grange	Winter 95/96	0.5	Dense *Pinus sylvestris* scrub c12 to 20 years old.	Trees were clear felled, site had not yet been litter stripped.
	Merritown	93	3	*Pinus sylvestris* c 30 years old.	Trees were clear felled, site was not litter stripped.
	Sopley & Ramsdown	Feb 93	3	Mature *Pinus* sylvestris 100% cover.	Trees were clear felled and the site was litter stripped leaving a 2-3 cm layer of litter on top of the mineral soil.
	Trigon	Dec 89	7	Mature *Pinus sylvestris*.	Trees were clear felled, and the litter was not stripped.

Table 4.2 cont.

Stage	Area	Date of Management	Age (years)	Vegetation before management	Details of management
mPA	Arne	84	12	Dense *Pteridium aquilinum* .	Bulldozed fronds, rhizomes and litter into a pile to one side.
	Blackhill(a)	Spring 92 & Aug 93	3	Dense *Pteridium aquilinum*.	Mowed 92 and sprayed August 93 with Asulox using a Micron ULVA sprayer.
	Blackhill(b)	91/92	4	Dense *Pteridium aquilinum*.	Sprayed with Asulox using a Micron ULVA sprayer.
	Cranborne	May-Aug 93 & Summer 94	2	Dense *Pteridium aquilinum* 100% cover with 5% of the area also having *Molinia caerulea* present in large tussocks.	Mowed in 93 and then sprayed with Asulox in 94.
	Trigon	Aug 90	6	Dense *Pteridium aquilinum* 90 - 100% cover.	Sprayed with Asulox using a Micron ULVA.
mR	Arne	Early spring 96	0.5	Dense mature *Rhododendron ponticum*.	*Rhododendron ponticum* cut and stumps and rootmat bulldozed out of the way.
	Blackhill	Jan - Mar 92	4	Very mature *Rhododendron ponticum*.	Cut to ground level using chain saws and stumps coated in a 12% solution of Garlon 4 in diesel.
	Sopley & Ramsdown(a)	Nov 93	3	Dense mature *Rhododendron ponticum*.	The *Rhododendron ponticum* was cut using hand tools, the brash was burnt and the stumps were treated a 8% solution of Garlon 4 in diesel.
	Sopley & Ramsdown(b)	Jan 90	6	Dense mature *Rhododendron ponticum*.	The *Rhododendron ponticum* was cut and the stumps treated with a 8% solution of Garlon 4 in diesel.
	Trigon	Aug 93	3	Mature *Rhododendron ponticum* 90% cover	The *Rhododendron ponticum* was cut with chain saws and the stumps were treated with a 12% solution of Garlon 4 in diesel.

but at other sites the stripping was not as thorough and 1-2 cm of litter were left on the surface. At the mPA sites three types of management were applied; (1) mown and sprayed, (2) sprayed and (3) bulldozed. Blackhill(a) and Cranborne were mown once and then sprayed with Asulox the following year, Blackhill(b) and Trigon were sprayed with Asulox once and at Arne the *Pteridium aquilinum* was bulldozed off site. At the mR sites two types of treatment were applied after felling and removal: herbicide treatment and bulldozing. At Blackhill, Trigon and Sopley & Ramsdown(a&b) the *Rhododendron* stumps were treated with herbicide, at Arne the root mats and stumps were bulldozed off site.

4.3.2 Vegetation survey

At each site ('start', managed and 'target') ten $1m^2$ quadrats were placed randomly and the cover (%) of all plant species, litter and bare ground estimated. The basal area of trees was estimated in the +B and +PS stages using a relascope (Manx Marker relascope x2, Stanton Hope Ltd, Essex, UK). A total of 570 quadrats was recorded, 90 from the open heath sites, 280 from managed sites, and 200 from successional sites (Table 4.1). Nomenclature follows Stace (1991) for higher plants, Duncan (1970) for lichens and Smith (1978) for mosses. From the centre of each quadrat a soil sample was taken to a depth of 21 cm using a Bi-partite Edelman auger (Eijkelkamp, Agrisearch Equipment, Giesbeck, The Netherlands). Soil samples were stored in a cold room (4 ^{o}C) until analysis.

4.3.3 Soil analysis

Fresh soil (5g) from each sample was shaken with 30 ml 1M potassium chloride for 1 hour for extraction of available nitrogen. The extract was analysed for ammonium-nitrogen and nitrate/nitrite-nitrogen using colorimetric methods (Allen *et al.* 1974).

The remainder of the soil samples were air dried and sieved through a 2 mm sieve. A 2.5g sample was extracted in 2.5% v/v acetic acid. The extractable phosphorus in this extract was measured using the stannous chloride method (Allen 1989). The same extract was used to measure exchangeable cations (calcium, magnesium, sodium and potassium). Ca and Mg were analysed by absorption spectrometry and Na and K by emission spectrometry (Unicam 1991). Organic matter present was estimated by loss-on-ignition (Allen 1989) and soil pH was recorded in a 1:2.5 slurry of soil and deionised water (Allen *et al.* 1974)

4.3.4 Data analysis

The sites were classified by TABLEFIT (Hill 1996) into NVC types (Rodwell 1991) using the cover and frequency of the species present.

Vegetation and soil data were analysed by Canonical Correspondence Analysis (CANOCO, Ter Braak 1988). CCA is a direct ordination technique in which the species/samples data in the ordination are constrained to optimise their linear relationship to the environmental variables, soil data in this case. The samples may be plotted in an ordination diagram with the environmental variables shown by vectors (arrows) with their lengths proportional to their importance and their directions showing their correlation with the axes. In this paper the vectors are displayed at x5 their actual length as the scores for the environmental variables and species/samples are of a different order of magnitude (Ter Braak 1988). The statistical validity of the ordination was tested using an unrestricted Monte Carlo permutation test (Ter Braak 1990). Here CANOCO was run without detrending (Palmer 1993) and the vegetation data (% cover) was transformed by a ln(ay+c) transformation, where a and c = 1. The option to downweight rare species was not used because here it would reduce the influence of species which occurred frequently but at low cover, mainly bryophytes. Instead species occurring in ≤ 5 quadrats (less than one percent of the samples) were removed from the data set. This removed 52 species, of which 25 only occurred once, and it reduced the inertia of the data set to levels similar to that when downweighting was used. The percentage cover of bare ground and litter were also included in the analysis because both were important components at some sites. Two different CANOCO analyses were done.

CCA analysis I

In the first CANOCO analysis all the samples (heath, managed and successional) were included as active samples to allow new species colonising managed sites, that were not present on the heath or successional sites to exert an influence on the direction of change; this is particularly important for the detection of model d.

CCA analysis II

In analysis II the managed sites were treated as passive samples. The heath and successional sites were used to produce the model and the positioning of the managed sites within this model calculated. This model fitted the managed sites on to the trajectories between the heath and successional sites without the managed sites influencing the trajectory. The distances of managed sites from the 'start' and 'target' points could then be calculated and used to measure the success of the management and the resilience of the sites. It is not possible to use model I for this as the objects being measured (the managed sites) have influenced the model.

The results from the CCA (analysis II) were used to calculate centroids for each site. As the CCA model has four axes the distances between these centroids was calculated in four dimensions using Euclidean distance (Manly 1986); this uses Pythagoras' theorem in four dimensions to calculate the distance between two points. As there are nine environmental variables and therefore nine axes, the distances could theoretically be calculated in nine dimensions. However, as over 80% of the explained species-environment relationship was explained in the first four axes, the calculations were confined to four dimensions. For any trajectory, the distance between the 'target' and managed site provided a measure of the success of the management to restore heathland and the distance between the managed and 'start' site provided a measure of the resilience of the managed site.

A measure of the linearity of the trajectory between 'start', managed and 'target' sites was also made in four dimensions. For a straight line A should equal zero, where $A = (T+S) - D$, and T is the distance from managed site to the 'target', S is the distance from the managed site to the 'start' and D is the distance from the 'start' to the 'target'. If the trajectory is a straight line then the managed site is moving towards the heath 'target', if A is large the trajectory is not a straight line and the managed site is moving in an different direction, towards a different community.

4.4 RESULTS

4.4.1 Description of vegetation

The vegetation of the heath and successional sites was similar to those described for the sites in Chapter 2 and Mitchell *et al.* (1997); here only brief descriptions of the heath and successional sites are given followed by more detailed descriptions of the managed sites. The heath sites (Table 4.3) were all dominated by *Calluna vulgaris*, usually at greater than 50% cover, with *Erica cinerea* and *Erica tetralix* often present. *Molinia caerulea* was the only grass recorded. The mosses *Dicranum scoparium, Hypnum jutlandicum, Hypnum cupressiforme* and *Pleurozium schreberi* were all common (>5% cover). Nine lichen species were recorded, *Cladonia portentosa* was the only one which occurred at greater than 5% cover.

On the +B sites the dominant species were *Betula* spp., *Gaultheria shallon, Hedera helix, Molinia caerulea, Poa annua, Pteridium aquilinum* and *Hypnum jutlandicum* (Table 4.4). A range of other invasive species were also present at lower cover, the few heathland species present were mainly mosses. On the mB sites *Betula* spp. were present with cover ranging from 39% (AHCP) to 1% (Merritown) (Table 4.4). Other successional species present at high cover included *Pteridium aquilinum* and *Rubus glandulosus*. *Calluna vulgaris* was present on all sites with 27% cover at Merritown and less than 15% cover at the other sites. The mosses *Campylopus introflexus, Hypnum jutlandicum, Polytrichum juniperinum* and *Pseudoschleropodium purum* were all common. Other species recorded included *Cladonia* lichens and species not recorded in either the successional or heath stage: *Achillea millefolium, Agrostis capillaris, Crataegus monogyna, Hypochaeris radicata* and *Leontodon saxatilis*.

Table 4.3. Mean % cover (n = 10) of species found in heathland sites in Dorset; only species with an average cover of 5% or more on any of the sites are shown in any detail.

Species	Arne^{1}	Avon^{2} Heath Country Park	Blackhill^{3}	Cranborne^{4} Common	East^{5} Holton Heath	Grange^{6} Heath	Merri-^{7} town heath	Sopley^{8} & Ramsdown	Trigon^{9}
Calluna vulgaris	51.8	57.8	62.8	53.0	37.4	53.3	95.2	55.0	79.3
Erica cinerea	9.8	13.8	31.3	0.5	0.0	<0.1	2.4	0.5	6.4
Erica tetralix	23.1	0.0	4.2	32.2	24.0	27.0	0.0	11.0	2.4
Molinia caerulea	0.0	0.0	0.0	3.3	11.3	8.1	0.0	1.1	<0.1
Ulex minor	0.3	9.3	1.5	1.8	0.0	0.0	0.0	0.0	1.1
Dicranum scoparium	0.2	4.3	<0.1	<0.1	0.3	0.0	2.8	0.0	0.0
Hypnum cupressiforme	0.0	10.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hypnum jutlandicum	12.6	0.0	7.1	1.2	14.0	0.0	14.4	2.2	19.9
Pleurozium schreberi	0.0	30.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cladonia portentosa	18.1	<0.1	0.0	20.1	15.7	2.2	6.2	76.2	38.9
Litter	10.1	42.6	28.0	11.0	5.2	3.3	31.3	7.8	31.2
Bare Ground	0.6	1.1	0.0	0.0	1.9	5.1	0.0	0.0	0.0

The following species were also recorded: *Betula* spp. ^{5} *Carex panicea* ^{6} *Cuscuta epithymum* ^{3} *Juncus articulatus* ^{5} *Pinus sylvestris* $^{2\ 5}$ *Quercus robur* ^{5} *Rumex acetosella* ^{2} *Brachythecium rutabulum* ^{2} *Campylopus introflexus* $^{1\ 5\ 7\ 8\ 9}$ *Campylopus paradoxus* ^{6} *Campylopus pyriformis* ^{5} *Leucobryum glaucum* ^{5} *Sphagnum palustre* ^{6} *Cladonia cervicornis* ^{6} *Cladonia chlorophaea* $^{2\ 8}$ *Cladonia coniocraea* ^{1} *Cladonia gracilis* ^{6} *Cladonia pyxidata* $^{1\ 2\ 5}$ *Cladonia uncialis* ^{5} *Hypogymnia physodes* $^{1\ 2\ 7}$ The superscripts relate to the areas shown in the table heading above, and indicate the areas at which the species occurred.

Table 4.4. Mean % cover (n = 10) of species found in +B and mB sites in Dorset; only species with an average cover of 5% or more on any of the sites are shown in any detail.

Species	Avon Heath Country Park		Merritown Heath		Sopley & Ramsdown		Trigon	
	+B^{1}	mB^{2}	+B^{3}	mB^{4}	+B^{5}	mB^{6}	+B^{7}	mB^{8}
Agrostis capillaris	0.0	0.0	0.0	0.0	0.0	17.1	0.0	0.0
Agrostis curtisii	0.0	0.1	0.0	0.0	<0.1	0.0	0.1	13.7
Betula spp	3.6	38.9	4.4	1.0	3.2	2.4	2.6	5.6
Betula relascope (m^2 ha^{-1})	12.6	0.0	25.2	0.0	17.6	0.0	19.6	0.0
Calluna vulgaris	0.0	13.9	0.0	26.8	0.0	6.6	0.0	1.6
Cirsium palustre	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.6
Erica cinerea	0.0	7.7	<0.1	4.6	0.0	2.7	0.0	0.5
Gaultheria shallon	14.3	28.4	0.0	0.0	0.0	0.0	0.0	0.0
Hedera helix	0.0	0.0	0.0	0.0	6.5	0.0	4.0	2.1
Molinia caerulea	0.0	0.2	0.0	0.0	0.2	0.0	11.2	26.0
Poa annua	0.0	0.0	0.0	0.0	15.0	0.0	10.7	0.0
Pteridium aquilinum	21.3	0.1	17.1	2.3	12.9	3.3	13.2	7.0
Rubus glandulosus	3.6	0.8	0.0	0.0	3.6	7.6	1.9	3.3
Rumex acetosella	0.0	0.0	0.0	0.5	0.0	10.6	0.0	1.5
Campylopus introflexus	0.1	0.9	0.6	39.0	0.0	14.7	0.4	14.0
Hypnum jutlandicum	0.0	0.0	0.0	6.5	15.6	0.0	0.7	2.0
Polytrichum jutlandicum	0.3	0.3	0.1	10.9	0.1	1.7	0.0	0.3
Pseudoscleropodium purum	3.1	0.2	0.0	0.0	0.0	13.1	0.0	0.0
Litter	91.0	51.9	94.9	10.3	56.6	17.8	79.0	12.4

The following species were also recorded: *Achillea millefolium* ^{6} *Agrostis vinealis* ^{5} *Aria praecox* ^{468} *Brachypodium sylvaticum* ^{8} *Carex nigra* ^{5} *Carex pilulifera* ^{1} *Carex viridula* spp. *oedocarpa* ^{8} *Centaurium erythraea* ^{6} *Cerastium fontanum* ^{568} *Crataegus monogyna* ^{8} *Cuscuta epithymum* ^{6} *Digitalis purpurea* ^{5} *Erica tetralix* ^{28} *Frangula alnus* ^{78} *Galium aparine* ^{8} *Glechoma hederacea* ^{5} *Holcus lanatus* ^{568} *Hypochaeris radicata* ^{8} *Ilex aquifolium* ^{28} *Juncus conglomeratus* ^{8} *Leontodon saxatilis* ^{6} *Lonicera periclymenum* ^{3578} *Lotus penduncculatus* ^{8} *Luzula campestris* ^{568} *Pinus pinaster* ^{8} *Pinus sylvestris* ^{128} *Potentilla erecta* ^{78} *Quercus robur* ^{8} *Rosa* spp. ^{568} *Sagina procumbens* ^{6} *Salix caprea* ^{78} *Senecio erucifolius* ^{568} *Sorbus aucuparia* ^{5} *Taraxacum* spp. ^{28} *Teucrium scorodonia* ^{12} *Ulex europaeus* ^{368} *Ulex minor* ^{248} *Urtica dioica* ^{1} *Viola reichenbachiana* ^{78} *Brachythecium rutabulum* ^{127} *Campylopus pyriformis* ^{7} *Dicranum scoparium* ^{12478} *Hypnum cupressiforme var. resupinatum* ^{3} *Mnium hornum* ^{7} *Cladonia chlorophaea* ^{2458} *Cladonia coniocraea* ^{2} *Hypogymnia physodes* ^{3} *Cladonia portentosa* ^{48} *Cladonia pyxidata* ^{6} Bare ground ^{124568789}. The superscripts relate to the areas shown in the table heading above, and indicate the areas at which the species occurred.

Table 4.5. Mean % cover (n = 10) of species found in +PS and mPS sites in Dorset; only species with an average cover of 5% or more on any of the sites are shown in any detail.

Species	Arne						Avon Heath Country Park		
	+PS[1]	mPS(a)[2]	mPS(b)[3]	mPS(c)[4]	mPS(d)[5]	mPS(e)[6]	+PS[7]	mPS(a)[8]	mPS(b)[9]
Betula spp.	0.1	1.6	1.9	2.4	0.2	0.1	<0.1	0.1	<0.1
Calluna vulgaris	<0.1	44.0	7.0	11.0	2.3	28.8	0.2	1.9	0.3
Erica cinerea	<0.1	17.5	2.7	1.5	0.3	8.9	0.0	0.4	1.5
Molinia caerulea	0.0	0.0	0.0	0.3	0.0	<0.1	0.1	0.0	0.0
Pinus sylvestris	1.4	0.1	0.4	0.1	<0.1	0.1	4.8	0.1	0.2
Pinus sylvestris relascope (m^2 ha^{-1})	41.8	0.0	0.0	0.0	0.0	0.0	42.2	0.0	0.0
Pteridium aquilinum	2.4	0.3	4.1	9.4	14.1	0.0	29.0	0.0	9.0
Brachythecium rutabulum	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Campylopus introflexus	0.0	0.0	25.6	20.2	0.1	36.7	0.0	<0.1	0.0
Dicranum scoparium	0.0	1.0	0.1	0.4	0.1	0.4	<0.1	0.4	<0.1
Hypnum jutlandicum	0.4	0.6	4.7	0.3	<0.1	0.7	13.5	0.3	1.7
Pleurozium schreberi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polytrichum juniperinum	0.0	18.0	24.5	0.3	<0.1	0.2	0.0	<0.1	0.0
Litter	98.2	8.0	36.5	59.6	25.7	23.7	82.5	96.7	98.1
Bare Ground	0.2	7.3	0.3	0.8	71.6	1.1	0.0	0.0	0.0

Table 4.5 cont.

Species	Blackhill		East Holton			Grange		Merritown	
	+PS[10]	mPS[11]	+PS[12]	mPS(a)[13]	mPS(b)[14]	+PS[15]	mPS[16]	+PS[17]	mPS[18]
Betula spp.	<0.1	0.5	0.6	0.1	0.4	0.0	<0.1	0.0	0.4
Calluna vulgaris	0.0	3.6	0.2	0.6	5.1	0.0	<0.1	0.2	0.7
Erica cinerea	0.0	1.7	0.0	<0.1	3.5	0.1	0.3	0.0	0.0
Molinia caerulea	0.0	<0.1	35.1	0.1	37.1	2.6	0.0	0.0	0.6
Pinus sylvestris	3.6	<0.1	2.2	<0.1	0.2	0.7	<0.1	1.1	<0.1
Pinus sylvestris relascope (m^2 ha^{-1})	44.2	0.0	27.4	0.0	0.0	32.2	0.0	17.6	0.0
Pteridium aquilinum	37.0	43.9	0.0	10.0	0.0	18.0	20.1	2.5	2.3
Brachythecium rutabulum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Campylopus introflexus	0.0	0.5	0.0	<0.1	0.1	0.3	0.1	0.0	0.1
Dicranum scoparium	0.0	0.6	0.9	0.0	0.0	0.0	0.3	6.9	<0.1
Hypnum jutlandicum	0.0	8.6	0.0	0.0	4.5	0.0	0.0	0.0	0.1
Pleurozium schreberi	0.0	0.0	20.2	0.0	0.0	0.0	2.9	4.9	0.0
Polytrichum juniperinum	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Litter	96.4	86.5	55.6	98.6	52.3	96.2	96.8	87.0	98.3
Bare Ground	0.0	0.0	0.0	1.1	0.0	0.0	0.3	<0.1	0.0

Table 4.5 cont.

Species	Sopley & Ramsdown		Trigon	
	+PS^{19}	mPS^{20}	+PS^{21}	mPS^{22}
Betula spp.	0.0	33.5	0.0	0.0
Calluna vulgaris	0.3	11.9	<0.1	20.2
Erica cinerea	0.2	0.1	4.1	8.4
Molinia caerulea	6.2	6.1	0.0	0.0
Pinus sylvestris	1.4	<0.1	1.0	<0.1
Pinus sylvestris relascope (m^2 ha^{-1})	38.2	0.0	27.8	0.0
Pteridium aquilinum	6.8	4.3	11.5	0.0
Brachythecium rutabulum	0.1	0.0	0.0	0.0
Campylopus introflexus	0.1	23.8	0.0	10.8
Dicranum scoparium	0.1	0.6	<0.1	11.4
Hypnum jutlandicum	0.0	13.4	7.4	17.3
Pleurozium schreberi	0.0	0.0	0.0	0.0
Polytrichum juniperinum	0.0	0.0	0.0	8.9
Litter	88.7	33.2	92.4	29.6
Bare Ground	0.0	0.0	0.0	0.0

The following species were also recorded: *Agrostis curtisii* $^{6\ 13\ 15\ 22}$ *Agrostis gigantea* ^{22} *Aira praecox* $^{4\ 18\ 22}$ *Carex pilulifera* ^{11} *Carex nigra* $^{3\ 4}$ *Cerastium fontanum* $^{1\ 14\ 22}$ *Chamerion angustifolium* $^{8\ 14}$ *Deschampsia flexuosa* ^{18} *Digitalis purpurea* $^{1\ 4}$ *Erica tetralix* $^{12\ 13\ 20\ 22}$ *Hedera helix* $^{1\ 11}$ *Holcus lanatus* ^{22} *Hypochaeris radicata* ^{9} *Ilex aquifolium* $^{10\ 11\ 12\ 15}$ *Juncus effusus* ^{20} *Lonicera periclymenum* $^{10\ 11}$ *Luzula campestris* $^{3\ 4\ 16}$ *Moehringia trinervia* ^{1} *Pinus pinaster* relascope ^{21} *Poa annua* $^{1\ 3}$ *Quercus robur* $^{1\ 4\ 9\ 14\ 21}$ *Rhododendron ponticum* ^{20} *Rubus glandulosus* $^{1\ 3\ 5\ 8\ 10\ 16\ 22}$ *Rumex acetosella* $^{2\ 3\ 4\ 6\ 18\ 22}$ *Senecio vulgaris* $^{3\ 4\ 6}$ *Sorbus aucuparia* $^{1\ 4}$ *Tripleurosperum inodorum* ^{22} *Ulex europaeus* $^{1\ 4\ 5\ 6\ 9\ 11\ 13\ 14\ 15\ 16\ 18\ 20\ 22}$ *Ulex minor* $^{2\ 3\ 4}$ *Urtica dioica* ^{17} *Campylopus pyriformis* $^{1\ 3\ 9\ 12\ 13\ 14\ 18}$ *Eurhynchium praelongum* ^{10} *Leucobryum glaucum* $^{2\ 3\ 7\ 12\ 14\ 16}$ *Pseudoscleropodium purum* $^{12\ 15\ 16\ 19}$ *Cladonia cervicornis* $^{1\ 6}$ *Cladonia chlorophaea* $^{2\ 4\ 22}$ *Cladonia coniocraea* $^{2\ 4\ 5\ 6\ 22}$ *Cladonia floerkeana* $^{6\ 22}$ *Cladonia portentosa* $^{2\ 4\ 6\ 14\ 16\ 17}$ *Cladonia pyxidata* $^{2\ 3\ 6\ 14}$ *Cladonia squamosa* ^{4} *Hypogymnia physodes* $^{1\ 6\ 7\ 12}$.

The superscripts relate to the areas shown in the table heading above, and indicate the areas at which the species occurred.

Table 4.6. Mean % cover (n = 10) of species found in +PA and mPA sites in Dorset; only species with an average cover of 5% or more on any of the sites are shown in any detail.

Species	Arne		Blackhill			Cranborne		Trigon	
	+PA^{1}	mPA^{2}	+PA^{3}	mPA(a)^{4}	mPA(b)^{5}	+PA^{6}	mPA^{7}	+PA^{8}	mPA^{9}
Aira praecox	7.7	0.0	0.0	0.2	1.6	0.0	0.0	0.0	0.0
Agrostis curtisii	0.1	6.9	0.0	5.8	5.3	0.0	0.0	0.8	2.9
Calluna vulgaris	5.8	83.9	1.8	0.8	3.3	0.0	<0.1	0.3	16.4
Molinia caerulea	0.3	0.2	2.1	0.0	0.0	7.0	49.0	0.0	2.5
Pteridium aquilinum	84.9	2.7	99.7	60.1	14.1	95.5	1.8	97.3	88.0
Rubus glandulosus	0.1	0.0	0.0	6.1	0.0	0.0	0.0	2.3	0.4
Rumex acetosella	0.2	0.0	0.0	7.7	6.3	0.0	0.0	0.0	0.0
Vaccinium myrtillus	0.0	0.0	1.7	36.6	0.0	0.0	0.0	0.0	0.0
Campylopus introflexus	3.4	7.9	0.4	0.0	0.1	0.1	29.3	0.1	0.6
Hypnum jutlandicum	5.4	0.2	<0.1	0.1	0.0	0.0	0.0	0.0	5.2
Pseudoscleropodium purum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.1	0.0
Litter	75.7	34.9	94.2	42.2	77.3	97.1	27.4	92.2	74.2

The following species were also recorded: *Agrostis capillaris* $^{2 4 7}$ *Agrostis vinealis* ^{7} *Anthoxanthum odoratum* $^{4 9}$ *Betula* spp. $^{1 2 3 4 7 8 9}$ *Carex pilulifera* $^{1 2 5 7}$ *Centaurea nigra* ^{8} *Cerastium fontanum* ^{4} *Crataegus monogyna* $^{8 9}$ *Digitalis purpurea* ^{4} *Erica cinerea* $^{1 2 3 4 5 7 8 9}$ *Erica tetralix* $^{1 3 4 9}$ *Frangula alnus* ^{6} *Galium saxatile* $^{2 4 7}$ *Geranium dissectum* ^{1} *Hedera helix* ^{9} *Luzula multiflora* ^{7} *Lonicera periclymenum* $^{3 4 8 9}$ *Pinus sylvestris* ^{9} *Polygala serpyllifolia* $^{7 9}$ *Potentilla erecta* $^{2 7 9}$ *Prunus spinosa* ^{8} *Stellaria media* ^{4} *Teucrium scorodonia* $^{5 8 9}$ *Trigonella caerulea* ^{1} *Ulex europaeus* $^{1 2 4 5 7 8 9}$ *Ulex minor* $^{3 9}$ *Bryum* spp. ^{7} *Campylopus pyriformis* $^{5 7}$ *Ceratodon purpureus* ^{3} *Dicranum scoparium* $^{1 2 4 5 6 8}$ *Leucobryum glaucum* ^{1} *Polytrichum juniperinum* $^{3 4 5 7}$ *Cladonia chlorophaea* $^{1 2 9}$ *Cladonia coniocraea* $^{2 5}$ *Cladonia macilenta* ^{2} *Cladonia portentosa* $^{1 2}$ Bare ground $^{1 2 5}$. The superscripts relate to the areas shown in the table heading above, and indicate the areas at which the species occurred.

Table 4.7. Mean % cover (n = 10) of species found in +R and mR sites in Dorset; only species with an average cover of 5% or more on any of the sites are shown in any detail.

Species	Arne		Blackhill		Sopley & Ramsdown			Trigon	
	+R^{1}	mR^{2}	+R^{3}	mR^{4}	+R^{5}	mR(a)^{6}	mR(b)^{7}	+R^{8}	mR^{9}
Calluna vulgaris	0.0	0.1	0.0	2.9	0.0	7.2	21.0	0.5	0.2
Pteridium aquilinum	1.0	0.6	0.0	1.7	0.2	1.5	20.0	0.0	7.1
Rhododendron ponticum	98.1	0.0	92.1	0.7	96.2	0.0	0.7	86.8	0.9
Campylopus introflexus	0.3	0.0	0.0	28.7	0.0	34.8	49.7	0.3	2.3
Dicranum scoparium	0.0	0.0	0.0	5.6	0.0	<0.1	1.3	0.1	<0.1
Litter	93.0	13.2	95.9	56.9	92.7	59.7	25.2	97.5	96.5
Bare Ground	0.0	85.9	0.0	1.0	0.0	0.0	0.0	0.1	0.0

The following species were also recorded: *Agrostis capillaris* ^{2} *Agrostis curtisii* ^{4} *Aira praecox* ^{79} *Betula* spp. ^{126789} *Carex nigra* ^{2} *Cerastium fontanum* ^{29} *Chamerion angustifolium* ^{26} *Cirsium arvense* ^{9} *Digitalis purpurea* ^{24} *Erica cinerea* ^{28} *Erica tetralix* ^{4678} *Hedera helix* ^{8} *Ilex aquifolium* ^{1} *Juncus bufonius* ^{2} *Luzula campestris* ^{2} *Molinia caerulea* ^{14678} *Pinus pinaster* ^{9} *Pinus sylvestris* ^{269} *Poa annua* ^{2} *Quercus robur* ^{36} *Rhododendron ponticum* ^{479} *Rubus glandulosus* ^{249} *Rumex acetosella* ^{29} *Senecio vulgaris* ^{1} *Sorbus aucuparia* ^{1} ^{2} *Trifolium repens* ^{2} *Ulex europaeus* ^{124} *Urtica dioica* ^{2} *Vaccinium myrtillus* ^{4} *Vulpia bromoides* ^{9} *Campylopus pyriformis* ^{249} *Hypnum jutlandicum* ^{124689} *Hypnum mammillatum* ^{1367} *Leucobryum glaucum* ^{47} *Polytrichum juniperinum* ^{1479} *Sphagnum capillifolium* ^{7} *Cladonia bellidiflora* ^{4} *Cladonia chlorophaea* ^{67} *Cladonia coniocraea* ^{67} *Cladonia gracilis* ^{4} *Cladonia portentosa* ^{67} *Cladonia pyxidata* ^{8} *Cladonia uncialis* ^{7}. The superscripts relate to the areas shown in the table heading above, and indicate the areas at which the species occurred.

On the +PS sites *Pinus sylvestris, Molinia caerulea, Pteridium aquilinum, Dicranum scoparium, Hypnum jutlandicum* and *Pleurozium schreberi* were the only species to occur at greater than 5% cover on at least one site (Table 4.5). On the mPS sites *Pinus sylvestris* was present at low cover (Table 4.5). *Pteridium aquilinum* occurred in 10 of the 14 sites and was the dominant species at Arne(d), AHCP(b), Blackhill, East Holton(a), Grange and Merritown. *Betula* spp. were present at all sites except Trigon. *Calluna vulgaris* occurred at all sites, with greater than 20% cover at Arne(a&e) and Trigon. *Campylopus introflexus, Hypnum jutlandicum* and *Polytrichum juniperinum* were all common (> 5% cover). Species present on the managed sites but not on the successional or heath sites included *Agrostis gigantea, Chamerion angustifolium, Holcus lanatus, Luzula campestris* and *Senecio vulgaris.* Eight lichen species were also recorded at low cover.

On the +PA sites *Aira praecox, Calluna vulgaris, Molinia caerulea, Pteridium aquilinum, Hypnum jutlandicum* and *Pseudoscleropodium purum* occurred at greater than 5% cover on at least one site (Table 4.6). At the mPA sites *Pteridium aquilinum* was the dominant species at Trigon and Blackhill(a) and occurred occasionally and at low cover at the other sites (Table 4.6). *Calluna vulgaris* occurred at all the sites with 84% cover at Arne and 16% at Trigon, but the other sites had less than 5% cover. *Agrostis curtisii, Rubus glandulosus, Rumex acetosella, Vaccinium myrtillus, Campylopus introflexus* and *Hypnum jutlandicum* were the only other species to occur at any site at greater than 5% cover.

Rhododendron ponticum was the only species to occur at greater than 5% cover on any of the +R sites (Table 4.7). On the mR sites *Rhododendron ponticum* was only recorded at three sites (Table 4.7). Species occurring at greater than 5% cover were *Calluna vulgaris, Pteridium aquilinum, Campylopus introflexus* and *Dicranum scoparium.* Although few species occurred at high cover many species were present at low cover; these were mostly young seedlings and they including *Agrostis capillaris, Agrostis curtisii, Aira praecox,* *Erica cinerea, Erica tetralix, Molinia caerulea, Rubus glandulosus, Rumex acetosella* and *Ulex europaeus.* Six lichen species were also recorded at low cover.

Table 4.8. Species found on managed stages classified as heath, successional or additional species; also shown are those species occurring in the heath and successional stages that were not found on the managed stages.

Managed stage	Heath Species		Successional Species		Additional Species
	Present	Absent	Present	Absent	
Managed +B stage *Betula* spp. was the major invader	*Calluna vulgaris*$^{\bullet}$	*Carex panicea*	*Agrostis curtisii*$^{+}$	*Agrostis vinealis*	*Achillea millefolium*$^{+}$
	Cuscuta epithymum	*Juncus articulatus*	*Betula* spp.$^{+}$	*Carex nigra*	*Agrostis capillaris*
	Erica cinerea$^{\bullet}$	*Campylopus paradoxus*	*Cerastium fontanum*	*Digitalis purpurea*	*Aria praecox*
	Erica tetralix^{--}	*Campylopus pyriformis*	*Frangula alnus*	*Glechoma hederacea*	*Brachypodium sylvaticum*
	Molinia caerulea$^{\bullet}$	*Hypnum cupressiforme*$^{--}$	*Gaultheria shallon*$^{\bullet}$	*Poa annua*$^{--}$	*Carex viridula* ssp. *oedocarpa*
	Rumex acetosella^{+}	*Leucobryum glaucum*	*Hedera helix*	*Rubus glandulosus*	*Centaurium erythraea*
	Ulex minor^{--}	*Pleurozium schreberi*$^{--}$	*Holcus lanatus*	*Sorbus aucuparia*	*Cirsium palustre*$^{+}$
	Brachythecium rutabulum	*Sphagnum palustre*	*Lonicera periclymenum*	*Urtica dioica*	*Crataegus monogyna*
	Campylopus introflexus^{+}	*Cladonia cervicornis*	*Luzula campestris*	*Campylopus pyriformis*	*Galium aparine*
	Dicranum scoparium^{--}	*Cladonia gracilis*	*Pinus sylvestris*	*Hypnum cupressiforme* var. *resupinatum*	*Hypochaeris radicata*
	Hypnum jutlandicum$^{\bullet}$	*Cladonia uncialis*	*Potentilla erecta*	*Mnium hornum*	*Ilex aquifolium*
	Cladonia chlorophaea	*Hypogymnia physodes*	*Pteridium aquilinum*$^{\bullet}$		*Juncus conglomeratus*
	Cladonia coniocraea		*Rosa* spp.		*Leontodon saxatilis*
	Cladonia portentosa^{--}		*Rubus gladulosus*$^{+}$		*Lotus pendunculatus*
	Cladonia pyxidata		*Salix caprea*		*Pinus pinaster*
			Senecio erucifolius		*Sagina procumbens*
			Teucrium scorodonia		
			Ulex europaeus		
			Viola reichenbachiana		
			Polytrichum juniperinum^{+}		
			Pseudoscleropodium purum^{+}		

Table 4.8 cont.

	Heath Species		Successional Species		Additional Species
	Present	Absent	Present	Absent	
Managed +PS stage *Pinus sylvestris* was the major invader	*Calluna vulgaris*$^{\bullet}$ *Erica cinerea*$^{\bullet}$ *Erica tetralix*$^{--}$ *Molinia caerulea*$^{\bullet}$ *Rumex acetosella* *Ulex minor*$^{--}$ *Brachythecium rutabulum*$^{\bullet}$ *Campylopus introflexus*$^{+}$ *Campylopus pyriformis* *Dicranum scoparium*$^{--}$ *Hypnum jutlandicum*$^{\bullet}$ *Leucobryum glaucum* *Cladonia cervicornis* *Cladonia chlorophaea* *Cladonia coniocraea* *Cladonia portentosa* *Cladonia pyxidata* *Hypogymnia physodes*	*Carex panicea* *Cuscuta epithymum* *Juncus articulatus* *Campylopus paradoxus* *Hypnum cupressiforme* *Pleurozium schreberi* *Sphagnum palustre* *Cladonia gracilis* *Cladonia uncialis*	*Agrostis curtisii* *Betula* spp.$^{+}$ *Cerastium fontanum* *Digitalis purpurea* *Hedera helix* *Ilex aquifolium* *Lonicera periclymenum* *Pinus sylvestris* *Poa annua* *Rubus glandulosus* *Pteridium aquilinum*$^{\bullet}$ *Quercus robur* *Sorbus aucuparia* *Ulex europaeus* *Pseudoscleropodium purum*	*Crataegus monogyna* *Galium aparine* *Moehringia trinervia* *Urtica dioica* *Eurhynchium praelongum*	*Agrostis gigantea* *Aira praecox* *Carex pilulifera* *Carex nigra* *Chamerion angustifolium* *Deschampsia flexuosa* *Holcus lanatus* *Hypochaeris radicata* *Juncus effusus* *Luzula campestris* *Rhododendron ponticum* *Senecio vulgaris* *Tripleurosperum inodorum* *Polytrichum juniperinum*$^{+}$ *Cladonia floerkeana* *Cladonia squamosa*
Managed +PA stage *Pteridium aquilinum* was the major invader	*Calluna vulgaris*$^{\bullet}$ *Erica cinerea*$^{--}$ *Erica tetralix*$^{--}$ *Molinia caerulea*$^{\bullet}$ *Rumex acetosella*$^{+}$ *Vaccinium myrtillus*$^{\bullet}$ *Ulex minor*$^{--}$ *Campylopus introflexus*$^{+}$ *Campylopus pyriformis* *Dicranum scoparium*$^{--}$ *Hypnum jutlandicum*$^{\bullet}$ *Cladonia chlorophaea* *Cladonia coniocraea* *Cladonia portentosa*$^{--}$	*Carex panicea* *Cuscuta epithymum* *Juncus articulatus* *Brachythecium rutabulum* *Campylopus paradoxus* *Hypnum cupressiforme* *Pleurozium schreberi* *Sphagnum palustre* *Cladonia gracilis* *Cladonia pyxidata* *Cladonia uncialis* *Hypogymnia physodes*	*Agrostis curtisii*$^{+}$ *Aira praecox*$^{--}$ *Betula* spp. *Carex pilulifera* *Crataegus monogyna* *Lonicera periclymenum* *Polygala serpyllifolia* *Pteridium aquilinum*$^{\bullet}$ *Rubus glandulosus*$^{+}$ *Teucrium scorodonia* *Ulex europaeus* *Polytrichum juniperinum*	*Centaurea nigra* *Frangula alnus* *Geranium dissectum* *Prunus spinosa* *Quercus robur* *Trigonella caerulea* *Ceratodon purpureus* *Pseudoscleropodium purum*	*Agrostis capillaris* *Agrostis vinealis* *Anthoxanthum odoratum* *Cerastium fontanum* *Digitalis purpurea* *Galium saxatile* *Hedera helix* *Luzula multiflora* *Pinus sylvestris* *Potentilla erecta* *Stellaria media* *Bryum* spp. *Cladonia macilenta*

Table 4.8 cont.

Managed Stage	Heath Species		Successional Stage		Additional Species
	Present	Absent	Present	Absent	
Managed +R stage *Rhododendron ponticum* was the major invader	*Calluna vulgaris** *Erica cinerea*$^{--}$ *Erica tetralix*$^{--}$ *Molinia caerulea*$^{--}$ *Rumex acetosella* *Campylopus introflexus** *Campylopus pyriformis* *Dicranum scoparium** *Hypnum jutlandicum*$^{--}$ *Leucobryum glaucum* *Cladonia chlorophaea* *Cladonia coniocraea* *Cladonia gracilis* *Cladonia portentosa*$^{--}$ *Cladonia uncialis*	*Carex panicea* *Cuscuta epithymum* *Juncus articulatus* *Ulex minor* *Brachythecium rutabulum* *Campylopus paradoxus* *Hypnum cupressiforme* *Pleurozium schreberi* *Sphagnum palustre* *Cladonia pyxidata* *Hypogymnia physodes*	*Betula* spp. *Pteridium aquilinum** *Quercus robur* *Rhododendron ponticum* *Sorbus aucuparia* *Ulex europaeus* *Hypnum mammillatum* *Polytrichum juniperinum*	*Ilex aquifolium* *Hedera helix* *Senecio vulgaris*	*Agrostis capillaris* *Agrostis curtisii* *Aira praecox* *Carex nigra* *Cerastium fontanum* *Chamerion angustifolium* *Cirsium arvense* *Digitalis purpurea* *Juncus bufonius* *Luzula campestris* *Pinus pinaster* *Pinus sylvestris* *Poa annua* *Rubus glandulosus* *Sorbus aucuparia* *Trifolium repens* *Urtica dioica* *Vaccinium myrtillus* *Vulpia bromoides* *Sphagnum capillifolium* *Cladonia bellidiflora*

* Species present at greater than 5% on some managed sites and some successional/heath sites

\+ Species present at greater than 5% on some managed sites but at less than 5% on the successional/heath sites

-- Species present at less than 5% on the managed sites but at greater than 5% on some successional/heath sites

4.4.2 Managed sites, classification of species

The species present on the managed sites can be classified into three groups, heathland species, successional species and others (Table 4.8). Heathland species were taken as those species recorded in the heath quadrats in this study with the exception of *Betula* spp., *Pinus sylvestris* and *Quercus robur* which were classified as successional species. Successional species were those recorded in the corresponding successional stage to the managed site. Other species were those present on the managed site but not on the heath or successional sites. Of the heathland species *Calluna vulgaris* is present at ≥ 5% cover in each of the managed stages. *Erica tetralix* is present at each managed stage but at much lower cover than in the heath sites. In contrast *Campylopus introflexus* is found at low cover on the heath sites but at greater than 5% cover on all the different managed stages. A similar pattern is shown for *Rumex acetosella* for some stages. Similarly some successional species are present in larger amounts in the managed sites than in the successional sites.

4.4.3 NVC classification

The managed sites with the best fit to dry heaths types were Arne mPS(a), Arne mPA, Trigon mPS, Merritown mB and Arne mPS(e) with G values of 60, 54, 52, 45 and 43 respectively (Table 4.9). Most of the sites were classified as heaths but with a very poor fit, G less than 40 (G = 100 is a perfect fit, (Hill 1996)). Some sites were not classified as dry heaths but mires (Cranborne mPA and Trigon mB); *Pteridium aquilinum* communities (Arne mPS(d), AHCP mPS(b), Grange mPS, Blackhill mPA(a&b), Trigon mPA and mR), grassland: (Sopley & Ramsdown mB) and *Ulex europaeus* scrub communities (Arne mR).

Table 4.9. Classification of the managed sites by TABLEFIT according to NVC. The NVC communities of the corresponding heath site for each area are also shown for comparison.

Stage	Area	NVC		Goodness of fit value (G)	NVC of heath	
mB	AHCP	H2	*Calluna vulgaris-Ulex minor* heath	22	H2a	*Calluna vulgaris-Ulex minor* heath
	Merritown	H2a	*Calluna vulgaris-Ulex minor* heath	45	H1b	*Calluna vulgaris-Festuca ovina* heath
	Sopley & Ramsdown	U1f	*Festuca ovina-Agrostis capillaris-Rumex acetosella* grassland	36	H1b	*Calluna vulgaris-Festuca ovina* heath
	Trigon	M25	*Molinia caerulea-Potentilla erecta* mire	26	H1b	*Calluna vulgaris-Festuca ovina* heath
mPS	Arne(a)	H10	*Calluna vulgaris-Erica cinerea* heath	60	H1b	*Calluna vulgaris-Festuca ovina* heath
	Arne(b)	H2	*Calluna vulgaris-Ulex minor* heath	22	H1b	*Calluna vulgaris-Festuca ovina* heath
	Arne(c)	H11	*Calluna vulgaris-Carex arenaria* heath	23	H1b	*Calluna vulgaris-Festuca ovina* heath
	Arne(d)	U20c	*Pteridium aquilinum-Galium saxatile* community	33	H1b	*Calluna vulgaris-Festuca ovina* heath
	Arne(e)	H10	*Calluna vulgaris-Erica cinerea* heath	43	H1b	*Calluna vulgaris-Festuca ovina* heath
	AHCP(a)	H2	*Calluna vulgaris-Ulex minor* heath	14	H2a	*Calluna vulgaris-Ulex minor* heath
	AHCP(b)	U20c	*Pteridium aquilinum-Galium saxatile* community	21	H2a	*Calluna vulgaris-Ulex minor* heath
	Blackhill	U20c	*Pteridium aquilinum-Galium saxatile* community	50	H10	*Calluna vulgaris-Erica cinerea* heath
	East Holton(a)	M16	*Erica tetralix-Sphagnum compactum* wet heath	31	M16	*Erica tetralix-Sphagnum compactum* wet heath
	East Holton(b)	H1e	*Calluna vulgaris-Festuca ovina* heath	18	M16	*Erica tetralix-Sphagnum compactum* wet heath
	Grange	U20c	*Pteridium aquilinum-Galium saxatile* community	50	M16	*Erica tetralix-Sphagnum compactum* wet heath
	Merritown	H1	*Calluna vulgaris-Festuca ovina* heath	18	H1b	*Calluna vulgaris-Festuca ovina* heath
	Sopley & Ramsdown	H12a	*Calluna vulgaris-Vaccinium myrtillus* heath	29	H1b	*Calluna vulgaris-Festuca ovina* heath
	Trigon	H12a	*Calluna vulgaris-Vaccinium myrtillus* heath	52	H1b	*Calluna vulgaris-Festuca ovina* heath
mPA	Arne	H1b	*Calluna vulgaris-Festuca ovina* heath	54	H1b	*Calluna vulgaris-Festuca ovina* heath
	Blackhill(a)	U20c	*Pteridium aquilinum-Galium saxatile* community	56	H10	*Calluna vulgaris-Erica cinerea* heath
	Blackhill(b)	U20c	*Pteridium aquilinum-Galium saxatile* community	16	H10	*Calluna vulgaris-Erica cinerea* heath
	Cranborne	M25a	*Molinia caerulea-Potentilla erecta* mire	48	M16	*Erica tetralix-Sphagnum compactum* wet heath
	Trigon	W25b	*Pteridium aquilinum-Rubus fruticosus* underscrub	54	H1b	*Calluna vulgaris-Festuca ovina* heath
mR	Arne	W23a	*Ulex europaeus-Rubus fruticosus* scrub	11	H1b	*Calluna vulgaris-Festuca ovina* heath
	Blackhill	H12a	*Calluna vulgaris-Vaccinium myrtillus* heath	25	H10	*Calluna vulgaris-Erica cinerea* heath
	Sopley & Ramsdown(a)	H1b	*Calluna vulgaris-Festuca ovina* heath	29	H1b	*Calluna vulgaris-Festuca ovina* heath
	Sopley & Ramsdown(b)	H1e	*Calluna vulgaris-Festuca ovina* heath	20	H1b	*Calluna vulgaris Festuca ovina* heath
	Trigon	U20C	*Pteridium aquilinum-Galium saxatile* community	10	H1b	*Calluna vulgaris-Festuca ovina* heath

4.4.4 Soil results

The soil results are shown in detail in Table 4.10, here only important trends are highlighted. The heath soil samples were very acidic pH 3.9 to 4.2 with the exception of AHCP at pH 5.0 (this was checked and was not an analytical error). The +B sites were less acidic than the heath sites (except for AHCP) (pH 4.1 - 4.9); the mB sites were more acidic than the +B sites (pH 4.0 - 5.6). The +PS soils were often more acidic then the heath soils (pH 3.7 - 4.2) and the mPS soils generally less acidic than the +PS soils (pH 3.9 - 4.4). The mPA sites (pH 3.8 - 4.5) and mR sites (pH 3.6 - 4.5) were all less acidic than the corresponding successional stages. The loss-on-ignition generally ranged from 5 to 10% for all stages and all sites, with a few results of 10 to 20%. The most noticeable effect was that of litter stripping in the mPS sites with results at Arne managed during 90/91 having values of 4.5, 6.5 and 7.7% for litter-stripped, partially litter-stripped and not litter-stripped sites respectively. Trigon, Merritown and Grange mPS sites all had greater loss-on-ignition than +PS sites, but none of these sites had been litter-stripped.

The heath soils had very low extractable ammonium-nitrogen values (0.9 - 2.3 μg N g^{-1}). With the exception of the +R site at Arne all successional stages had greater ammonium-nitrogen concentrations than the heaths (1.3 - 76.2 μg N g^{-1}). The managed sites had greater concentrations than the successional sites except were management removed the litter layer to the mineral soil (Arne mPS(a), mPA and mR). The extractable nitrate/nitrite-nitrogen of the heath samples was also low (0.5 - 1.1 μg N g^{-1}). The results for managed sites showed similar patterns to those for the ammonium-nitrogen although differences due to litter stripping were not as obvious as for ammonium-nitrogen, however bulldozing of the site once again lowered the nitrogen level.

Table 4.10. Chemical properties of soil samples from heath, successional and managed sites in Dorset, mean values ± SE (n = 10) are presented (ions are expressed as ug g^{-1}).

Stage	Area	pH	% Loss on Ignition	Extractable NH_4	Extractable NO_3	Extractable P	Exchangeable Ca	Exchangeable Mg	Exchangeable Na	Exchangeable K
Heath	Arne	4.20 ± 0.02	8.45 ± 2.24	1.88 ± 0.33	0.91 ± 0.07	1.15 ± 0.11	45.64 ± 3.18	26.65 ± 2.28	17.79 ± 1.62	20.03 ± 2.74
	Avon Heath Country Park	4.95 ± 0.29	7.67 ± 0.71	2.01 ± 0.38	1.12 ± 0.25	3.11 ± 0.52	1167.27 ± 649.30	40.80 ± 6.94	12.07 ± 1.20	15.32 ± 1.98
	Blackhill	3.85 ± 0.04	10.10 ± 0.91	1.83 ± 0.25	0.75 ± 0.06	3.11 ± 0.32	104.72 ± 8.41	53.38 ± 3.69	26.37 ± 3.45	37.32 ± 6.01
	Cranborne	4.06 ± 0.03	7.26 ± 1.21	1.91 ± 0.61	0.48 ± 0.02	2.46 ± 0.47	50.08 ± 4.28	23.58 ± 3.44	13.07 ± 2.45	32.94 ± 5.60
	East Holton	4.20 ± 0.05	2.53 ± 0.33	2.33 ± 0.39	0.65 ± 0.02	1.05 ± 0.10	13.20 ± 1.87	11.98 ± 1.23	9.30 ± 1.23	6.96 ± 0.82
	Grange	4.17 ± 0.13	9.13 ± 1.89	1.19 ± 0.20	0.92 ± 0.12	2.05 ± 0.50	57.18 ± 10.81	41.39 ±10.98	36.25 ± 9.24	44.40 ±13.63
	Merritown	4.04 ± 0.02	7.31 ± 0.88	1.11 ± 0.14	0.86 ± 0.17	3.82 ± 0.27	72.51 ± 9.27	31.46 ± 4.39	22.06 ± 3.03	37.79 ± 5.82
	Sopley & Ramsdown	4.17 ± 0.05	4.27 ± 0.67	1.09 ± 0.21	0.66 ± 0.08	1.38 ± 0.23	12.38 ± 1.48	13.46 ± 1.31	7.56 ± 1.82	14.99 ± 3.31
	Trigon	4.09 ± 0.03	10.28 ± 1.37	0.86 ± 0.10	0.62 ± 0.03	2.77 ± 0.26	121.99 ± 15.28	65.00 ± 9.91	24.90 ± 3.42	25.35 ± 4.45
+B	Avon Heath Country Park	4.27 ± 0.08	6.79 ± 0.69	4.18 ± 1.01	0.99 ± 0.12	7.29 ± 1.60	246.48 ± 78.92	39.28 ± 9.61	21.72 ± 3.50	38.51 ± 6.41
	Merritown	3.96 ± 0.04	8.75 ± 0.73	3.83 ± 0.63	0.68 ± 0.05	5.37 ± 0.71	94.08 ± 7.88	54.84 ± 5.10	53.55 ± 7.91	47.83 ± 9.17
	Sopley & Ramsdown	5.62 ± 0.17	3.73 ± 0.42	3.29 ± 0.72	1.04 ± 0.11	3.88 ± 0.80	561.43 ± 104.94	56.81 ± 5.99	20.20 ± 1.82	28.16 ± 3.04
	Trigon	5.10 ± 0.28	17.91 ± 1.70	5.26 ± 1.94	2.94 ± 0.80	0.80 ± 0.07	1429.19 ± 347.93	132.57 ±23.43	75.51 ± 8.04	87.36 ±14.37
mB	Avon Heath Country Park	4.72 ± 0.32	5.83 ± 0.49	2.90 ± 0.89	1.38 ± 0.44	3.37 ± 0.39	455.54 ± 179.88	36.12 ± 3.95	11.55 ± 2.14	16.53 ± 2.52
	Merritown	4.10 ± 0.08	6.90 ± 0.58	13.65 ± 5.48	0.85 ± 0.23	4.59 ± 0.75	88.78 ± 10.16	44.79 ± 3.55	19.04 ± 3.14	23.05 ± 5.55
	Sopley & Ramsdown	5.85 ± 0.42	5.44 ± 0.79	4.39 ± 1.20	3.75 ± 1.83	4.52 ± 0.99	1141.89 ± 406.73	59.52 ±10.31	9.16 ± 2.83	26.02 ± 4.07
	Trigon	4.90 ± 0.27	21.20 ± 1.87	5.69 ± 1.30	1.38 ± 0.22	1.48 ± 0.46	1367.60 ± 330.85	150.08 ±26.46	65.08 ± 7.63	90.32 ±27.90

Table 4.10. cont.

Stage	Area	pH	% Loss on Ignition	Extractable NH_4	Extractable NO_3	Extractable P	Exchangeable Ca	Exchangeable Mg	Exchangeable Na	Exchangeable K
+PS	Arne	3.92 ± 0.02	11.02 ± 1.07	4.55 ± 0.96	0.78 ± 0.08	3.63 ± 0.30	85.47 ± 11.32	48.03 ± 6.42	78.53 ± 7.17	39.37 ±10.77
	Avon Heath Country Park	3.84 ± 0.05	7.31 ± 0.90	4.31 ± 1.32	0.83 ± 0.09	0.98 ± 0.15	38.11 ± 7.45	26.50 ± 2.96	28.34 ± 4.69	10.98 ± 1.72
	Blackhill	3.77 ± 0.06	18.05 ± 1.72	14.10 ± 3.37	2.05 ± 0.95	4.34 ± 0.50	136.55 ± 13.24	86.27 ±10.47	101.67 ±14.33	66.46 ±12.30
	East Holton	4.17 ± 0.13	11.19 ± 2.78	4.63 ± 1.59	0.90 ± 0.12	2.24 ± 0.32	424.80 ± 180.66	46.25 ± 8.28	61.05 ±14.83	24.62 ± 5.51
	Grange	3.72 ± 0.05	9.88 ± 0.89	4.05 ± 0.75	0.83 ± 0.05	2.52 ± 0.23	111.03 ± 9.69	67.91 ± 5.62	65.11 ± 9.13	37.22 ± 6.04
	Merritown	4.05 ± 0.05	3.95 ± 0.33	2.14 ± 0.42	0.66 ± 0.04	2.77 ± 0.26	48.87 ± 7.21	19.90 ± 3.20	13.29 ± 2.53	11.46 ± 0.98
	Sopley & Ramsdown	3.92 ± 0.06	4.24 ± 0.50	1.99 ± 0.34	0.63 ± 0.04	0.84 ± 0.12	25.00 ± 3.66	15.58 ± 1.67	21.07 ± 3.35	14.79 ± 1.88
	Trigon	4.00 ± 0.05	7.02 ± 1.09	1.92 ± 0.08	0.63 ± 0.03	1.94 ± 0.27	74.46 ± 11.09	45.25 ± 8.72	38.75 ± 7.90	16.60 ± 4.57
mPS	Arne(a)	4.13 ± 0.03	4.47 ± 0.76	3.31 ± 1.53	0.88 ± 0.06	1.92 ± 0.48	49.45 ± 9.36	20.87 ± 3.26	10.76 ± 2.81	17.34 ± 4.91
	Arne(b)	3.88 ± 0.08	6.46 ± 0.91	12.91 ± 4.14	0.81 ± 0.19	3.65 ± 0.75	83.03 ± 20.99	47.18 ± 5.60	27.86 ± 6.28	66.19 ±17.02
	Arne(c)	3.87 ± 0.05	7.69 ± 0.69	22.96 ±10.54	0.92 ± 0.11	3.66 ± 0.83	85.91 ± 12.13	53.01 ± 7.31	28.21 ± 6.73	50.25 ±10.45
	Arne(d)	4.09 ± 0.11	6.47 ± 1.09	6.38 ± 1.53	1.11 ± 0.14	1.74 ± 0.35	54.18 ± 9.81	30.06 ± 5.66	14.78 ± 3.70	22.28 ± 3.72
	Arne(e)	4.04 ± 0.05	8.57 ± 0.84	11.93 ± 4.73	1.05 ± 0.19	4.14 ± 0.26	104.28 ± 10.67	55.34 ± 7.02	28.68 ± 3.99	19.47 ± 4.25
	Avon Heath Country Park(a)	4.14 ± 0.10	5.88 ± 0.76	18.12 ± 3.02	0.98 ± 0.08	1.72 ± 0.13	47.53 ± 6.59	24.63 ± 2.84	12.38 ± 1.48	30.29 ± 7.53
	Avon Heath Country Park(b)	3.96 ± 0.09	5.03 ± 1.15	14.78 ± 2.90	0.74 ± 0.05	1.63 ± 0.22	32.13 ± 9.83	22.35 ± 4.78	11.30 ± 3.73	19.85 ± 4.70
	Blackhill	3.92 ± 0.05	7.53 ± 0.56	13.09 ± 3.44	0.85 ± 0.11	2.62 ± 0.54	84.20 ± 10.14	45.16 ± 3.17	31.24 ± 4.29	33.52 ± 6.66
	East Holton(a)	4.41 ± 0.06	5.36 ± 0.51	22.73 ± 3.37	1.13 ± 0.35	1.53 ± 0.24	37.30 ± 6.33	20.49 ± 2.86	14.38 ± 3.94	22.82 ± 6.34
	East Holton(b)	4.13 ± 0.06	5.03 ± 0.63	8.98 ± 1.90	0.63 ± 0.05	1.34 ± 0.13	47.51 ± 10.09	27.23 ± 4.40	16.89 ± 2.43	12.89 ± 1.85
	Grange	3.86 ± 0.05	10.53 ± 0.92	6.84 ± 1.81	0.89 ± 0.04	2.73 ± 0.37	117.86 ± 10.88	54.82 ± 4.19	38.11 ± 5.12	39.52 ± 9.69
	Merritown	4.26 ± 0.06	7.30 ± 0.77	22.96 ± 4.73	0.82 ± 0.06	3.89 ± 0.26	60.22 ± 7.73	35.00 ± 4.49	21.28 ± 2.33	40.36 ± 7.58
	Sopley & Ramsdown	4.00 ± 0.04	7.22 ± 1.40	6.04 ± 2.04	0.90 ± 0.16	1.52 ± 0.32	50.77 ± 7.91	26.57 ± 4.89	16.24 ± 6.05	23.82 ± 8.45
	Trigon	4.27 ± 0.20	8.52 ± 1.40	1.61 ± 0.19	0.71 ± 0.06	7.59 ± 5.34	194.39 ± 76.58	68.47 ±16.99	22.23 ± 4.61	18.09 ± 4.19

Table 4.10. cont.

Stage	Area	pH	% Loss on Ignition	Extractable NH_4	Extractable NO_3	Extractable P	Exchangeable Ca	Exchangeable Mg	Exchangeable Na	Exchangeable K
+PA	Arne	3.66 ± 0.05	13.82 ± 1.98	11.79 ± 3.59	1.35 ± 0.27	9.63 ± 2.48	170.62 ± 20.83	78.96 ± 8.00	51.56 ± 4.96	102.52 ±16.17
	Blackhill	3.83 ± 0.06	10.29 ± 1.25	16.64 ± 3.97	0.65 ± 0.10	5.93 ± 0.72	99.17 ± 16.27	52.05 ± 7.41	63.80 ± 9.78	104.39 ±18.38
	Cranborne	4.10 ± 0.06	11.54 ± 1.04	76.18 ±15.50	13.51 ± 1.85	0.88 ± 0.11	50.79 ± 5.76	42.52 ± 8.09	110.88 ±14.15	319.19 ±62.68
	Trigon	3.87 ± 0.03	12.74 ± 1.33	5.08 ± 1.25	0.74 ± 0.12	2.72 ± 0.30	274.82 ± 46.39	69.63 ± 6.33	66.19 ± 9.29	60.73 ± 9.87
mPA	Arne	3.88 ± 0.04	11.70 ± 1.78	1.65 ± 0.32	1.00 ± 0.10	4.68 ± 0.74	119.78 ± 15.01	54.22 ± 8.55	31.29 ± 5.44	56.04 ±24.42
	Blackhill(a)	3.95 ± 0.15	20.17 ± 2.46	26.00 ± 9.75	3.80 ± 1.79	18.74 ± 6.00	471.99 ± 201.76	92.72 ±13.17	55.92 ±14.13	146.55 ±50.38
	Blackhill(b)	3.86 ± 0.05	9.03 ± 0.71	26.10 ± 5.32	1.03 ± 0.16	5.33 ± 0.62	124.94 ± 9.75	64.80 ± 5.35	52.97 ± 7.92	99.01 ±14.36
	Cranborne	4.21 ± 0.12	8.37 ± 0.65	34.77 ± 8.48	4.32 ± 0.80	0.94 ± 0.11	270.99 ± 138.20	25.99 ± 6.06	46.03 ± 4.90	97.75 ±10.86
	Trigon	4.12 ± 0.09	9.00 ± 1.03	3.50 ± 1.14	0.64 ± 0.05	3.01 ± 0.58	301.49 ± 44.62	61.05 ± 8.09	62.17 ± 9.39	41.99 ±11.18
+R	Arne	3.83 ± 0.03	10.69 ± 1.06	1.29 ± 0.16	0.81 ± 0.10	4.19 ± 0.36	81.10 ± 15.65	36.07 ± 3.54	32.52 ± 3.74	22.65 ± 1.78
	Blackhill	3.66 ± 0.04	12.65 ± 1.29	8.46 ± 0.81	0.47 ± 0.02	4.32 ± 0.68	82.75 ± 21.86	51.59 ± 7.69	39.58 ± 4.76	50.64 ±11.31
	Sopley & Ramsdown	3.61 ± 0.07	8.76 ± 1.51	1.12 ± 0.11	0.76 ± 0.06	2.94 ± 0.33	60.77 ± 25.96	25.31 ± 8.93	48.38 ±13.31	27.94 ± 5.87
	Trigon	4.54 ± 0.41	6.99 ± 1.20	1.58 ± 0.20	0.70 ± 0.04	1.89 ± 0.69	848.39 ± 741.08	49.10 ± 9.37	40.58 ± 5.19	18.02 ± 2.60
mR	Arne	4.06 ± 0.04	7.76 ± 0.61	1.17 ± 0.14	0.56 ± 0.03	2.63 ± 0.69	97.26 ± 22.94	33.89 ± 5.11	28.31 ± 4.77	51.32 ± 8.77
	Blackhill	3.75 ± 0.07	7.59 ± 1.00	14.11 ± 5.95	0.59 ± 0.06	3.65 ± 0.21	38.83 ± 7.18	54.09 ± 6.64	42.71 ± 8.03	70.36 ±13.57
	Sopley & Ramsdown(a)	4.20 ± 0.05	3.82 ± 0.75	3.35 ± 0.62	0.86 ± 0.07	2.23 ± 0.13	11.84 ± 1.74	8.32 ± 1.23	18.95 ± 2.80	6.12 ± 1.33
	Sopley & Ramsdown(b)	3.79 ± 0.05	5.67 ± 0.47	1.58 ± 0.28	0.71 ± 0.06	3.76 ± 1.01	53.90 ± 27.21	28.58 ± 9.86	7.25 ± 2.41	14.08 ± 3.04
	Trigon	4.86 ± 0.18	5.44 ± 0.68	2.07 ± 0.26	2.90 ± 2.10	0.64 ± 0.09	396.32 ± 111.72	26.09 ± 3.80	15.05 ± 2.62	7.68 ± 1.32

The heath soil samples had low concentrations of extractable phosphorus (1.1 - 3.1 μg P g^{-1}). The successional sites generally had higher phosphorus concentrations than the heath sites, with the +B sites having some of the highest concentrations recorded, (3.9 to 7.3 μg P g^{-1}) although Trigon at 0.8 μg P g^{-1} was an exception. The managed sites often had higher concentrations than the corresponding successional site. All managed sites which were litter-stripped to the mineral soil surface (Arne mPS, mPA and mR) had lower phosphorus concentrations than the successional sites.

The exchangeable calcium results showed large variability (the extreme values were checked and these were not analytical errors). The heath results ranging from 13.2 to 104.7 μg Ca g^{-1}, with the extreme of AHCP at 1168.3 μg Ca g^{-1}. All the successional sites except four had higher calcium concentrations than the corresponding heath sites. The results of the managed sites were variable when compared to the successional sites, but the mB, mPA and mR sites were all greater than the corresponding heath sites except mB at AHCP and mR at Blackhill; the calcium results for the mPS sites showed no pattern. The exchangeable magnesium levels in the heath samples ranged from 12.0 to 65.0 μg Mg g^{-1}. The majority of the managed sites had greater concentrations than the corresponding heath sites.

Exchangeable sodium ranged from 7.6 to 36.5 μg Na g^{-1} in the heath samples. The successional sites all had greater values than the corresponding heath except for +PS at Merritown. The managed sites were lower than the successional sites except for mR at Blackhill. Litter-stripping on the mPS sites decreased levels further, with values at Arne of 10.8, 27.9 and 28.2 μg Na g^{-1} for litter-stripped, partially litter-stripped and not litter-stripped sites respectively. Exchangeable potassium ranged from 7.0 to 44.4 μg K g^{-1} on the heath samples. The +PA samples had higher concentrations than the heath samples (60.7 -

319.2 μg K g^{-1}); except for Blackhill(a) the mPA had lower concentrations than the +PA sites (42.0 - 146.6 μg K g^{-1}). The other successional and managed sites showed no pattern.

The soil data of the managed sites were compared with the corresponding heath sites using a two tailed t-test (Table 4.11). Ammonium-nitrogen, pH, phosphorus, calcium and magnesium were frequently significantly different in the managed sites compared to the heath.

Table 4.11. Soil nutrient levels of managed sites in comparison with the heath sites, as tested by a two-tailed t-test.
* p = 0.05 ** p = 0.01 *** p = 0.001

Stage	Area	pH	LOI	NH_4	NO_3	P	Ca	Mg	Na	K
mB	AHCP		*							
	Merritown			*				*		
	Sopley & Ramsdown	**		*		**	*	**		*
	Trigon	*	***	**	**	*	**	*	***	*
mPS	Arne(a)								*	
	Arne(b)	**		*		**		**		*
	Arne(c)	***				*	**	**		*
	Arne(d)			*						
	Arne(e)	**				***	***	**	*	
	AHCP(a)	*		***		*		*		
	AHCP(b)	**		**		*		*		
	Blackhill		*	**						
	East Holton(a)	*	***	***			**	*		*
	East Holton(b)		**	**			**	**	*	*
	Grange	***		*			***			
	Merritown	**		***					*	
	Sopley & Ramsdown	**		*			***	*		
	Trigon			**						
mPA	Arne	***				***	***	**	*	
	Blackhill(a)		**	*		**		*		
	Blackhill(b)			***		**			**	**
	Cranborne			**	***	*			***	***
	Trigon			*			**		***	
mR	Arne	**			***					
	Blackhill						***			*
	Sopley & Ramsdown(a)			*		**		*		*
	Sopley & Ramsdown(b)	***				*			**	
	Trigon	***	**	***		***	*	**	*	**

4.4.5 The CCA model

CCA analysis I: managed sites as active samples

As expected the data set showed a large variation and therefore the CCA results had low eigenvalues, 0.2, 0.13 for the first 2 axes (Table 4.12) however, such models can still be quite informative (Gouch 1982; Ter Braak 1990). For the first axis there was a 0.77 correlation between the species data and the soil data which accounts for 33.9% of the explained species-environment relationships. Axis 2 has a species environment correlation of 0.57 and accounts for a further 20.8% of the species-environment relationship. The four axes explain 76.8% of the explained species-environment relationships. The intraset correlations show the correlation coefficients between the environmental variables and the ordination axes: pH, calcium, and magnesium are closely correlated with the first axis; sodium, loss-on-ignition and magnesium with the second; phosphorus, nitrite/nitrate-nitrogen and ammonium nitrogen with the third and loss-on-ignition, potassium, and magnesium with the fourth.

The ordination diagram (Fig. 4.2) plots the sample scores for the first two axes, and shows that samples from managed sites from all stages are generally clustered near the centre of the graph, the exception being a few mB samples which are spread out along the positive end of Axis 1. The heath samples are clustered together at the lower end of both axes. Samples from the same successional stage are clustered together and are positioned in an arch around the managed sites and further away from the heath samples than the managed sites. The first axis splits the samples into three groups, first the +B and some mB samples, second the heath, +PA and most managed sites samples and third +R and +PS samples. Axis 1 is mostly closely correlated to pH, calcium and magnesium. Axis 2 splits the samples into four groups, first the +PS samples, second the +R, +PA and +B samples, third the managed sites and fourth the heaths. This second axis is most closely correlated to the sodium vector.

Table 4.12. Eigenvalues and intra-set correlations of soil variables for the four CCA axes for analysis I (managed sites as active samples) and analysis II (managed sites as passive samples)

	Analysis I				Analysis II			
Axis	1	2	3	4	1	2	3	4
Eigenvalue	0.21	0.13	0.09	0.08	0.25	0.22	0.08	0.06
Species-environment correlations	0.77	0.57	0.59	0.53	0.77	0.66	0.62	0.57
Percentage variance								
of species data	3.4	2.1 (5.5)	1.5 (7.0)	1.0 (8.0)	5.3	4.8 (10.1)	1.7 (11.8)	1.2 (13.0)
of species-environment relation	33.9	21.0 (54.9)	14.2 (69.1)	9.7 (69.1)	36.0	31.6 (67.6)	12.0 (79.6)	8.1 (87.7)
Intra-set correlations								
pH	0.86 (1)	-0.12	0.05	-0.34 (3)	0.73 (1)	0.36	-0.24	0.05
Loss on ignition	0.33	0.47 (2)	0.21	0.48 (1)	-0.09	0.44	-0.20	0.52 (1)
NH_4-N	0.15	0.31	0.49 (3)	0.23	-0.26 (3)	0.47	0.06	0.33
NO_3-N	0.33	0.17	0.56 (2)	-0.04	-0.12	0.47	0.11	0.46 (2)
P	0.26	-0.16	0.77 (1)	0.01	0.02	0.46	0.72 (1)	0.24
Ca	0.73 (3)	0.17	0.07	0.08	0.26	0.27	-0.33 (2)	0.43
Mg	0.78 (2)	0.40 (3)	0.06	0.28	0.23	0.73 (2)	-0.26	0.45 (3)
K	0.32	0.39	0.37	0.46 (2)	-0.12	0.57 (3)	0.11	0.51
Na	0.10	0.92 (1)	0.26	0.03	-0.43 (2)	0.80 (1)	-0.26 (3)	0.12

Cumulative percentage variances are shown in parentheses.
On the intra-set correlation, the first three leading variables are shown in parentheses.

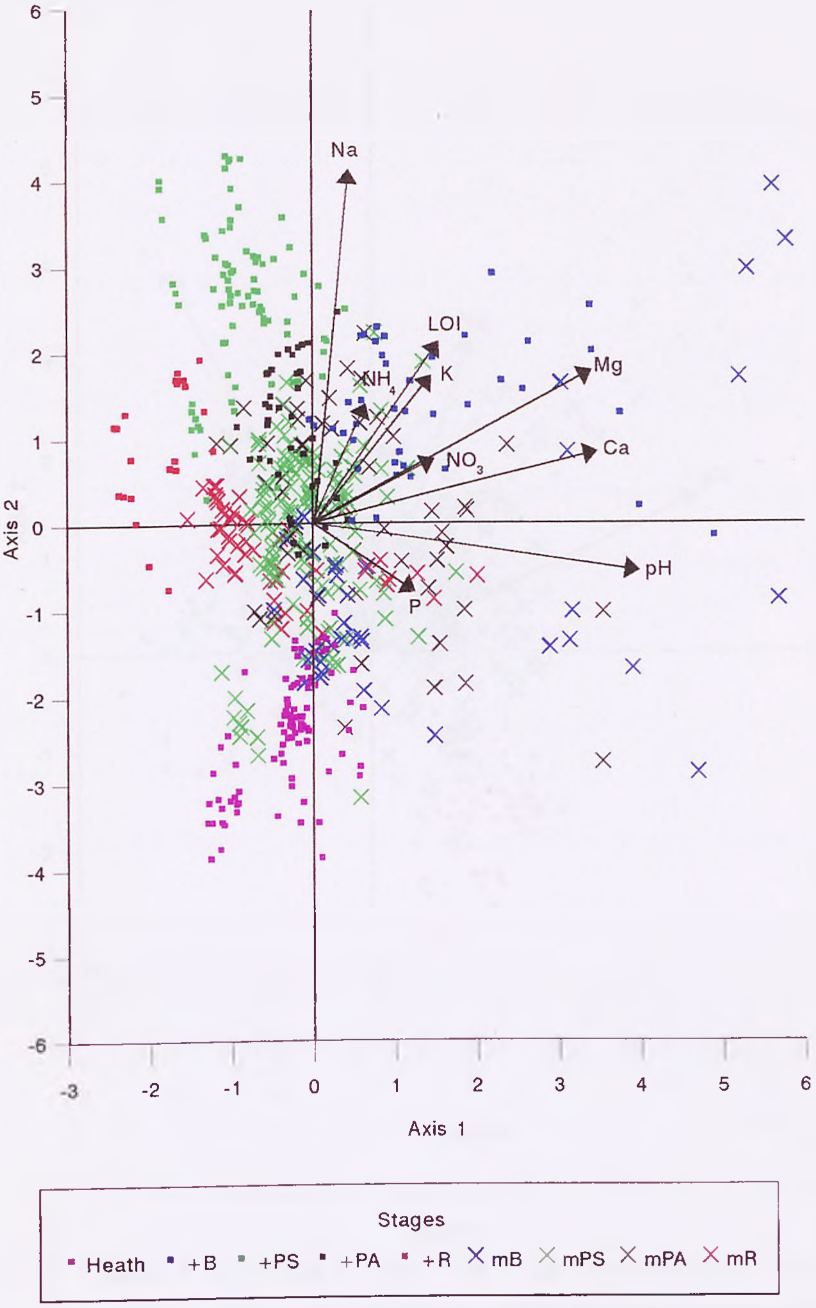


Fig. 4.2. Ordination diagram from CANOCO for analysis I (managed sites as active samples) for the first two axes showing the relationship between the different stages and the soil nutrients. The soil nutrient vectors are shown by arrows and their length is multiplied by a factor of five. Heath = open heathland, +B = *Betula* spp. is the major invader, +PS = *Pinus sylvestris* is the major invader, +PA = *Pteridium aquilinum* is the major invader, +R = *Rhododendron ponticum* is the major invader, mB = a managed +B site, mPS = a managed +PS site, mPA = a managed +PA site, mR = a managed +R site, Ca = exchangeable calcium, K = exchangeable potassium, LOI = percentage loss on ignition, Mg = exchangeable magnesium, Na = exchangeable sodium, NH_4 = extractable ammonium-nitrogen, NO_3 = extractable nitrate/nitrite-nitrogen, P = extractable phosphorus, pH = pH.

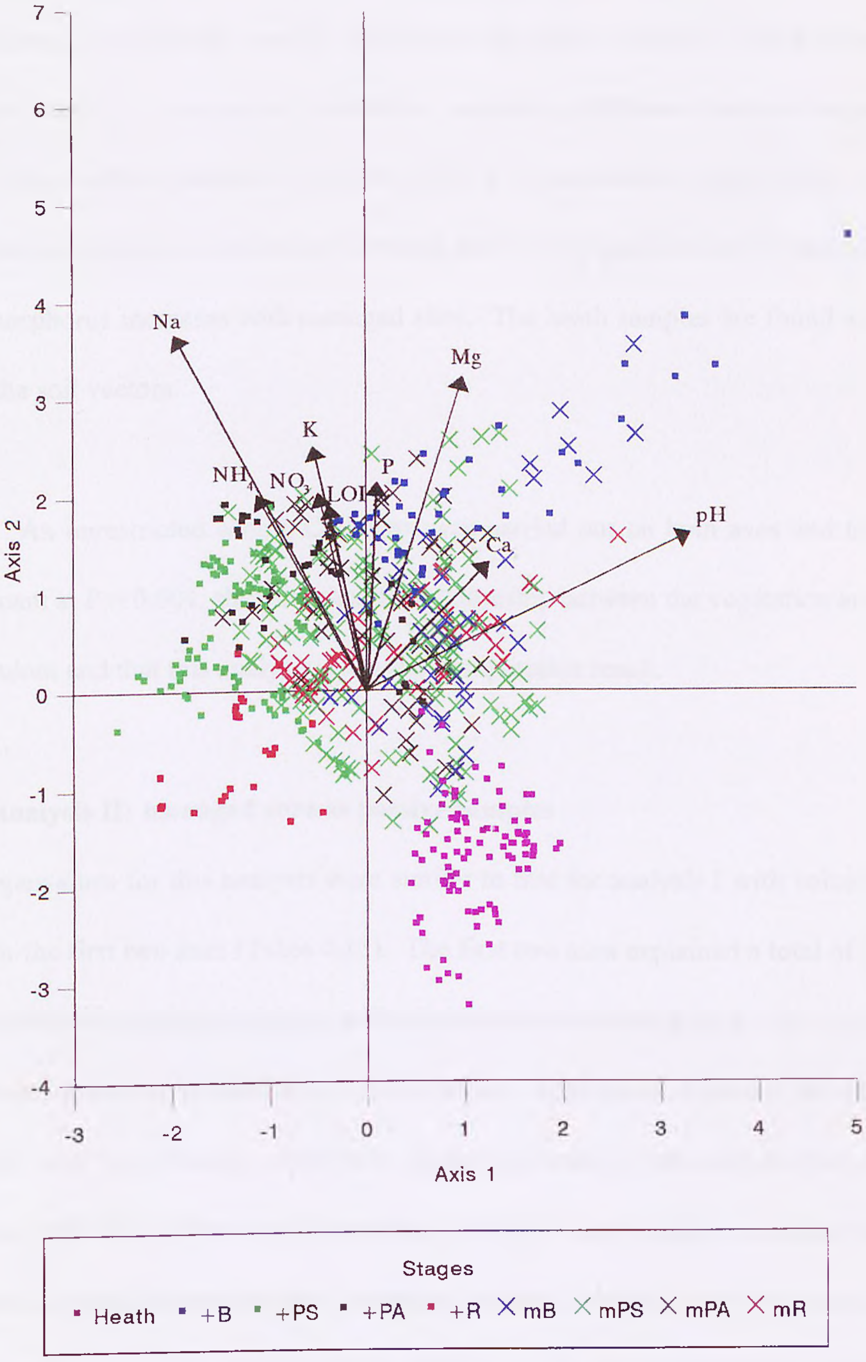


Fig. 4.3. Ordination diagram from CANOCO for analysis II (managed sites as passive samples) for the first two axes showing the relationship between the different stages and the soil nutrients. The soil nutrient vectors are shown by arrows and their length is multiplied by a factor of five. Heath = open heathland, +B = *Betula* spp. is the major invader, +PS = *Pinus sylvestris* is the major invader, +PA = *Pteridium aquilinum* is the major invader, +R = *Rhododendron ponticum* is the major invader, mB = a managed +B site, mPS = a managed +PS site, mPA = a managed +PA site, mR = a managed +R site, Ca = exchangeable calcium, K = exchangeable potassium, LOI = percentage loss on ignition, Mg = exchangeable magnesium, Na = exchangeable sodium, NH_4 = extractable ammonium-nitrogen, NO_3 = extractable nitrate/nitrite-nitrogen, P = extractable phosphorus, pH = pH.

The lengths of the vectors represent their relative importance, thus sodium, pH, magnesium, and calcium are the four most important vectors. The positioning of the samples relative to the vectors relates the samples to different chemical properties of the soil. Thus sodium increases with the +PA; pH, magnesium and calcium with the +B; ammonium-nitrogen, nitrite/nitrate-nitrogen and loss on ignition with +B and managed sites and phosphorus increases with managed sites. The heath samples are found at the low end of all the soil vectors.

An unrestricted Monte Carlo test was carried out on both axes and the result was significant at $P = 0.001$, showing that the relationship between the vegetation and soil data is not random and that this analysis gives the best possible result.

CCA analysis II: managed sites as passive samples

The eigenvalues for this analysis were similar to that for analysis I with values of 0.25 and 0.22 for the first two axes (Table 4.12). The first two axes explained a total of 67.6% of the species-environment relationships, with all four axes accounting for 87.7%. of the explained species-environment relationship. The intra-set correlations between the environmental variables and the ordination axes were slightly different in this analysis than the previous analysis, with pH, sodium and ammonium-nitrogen being closely correlated with the first axis and sodium, magnesium and potassium closely correlated with the second axis. The ordination diagram (Fig. 4.3) plots the sample scores for the first two axes. In this analysis the managed site samples are once again in the centre of the graph with the successional samples in an arch around them and the heath samples positioned at the opposite end of the second axis from the successional and managed sites. Sodium, pH, magnesium and potassium are the four most important vectors in this model. As with analysis I sodium increases with the +PA samples and pH, magnesium and calcium with the +B samples.

However in this analysis ammonium-nitrogen, nitrite/nitrate-nitrogen and potassium and loss-on-ignition all increase with the +PA rather than with the +B and the managed sites. These differences are due to this ordination being constructed using data only from the heath and successional sites.

Comparison of the CANOCO results with 1995 results.

Analysis II uses only the heath and successional sites to construct the model; this model was compared to the previous model produced in 1995 (Chapter 3). Phosphorus, pH and calcium once again increased during the +B stage, potassium, ammonium-nitrogen, nitrate/nitrite-nitrogen and potassium increased in the +PA stage. The major differences were that sodium increased with the +PA stage, rather than the +PA and +R stages and the +R stage was closer to the heath in this model than in the 1995 model. All of the samples from this study were then treated as passive samples in the previous model. The successional and heath samples from this studies fitted in to the corresponding samples in the 1995 model with the managed sites generally grouped between the heath and successional sites. These were seen as important tests as they showed that (a) the model is repeatable over time, (b) that this study validates the model from the previous study.

Managed sites

The centroids of each managed site and the overall centroids for the successional stages and heath were plotted (Fig. 4.4) using the data from analysis I. The mB sites are scattered, with Merritown and AHCP close to the heath, Trigon close to the +B and Sopley & Ramsdown moving in a different direction. The mPS sites generally cluster between the +PS and the heath, with some sites (Trigon and Arne(a)) closer to the heath than others (Blackhill and Grange). The mPA sites are scattered, some remain close to the +PA (Trigon), others move

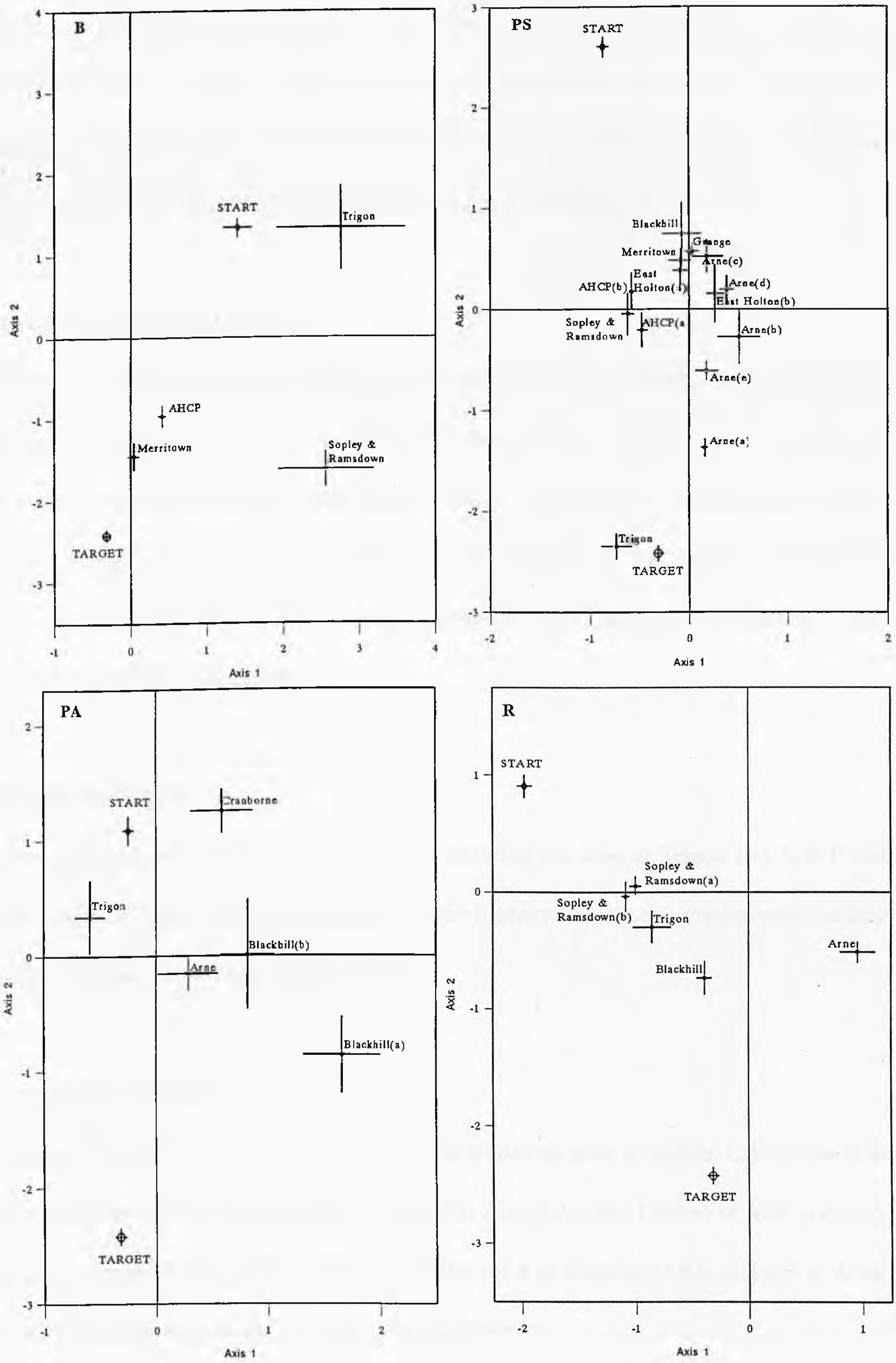


Fig. 4.4. Simplified CCA ordination diagrams from analysis I for B, *Betula*; PS, *Pinus sylvestris*; PA, *Pteridium aquilinum* and R, *Rhododendron ponticum* sites. The centroids and SE bars for the heath (TARGET), successional (START) and managed sites are shown. The centroids for the START and TARGET sites are average centroids for all the START and TARGET sites.

towards the +B trajectory (Blackhill(b) and Cranborne) while Blackhill(a) moved in a different direction altogether. The mR sites at Sopley & Ramsdown(a&b), Trigon and Blackhill are positioned between the +R and the heath, with Blackhill closer to the heath than the others. Arne appears to be moving in a different direction.

Measuring management success.

Centroids for all the sites were calculated using analysis II and the distances between these centroids are shown in Table 4.13. The sites closest to the heath 'target' were mB at Merritown and the mPS sites at Arne(a) and Trigon, the management on these sites can therefore be judged to be most successful. Those furthest from the 'target' were the mB sites at Sopley & Ramsdown, Trigon and AHCP and the mPA sites at Blackhill, these sites were least successfully managed.

Measuring resilience

Those sites that were closest to the 'start' sites were the mB sites at Trigon and AHCP and the mPA sites at Trigon. These sites may have the highest resilience to management as they remained close to the corresponding start site.

Measuring the trajectory

The managed sites that were closest to the target tended to have straighter trajectories than those sites further away from the target. Sites with a large A value (values of four or more), were mB at Sopley & Ramsdown, mPS at Arne(b), mPA at Blackhill(a&b) and mR at Arne, indicating that they may be moving to a different endpoint.

Table 4.13. Distances in four dimensions of managed sites from heath (target) and successional (start) sites and of start site from target. A measure of whether this trajectory (start to managed to target) is a straight line is also shown. The managed sites are ranked by distance from the heath and by how close they are to a straight line trajectory. Distances are calculated from CCA analysis II (managed sites treated as passive samples).

Stage	Area	Distance of managed site from		Distance of start from target ^{D}	A value*	Ranking, closest to heath		Ranking, closest to straight line	
		Target^T	Start^S			with in stage	over all	within stage	over all
+B	Sopley & Ramsdown	7.32	8.11	5.96	9.47	4	27	4	27
	Trigon	5.28	1.07	5.52	0.84	2	24	2	5
	AHCP	5.93	1.23	6.15	1.05	3	25	3	7
	Merritown	1.96	2.41	3.67	0.70	1	2	1	4
+PS	Grange	3.87	3.00	4.00	2.87	12	20	11	19
	Arne(d)	2.91	4.29	4.99	2.22	6	9	7	13
	E. Holton(a)	2.79	3.77	4.33	2.23	5	8	8	14
	AHCP(a)	2.64	2.28	4.57	0.35	4	6	1	2
	E. Holton(b)	3.67	1.76	4.32	1.09	11	17	3	8
	Merritown	2.46	3.16	3.89	1.74	3	4	6	11
	Sopley & Ramsdown	3.46	3.79	4.65	2.60	9	13	9	16
	Blackhill	3.24	2.91	4.28	1.87	8	11	5	12
	Arne(a)	1.71	4.67	4.99	1.40	1	1	4	9
	Arne(b)	4.31	6.52	4.99	5.92	13	21	13	24
	Arne(c)	3.49	5.00	4.99	3.51	10	14	12	22
	AHCP(b)	3.08	2.53	4.57	1.04	7	10	2	6
	Trigon	2.36	3.96	3.63	2.69	2	3	10	18
	Arne(e)	4.62	7.45	4.99	7.09	14	22	14	25
+PA	Cranborne	5.19	2.29	4.53	2.95	3	23	3	20
	Blackhill(a)	7.12	4.67	3.68	8.10	4	26	4	26
	Blackhill(b)	7.96	5.79	3.68	10.07	5	28	5	28
	Trigon	3.26	1.58	4.16	0.68	2	12	2	3
	Arne	2.65	2.58	5.14	0.10	1	7	1	1

Table 4.13 cont.

Stage	Area	Distance of managed site from		Distance of start from target ^{D}	A value*	Ranking, closest to heath		Ranking, closest to straight line	
		Target^{T}	Start^{S}			with in stage	over all	within stage	over all
+R	Arne	3.62	4.86	3.53	4.95	2	15	5	23
	Sopley & Ramsdown(a)	3.63	2.28	3.39	2.53	3	16	2	15
	Trigon	3.68	2.17	2.88	2.97	4	18	4	21
	Blackhill	2.61	2.03	2.93	1.71	1	5	1	10
	Sopley & Ramsdown(b)	3.70	2.31	3.39	2.62	5	19	3	17

[*] The A value gives a measure of whether the managed site is on a straight line trajectory from the successional site back to the heath.
It is calculated as (distance from managed site to target (T)) + (distance from managed site to start (S)) - (distance from start to target (D)) the closer this value is to zero the closer the trajectory is to a straight line.

4.5 DISCUSSION

4.5.1 Restoration of typical heathland vegetation

Management did not remove all of the successional species, just most of the major invaders; this disturbance allows the establishment of heathland and other species in addition to the recovery of the successional species already present (Table 4.8). Many heathland species are able to establish on the managed sites, including *Cladonia* spp., typical of heathland, but not present in the successional stages (Mitchell *et al* 1997). Many of the successional species are very resilient and able to recover quickly after management (Table 4.8). The success of management is therefore dependent on whether the heathland or the successional and other species end up dominating the site. This may be influenced by the continued management of the site, for example by grazing, to continue the movement of the site towards the 'target'.

The NVC classification results (Table 4.9) show that at Arne mPS(a), Arne mPA, Trigon mPS, Merritown mB, Arne mPS(e) it has been possible to re-establish vegetation that is relatively close to heathland. Most of the other sites are classified as heaths but have low G values and are only on target to become heathlands if the trend continues. Some of the classifications given are more typical of northern than southern England heaths (Rodwell 1991), this is because the Dorset heaths do not fit very well into the NVC classification (Webb pers. comm.). However the TABLEFIT analysis does allow a measure of how close to heatherlands if not heathlands the managed sites are. Some sites appear to be changing to a different community, often *Pteridium aquilinum* communities, and these sites are likely to be problematic. Further sampling is needed to test these suggestions.

4.5.2 Restoration of typical heathland soil chemical properties

The increased levels of soil nutrients that occur during succession do not automatically decrease following management. In general, if the soil nutrient concentrations are significantly different from the heath at the start site they are also significantly different in the managed site (Table 4.11). Levels of ammonium-nitrogen, nitrate/nitrite-nitrogen, phosphorus and calcium are generally greater in the managed sites than the successional sites. This increase may be due to a loss of biotic control following management (Bormann & Liken 1979). The sites that were similar to the heath soils were either those that were litter-stripped to the mineral surface (Arne mPS(a&b) and mR) or had corresponding successional sites that were not very different from the heath. Unless management involves litter-stripping, soil nutrient levels are unlikely to decrease to heathland levels, indeed for the major soil nutrients they are more likely to increase.

When management is simply the removal of the dominant species the quantity of nutrients removed from the ecosystem is unlikely to be as high as when the management involves burning or sodd cutting. Thus unless more "drastic" management is undertaken such as litter-stripping, sodd cutting or burning, the nutrient levels of the successional sites are unlikely to be returned to those of typical heathland levels.

Raised soil nutrient levels will make the restoration of heathland on successional sites more difficult (Marrs & Gough 1989). However, on the majority of sites studied here heathland species have established despite the higher nutrient levels. The increased nutrient levels are not inhibiting the establishment of *Calluna vulgaris* seedlings. However the raised nutrient levels may speed up the successional process so that management to remove successional species is required more regularly thus creating problems in the future. The effects of a long term build up of nutrients is unknown and further studies need to be done.

4.5.3 Testing of models

No site has reverted perfectly to coincide with the heath 'target' (model 1a) and none of the centroids of the managed sites overlap with the centroids of the corresponding successional stage, the 'start' point (model 1b) (Fig. 4). Most of the sites are positioned between the successional stage and heath sites indicating that Fig. 1c is the model along which most managed sites operate. Some managed sites however appear to be moving towards a different target, indicating that there is a risk of model 1d operating.

4.5.4 Measuring management success and the resilience of the sites

The distance between the managed and target sites allow a measure of the success of reversion to be made and these provide a method of judging restoration success in terms of both vegetation and soil nutrients. The distance between the managed site and the 'start' allows a measure of the combined impact of treatment and the resilience of the site. To measure resilience accurately the survey would have to be repeated over time. It would then be possible to monitor the managed sites and see if they continued to move towards the heath or if they showed high resilience and started to move back towards the 'start' point.

Ecosystems may have more than one equilibrium (Holling 1986) so management may not always revert the site to the desired equilibrium (heath); this is happening for sites that follow model 1d and have a high A value. Sites with a high A value are on a trajectory towards a different equilibrium, whereas sites with a low A value are moving in the desired direction, even if they have a long way to go. The sites with high A values are often those that the TABLEFIT and NVC results also show as reverting towards a community other than heathland. In this study sites with an A value of greater than four have been found, however we do not know how much greater than zero A has to be before it becomes a serious problem.

4.5.5 Conservation relevance: factors affecting the success of management

As model 1c is the predominant model that is operating on the heaths it is important to understand why some sites are further along the trajectory from 'start' to 'target' than others. Three factors that may influence this, age, stage and management, were examined by comparing the distances of the sites from the heath in multivariate space.

Age

Within each stage in Table 4.13 the sites are ordered by increasing age. For mB sites age correlates positively with closeness to the heath. However with so few samples it is impossible to say if this is just a coincidence. For the other stages the very young sites (less than 1.5 years) are furthest from the heath as they are dominated by bare ground and litter and contain little vegetation; the age of the other sites show no correlation to closeness to heath.

Stage

Mitchell *et al.* (1997) ranked successional stages in order of closeness to heath and suggested that the +PS stage was the easiest and the +B stage the most difficult to restore to heathland. The site closest to the heath is a managed +PS site (Arne(a)) (Table 4.13). However, the second closest site to the heath is a mB site (Merritown) indicating that the +B stage may not be as difficult to restore as Mitchell *et al.* (1997) suggested. However, the other mB sites were some of the sites furthest from the heath indicating that the success at Merritown may be the exception rather than the rule. The reason for the success at Merritown may be that the distance between the 'start' and 'target' points was smaller than for the other +B sites and for many of the other successional sites. The mPS sites at Trigon and Merritown and mR sites at Blackhill were ranked third, fourth and fifth closest to the heath. The closest mPA site (Arne) was ranked 7th out of 28; the other mPA sites together with the mB sites being some of the sites furthest from the heath. Generally mPS sites appear to be most successful followed by mR sites with mPA and mB sites being the least successful. However some mB and mPA sites may revert better than some mPS sites.

Sites that are close to either their 'target' (mPS at Arne(a) and mB at Merritown) or close to their 'start' point (mB at Trigon) have low A values. Compared to the number of mPS sites studied very few have high A values, this may indicate that +PS sites are more likely than the other stages to move back along a straight line towards their 'target' and not to veer off in a different direction.

Management

There is no clear difference between the two types of management at the mB sites (Table 4.13), however the *Betula* spp. was re-sprouting where stumps were not treated and this will cause problems in the future (Marrs 1985a). The effects of severe litter stripping at the mPS sites can be seen at Arne; site (a) where the mineral soil was exposed, is closer to the heath than the two areas managed at the same time. Indeed the litter-stripped site is ranked closer to the heath than a site managed at Arne in the 1980's and therefore 10 years older, indicating that litter-stripping improves and accelerates the success of reversion. The quality of the litter-stripping also appears important, it is better if the litter is removed to expose the mineral soil. This process will remove more nutrients from the site and uncover the buried *Calluna vulgaris* seed bank at the mineral soil surface which requires light to germinate (Grime, Hodgson & Hunt 1988; Gimingham 1960).

Of the three types of management at the mPA sites, the site closest to the heath was the bulldozed site. This was the most effective management as it removes the *Pteridium aquilinum* fronds, rhizomes and litter thus removing a potential source of propagules and nutrients. There is little difference in the success between the other two methods: spraying and mowing & spraying. Reversion of mR sites may be slow and only partially successful because of high concentrations of toxins and the deep root mat (Cross 1975). Bulldozing is, therefore, an attractive option as it solves these problems, however, the management at the bulldozed site (Arne) is too recent to compare it with the other sites.

Although this study is limited it does indicate that the type of management used is very important. More detailed comparisons between the success of the different management options outlined above would be worthwhile; especially on the effects of total litter-stripping to remove nutrients and release the available *Calluna vulgaris* seed bank, both in the management of +PS and other stages.

4.5.6 Comparing the two types of model

In this study two models have been used, treating the managed sites as I) active and II) passive samples. As model I treats the managed sites as active samples it shows the relationship between the heath, successional and managed sites. This model is especially useful for testing if the managed site is moving in a direction other than towards the 'target', eg towards grassland. Model II calculates the positioning of the managed sites, from the abundance of species occurring in successional and heath sites. Therefore if the site is dominated by species not present in the heath or successional communities then the true positioning of the site may not be shown. However model II enables the managed sites to be positioned along the trajectory between the heath and successional sites and a measurement of the closeness of the managed site to the 'target' to be made. Both models are therefore needed for a realistic judgement of management success to be made.

4.5.7 Future developments of the model

This study and the previous study in Chapter 3 (Mitchell *et al.* 1997) have shown that models such as these are repeatable over time and can be used to relate the managed sites to successional processes on nature reserves. The models can be used to place managed sites in relation to the 'start' and 'target' sites and provide:

1) a measure of the effectiveness of management
2) a measure of the resilience of the site
3) an early warning system.

The advantage of this method to assess the success of the management (the distance of the managed site from the 'target') is that it is not based on one factor alone, vegetation or soil, but combines abiotic and biotic factors to produce a combined measure of success. Such models may be used for a more detailed study of the effectiveness of different management treatments. Models such as these could also be developed for other habitats.

If the same site was surveyed repeatedly over time the resilience of the site could be measured quantitatively and help to provide information on basic ecological processes. Having moved along the successional trajectory towards the heath, does the site remain there or does it 'bounce' back towards the starting point? Thus for the first time we have a multivariate method using biotic and abiotic processes for measuring ecosystem resilience.

Moreover, the A value provides a measure of how straight a trajectory the managed site is on within the assumed successional trajectory. If the trajectory is not straight this provides an early warning system that the site is moving in an unexpected direction and that more management may be needed.

4.6 CONCLUSION

The management of the successional sites allows many heathland species to re-establish and the site starts to become similar to the neighbouring heath. The reversion of increased soil nutrients and pH is more problematic with ammonium-nitrogen, pH, phosphorus, calcium and magnesium frequently being significantly different in the managed sites compared to the heaths and sometimes being even higher than the successional stages. The stage and type of management of the site will effect the success of reversion. The study of successional, managed and plagioclimax habitats is of great value for the development of models which may then be used to monitor the success of the restoration of the managed site.

Chapter 5

A COMPARATIVE STUDY OF THE SEEDBANKS OF HEATHLAND AND SUCCESSIONAL HABITATS IN DORSET, SOUTHERN ENGLAND.

5.1 INTRODUCTION

The soil seedbank is an important part of the plant community (Miles 1979) as it acts as a potential pool of propagules for regeneration after disturbance (Donelan & Thompson 1980; Stieperaere & Timmerman 1983; Lavorel, Lebreton, Debussche & Lepart 1991; Hodgson & Grime 1992; Pakeman & Hay 1996). The viable seedbank and the vegetation on a site are dynamically linked, although some species may be present in one of these but not the other (Chippindale & Milton 1934; Thompson & Grime 1979).

The changes within seedbanks that occur during succession have been extensively investigated (Hayashi & Numata 1964; Thompson & Grime 1979; Donelan & Thompson 1980) with an increasing divergence found between the composition of the vegetation and the seedbank during the course of succession. Early, more disturbed, successional communities tend to have a higher density of seeds per unit volume of soil than the later, more stable, successional communities (Donelan & Thompson 1980; Fenner 1985).

The role of seedbanks in secondary succession in many communities is important as the content of the seedbank will influence the initial floristic composition of the site after disturbance (Hobbs & Gimingham 1984; Mallik, Hobbs & Legg 1984). This in turn will determine the future floristic development of the site (Egler 1954; Connell & Slatyer 1977; Noble & Slatyer 1980; Hobbs & Gimingham 1984; Hobbs & Legg 1984). Thus if species commonly thought of as late successional species are present in the seedbank they may become established early on in the succession instead of species commonly regarded as early successional species (Connell & Slatyer 1977).

Lowland heaths are one of many man-made habitats where the vegetation is often threatened by successional change to other communities (Marrs, Hicks & Fuller 1986; Webb & Haskins 1980; Webb 1990). Lowland heaths are an important biotope in the U.K., and as Britain has an international obligation to conserve its lowland heaths (Department of the Environment 1995a,b) considerable resources are being spent on restoring successional areas to heathland. The success of this restoration work at least partially depends on the content of the viable seedbank of the managed site (Putwain & Gillham 1990; Gimingham 1992).

Calluna vulgaris has long been recognised as having a large buried seedbank (Chippendale & Milton 1934) and has been shown to survive under 73 year old *Pinus abies* forest (Granström 1988). If this buried seedbank can be made to germinate then biotope restoration will be considerably cheaper than if propagules have to be added as seed, or within litter or topsoil (Gimingham 1992; Pywell, Webb & Putwain 1995). Many seedbank studies of heathland species concern the survival of seeds beneath arable/reclaimed land (Chippendale & Milton 1936; Stieperaere & Timmerman 1983, Pywell, Putwain & Webb 1997) or beneath plantations (Hill & Stevens 1981; Granström 1987 & 1988). Few studies have looked at the way that heathland seedbanks change during succession (Pakeman & Hay 1996). Miles and Young (1980) note changes in the species composition of the seedbank on moorland during *Betula* spp. succession, with the buried seed flora slowly changing to one characteristic of a woodland. Similarly Pakeman and Hay (1996) showed that the seedbank of heathland which has been under *Pteridium aquilinum* for more than 50 years was very small and propagule introduction was thought necessary for successful restoration. These authors concluded that both the size and quality of the viable seedbank were determinants of the success of heathland restoration on successional sites, and it was important to take this into account when planning restoration schemes.

In order that restoration is successful it is important to take into account both the presence of heathland species and non-heathland ones. If the seedbank contains non-heathland species which are more competitive than the heathland ones then the disturbance caused by management may allow these more competitive species to dominate and prevent establishment of heathland species.

Dorset has the third largest area of lowland heath in England after Hampshire and Surrey (British Gas 1988; Cadbury 1989). These heaths have been considerably fragmented and reduced in area over the last century (Moore 1962; Webb & Haskins 1980; Webb 1980, 1990). Thus the conservation of the remaining Dorset heaths and the restoration of heathland on areas that have been invaded by successional species is of great importance (Auld, Davies & Pickess 1992; Woodrow *et al.* 1996a)

On the Dorset heaths a range of successions are commonly found (Chapter 2; Mitchell *et al.* 1997) and it is possible that some successions may have a greater effect on the seedbank than others. Here we aimed to compare the seedbanks of both heathlands and different successional communities to test the following hypotheses;

1) That the seedbanks of successional communities were significantly different from those of the heathland,

2) That the seedbanks of some successional communities are more similar to the heathland than others and conversely some have suffered greater depletion,

3) That the balance of heathland and non-heathland species in the seedbanks was different in some successions.

Ultimately the aim was to use the results from this study to help develop practical conservation management strategies for heathland restoration on sites where succession has occurred. Through out this paper the term heathland restoration means the establishment of a dwarf shrub community dominated by *Calluna vulgaris*.

5.2 MATERIALS AND METHODS

Ten heathland areas in the Poole Basin of Dorset (Southern England) were chosen (Table 5.1), all these areas were within a 20 km radius of each other. At each area there was an open heath stage that had not been invaded by any of the successional species and a range of successional stages. The heathland sites were all dry heaths and as similar as possible to the successional stages before invasion occurred on these sites. The successional stages were classed on the basis of the dominant invasive species as follows:

+B - major invader is *Betula* spp.,

+PS - major invader is *Pinus sylvestris,*

+PA - major invader is *Pteridium aquilinum,*

+R - major invader is *Rhododendron ponticum,*

+U - major invader is *Ulex europaeus.*

Table 5.1. The heathland areas in Dorset, their location, successional stages noted as the approximate time (years before 1995) over which these stages have occurred (x); data derived from aerial photographs.

Site	Grid Reference	Successional Stage					
		Heath	+B	+PS	+PA	+R	+U
Arne	SY973882	H	$30 > x > 23$	$43 > x > 23$	$49 > x > 43$	$49 > x > 43$	$49 > x > 30$
Avon Heath County Park (AHCP)	SU128035	H	$x > 23$	$x > 23$	$23 > x$	?	$23 > x$
Blackhill	SY840940	H	$23 > x > 9$	$23 > x > 9$	$48 > x > 23$	$48 > x > 23$	$48 > x > 23$
Canford Heath	SZ030950	H	$23 > x$	$x > 49$	$48 > x > 23$	$48 > x > 23$	$23 > x$
Cranborne Common	SU104112	H			$x > 49$		$x > 49$
Higher Hyde Heath	SY851907	H	$48 > x > 23$		$23 > x > 9$	$48 > x > 23$	$48 > x > 23$
St Catherines Hill & Town Common	SZ142955	H	$48 > x$	$48 > x$		$48 > x$	
Sopley & Ramsdown	SZ133974	H	$x > 48$	$x > 48$		$x > 48$	
Trigon	SY884908	H		$48 > x > 23$	$48 > x > 23$	$48 > x > 23$	
Winfrith Heath	SY805865	H			$23 > x > 9$		$x > 23$
Number of paired samples		30	21	21	24	24	21

H = Open Heath site
? = stage sampled but time over which successional stage occurred unknown
$>$ = greater than sign used to indicate the range of years over which the successional stage (x) has occurred, for some stages the data was incomplete and only the maximum or minimum of the range is shown

Aerial photographs of the sites taken in 1946/47, 1972/73 and 1986 showed that the successional stages were all heathland 20-50 years ago (Table 5.1). The successional stages were positioned as close as possible to the heathlands to enable comparisons of the stages to be as valid as possible. The vegetation of these sites has been described in detail in Chapter 2.

5.2.1 Sampling

In late February 1996 six soil cores (diameter 5.0 cm, depth 6.3 cm), were sampled from each site. The cores were grouped into three pairs, and the paired samples were then mixed to form a sample from an area of 39 cm^2 with a volume of 247 cm^3. This gave 30 samples from the heath sites, 21 samples from +B, +PS, and +U stages and 24 samples from +PA and +R sites. All samples were stored in a cold room at 4° C until the experiment was set up.

Each sample was sieved through a 4 mm mesh to remove large stones and then spread thinly on to a tray (21 x 35 cm) containing sterile sand. The trays were randomly placed in a polytunnel and watered regularly. Eleven control trays containing sterile sand were also set up to detect wind blown seed. The seedlings were identified using Muller (1978) and counted as they emerged over the following 15 months. Those species which could not be identified at the seedling stage were potted on until identification was possible. It was not possible to distinguish between the three *Ulex* species and two *Erica* species and these were recorded as *Ulex* spp. and *Erica* spp. respectively. Species recorded in both the control trays and the experimental trays, mainly glasshouse weeds, were not included in the analysis. Results were expressed as seeds m^{-2} to a depth of 6.3 cm. Species nomenclature follows Stace (1991).

5.2.2 Statistical analysis

The data was analysed using the linear multivariate technique Canonical Discriminant Analysis (CDA), using the CANDISC procedure (SAS Institute Inc. 1988). This technique can be used to detect differences in species composition between groups (Benoit, Derksen & Panneton 1992). The data was transformed using a square root transformation prior to analysis. CDA finds linear combinations of discriminating variables which maximise the differences between groups (the six stages in this case) and minimises the differences within the groups. It performs this by maximising the ratio of the between-group sum of squares and the within-group sum of squares of the site scores (Jongman, Ter Braak & Van Tongeren 1995). The maximum number of discriminating variables is the number of groups minus one, 5 in this case.

The Wilks's lambda test, a multivariate measure of group (stage) differences over several variables, was used to test whether the differences explained by the discriminating variables are significant (Klecka 1980), ie whether the differences between the stages indicated by that discriminating variable are likely to occur in the population as well as in the samples. Only discriminating variables that were statistically significant were used in the explanation of the results.

The test statistic used to discriminate between groups is the Mahalanobis distance (D^2) (Klecka 1980) and is calculated by the CANDISC procedure (SAS 1988). A large value of D^2 indicates good discrimination between groups. The Mahalanobis distance was converted to an F statistic (SAS 1988) to test if the stages were significantly different from each other.

5.3 RESULTS

5.3.1 Species composition of the seedbanks

All of the results are presented in Table 5.2, here only the major differences between the stages are discussed.

The samples from the heath sites contained large numbers of *Calluna vulgaris* seedlings (2000-28000 m^{-2}); *Erica* spp. were also present at seven of the ten sites although at lower densities (100-8000 m^{-2}) than *Calluna vulgaris.* Other species present included *Betula* spp., *Carex pilulifera, Molinia caerulea* and *Ulex* spp. and these had much lower densities (< 800 m^{-2}).

Betula spp. were present at all +B sites at densities of between 400-8000 m^{-2}. *Calluna vulgaris* was also present in all +B sites, usually at much lower densities than the heath sites, AHCP being an exception The heathland species *Agrostis curtisii, Erica* spp., *Molinia caerulea, Carex pilulifera* and *Ulex* spp. were also present in some samples. Other non-heathland species were also recorded, *Digitalis purpurea, Geranium robertianum, Holcus lanatus, Juncus bufonius, Rubus glandulosus* and *Rumex acetosella*; of these *Juncus bufonius* was the most common.

The +PS stage contained fewer species than the +B stage. These were mainly heathland species, *Calluna vulgaris, Carex pilulifera, Erica* spp., *Molinia caerulea* and *Ulex* spp. The *Calluna vulgaris* content of the samples was variable with some sites having very high densities, similar to the heathland (AHCP and Blackhill) and others having much lower densities (Canford). *Betula* spp. and *Juncus bufonius* were also recorded although at lower densities than in the +B stage. *Sagina procumbens* and *Teucrium scorodonia* were also present.

Table 5.2. Species recorded in soil samples at Heath (H), and successional stages (*Betula* spp. (+B), *Pinus sylvestris* (+PS), *Pteridium aquilinum* (+PA), *Rhododendron ponticum* (+R), *Ulex europaeus* (+U)) on Dorset Heaths. Means ± SE (n = 3) are shown, results are number of seedlings m^{-2} to a depth of 6.3 cm.

Stage	Species	Arne	AHCP	Blackhill	Canford Heath	Cranborne Common	Higher Hyde Heath	St Catherines Hill	Sopley & Ramsdown	Trigon	Winfrith
H	*Betula* spp.	255 ± 255	85 ± 85	170 ± 85	85 ± 85	0	170 ± 170	0	85 ± 85	0	0
	Calluna vulgaris	24276 ± 8454	15363 ± 2728	7894 ± 4116	5942 ± 4200	11466 ± 3949	21475 ± 5374	3225 ± 1861	28435 ±16722	4668 ± 2091	2205 ± 1266
	Carex pilulifera	0	0	0	0	0	0	0	0	0	85 ± 85
	Erica spp.	5772 ± 5772	170 ± 170	1782 ± 1535	0	7810 ± 3749	1613 ± 740	85 ± 85	6536 ± 6281	0	0
	Holcus lanatus	0	0	0	170 ± 170	0	0	0	0	0	0
	Hypochaeris radicata	0	0	0	0	0	85 ± 85	0	0	0	0
	Juncus bufonius	170 ± 170	0	0	0	85 ± 85	85 ± 85	85 ± 85	0	0	170 ± 170
	Molinia caerulea	0	0	0	0	764 ± 530	0	0	0	0	0
	Sagina procumbens	0	0	0	0	0	0	85 ± 85	0	0	85 ± 85
	Tripleurospermum inodorum	0	255 ± 147	0	0	0	0	0	0	0	0
	Ulex europaeus	0	0	0	255 ± 147	0	0	0	0	0	0
+B	*Agrostis curtisii*	0	0	509 ± 509	0		0	0	85 ± 85		
	Betula spp.	849 ± 473	1443 ± 663	679 ± 306	3650 ± 2007		7300 ± 3483	3395 ± 1113	425 ± 306		
	Calluna vulgaris	85 ± 85	19608 ± 1789	1698 ± 1318	5433 ± 2752		2716 ± 1480	934 ± 695	1613 ± 1001		
	Carex pilulifera	0	0	2122 ± 1983	0		0	0	255 ± 255		
	Digitalis purpurea	2292 ± 2292	0	0	0		0	0	85 ± 85		
	Erica spp.	0	12818 ±10150	340 ± 340	441 ± 441		425 ± 306	0	85 ± 85		
	Geranium robertianum	0	0	0	0		0	255 ± 147	85 ± 85		
	Holcus lanatus	0	85 ± 85	0	0		255 ± 255	764 ± 0	0		
	Juncus bufonius	0	5263 ± 2736	2122 ± 1334	339 ± 170		4838 ± 1403	9082 ± 7489	85 ± 85		
	Molinia caerulea	0	340 ± 225	0	340 ± 340		85 ± 85	85 ± 85	0		
	Rubus glandulosus	0	0	0	0		0	170 ± 85	0		
	Rumex acetosella	0	255 ± 255	0	0		0	85 ± 85	255 ± 255		
	Ulex spp.	85 ± 85	0	1019 ± 255	0		0	0	0		

Table 5.2 cont.

Stage	Species	Arne	AHCP	Blackhill	Canford Heath	Cranborne Common	Higher Hyde Heath	St Catherines Hill	Sopley & Ramsdown	Trigon	Winfrith
+PS	*Betula* spp.	170 ± 85	170 ± 170	0	424 ± 225			594 ± 594	0	0	
	Calluna vulgaris	509 ± 147	10016 ± 5144	44224 ±42696	170 ± 170			1358 ± 898	2462 ± 1084	9422 ± 2723	
	Carex pilulifera	85 ± 85	0	0	0			0	0	0	
	Erica spp.	85 ± 85	0	0	0			0	0	85 ± 85	
	Juncus bufonius	509 ± 255	85 ± 85	0	0			424 ± 225	1443 ± 740	85 ± 85	
	Molinia caerulea	85 ± 85	170 ± 170	0	0			0	0	0	
	Sagina procumbens	0	170 ± 170	0	0			0	0	0	
	Teucrium scorodonia	85 ± 85	0	0	0			0	0	0	
	Ulex spp.	0	0	0	0			0	85 ± 85	0	
+PA	*Agrostis curtisii*	0	0	0	0	85 ± 85	0			0	0
	Betula spp.	424 ± 424	170 ± 170	0	85 ± 85	85 ± 85	0			594 ± 225	0
	Calluna vulgaris	425 ± 170	10950 ± 6180	11629 ± 3700	6027 ± 4520	170 ± 170	2886 ± 1366			4946 ± 3968	2799 ± 1417
	Carex pilulifera	0	0	0	0	0	0				170 ± 170
	Erica spp.	0	0	2283 ± 1648	509 ± 509	0	0			340 ± 340	0
	Geranium robertianum	0	0	0	0	0	0			0	85 ± 85
	Holcus lanatus	0	85 ± 85	0	0	0	0			0	85 ± 85
	Juncus bufonius	1019 ± 894	0	0	85 ± 85	255 ± 255	255 ± 147			2460 ± 1316	0
	Luzula campestris	0	0	0	0	0	0			85 ± 85	0
	Molinia caerulea	0	0	85 ± 85	0	85 ± 85	85 ± 85			170 ± 170	0
	Rubus glandulosus	0	0	0	0	0	0			85 ± 85	0
	Rumex acetosella	0	170 ± 170	0	0	0	0			0	0
	Teucrium scorodonia	0	85 ± 85	0	0	0	0			170 ± 170	0
	Ulex spp.	0	0	170 ± 85	0	934 ± 810	85 ± 85			170 ± 170	0

Table 5.2 cont.

Stage	Species	Arne	AHCP	Blackhill	Canford Heath	Cranborne Common	Higher Hyde Heath	St Catherines Hill	Sopley & Ramsdown	Trigon	Winfrith
+R	*Betula* spp.	764 ± 530	85 ± 85	2292 ± 1167	0		2377 ± 557	85 ± 85	594 ± 225	0	
	Calluna vulgaris	2632 ± 2007	255 ± 147	679 ± 306	85 ± 85		4584 ± 3251	0	509 ± 85	9075 ± 6913	
	Erica spp.	0	0	0	0		0	0	85 ± 85	1527 ± 1527	
	Hypochaeris radicata	0	85 ± 85	0	0		0	0	0	0	
	Juncus bufonius	894 ± 340	509 ± 294	85 ± 85	0		9337 ± 5892	0	170 ± 85	509 ± 255	
	Molinia caerulea	0	85 ± 85	0	0		0	0	0	0	
	Rubus glandulosus	0	85 ± 85	0	0		0	0	0	0	
	Rumex acetosella	0	85 ± 85	0	0		0	85 ± 85	0	0	
	Sagina procumbens	0	0	0	0		0	0	85 ± 85	0	
	Tripleurospermum inodorum	0	0	170 ± 170	0		0	0	0	0	
+U	*Agrostis curtisii*	0	0	0	0	85 ± 85	0				1188 ± 1063
	Betula spp.	85 ± 85	255 ± 147	85 ± 85	0	85 ± 85	85 ± 85				0
	Calluna vulgaris	679 ± 370	6536 ± 1919	3905 ± 2142	255 ± 255	2037 ± 509	4244 ± 2426				10093 ± 3192
	Carex pilulifera	85 ± 85	0	0	0	0	0				0
	Erica spp.	0	255 ± 147	0	85 ± 85	0	424 ± 424				1272 ± 640
	Juncus bufonius	255 ± 147	340 ± 85	0	170 ± 85	255 ± 147	0				1018 ± 1018
	Leucanthemum vulgaris	0	0	0	0	85 ± 85	0				0
	Molinia caerulea	0	0	0	0	1188 ± 370	340 ± 340				934 ± 810
	Rubus glandulosus	0	0	0	0	0	0				85 ± 85
	Taraxacum spp.	0	85 ± 85	0	0	0	0				0
	Tripleurospermum inodorum	0	0	0	0	0	85 ± 85				0
	Ulex spp.	0	340 ± 225	85 ± 85	0	679 ± 306	340 ± 170				510 ± 255

The +PA stage was similar to the +B stage as it contained a greater variety of non-heathland species than the other stages, including *Betula* spp., *Geranium robertianum, Holcus lanatus, Luzula campestris, Rubus glandulosus, Rumex acetosella* and *Teucrium scorodonia.* The heath species *Agrostis curtisii, Calluna vulgaris, Carex pilulifera, Erica* spp. and *Ulex* spp. were also present.

The +R stage generally contained few viable seeds compared to the other stages. *Calluna vulgaris* was present at all sites except St Catherine's Hill. *Betula* spp. and *Juncus bufonius* were the most frequent species other than *Calluna vulgaris.* Other species which occurred occasionally were *Erica* spp., *Hypochaeris radicata, Tripleurospermum inodorum, Molinia caerulea, Rubus glandulosus, Rumex acetosella* and *Sagina procumbens.*

At the +U sites the most common species were heathland species, *Agrostis curtisii, Calluna vulgaris, Erica* spp., *Molinia caerulea* and *Ulex* spp. Other species which occurred were *Betula* spp., *Juncus bufonius, Leucanthemum vulgaris, Tripleurospermum inodorum, Rubus glandulosus* and *Taraxacum* spp.

5.3.2 CDA results

The eigenvalues for the first two discriminating variables show that these two variables have the greatest discriminating power; 81% of the total (Table 5.3). The squared canonical correlation indicates that the first two discriminating variables were highly correlated with the stages and that the stages were different when analysed according to the species present in the seedbank (Table 5.3). The Wilks's lambda test (Table 5.3) showed that the first two discriminant variables were significant ($P<0.0001$ and $P<0.05$) and that the remaining three were not. Therefore, here the interpretation of results is confined to the first two discriminating variables.

Table 5.3. CDA results for the five discriminating variables obtained from analysis of the species present in seedbanks on Dorset heaths and successional stages.

Discriminating variable	Eigenvalue	Eigenvalue proportion	Eigenvalue Cumulative proportion	Squared Canonical Correlation	Wilk's lambda	Wilk's lambda Pr > F
1	1.5499	0.6211	0.6211	0.6077	0.1733	0.0001
2	0.4631	0.1856	0.8067	0.3165	0.4420	0.0426
3	0.3037	0.1218	0.9285	0.3239	0.6467	0.5494
4	0.1108	0.0444	0.9729	0.0998	0.8431	0.9728
5	0.0677	0.0271	1.0000	0.0634	0.9366	0.9604

The discriminating variables (which may be treated as axes) are composed of discriminating species. The following species were positively correlated with the first axis: *Betula* spp., *Juncus bufonius, Holcus lanatus, Geranium robertianum, Rumex acetosella, Carex pilulifera, Digitalis purpurea* and *Rubus glandulosus. Calluna vulgaris* and *Erica* spp. were positively correlated with the second axis and *Ulex* spp. was negatively correlated with this axis.

The distribution of samples on the first two canonical axes (Fig. 5.1) separated out the +B stage at the positive end of Axis 1 from other samples. In the middle of this axis the +PS, +PA and +R samples were intermixed with some of the +B samples. The heath and +U samples were found at the negative end of this axis. There is a considerable amount of intermixing between groups on this axis. The heath samples were positioned at the positive end of the second axis, these intermixed with the +PA and +PS samples in the middle of this axis and the +U samples occurred at the negative end of this axis.

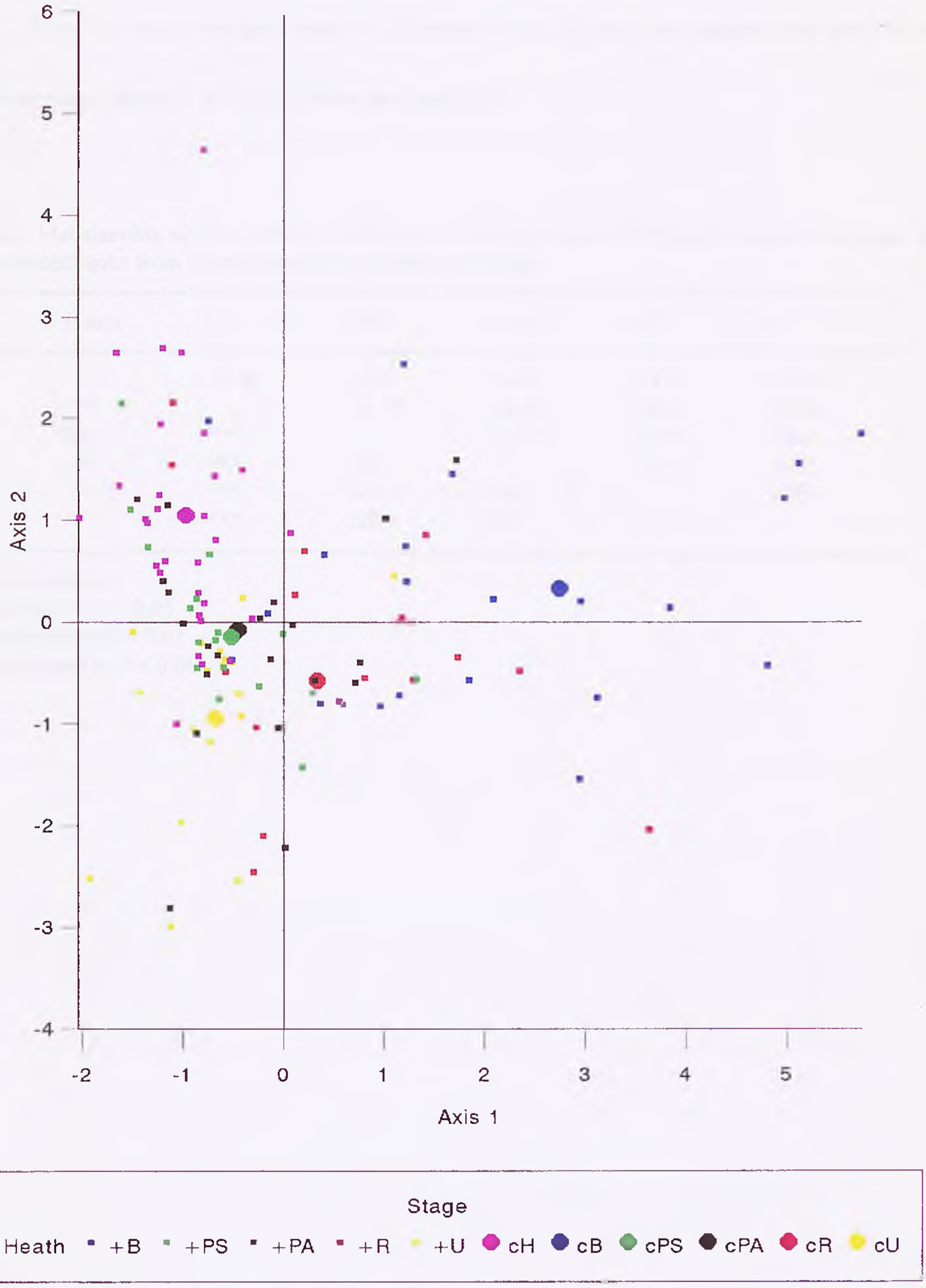


Fig. 5.1. Samples plotted by their scores for the first two canonical variables as calculated by CDA. The centroids for each stage are also shown and are labelled cH, cB, cPS, cPA, cR and cU for the centroids of heath, +B (stage dominated by *Betula* spp.), +PS (stage dominated by *Pinus sylvestris*), +PA (stage dominated by *Pteridium aquilinum*), +R (stage dominated by *Rhododendron ponticum*) and +U (stage dominated by *Ulex europaeus*) respectively.

The differences between the Mahalanobis distances (Table 5.4) show that the +B, +R and +U stages are significantly different from the heath whereas the +PS and +PA stages are not. The +B stage is significantly different from all the other stages and the +R and +U stages are significantly different from each other.

Table 5.4. Mahalanobis squared distances (D^2) and level of significant differences between sites from the CDA analysis of seedbanks from Dorset heaths and successional stages.

	Heath	+B	+PS	+PA	+R	+U
Heath	-	14.43	2.42	2.42	5.14	4.66
+B	***	-	11.78	10.92	8.08	13.69
+PS	NS	***	-	1.59	1.77	2.85
+PA	NS	***	NS	-	2.98	2.02
+R	***	***	NS	NS	-	3.97
+U	**	***	NS	NS	*	-

NS = Not significant
* = Significant at $P < 0.05$
** = Significant at $P < 0.01$
*** = Significant at $P < 0.001$

5.4 DISCUSSION

5.4.1 Experimental technique

Seedbank studies are beset by a number of limitations which need to be considered when discussing the results of this experiment. Studies often suffer from insufficient replication and sampling size (Benoit, Kenkel & Cavers 1989; Gross 1990) and the limited area of soil sampled in this study may have given rarer species little chance to be present as a seed in the sample and restricted the precision of the other estimates. However these rarer species are unlikely to be important in terms of restoration. Although it may be argued that more accurate results could have been obtained by an increased number of samples from fewer sites, all these sites were studied so that the results could be related to other studies on these sites (Chapters 2,3 & 4; Mitchell *et al.* 1997 & in prep). The seedbank was only sampled once rather than consecutively throughout the year, but this is unlikely to influence the estimates for heath species greatly because these species tend to have a large persistent seedbank relative to annual seed inputs (Thompson & Grime 1979) and sampling was timed to take place after the heath plants had dispersed their seed. Timing may however have influenced the estimates for some non-heathland species.

It is also unlikely that optimum conditions for the germination of all species present in the seedbank were provided. The samples were, however, collected at the end of a cold winter and a chilling pre-treatment was thought unnecessary. As the experiment was done in an unheated polytunnel with widely varying diurnal temperature changes and the soil was spread thinly on each tray, conditions should have been suitable for the germination of most heathland species. However, those autumn-germinating species which do not form a persistent seedbank may be under represented.

It is also possible that new germinations would have occurred several years after the start of the germination trials (Chippindale & Milton 1934). The proportion of innately dormant seeds is unknown and varies with species, so the term seed population in this discussion refers specifically to the immediately germinable seeds. The period of the experiment (15 months) may not have allowed all the seeds to germinate and hence underestimated the size of the seedbank. However a period of more than a year provided opportunity for both spring and autumn germinating seeds to germinate and other studies have shown that most seeds germinate in the first 8 months of the study (Hill & Stevens 1981). The 15 months of this study is longer than many studies. In spite of these uncertainties the values obtained are adequate for the purposes of this comparative study; they provided a general indication of seed density and allowed comparisons between the heath and successional stages to be made.

5.4.2 Comparisons of the seedbanks of the different stages

The CDA analysis showed that the +B stage was the most different from both the heath and all the other successional stages. This was due to the presence of (1) a large number of *Betula* spp. seedlings, (2) a few other non-heathland species and (3) relatively fewer *Calluna vulgaris* seedlings than the other stages, (except at AHCP). The stages next furthest from the heath are +R and +U. The +R contained few seedlings of any species while the +U stage contained more *Ulex* spp. seedlings than the heath samples. The +PS and +PA stages were closer to the heath than the other samples.

The sites can therefore be ranked in order of closeness to heath: +PS & +PA < +U & +R < +B, (where < represents increasing distance from the heath). This ranking is similar to the order given when only the species composition of the vegetation was analysed, +U & +PS < +PA < +R & +B (Chapter 2; Mitchell *et al.* 1997). Once again the +R and +B stages are furthest from the heath vegetation and the +PS is close to the heath. The major difference is that +U stage is further from the heath in the seedbank ranking than in the vegetation ranking and the +PA stage is closer to the heath in the seedbank ranking than in the vegetation ranking, a result of the persistent seedbank of *Ulex* spp.

Although similar patterns between the seedbank and the vegetation data were found, the separation in the seedbank analysis was less clear, with the heath and the successional stages being more intermixed. This result indicates that while the vegetation flora may have changed completely from that of open heathland (Chapter 2; Mitchell *et al.* 1997), the seedbank flora remains fairly similar to that of the heath for a longer period although some successional stages are more similar to the heath than others.

5.4.3 The seedbank flora

Calluna vulgaris was present in the seedbanks of all the stages, the numbers recorded were fairly typical of heathland seedbanks present beneath plantations or *Pteridium aquilinum* on former heathland (Hill & Stevens 1981; Granström 1988; Pakeman & Hay 1996). The higher values recorded here are greater than those recorded by Miles (1973) for various Callunetum soils in Scotland but are similar to the values of Chippendale & Milton (1934) for a Callunetum in Wales and are typical of heathland seedbanks in Dorset (Pywell 1993). These results confirm that *Calluna vulgaris* seeds can survive buried beneath successional stages for up to 50 years. However the total density of seeds appears to vary between the stages with +B and +R stages having the lowest densities. The decline in the +B stage may be due to an increase in earthworm and other soil fauna and flora activity as the soil beneath a *Betula* spp. wood slowly changes from a mor to a mull soil (Satchell 1980b; Miles 1981a, 1985). The decline in numbers in the +R stage may be due to toxins released by the *Rhododendron ponticum* (Cross 1975) decreasing the viability of the *Calluna vulgaris* seeds. Although *Calluna vulgaris* is present in the seedbanks of the successional stages, whether the density is high enough to allow a sufficiently dense *Calluna vulgaris* sward to establish thus preventing the invasion of more competitive species is unknown. For those stages and sites with small *Calluna vulgaris* seedbanks, propagules must be added for successful restoration (Pakeman & Hay 1996). *Erica* spp. were also present at many sites and may also help restoration.

After *Calluna vulgaris, Juncus bufonius* was the most common species in the seedbank. *Juncus* spp are often present in large densities in the seedbanks of heathland and former heathland sites (Stieperaere & Timmerman 1983; Hill & Stevens 1981; Granström 1988; Putwain & Gillham 1990) even if they are absent from or only present at low cover in the vegetation (Stieperaere & Timmerman 1983). *Juncus* species may be present in sufficient numbers in the top soil of managed sites to become an undesirable component of the developing heathland plant community (Putwain & Gillham 1990) and are a common species on managed successional sites (Chapter 4; Mitchell *et al.* in prep). *Carex* spp. were frequently present in the seedbanks of the successional stages and are commonly found in heathland seedbank studies (Hill & Stevens 1981; Granström 1988; Pakeman & Hay 1996).

Of the major successional species *Betula* spp. and *Ulex* spp. were the only ones occurring in the seedbank. Some *Betula* spp. seeds germinate soon after release, while others may form a more persistent seedbank (Grime, Hodgson & Hunt 1988), remaining viable for at least 5 years in a forest soil (Granström 1987). These seeds would become a problem in restoration work if a large seedling population emerged (Putwain & Gillham 1990). *Ulex* spp. are known to have large persistent seedbanks (Grime, Hodgson & Hunt 1988) and may become a problem if large seedling populations emerge from the topsoil in managed sites (Putwain & Gillham 1990). Both *Betula* and *Ulex* spp. were frequently present as seedlings on recently managed successional sites on the Dorset heaths (Chapter 4). Whether these plants become a problem and limit the success of the restoration depends on the survival rate of the seedlings relative to the development of the heathland species. *Pinus sylvestris* and *Rhododendron ponticum* have transient seedbanks with no dormancy (Cross 1975; Granström 1987), and so the seeds of these species are unlikely to be problematic in terms of restoration. *Pteridium aquilinum* can propagate by spores, although the significance of this as a means of regeneration is unknown (Dyer 1989) and no spores germinated from the soil sample here. *Pteridium aquilinum* also spreads by means of extensive rhizomes, so while not present in the seedbank it may still be difficult to control (Marrs, Pakeman & Lowday 1993).

Other potentially problematic species, from a restoration viewpoint, that were detected in the seedbanks included *Holcus lanatus, Rubus glandulosus, Rumex acetosella, Tripleurospermum inodorum, Geranium robertianum, Teucrium scorodonia, Hypochaeris radicata* and *Leucanthemum vulgaris.* Whether these species cause problems for the restoration of heathland depends on their density in the seedbank and whether increases in soil nutrients that occur during succession are reversed by management intervention (Chapter 3; Mitchell *et al.* 1997). The increase in nutrients may give these competitive species an advantage over the heathland species (Marrs & Gough 1989).

5.4.4 Comparison of vegetation and seedbank floras

The sites sampled were the same as those surveyed by Mitchell *et al.* (1997) (Chapter 2). This allows a comparison of the species present in the vegetation and the seedbanks to be made (Table 5.5). Most heathland species are found in both the vegetation and the seedbank. *Carex pilulifera, Juncus bufonius* and *Sagina procumbens* were only found in the seedbanks (Table 5.5). These species are often found surviving in heathland/ex-heathland

Table 5.5. Species present in the vegetation and/or seedbank samples at five successional stages on the Dorset heaths. Numbers in parenthesis refer to the seedbank type of Grime *et al.* (1988); type I = most seed germinates shortly after shedding; type II = most seed persistent only until start of next growing season; types III = a small amount of seed persists in soil but concentrations high only immediately after shedding; type IV = a large persistent seedbank; ? = strategy of regeneration by seed uncertain.

Stage	Present in seedbank and the vegetation		Present only in the seedbank		Present only in the vegetation	
+B	*Agrostis curtisii*	(?)	*Carex pilulifera*	(IV)	*Agrostis capillaris*	(III/IV)
	Betula spp.	(III)	*Geranium robertianum*	(?)	*Carex nigra*	(?)
	Calluna vulgaris	(IV)	*Juncus bufonius*	(IV)	*Chamerion angustifolium*	(I)
	Digitalis purpurea	(III)			*Galium saxatile*	(IV)
	Erica spp.	(IV)			*Hedera helix*	(?)
	Holcus lanatus	(III)			*Ilex aquifolium*	(?)
	Molinia caerulea	(II-IV)			*Juncus effusus*	(IV)
	Rubus glandulosus	(IV)			*Lonicera periclymenum*	(II)
	Rumex acetosella	(IV)			*Luzula campestris*	(IV)
	Ulex spp	(IV)			*Pinus sylvestris*	(?)
					Pteridium aquilinum	
					Quercus robur	(I)
					Rhododendron ponticum	(I)
					Senecio erucifolius	(?)
					Sorbus aucuparia	(II)
					Teucrium scorodonia	(II/IV)
+PS	*Betula* spp.	(III)	*Carex pilulifera*	(IV)	*Castanea sativa*	(?)
	Calluna vulgaris	(IV)	*Juncus bufonius*	(IV)	*Hedera helix*	(?)
	Erica spp.	(IV)	*Sagina procumbens*	(IV)	*Holcus lanatus*	(III)
	Molinia caerulea	(II-IV)	*Teucrium scorodonia*	(II/IV)	*Ilex aquifolium*	(?)
			Ulex spp	(IV)	*Lonicera periclymenum*	(II)
					Pinus sylvestris	(?)
					Pteridium aquilinum	
					Quercus robur	(I)
					Rhododendron ponticum	(I)
					Rubus glandulosus	(IV)
					Sorbus aucuparia	(II)
+PA	*Agrostis curtisii*	(?)	*Geranium robertianum*	(?)	*Agrostis capillaris*	(III/IV)
	Betula spp.	(III)	*Holcus lanatus*	(III)	*Agrostis gigantea*	(III)
	Calluna vulgaris	(IV)	*Juncus bufonius*	(IV)	*Aira praecox*	(I/III)
	Carex pilulifera	(IV)			*Anthoxanthum odoratum*	(III)
	Erica spp.	(IV)			*Crataegus monogyna*	(?)
	Luzula campestris	(IV)			*Lonicera periclymenum*	(II)
	Molinia caerulea	(II-IV)			*Pinus pinaster*	(?)
	Rubus glandulosus	(IV)			*Pinus sylvestris*	(?)
	Rumex acetosella	(IV)			*Potentilla erecta*	(I)
	Teucrium scorodonia	(II/IV)			*Prunus spinosa*	(?)
	Ulex spp.	(IV)			*Pteridium aquilinum*	
					Quercus robur	(I)
					Serratula tinctoria	(?)
					Vaccinium myrtillus	(IV)
+R	*Calluna vulgaris*	(IV)	*Betula* spp.	(III)	*Hedera helix*	(?)
	Erica spp.	(IV)	*Hypochaeris radicata*	(I)	*Luzula campestris*	(IV)
	Molinia caerulea	(II-IV)	*Juncus bufonius*	(IV)	*Pinus pinaster*	(?)
	Rubus glandulosus	(IV)	*Rumex acetosella*	(IV)	*Pinus sylvestris*	(?)
			Sagina procumbens	(IV)	*Pteridium aquilinum*	
			Tripleurospermum inodorum	(III)	*Rhododendron ponticum*	(I)
					Sorbus aucuparia	(II)
					Ulex spp.	(IV)

Table 5.5 cont.

Stage	Present in seedbank and the vegetation		Present only in the seedbank		Present only in the vegetation	
+U	*Agrostis curtisii*	(?)	*Carex pilulifera*	(IV)	*Agrostis gigantea*	(III)
	Betula spp.	(III)	*Juncus bufonius*	(IV)	*Cuscuta epithymum*	(?)
	Calluna vulgaris	(IV)	*Leucanthemum vulgaris*	(III)	*Hedera helix*	(?)
	Erica spp.	(IV)	*Taraxacum* spp.	(I)	*Pinus sylvestris*	(?)
	Molinia caerulea	(II-IV)	*Tripleurospermum inodorum*	(III)	*Potentilla erecta*	(I)
	Rubus glandulosus	(IV)			*Pteridium aquilinum*	
	Ulex spp.	(IV)			*Quercus robur*	(I)
					Vaccinium myrtillus	(IV)

Sources: Grime, Hodgson & Hunt (1988) and Mitchell *et al.* (1997).

seedbanks but not occurring in the vegetation (Miles 1973; Hill & Stevens 1981; Stieperaere & Timmerman 1983; Mallik, Hobbs & Legg 1984; Granström 1988;); they may establish once the ground is cleared (Miles 1973).

In most stages few species typical of successional communities except *Betula* spp. and *Rubus glandulosus* were present in both the seedbank and the vegetation (Table 5.5). Many of the additional invaders present in the flora (Mitchell *et al.* 1997) are not present in the seedbank. This discrepancy between vegetation and seedbank flora is common for late-successional communities (Donelan & Thompson 1980; Fenner 1985), and shows that the seedbanks do not change as quickly as the vegetation during succession. Most non-heathland species found in the vegetation are colonising by seed ingress.

The exception to this is the +B stage which does have a few more successional species present in its seedbank; this may be the start of the buried seed flora slowly changing to one characteristic of woodland (Miles & Young 1980). However very few of these species occurred in the seedbank compared to the numbers of non-heathland species present in the +B stage ground flora (Table 5.5).

The majority of species (80%) present only in the seedbank or present in the vegetation and the seedbank (Table 5.5) belong to seedbank type III or IV (Grime, Hodgson & Hunt 1988). These groups contain species which form persistent seedbanks. The species present only in the vegetation belong to all four seedbank categories (Table 5.5). However over half (64%) of these species belong to groups I or II, which do not form persistent seedbanks, or their strategy for regeneration by seed is unknown. Thus many of the successional species present in the ground flora are not present in the seedbank because they do not form a persistent seedbank.

5.4.5 Relevance to conservation management

This study has shown that successional changes are not occurring as quickly in the seedbank flora as in the vegetation and that a viable population of *Calluna vulgaris* seeds is present in the soil for at least 50 years. Thus for the time being, there is a reasonable hope of successful restoration of heathland on these stages. However, with time, the viable *Calluna vulgaris* seed population will decrease, the population of successional species will increase and the capacity of the seedbank to act as a source of heathland propagules will slowly decline. Restoration should therefore be undertaken sooner rather than later and is likely to be more successful on the younger sites.

Despite heathland species being present in all stages, some stages are closer to the heath than others, (+PS and +PA). Restoration of these stages are likely to be more successful than for +B, +R or +U. When deciding where to target resources the results from this study should be combined with information on the changes that occur during succession in soil nutrient concentration (Chapter 3; Mitchell *et al.* 1997), the ease with which the invasive species may be controlled (Marrs 1984, 1987; Marrs & Lowday 1992; Squires 1991) and the cost involved (Woodrow, Symes & Auld 1996b).

Although many heathland species are obviously present in the buried seed flora of successional sites the seeds may need to be brought to the surface to stimulate germination. Areas where the soil has been disturbed by scarifying, turf or litter-stripping have a greater *Calluna vulgaris* establishment than where the soil/litter is undisturbed (Granström 1988; Putwain & Gillham 1990; Smith, Webb & Clarke 1991; Bruggink 1993; Chapter 4). Litter-stripping of successional sites is therefore strongly advised as this releases the dormant seedbank and removes nutrients from the system (Chapter 4), both of which will help to increase the probability of successful restoration. However, as 96% of *Calluna vulgaris* seeds may be in the top 50 mm of the mineral soil (Putwain & Gillham 1990), this disturbance must be done with care. Where litter is removed the aim should be to leave the surface mineral soil intact.

5.5 CONCLUSION

The seedbanks of all the successional sites contained some heathland species, although densities varied, with *Pinus sylvestris* and *Pteridium aquilinum* sites having higher densities than the other successional communities. *Betula* spp. and *Ulex europaeus* successional sites contained more seeds of invasive/successional species than the other sites and the *Rhododendron ponticum* sites had a poor seedbank flora.

The seedbanks from the *Betula* spp., *Rhododendron ponticum* and *Ulex europaeus* successional sites were found to be significantly different from the heathland seedbanks, whereas those of the *Pinus sylvestris* and *Pteridium aquilinum* successional sites were not found to be significantly different from the heathland seedbanks. The seedbanks from the *Betula* spp., successional sites were also found to be significantly different from the other successional communities.

When compared to the vegetation of the sites, many heathland species were present in the seedbank that were not present in the vegetation and many successional species that were present in the vegetation were not present in the seedbank.

The seedbanks beneath *Pinus sylvestris* and *Pteridium aquilinum* successional sites are likely to provide a better source of seed for recolonisation than the seedbanks beneath *Betula* spp., *Rhododendron ponticum* and *Ulex europaeus* successional sites.

Chapter 6

TOWARDS AN IMPROVED UNDERSTANDING OF ECOSYSTEM STABILITY - A STUDY OF THE DORSET HEATHS, SOUTHERN ENGLAND

6.1 INTRODUCTION

There have been many attempts to define ecosystem stability, but often stability is reduced to two components - resilience and resistance (Webster, Waide & Patten 1975; Westman 1978; Leps, Osbornová-Kosinová & Rejmánek 1982). Ecosystem resilience is usually defined as the ability of the system to recover after disturbance (Webster, Waide & Patten 1975; Leps, Osbornová-Kosinová & Rejmánek 1982; Pimm 1984), although this concept has been referred to as stability by some workers (Holling 1973; May 1973). By definition the greater the resilience the shorter the recovery time to equilibrium (T_r), and resilience is measured as $1/T_r$. Resistance is the ability of the ecosystem to avoid displacement from its equilibrium position (Leps *et al.* 1982), although this property has also been referred to as resilience (Holling 1973).

Most studies on ecosystem stability start from a basic assumption that the ecosystem is at equilibrium (Williamson 1987), even if it is aknowledged that this equilibrium is notional. Moreover, it is often assumed that after disturbance there is a return to an equilibrium approximating the original system. This is in the view of this study a major flaw in any generalised theory of ecosystem stability. Investigations of stability have usually measured parameters of either ecosystem structure - vegetation biomass, cover or species diversity (Frank & McNaughton 1991; Tilman & Downing 1994; Collins 1995; Dodd *et al.* 1995) or ecosystem function - often nutrient loss (Jordan, Kline & Sasscer 1972; Webster *et al.* 1975; Borman & Likens 1979), where it is often assumed that the ecosystem has supra-organism properties (Odum 1969).

6.2 CRITERIA FOR A MODEL MEASURING ECOSYSTEM STABILITY

Any generalised model for investigating ecosystem stability and measuring resilience should ideally satisfy the following criteria:

- A test of the assumption that the ecosystem is at an 'approximate equilibrium'.
- A test of the assumption that the disturbed ecosystem will return to an approximation of its undisturbed state.
- Provide a mechanism for bringing together measurements of both structure (species composition) and function (ecosystem properties, both biotic and abiotic).
- Provide a measure of the variability within the ecosystem under investigation; for practical resource management this should be independent of scale and operate at the individual site level, but allow expansion to cover biotopes at regional, national and global scales.
- Accommodate unforeseen ecosystem change associated with stochastic or other factors.
- Be statistically rigorous, and be able to determine which environmental variables are most important for describing the system.
- Be useful in practical resource management.

This paper illustrates a hypothetical model which, for the first time, satisfies all of these criteria, and has the potential to measure resilience rates directly. Moreover, the models produced have direct relevance for conservation managers. A key factor in this approach is the use of multivariate models where a minimum of two ecosystems on a successional trajectory are compared. The models are tested using data collected from the lowland heaths of Dorset which have a high nature conservation profile. The Dorset heaths are an important regional subset of the lowland heath biotope within the European Community. Lowland heaths are man-created and man-managed biotopes termed plagio-climax communities or arrested seres. However, many such heaths are threatened by succession and previous work has identified a range of successional problems on the Dorset heaths (Mitchell *et al.* 1997; Chapter 2). These successions must be reversed by conservation agencies and the heathlands restored if the heaths are to be conserved.

6.3 THEORETICAL FRAMEWORK AND DEFINITION OF TERMS

The starting point of this study is to assume that at least two ecosystems (early- and late-successional sites) exist on a trajectory in multivariate space. In the case of the Dorset heaths the early-successional communities are the heaths themselves and there are a range of late-successional communities (Mitchell *et al.* 1997), dominated by invasive species; for example *Betula* spp. or *Pinus sylvestris.* Obviously it is important to use historical records such as aerial photographs to ensure that the communities are part of such a successional trajectory. In conservation management terms the late-successional site would be the 'startpoint' and the heathland sites would be the 'target', ie the reversal of the succession. The 'startpoint' sites have to be managed and the ideal aim is to reverse them to the 'target' as quickly as possible (Fig. 6.1a). Three factors are involved in the initial ecosystem response, (1) the distance that the 'startpoint' sites are from the 'target', (2) the resistance of the 'startpoint' ecosystem and the management force applied, which together determine the proximity to the 'target' after treatment, and thereafter (3) the resilience of the site after management, which determines the speed of recovery (Fig. 6.1a). The use of constrained ordination techniques such as CANOCO (Ter Braak 1988) allows this approach to be tested and moreover, provides the option of incorporating both species data plus the most important environmental variables which drive the system; in the case of the Dorset heaths - soil nutrients (Chapman 1967). Moreover, CANOCO allows an assessment of the amount of variation explained by the model and through its forward selection procedure and the technique of variation partitioning (Legendre & Fortin 1989; Borcard, Legendre & Drapeau 1992, Økland & Eilertsen 1994) it is possible to assess which environmental variables are most important.

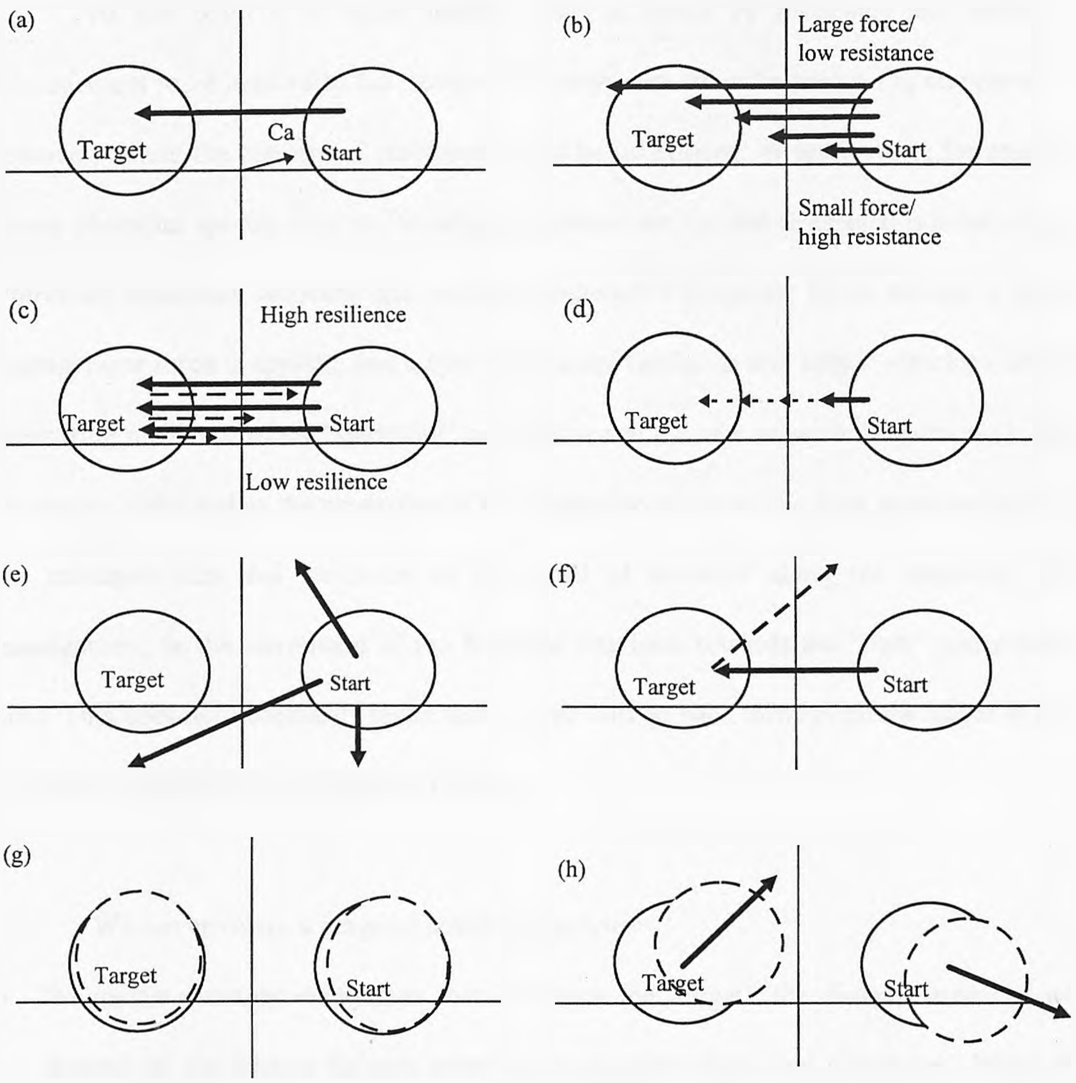


Fig. 6.1. Hypothetical models based on CANOCO type models illustrating the different trajectories of a disturbed ecosystem (managed site) between 'start' site (successional community) and 'target' site (heathland). In Fig (a) the vector Ca represents increasing calcium availability and shows how increasing soil nutrients may be represented within the diagram. For clarity this is omitted in the other figures. (a) Ideal scenario where the 'startpoint' community moves direct to the 'target' community. (b) Different levels of management force are applied to the same ecosytem or applying the same force to ecosystems with different levels of resistance. (c) 'Startpoint' sites given the same management force, but with differing resilience levels; dashed line indicates the resilience trajectory over a similar time period. (d) The initial management force does not push the site to the 'target', but there is sufficient momentum to carry it on the correct trajectory thereafter (dotted line). (e) The initial management force applied enforces a trajectory away from the 'target' in an unexpected trajectory. (f) Initial management maintained the correct trajectory, but recovery veered off on an unexpected trajectory away from both 'target' and 'startpoint'. (g) Ecosystems at different time points where there has been no detectable movement, ie the ecosystem are at 'approximate equilibrium: T0 = solid circle, T1 = dashed circle. (h) Ecosystems at different time points where there has been some detectable movement, ie the ecosystems are not at 'equilibrium' and are moving relative to their baseline positions; T0 = solid circle, T1 = dashed circle.

At this point it is worth debating what is meant by resistance and resilience. Management force applied to the 'startpoint' system can either be severe (eg complete tree removal) where the concept of resistance could be questioned, or less severe, for example where perennial species such as *Pteridium aquilinum* are cut and resistance is a function of *Pteridium aquilinum* recovery and would be relevant. However, let us assume a severe management force is applied, and a new community similar to the 'target' develops, are we measuring resilience of the 'startpoint' or resistance of the new ecosystem to change? Here resistance is defined as the properties of the 'startpoint' ecosystem which reduces change in the managed sites and resilience as the speed of recovery along the trajectory after management, ie the movement of the managed site back towards the 'start' (successional site). This does not necessarily mean that the site will go back through all the stages it went through in reaching its pre-managed position.

We can envisage a range of possible scenarios:

- Where the managed ecosystem does not reach the 'target', the distance achieved will depend on the relative balance between management force and resistance. When the force is much greater than the resistance the ecosystem should be closer to the 'target' than when the force is less than the resistance. A good manager will ensure that management force is sufficient, but this approach allows different levels of force to be compared relative to the resistance of the 'startpoint' ecosystem (Fig. 6.1b).
- Managed ecosystems which achieve the same initial position but differ in their resilience will revert to the 'startpoint' at differing rates (Fig. 6.1c).
- It is possible that after the initial management the site does not quite reach the 'target' but the momentum of change brought about by the initial management force is sufficient to ensure that the site continues along the correct trajectory (Fig. 6.1d).

Where this occurs the initial force applied has a long-term impact and the resilience is low, or the resilience of the new ecosystem produced is different.

- It is also possible that none of these simple models apply. Either the management force is inappropriate or stochastic factors interfere and the successional trajectory moves away from the 'target' (Fig. 6.1e). Alternatively, the management could provide a good initial movement in the correct direction, but thereafter a completely new succession takes over (Fig. 6.1f).
- Lastly, the models noted above make the assumption that the 'startpoint' and 'target' ecosystems are at equilibrium and do not change through time. Comparisons of repeated samples on the same ecosystems through time can be made to ensure that there is no great change (Fig. 6.1g), or alternatively that any change from the equilibrium baseline is detected (Fig. 6.1h).

These examples are given to illustrate the generality of this proposal, other options are possible, ie a severe management force could push the succession beyond the 'target' but the recovery trajectory would pass through it. All combinations are clearly possible, but the important point is that they are detectable and the speed of change measurable. Moreover it will be possible to detect, given sufficient time-series data, if a site is continually moving or whether there are 'preferred' points where the rate of change is reduced.

6.4 VALIDATION - DOES IT WORK?

Unfortunately this study does not have data over a long enough time period to test all of the models and hypotheses noted above. Data would need to be collected over many years and possibly decades. However, there is sufficient data to at least explore some of these ideas and to show the relevance of this work for conservation management.

The initial data set was collected in 1995 purely from 'startpoint' and 'target' sites, the initial aims were (1) to assess whether there were successional trajectories on these sites, or whether the observed change was merely the invasion of a single dominant, (2) to determine whether the same or different successions occurred depending on the dominant invasive species - four invasive species were tested (*Betula* spp., *Pinus sylvestris, Pteridium aquilinum* and *Rhododendron ponticum*), (3) to test whether there were any changes in soil nutrients associated with these different successions. Lowland heaths are generally found on very infertile soils and any increase in nutrients would have a deleterious effect on heathland restoration (Heil & Diemont 1983; Aerts & Berendse 1988; Van Der Eerden *et al.* 1991). An array of 10 heath sites across the Dorset area were surveyed to get a reasonable estimate of variability within the biotope at the regional scale, and at each site both the heathland ('targets') and a range of successions ('startpoints') were sampled, the time over which these successions occurred was known. A minimum of 7 areas invaded by each successional species were sampled. A second data set was collected in 1996 when a subset of sites were revisited, the aim here was to compare the 'start' and 'target' sites with adjacent areas where late-successional communities had been managed to differing degrees of intensity.

Analysis of the first dataset showed a clear separation between the different successions. Each succession appeared to occur in a different direction, (Fig. 6.2). The

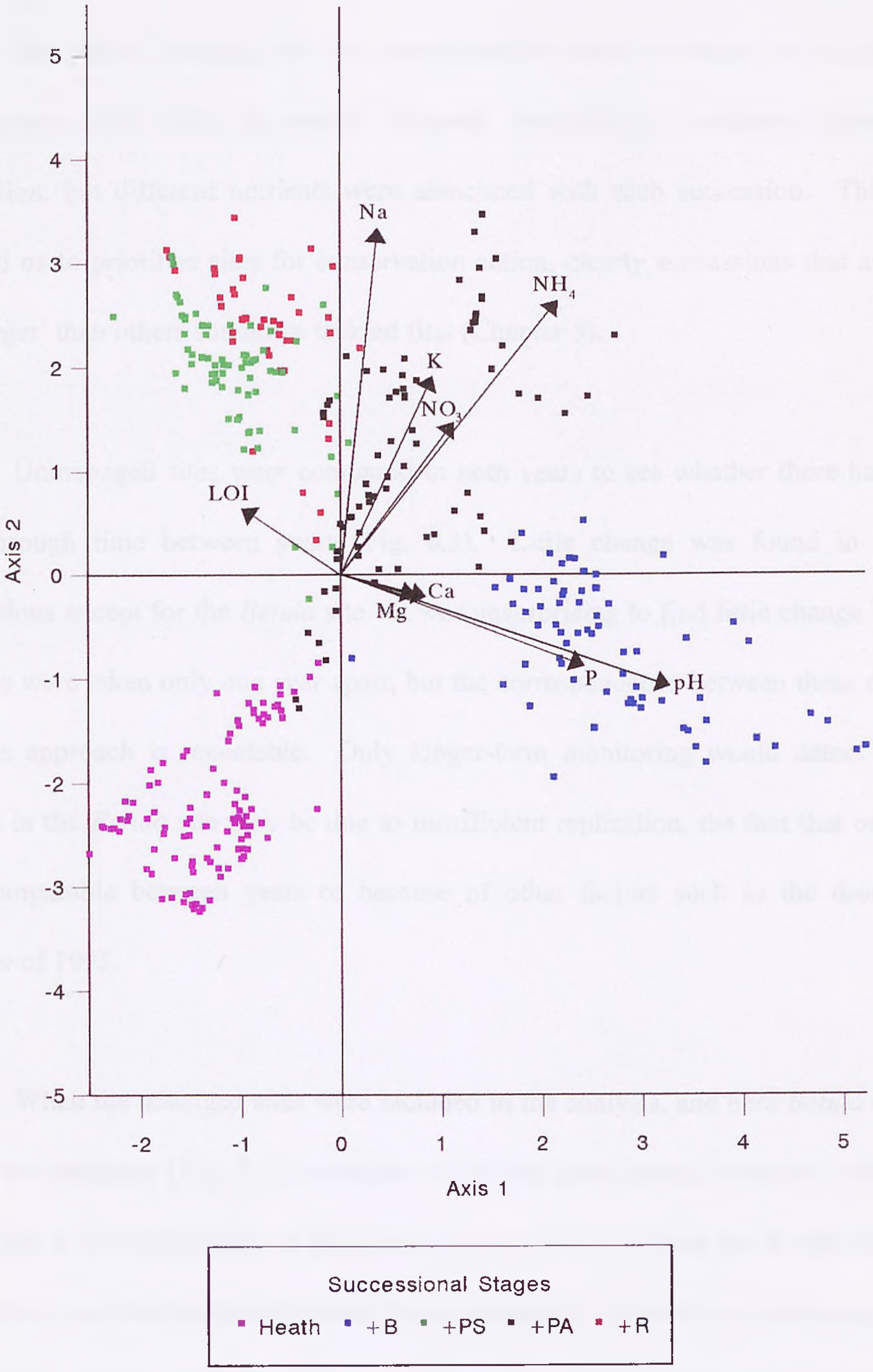


Fig. 6.2. Ordination diagram from CANOCO for the first two axes showing the relationship between the different successional stages and the soil nutrients on the Dorset Heaths. The soil nutrient vectors are shown by arrows. Heath = open heathland, +B = *Betula* spp. is the major invader, +PS = *Pinus sylvestris* is the major invader, +PA = *Pteridium aquilinum* is the major invader, +R = *Rhododendron ponticum* is the major invader. Ca = exchangeable calcium, K = exchangeable potassium, LOI = percentage loss on ignition, Mg = exchangeable magnesium, Na = exchangeable sodium, NH_4 = extractable ammonium-nitrogen, NO_3 = extractable nitrate/nitrite-nitrogen, P = extractable phosphorus, pH = pH.

analysis highlighted two other results. First, some successions were further away from the 'target' than others, meaning that they were probably harder to restore, or at least a greater management force might be needed. Second, available soil nutrients increased during succession, but different nutrients were associated with each succession. This approach allowed us to prioritise sites for conservation action, clearly successions that are closer to the 'target' than others should be tackled first (Chapter 3).

Unmanaged sites were compared in both years to see whether there had been any drift through time between years (Fig. 6.3). Little change was found in any of the successions except for the *Betula* site. It was unsurprising to find little change because the samples were taken only one year apart, but the correspondence between these data implies that the approach is repeatable. Only longer-term monitoring would detect drift. The change in the *Betula* site may be due to insufficient replication, the fact that only one site was comparable between years or because of other factors such as the drought in the summer of 1995.

When the managed sites were included in the analysis, and here *Betula* spp. is used as the test example (Fig. 6.4), examples of at least three models described above can be seen. Site 1 has moved close to the heath ('target'), the site either had a high level of force applied to it, or low resilience or both, thus enabling it to revert to a community similar to that of the heathland, (example of model Fig. 6.1b). Site 2 appears to be heading towards the target, but it has not yet reached it (example of model Fig. 6.1d). Only time will tell whether there is enough momentum for the site to continue towards the 'target' or if it will return towards the 'startpoint'. Sites 3 and 4 appear to be heading in directions other than towards the 'target' (examples of model Fig. 6.1e).

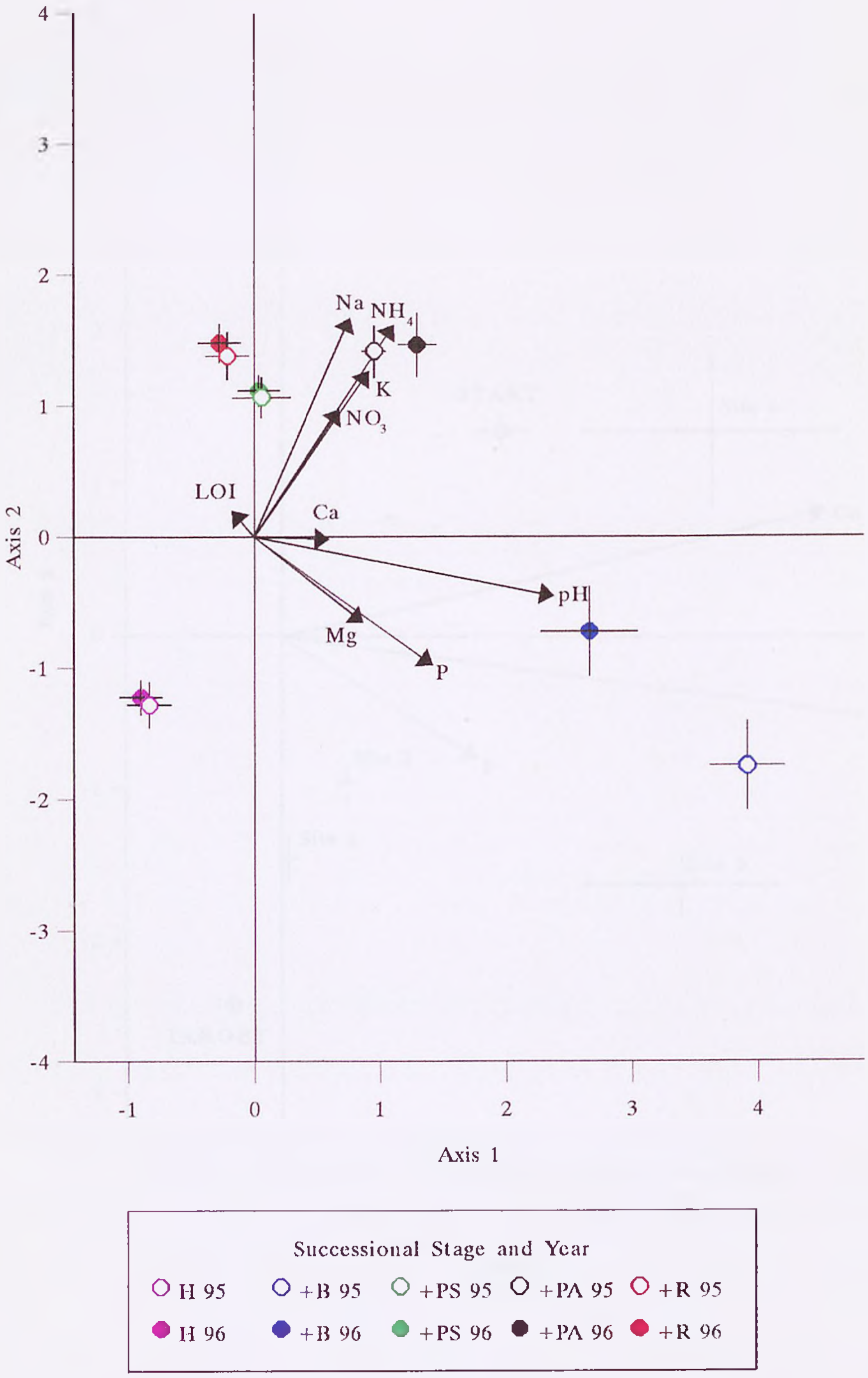


Fig. 6.3. Ordination diagram from CANOCO for sites sampled in both 1995 and 1996. The 1996 sites were put into the 1995 model as passive samples and the figure shows the movement of the sites between years. The symbols are centroids for the sites and the lines are standard error bars. Heath = open heathland, +B = *Betula* spp. is the major invader, +PS = *Pinus sylvestris* is the major invader, +PA = *Pteridium aquilinum* is the major invader, +R = *Rhododendron ponticum* is the major invader.

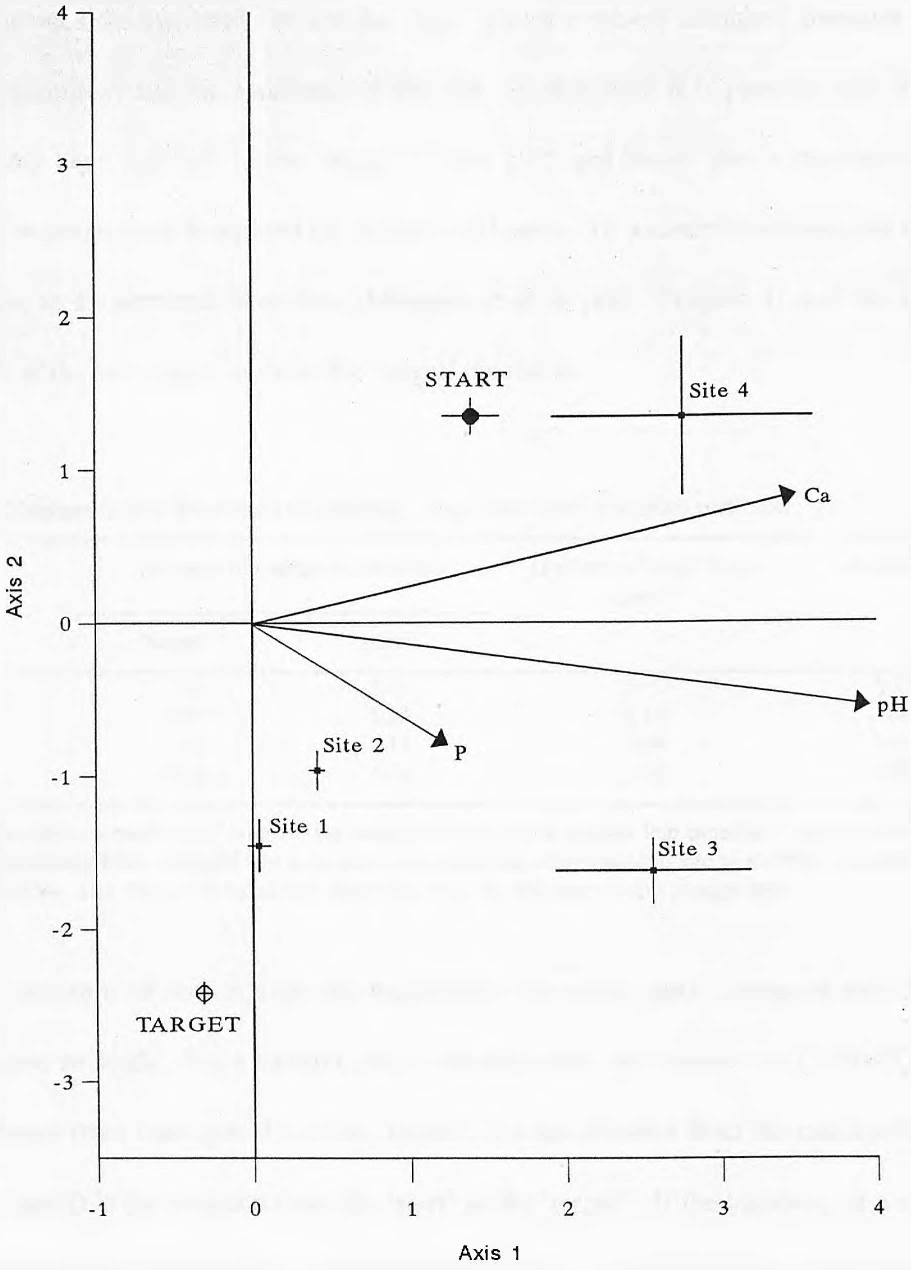


Fig. 6.4. CANOCO diagram to show the movement of managed *Betula* sites (sites 1, 2, 3 & 4) from the 'start' site. The symbols represent centroids of the managed, 'start' and 'target' sites and the lines are standard error bars. Increasing levels of exchangeable calcium (Ca), extractable phosphorus (P) and pH (pH) are shown by the arrows.

The distances between the 'start', 'target' and managed sites may be measured in multi-dimensional space and here 4 axes were used, the CANOCO default (Table 6.1). The distance between the managed site and the 'start' allows a one-off combined measure of the impact of treatment and the resistance of the site. At this point it is possible only to rank sites on how near they are to the 'target' (Table 6.1), and hence give a measure of the success of restoration of heathland on successional sites. To measure resilience the survey would have to be repeated over time (Mitchell *et al* in prep; Chapter 4) and the rate of movement of the ecosystem towards the 'target' measured.

Table 6.1. Distances in four dimensions of managed, 'target' and 'start' sites from each other.

Site	Distance of managed site from		Distance of 'start' from 'target' ^{D}	A value *
	'target' ^{T}	'start' ^{S}		
Site 1	1.96	2.41	3.67	0.70
Site 2	5.93	1.23	6.15	1.05
Site 3	7.32	8.11	5.96	9.47
Site 4	5.28	1.07	5.52	0.84

* The A value gives a measure of whether the managed site is on a straight line trajectory from the start to the target. A = (distance from managed site to target (T)) + (distance from managed site to start(S)) - (distance from start to target(D)). The closer this value is to zero the closer the trajectory is to a straight line.

A measure of how straight the trajectory is between 'start', managed and 'target' sites can also be made. For a straight line, A should equal zero where $A = (T+S)-D$, and T is the distance from managed site to the 'target', S is the distance from the managed site to the 'start' and D is the distance from the 'start' to the 'target'. If the trajectory is a straight line then the managed site is moving towards the 'target'. However, if A is large then the trajectory is not straight and the managed site is moving in a different direction. In this data sites 3 and 4 have high A values (Table 6.1) and are moving in a direction other than towards the desired 'target' (Fig. 6.4).

For simplicity it has been assumed that the trajectories are linear, but it is possible that many trajectories will be curvilinear, and where this occurs the implications must be accommodated in the management of the site. However, the use of this approach allows the manager to detect this relationship and make a judgement as to whether it is acceptable for conservation purposes or whether other management must be applied to correct the direction of change.

This approach offers a potential method to measure resilience rates in at least some communities. It satisfies all of the criteria noted above, ie it (1) tests for equilibrium conditions by measuring drift, (2) tests whether the ecosystems returns to its undisturbed state, (3) brings together both structure and function data, (4) measures variability and is scale independent, (5) is statistically rigorous, (6) accommodates stochastic factors and (7) has a practical use. Moreover, this study has merely considered the composition of plant species in the model; other organisms could be included in the future, for example invertebrates and soil micro-organisms.

This approach based on a theoretical appreciation of succession has direct relevance to practical conservation management. It provides information that helps prioritise action, monitor progress and detect when things go wrong; for example, where the community is moving in the wrong direction after management. With greater insight into these successional trajectories it may be possible, in the future, to apply additional management to 'problem sites' to subtly correct or fine-tune the direction of change. It may also be possible to rank different management practices with respect to success in achieving the correct trajectory, and identifying those management techniques which result in different trajectories. These studies on the Dorset heaths covered the lowland heath biotope at the individual site and regional scale. There is no reason to suppose it could not be extended to include other regions (test of regional responses) or indeed the entire heathland biotope. Other biotopes with high conservation interest such as reed-beds and grassland communities could also be studied using the same type of model.

This approach shows real promise as a model system for assessing perturbations and resulting impacts in conservation biology. Measurements of ecosystem resilience based on properties of both ecosystem structure and function can be calculated if repeat data were collected over a longer time period. However, these models merely measure direction and change through time, they do not give information on either the processes involved or the genetic properties of the populations, all of which may be important factors contributing to ecosystem resilience. However, they show important hypotheses that can be tested by further experiments and put conservation experiments on a sound theoretical basis.

6.5 CONCLUSION

Understanding and measuring ecosystem stability and resilience is of critical importance if our knowledge of the way ecosystems recover from disturbance is to be increased. This study has advanced a model which provides a new way to measure ecosystem stability and resilience. It enables changes to be measured not only in the ecosystem structure but also enables inclusion of the important driving variables of the ecosystem. The changes in the disturbed ecosystem may be measured against two fixed points, two ecosystems at notional equilibrium along a successional trajectory. However, the model is designed to include any variability or movement over time caused by these ecosystems not being at equilibrium. This has direct relevance to the conservation and management of many of our declining habitats and here it has been related to the lowland heaths of Dorset.

Chapter 7

DISCUSSION

7.1 INTRODUCTION

This project has encompassed a range of studies on aspects of succession on Dorset lowland heaths. Previous work has shown that succession, especially scrub encroachment, on these heaths is now a major cause of loss of heathland area (Webb 1990). As the Dorset heaths are of international importance for nature conservation, an improved understanding of the changes that occur in the vegetation, soil and seedbanks during succession is essential if attempts to reverse succession and restore heathland are to be successful. Soil nutrients are of particular importance because lowland heaths are only found on infertile soils (Gimingham 1972) and any increase in growth limiting nutrients may lead to a change in species composition. In this thesis selected aspects of successional change have been studied and an attempt has been made to draw some of the results together into a model of heathland resilience, which has relevance for practical land management.

7.2 VEGETATION TRAJECTORIES AND CHANGES IN SPECIES COMPOSITION

In a large survey of succession on the Dorset heaths, it was shown that the successions were not site dependent nor were they a simple case of relay floristics or facilitation succession. The facilitation model may occur in some situations, eg primary successions, but there has been a growing recognition that this model does not provide a general explanation of many secondary successions (Egler 1954; Connel & Slayter 1977; Noble & Slayter 1978). A multi-trajectory model was found to describe the range of successions found; the successions were classified by the dominant species invading (*Betula* spp. (+B), *Pinus sylvestris* (+PS), *Pteridium aquilinum* (+PA), *Rhododendron ponticum* (+R) and *Ulex europaeus* (+U)). A separate successional trajectory was found from the heath for each major invasive species. However, succession was not just the addition of the single dominant species to the heathland flora; many heathland species were lost, in particular the lichens which may be dominant species on some heathland sites. In some successions, especially +PS and +U, heathland plants may survive, but in the +R succession the *Rhododendron ponticum* achieves almost complete dominance with few other species surviving. In the +B flora many new species characteristic of a woodland flora have invaded (Miles 1981a). It is thought that the major determinant of the fate of the sub-dominant species, the ground flora, is the successional changes occurring in the dominant species (Grime 1987). Thus changes in shading (Hester 1987) and soil nutrients (Miles 1981a) caused by the invasion of the dominant species may be the driving force behind the loss of many of the heathland species in the successional community and these changes may have created suitable conditions for the other sub-dominant invaders to establish.

Which successional trajectory occurs on a given site depends on a variety of factors, the closeness of the site to a propagule source, soil disturbance, soil chemistry (Chapman, Rose & Basanta 1989), the species available for soil colonisation and stochastic processes. The vital attributes (Noble & Slayter 1980) or establishment strategy (CSR characteristics) (Grime 1987) are also likely to play a part.

The detection of a range of different successional trajectories was an important factor because it went on to identify those successions which were closest to the heath (+PS and +U) and those that were further away (+R and +B). This gave an assessment of those successions which were likely to be easiest to restore.

7.3 CHANGES IN SOIL NUTRIENTS

Most studies on changing soil nutrients with succession have been conducted either on British moorlands (Dimbleby 1952; Miles & Young 1980; Satchell 1980a; Miles 1981a; Miles 1988) or on heath to woodland successions in Europe (Nielsen, Dalsgaard & Nørnberg 1987a&b; Leuschner 1993). The only English lowland heath study of soil nutrient change through succession was that of Chapman, Rose & Basanta (1989), who related the soil phosphorus adsorption capacity to the risk of the heath being invaded by *Betula* spp. or *Ulex europaeus*. In the present study successional change in vegetation has been related to nine different soil chemical properties. Not only has it been shown that soil nutrients increase as succession occurs but that different soil nutrients increase with different successional trajectories. This result has not been detected before and it implies that specific soil nutrients, known to be essential for plant growth, will have to be reduced in order to restore heathland in different successions.

With studies such as this it could be argued whether the increased soil nutrient levels were caused by the vegetation or whether the changes in vegetation were caused by the soil. Unless it were possible to follow plots through time to test this in a true chronosequence (*sensu* Jenny 1980), this problem will not be resolved. However, all that has been shown here is that increased soil chemical properties are associated with certain successions. Whether it is a cause or effect is to some extent irrelevant as far as management for heathland restoration is concerned. The soil problems exist and need to be tackled. Alternatively, a different conservation endpoint could be selected.

The problems of high soil fertility in habitat restoration work is widely known (Marrs & Gough 1989; Marrs 1993a). However, such problems are usually found when restoring habitats on ex-arable land or other land on which soil fertility has been increased by man (Marrs 1985b; Marrs & Gough 1989; Marrs 1993a; Pywell, Webb & Putwain 1994; Snow 1995; Owen *et al.* 1996). Soil nutrient increase during succession may also be detrimental to restoration (Marrs 1993a). However, experiments are needed to test whether the relatively small increases found on the Dorset heaths would hinder heathland restoration. Such experiments may be difficult as (1) the effects may only be observed over long time periods (tens or hundreds of years), well beyond the scope of most management plans or research projects; and (2) the detrimental effects of succession may be site dependent as increased fertility is likely to be more problematic on sites where there is a seed source of successional species nearby. Elevated soil fertility may lead to either a rapid invasion of late-successional species, helped by the high fertility, a man-modified relay floristics succession (Clements 1916), or a shorter period of dominance by early successional species, an accelerated initial floristics composition (Egler 1954; Marrs & Gough 1989). High nutrient concentrations, especially of nitrogen, may, in certain circumstances increase the risk of the *Calluna vulgaris* being attacked by the heather beetle (*Lochmaea suturalis* Thomson) (Berdowski 1987a), and this can lead to large areas of *Calluna vulgaris* loss and replacement by grass (Heil & Diemont 1983; Berdowski 1987b; Berdowski & Zeilinga 1987).

7.4 THE EFFICACY OF CONSERVATION MANAGEMENT TO REVERSE SUCCESSIONAL CHANGES

The reversion of succession is not a new idea to conservation managers (Pickess, Burgess, Evans 1989; Pickess & Auld 1992); however much conservation management is done in an *ad hoc* way with little certainty of the final out come. There have been few scientific studies of the success of heathland management and how it relates to wider issues of manipulating succession.

Chapter 4 showed that it was possible to restore heathland communities on some successional sites. It is difficult to produce any ranking as to which stages reverted best; generally +PS stages seemed to be more successful or at least less likely to move in an undesirable direction, +R and +PA stages were probably the next most successful and +B was the most difficult although some +B sites may be very successful. Obviously success is not a simple matter of stage, other factors such as site, management and factors yet unknown will influence success.

The results (Chapter 4) showed that on many sites heathland species did re-establish. It was encouraging to note that many of the lichen species that quickly disappeared during succession were able to re-establish. However, non-heathland species may also re-establish particularly *Ulex europaeus, Pteridium aquilinum, Betula* spp. and some grassland species. Bryophytes were also dominant on many of the managed sites and may influence the success of seedling establishment of some species and hence the successional trajectory of the site (Grime 1987; Legg, Maltby & Proctor 1992).

Soil nutrient levels were not necessarily restored to typical heathland levels after management. Reversal of pH, phosphorus and nitrogen appeared to be the most difficult and as the Dorset soils are phosphorus limited this could have a significant effect for long term change. The most effective management treatment appeared to be that of litter-stripping. This was tested on several +PS sites but only on one +R and +PA sites. It would be worth carrying out further research on the effects of litter-stripping on all stages, but especially on the +B sites where the greatest changes in soil nutrients occurred and where restoration was most difficult.

By analysing these data with CANOCO it has been possible to assess the success of management using both vegetation and soil data, and to measure how close to the heath target the managed site is. This is a new way of measuring management success. When trying to assess the success of management one must be very clear as to what the aim is, whether it is complete ecosystem restoration, rehabilitation (in which progress towards complete ecosystem restoration is made but the progress is not complete) or replacement (where the original ecosystem is substituted by another usually different and simpler one) (Bradshaw 1984). The present study is concerned with measuring the success of management relative to the desired objective, it allows us to measure success and resilience.

7.5 SEEDBANKS

The viable content of the seedbank will play a critical role in determining the success of restoration. It was shown in Chapter 5 (Mitchell, Marrs & Auld in prep) that in common with many other studies there were many late-successional species present in the vegetation that were not present in the seedbank, and that many early-successional species (heathland ones) were present in the seedbank that were not present in the vegetation. On at least some of the sites the seedbanks may be relied upon to provide a source of viable propagules for heathland restoration. However, some sites (+PS) were closer to the heath and hence had a greater proportion of heathland species relative to late-successional ones than others (+R and +B). Those sites with low densities of heathland species and high densities of late-successional species in their seedbanks are more likely to be harder to restore to heathland.

7.6 MODELS OF STABILITY AND RESILIENCE

The model developed in Chapter 6 allows the change in a managed successional site to be related to two reference points; a late-successional stage ('startpoint') and the heath ('target'). The model developed in CANOCO (Ter Braak 1988) provides a new way of measuring ecosystem stability and resilience rates. While this study does not have all the data needed to measure the resilience rates of the managed sites, it presents enough data to show the theoretical possibilities of such a model. This way of studying ecosystem resilience has several new ideas and provides an integrated approach, specifically:

- 'Start' and 'target' sites as reference points to relate movement of disturbed/managed sites to.
- The model can accommodate movement of the 'start' and 'target' sites, ie non-equilibrium circumstances.
- Provides measurements of resilience and resistance in terms of distance moved in multivariate space over time.
- Can include both the vegetation and abiotic and biotic driving variables of the ecosystem.
- Can provide a measure of the variability within the ecosystem under investigation, which can operate at a range of scales from the individual site to national levels.
- Can accommodate unforeseen ecosystem change associated with stochastic or other factors.
- It can identify which environmental variables are likely to be the most important driving variables in the ecosystem.
- It is statistically rigorous.
- It has direct relevance to practical conservation management.

7.7 RELEVANCE TO PRACTICAL CONSERVATION MANAGEMENT

This project had a dual purpose, first to advance our understanding of succession and second to relate it to practical conservation management. Changes in vegetation, soil and seedbanks have all been studied and ranked in order of closeness to heath.

+PS & +U < +PA < +R & +B Vegetation

+U < +PS & +PA < +R & +B Soil and vegetation

+PS & +PA < +U & +R < +B Seedbanks

On all criteria a similar pattern emerges. The +R and +B sites are likely to be the most difficult to restore to heathland. Although the seedbanks of the +PA sites are close to those of the heath, the vegetation and soil ranking place +PA in the middle of the sequence therefore suggesting that +PA may be more difficult to restore. The +U and +PS are the two easiest stages to restore, the +PS being further away than the +U in terms of the soil but the +U is further away than the +PS in terms of the seedbank content. The collective rankings (Table 7.1) can then be added together to produce an overall likelihood of success score for the stages. The +PS has the lowest score and is therefore "best" followed by +U and the +PA. The +R and +B stages have much higher scores with +B having the highest score and therefore the least likelihood of success.

Table 7.1. Proximity to heath of the successional stages when ranked by their vegetation, soil and vegetation and seedbanks. 1 = closest to heath, 5 = furthest from heath, therefore those stages with the highest total score are furthest from the heath.

Ranked by	Successional Stage				
	+B	+PS	+PA	+R	+U
Vegetation	$^{=}4$	$^{=}1$	3	$^{=}4$	$^{=}1$
Soil and Vegetation	$^{=}4$	$^{=}2$	$^{=}2$	$^{=}4$	1
Seedbank	5	$^{=}1$	$^{=}1$	$^{=}3$	$^{=}3$
Total score	13	4	6	11	5

Whether assessed on individual attributes or overall ranking the +PS sites have the greatest chance of success. Therefore when targeting conservation resources it is better to target heathland restoration projects at +PS sites than +R or +B sites.

However, other factors such as the cost of the management technique and the ease of control of the major species should also be taken into account when devising management plans. The costings of these types of projects has been covered by Woodrow, Symes & Auld (1996). *Rhododendron ponticum* and *Betula* spp. are difficult to remove because of their ability to resprout from cut stumps unless treated by herbicide (Marrs 1985a). *Pteridium aquilinum* is difficult to control successfully because of its extensive rhizomes (Marrs, Pakeman & Lowday 1993) and *Ulex europaeus* may be difficult due to the ability of young stumps to resprout and its extensive seedbank (Grime, Hodgson & Hunt 1988). *Pinus sylvestris* neither resprouts nor has extensive seedbanks (Carlisle & Brown 1968), and should be the easiest to remove. This management information reinforces the above results; that if conservation managers have a choice the restoration of heathland on sites dominated *Pinus sylvestris* is likely to be most successful.

Chapter 4 tests whether the above conclusions were correct. While it was very difficult to establish simple rankings as in the other three chapters the results confirm the above conclusions. The +PS sites were more likely to be successful than +B. The +B could be managed successfully but there was a much greater tendency to move in a different direction other than the desired one. Similarly +R and +PA were shown to be difficult to restore.

7.8 FUTURE WORK

This study has shown the great potential there is for using multivariate analysis to study successional change on plagio-climax successions. Many aspects of the work here could be extended or developed as outlined below.

7.8.1 Heathland in other regions

The studies here were based on the Dorset heathlands; however, the hypothetical models outlined in Chapters 2 and 3 could be tested on other lowland heaths, especially the Hampshire, Surrey and Breckland heaths which are the other remaining large areas of lowland heaths in England. Hypotheses to be tested would include:

- Are the vegetation successional trajectories the same in each region?
- Are there other successional trajectories that occur, eg towards grassland on the Breckland sites (Marrs 1993b)?
- Do the soil nutrients that increase with each stage on the Dorset heaths also increase in the corresponding stages in other heathland regions?
- Is the CANOCO model for vegetation and soil chemical properties similar to the Dorset model but operating at a “higher soil nutrient level”? The Hampshire, Surrey and Breckland heaths are inherently more fertile than the Dorset heaths. If the Dorset, Hampshire, Surrey and Breckland heaths were examined together the results might be confusing, for example the Hampshire heaths may have soil nutrient concentrations similar to the Dorset +B stages. However, if the heaths were examined regionally the same model might work with pH, phosphorus, and calcium increasing with the +B stage, and nitrogen increasing with the +PA and +U stages etc, but the whole process starting at a higher threshold.

7.8.2 Other habitats

There are many other plagio-climax habitats were scrub encroachment occurs, for example reedbeds and grassland, and management is needed for their conservation. These habitats have also been fragmented and have declined dramatically in area within the last century. They have important species associated with them and thus also have a high nature conservation profile. Studies could be done to test the following hypotheses:

- Do different successional trajectories occur?
- Do soil nutrient concentrations change during succession?
- If soil nutrient concentrations do increase, which soil nutrients increase and with which successional trajectories are they associated?
- If a CANOCO type model, similar to that for the Dorset heaths, can be developed for these other habitats can managed sites be fitted into it?

7.8.3 Development of the model for monitoring conservation management success

Conservation managers are interested in measuring success and the models developed here could be used to allow them to measure restoration success directly. The model reduces the numerous variables of species diversity, species composition and environmental variables down to a single figure, the distance from the 'target'. If conservation managers were able to add the latest survey data from a managed site into a computer model which calculated the distance from the 'target' site, they could immediately have a measure of success. If such surveys were repeated regularly the progress towards the 'target' could be assessed in terms of both direction and speed. Such a system would provide an early warning if the managed site started to move in an undesirable direction. It would also allow corrective management to a given trajectory to be applied and its success monitored.

7.8.4 The inclusion of other groups of species within the model

This model has concentrated on vegetation and soil. However heathlands are species poor in terms of the plants present and while both the plants and soils have to be correct for the establishment of a heath they are but the initial building blocks on which to establish a heathland ecosystem. The study could be expanded to include invertebrates, eg *Hymenoptera*, many of which are specialised heathland species, soil fauna and soil microbial species. The model could even be expanded to include paired heathland and non-heathland species *sensu* Moore (1964). Moore (1964) studied changes in heathland distribution and fragmentation by studying changes in the species distribution of the following pairs: The Small Red Damselfly (*Ceriagrion tenellum*) and The Large Red Damselfly (*Pyrrhosoma nymphula*), insects *Odonata;* Silver Studded Blue (*Plebejus argus*) and Common Blue (*Polyommatus icarus*), insects *Lepidoptera*; Sand Lizard (*Lacerta agilis*) and Common Lizard (*Lacerta vivipara*), reptiles; Dartford Warbler (*Sylvia undata*) and Stonechat (*Saxicola torquata*), birds passerines. The first one of each pair is restricted to heathland in its distribution, while the second one occupies a similar niche in the ecosystem but occurs across a wider range of habitats. This might allow a much broader measure of the success of establishing the whole heathland ecosystem. (Nomenclature follows Hammond (1985) for *Odonata*; Thomas & Lewington (1991) for *Lepidoptera*; Morrison (1994) for reptiles and Jonsson (1993) for birds.)

7.8.5 Measurement of resilience, resistance and movement towards the target.

The potential of this model to measure ecosystem resilience and resistance has already been discussed, but this needs to be tested. To do this the array of sites studied in Chapter 4 would have to be resurveyed over the next 5 years or more at regular intervals. Then the distance that the managed site has moved in multi-variate space during a fixed time could be measured and rates of resilience or speed of movement towards the 'target' measured. As the speed with which the site moves towards the 'target' might be expected to decrease with time this deceleration could be measured. Some stages may be found to decelerate quicker than others and the speed at which they decelerate may depend on the management techniques applied.

7.8.6 Starting from time zero and testing previous assumptions

These models and calculations have been conducted on the assumption that the managed site was the same as the 'start' site before management. While this assumption is reasonable as the 'start' sites are adjacent to managed sites, experiments should be set up to test this. The whole site should be surveyed for vegetation and soil. Part of the site could then be managed and part left as a control. The trajectory could then be followed from time zero.

7.8.7 Force of management

Experiments could be established to assess the effects of differences in force of management, ie management technique. It has been shown that litter-stripping has an important influence over the direction of the trajectory and speed of movement towards the 'target' in terms of both vegetation and soil (Chapter 4). Experiments could be set up for all major stages where the major species were cut or felled and then varying degrees of management force applied: no litter-stripping, partial litter-stripping, total litter-stripping, top soil removal.

7.8.8 The probability of success

If enough data were gathered from a range of sites, stages and management techniques, it would be possible to start to calculate the probability of successful restoration of heathland for any given stage and management technique. The probability of hitting the 'target' may be very low if the ‘target’ is small; it may therefore be better to calculate the probability of getting the site to within a critical distance of the ‘target’. This critical distance would also have to be assessed.

7.8.9 Species biology

If the biological characteristics of the species eg vital attributes (Noble & Slayter 1978) or CSR characteristics (Grime 1977; Grime, Hodgson & Hunt 1988), could be fitted into the model as functional types then it might be possible to select species or species groups for management action in order to push the ecosystem in the desired direction.

7.8.10 Correcting the direction of the trajectory

Some managed sites invariably “mis-fire” and head in an undesirable direction either due to stochastic effects or mismanagement. Future work could establish whether it is possible to “fine-tune” the trajectories and to apply an additional management force which would correct these trajectories and move them back towards the target. Such correction methods could involve grazing, burning and respraying to control invasive species.

7.8.11 Unexplained variation

The differences of success between some sites may be due to obvious causes such as management differences or stage differences. However some sites that appear to be “identical” may have differing success rates, this unexplained variation may for example be due to differences in species diversity, genetic diversity, effects of the neighbouring patch, size effects, edge effects, fragmentation effects, pollution effects, etc. Further work could try to account for more of this unexplained variation thus making it an even more powerful model and management tool.

7.8.12 Using the model to generate new hypotheses

This model enables us to measure ecosystem resilience and resistance and to assess the success of management, and acts as an advanced warning system when things start to go wrong. However beyond the possibility of having the power to attach a "probability of success" to any management application this model has no predictive powers and does not advance our understanding of why things are happening within an ecosystem. It does however show us what is happening even if we do not know why. This can then lead to the development of hypotheses to be tested by experiment, in order to explain what is happening.

7.9 CONCLUDING REMARKS

This work has shown the value of studying successional pathways in plagio-climax communities. It has increased our understanding of the changes that occur during succession in the vegetation, soil chemical properties and seedbanks of the lowland heaths in Dorset. These results have been related to practical conservation with the aim of helping to target resources for the restoration of heathland. This shows how ecological research may be of direct value to conservation managers. Successional sites, managed to restore heathland were studied and the success of management to reverse successional changes assessed. Canonical Correspondence Analysis was used through out this work to assess changes in vegetation and soil nutrients. This led to the idea of using CCA type models for studying ecosystems in general and measuring ecosystem resilience and resistance. The potential for further work using this type of model has been discussed.

REFERENCES

Aerts, R. & Berendse, F. (1988) The effect of increased nutrient availability on vegetation dynamics in wet heathlands. *Vegetatio*, **76**, 63-69.

Allen, S.E. (Ed) (1989) *Chemical Analysis of Ecological Materials 2nd ed.* Blackwell Scientific Publications, London.

Allen, S.E., Grimshaw, H.M., Parkinson, J.A. & Quarmby, C. (1974) *Chemical Analysis of Ecological Materials 1st ed.* Blackwell Scientific Publications, Oxford.

Andrews, J. (1990) Wildlife habitat management. Management of lowland heathlands for wildlife. *British Wildlife*, **1**, 336-346.

Armstrong, P.H. (1971) *The heathlands of the East Suffolk Sanderlings*. Lavenham, Dalton.

Auld, M., Davies, S. & Pickess, B. (1992) Restoration of lowland heaths in Dorset. *RSPB Conservation Review*, **6**, 68-73.

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

Batten, L.A, Bibby, C.J., Clement, P., Elliott, G.D. & Porter, R.F. (1990) *Red data birds in Britain*. T & AD Poyser, London.

Benoit, D.L., Kenkel, N.C. & Cavers, P.B. (1989) Factors influencing the precision of soil seedbank estimates. *Canadian Journal of Botany*, **67**, 2833-2840.

Benoit, D.L., Derksen, D.A. & Panneton, B. (1992) Innovative approaches to seedbank studies. *Weed Science*, **40**, 660-669.

Berdowski, J.J.M. (1987a) *The catastrophic death of Calluna vulgaris in Dutch heathlands.* Drukkerij Elinkwijk BV, Utrecht, The Netherlands.

Berdowski, J.J.M. (1987b) Transition from heathland to grassland initiated by the heather beetle. *Vegetatio*, **72,** 167-173.

Berdowski, J.J.M. & Zeilinga, R. (1987) Transition from heathland to grassland: damaging effects of the heather beetle. *Journal of Ecology*, **75,** 159-175.

Berendse, F. (1990) Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. *Journal of Ecology*, **78**, 413-427.

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

Borcard, D., Legendre P. & Drapeau P. (1992) Partialling out the spatial component of ecological variation. *Ecology,* **73,** 1045-1055.

Bormann, F.H. & Likens, G.E. (1979) *Pattern and processes in a forested ecosystem.* Springer, New York.

Bradshaw, A.D. (1984) Land restoration: now and in the future. *Proceedings of the Royal Society*, **233,** 1-23.

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

Bruggink, M. (1993) Seed bank, germination and establishment of ericaceous and gramineous species in heathlands. *Heathlands: Patterns and processes in a changing environment* (eds R. Aerts & G.W. Heil), pp.153-180. Kluwer Academic Publishers, The Netherlands.

Bullock, J.M & Webb, N.R (1995) Responses to severe fires in heathland mosaics in Southern England. *Biological Conservation*, **73**, 207-214.

Bullock, J.M. & Pakeman, R.J. (1997) Grazing of lowland heaths in England: Mangement methods and their effects on heathland vegetation. *Biological Conservation*, **79**, 1-13.

Byfields, A. & Pearman, D. (1995) Dorset's disappearing heathland flora: a case for reinstating grazing. *RSPB Conservation Review*, **9**, 84-89.

Cadbury, C.J. (1989) What future for lowland heaths in Southern Britain? *RSPB Conservation Review*, **3**, 61-67.

Carlisle, A. & Brown A.H.F. (1968) Biological flora of the British Isles *Pinus sylvestris*. *Journal of Ecology*, **56**, 269-307.

Chapman, S.B. (1967) Nutrient budgets for a dry heath ecosystem in the south of England. Journal of Ecology, **55**, 677-689.

Chapman, S.B. (1979) Some interrelationships between soil and root respiration in lowland *Calluna* heathland in Southern England. *Journal of Ecology*, **67**, 1-20.

Chapman, S.B., Clarke, R.T. & Webb, N.R. (1989) The survey and assessment of heathland in Dorset, England for conservation. *Biological Conservation*, **47,** 137-152.

Chapman, S.B, Rose, R.J. & Basanta, M. (1989) Phosphorus adsorption by soils from heathlands in Southern England in relation to successional change. *Journal of Applied Ecology*, **26**, 673-690.

Chapman, S.B., Rose, R.J., Clarke, R.T, (1989) A model of the phosphorus dynamics of *Calluna* heathland. *Journal of Ecology*, **77**, 35-48.

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

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

Collins, S.L. (1995) The measurement of stability in grassland. *Trends in Ecology and Evolution*, **10**, 95-96.

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

Cross, J.R (1975) Biological flora of the British Isles *Rhododendron ponticum* L. *Journal of Ecology*, **63**, 345-364.

Department of Environment (1995a) *Biodiversity: UK Steering Group Report. Volume 1: Meeting the Rio challenge.* HMSO, London.

Department of Environment (1995b) *Biodiversity: UK Steering Group Report. Volume 2: Action plans.* HMSO, London.

Diemont, W.H. (1994) Effects of removal of organic matter on the productivity of heathlands. *Journal of Vegetation Science*, **5**, 409-414.

Diemont, W.H. (1996) *Survivial of Dutch heathlands.* IBN Scientific contributions 1, DLO Institute for Forestry and Nature Research, Wageningen.

Dimbleby, G.W. (1952) Soil regeneration on the north-east Yorkshire moors. *Journal of Ecology*, **40**, 331-341.

Dimbleby, G.W. (1962) *The development of British Heathlands and their soils.* Clarendon Press, Oxford

Dodd, M., Silvertown, J., McConway, K., Potts, J. & Crawley, M. (1995) Community stability: a 60 year record of trends and out breaks in the occurrence of species in the Park Grass experiment. *Journal of Ecology*, **83**, 277-285.

Donelan, M. & Thompson, K. (1980) Distribution of buried viable seeds along a successional series. *Biological Conservation*, **17**, 297-311.

Duncan U.K. (1970) *Introduction to British Lichens.* T. Buncle & Co. Ltd, Arbroath.

Dyer, A.F. (1990) Does bracken spread by spores? *Bracken biology and management.* (eds J.A. Thompson & R.J. Smith) pp. 35-42. Australian Institute of Agricultural Science, occasional publication No. 40, Sydney.

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

Ernst, W. (1978) Discrepancy between ecological and physiological optima of plant species. A re-interpretation. *Oecologia Plantarum*, **13**, 175-188.

Farrell, L. (1989) The different types and importance of British heaths. *Botanical Journal of the Linnean Society*, **101**, 291-299.

Fenner, M. (1985) Soil seedbanks. *Seed Ecology*, pp. 57-71. Chapman & Hall Ltd, London.

Frank, D.A. & McNaughton, S.J. (1991) Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. *Oikos*, **62**, 360-362.

Gardeniner, A.S. (1968) The reputation of birch for soil improvement. *Forestry Commission Research & Development Paper 67.* Forestry Commission, London.

Gauch, H.G. (1982) *Multivariate Analysis in Community Ecology.* Cambridge University Press, Cambridge.

Gimingham, C.H. (1960) Biological Flora of the British Isles *Calluna vulgaris* (L) Hull. *Journal of Ecology*, **48**, 455-483.

Gimingham, C.H. (1972) *Ecology of Heathlands.* Chapman & Hall, London.

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

Good, R. (1948) *A geographical handbook of the Dorset flora.* The Dorset Natural History and Archaeological Society, Dorset.

Granström, A. (1987) Seed viability of fourteen species during five years of storage in a forest soil. *Journal of Ecology*, **75**, 321-331.

Granström, A. (1988) Seedbanks at six open and afforested heathland sites in Southern Sweden. *Journal of Applied Ecology*, **25**, 297-306.

Green, B.H. (1972) The relevance of serial eutrophication and plant competition to the management of successional communities. *Biological Conservation*, **4**, 378-384.

Grime, J.P. (1979) *Plant Strategies & Vegetation Processes*. John Wiley & Sons Ltd, Chichester.

Grime, J.P. (1987) Dominant and subordinate components of plant communities: implications for succession, stability and diversity. *Colonization, succession and stability. 26th Symposium of the British Ecological Society.* eds A.J. Gray, M.J. Crawley & P.J. Edwards, pp. 413-428. Blackwell Scientific Publications, Oxford.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology. A functional approach to common British species.* Unwin Hyman Ltd, London.

Gross, K.L. (1990) A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology*, **78,** 1079-1093.

Groves, R.H. (1981) Heathland soils and their fertility status. *Ecosystems of the world, 9B. Heathland and related shrublands. Analytical studies* (ed R.L.Specht), pp143-150. Elsevier Scientific Publishing Company, Amsterdam.

Grubb, P.J., Green, H.E. & Merrifield, R.C.J. (1969) The ecology of chalk heath: its relevance to the calcicole-calcifuge and soil acidification problems. *Journal of Ecology*, **57**, 175-212.

Hammond, C.O. (1985) *The dragonflies of Great Britain and Ireland*, 2nd ed. Harley Books, Essex.

Harrison, C.M. (1976) Heathland management in Surrey, England. *Biological Conservation*, **10**, 211-220.

Haskins, L.E. (1978) *The vegetational history of south-east Dorset.* Ph.D. thesis, University of Southampton.

Hayashi, I. & Numata, M. (1964) Ecological studies on the buried-seed population in the soil from the view point of plant succession III A mature stand of *Pinus thunbergii. Physiological Ecology*, **12**, 185-190.

Heil, G.W. & Diemont, W.H. (1983) Raised nutrient levels change heathland into grassland. *Vegetatio*, **53**, 113-120.

Hester, A.J. (1987) Successional vegetation change: the effect of shading on *Calluna vulgaris* (L) Hull. *Transactions of the Botanical Society of Edinburgh,* **45**, 121-126.

Hester, A.J., Miles, J. & Gimingham, C.H. (1991) Succession from heather moorland to birch woodland. 1 Experimental alteration of specific environmental conditions in the field. *Journal of Ecology*, **79**, 303-315.

Hill, M.O, (1979) *DECORANA, A FORTRAN program for detrended correspondence analysis and reciprocal averaging.* Cornell University, New York.

Hill, M.O. (1996) *TABLEFIT version 1.0 for identification of vegetation types.* Institute of Terrestrial Ecology, Monks Wood, Huntingdon.

Hill, M.O. & Stevens, P.A. (1981) The density of viable seed in soils of forest plantations in upland Britain. *Journal of Ecology*, **69**, 693-709.

Hobbs, R.J. & Gimingham, C.H. (1984) Studies of fire in Scottish heathland communities II Post-fire vegetation development. *Journal of Ecology*, **72**, 585-610.

Hobbs, R.J. & Legg, C.J. (1984) Markov models and initial floristic composition in heathland vegetation dynamics. *Vegetatio,* **56**, 31-43.

Hodgson, J.G. & Grime, J.P. (1992) The role of dispersal mechanism, regenerative strategies and seedbanks in the vegetation dynamics of the British landscape. *Seeds, the ecology of regeneration in plant communities* (ed M. Fenner), pp. 65-81. CAB International, Wallingford.

Holling, C.S. (1973) Resilience and stability of ecological systems. *Annual review of Ecology and Systematics*, **4**, 1-23.

Holling, C.S. (1986) The resilience of ecosystems: local surprise and global change. *Sustainable development of the biosphere* eds W.C. Clark & R.E. Munn, pp. 292-317. Cambridge University Press, Cambridge.

Hutchins, J. (1861) *History and antiquities of the county of Dorset compiled from the best and most ancient of historians with a copy of the Domesday Book.* John Bowyer Nicholls and Sons, Westminster.

Jarvis, M.C. & Duncan, H.J. (1976) Profile distribution of organic carbon, iron, aluminium and manganese in soils under bracken and heather. *Plant and Soil*, **44**, 129-140.

Jenny, H. (1980) *The soil resource- origin and behaviour.* Springer, New York.

Jongman, R.H.G., Ter Braak, C.J.F., & Van Tongeren, O.F.R.(eds) (1995) *Data analysis in community and landscape ecology* (2nd ed). Cambridge University Press, Cambridge.

Jonsson, L. (1993) *Birds of Europe with North Africa and the Middle East.* Princeton University Press, Princeton, New Jersey.

Jordan, C.F., Kline, J.R. & Sasscer, D.S. (1972) Relative stability of mineral cycles in forest ecosystems. *The American Naturalist*, **106**, 237-253.

Khoon, G. W. & Gimingham, C.H. (1984) Birch regeneration in heath vegetation. *Proceedings of the Royal Society of Edinburgh*, **85B**, 73-81.

Klecka, W.R. (1980) *Discriminant analysis.* Sage Publication, Beverly Hills and London.

Lavorel, S., Lebreton, J.D., Debussche, M. & Lepart, J. (1991) Nested spatial patterns in seedbank and vegetation of Mediterranean old fields. *Journal of Vegetation Science*, **2**, 367-376.

Legendre, P & Fortin, M.J. (1989) Spatial pattern and ecological analysis. *Vegetatio,* **80,** 107-138.

Legg, C.J., Maltby, E. & Proctor, M.C.F. (1992) The ecology of severe moorland fire on the North York Moors: seed distribution and seedling establishment of *Calluna vulgaris*. *Journal of Ecology*, **80,** 737-752.

Leps, J., Osbornová-Kosinová, J. & Rejmánek, M. (1982) Community stability, complexity and species life history strategies. *Vegetatio*, **50**, 53-63.

Leuschner, C. (1993) Resource availability at three presumed stages of a heathland succession on the Lüneburge Heide, Germany. *Journal of Vegetation Science*, **4**, 255-262.

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

Mackney, D. (1961) A podzol development sequence in oakwoods and heath in central England. *Journal of Soil Science*, **12**, 23-40.

Mallik, A.U., Hobbs, R.J. & Legg, C.J. (1984) Seed dynamics in *Calluna-arctostophylos* heath in North-Eastern Scotland. *Journal of Ecology*, **72**, 855-871.

Manly, B.F.J. (1986) *Multivariate Statistical Methods.* Chapman and Hall, London.

Marrs, R.H. (1984) Birch control on lowland heaths: mechanical control and the application of selective herbicides by foliar spray. *Journal of Applied Ecology*, **21**, 703-716.

Marrs, R.H. (1985a) Birch control by the treatment of cut stumps with herbicide. *Arboricultural Journal*, **9**, 173-182.

Marrs, R.H. (1985b) Techniques for reducing soil fertility for nature conservation purposes: A review in relation to research at Ropers Heath, Suffolk, England. *Biological Conservation*, **34**, 307-332.

Marrs, R.H. (1987) Studies on the conservation of lowland *Calluna* heaths I. Control of birch and bracken and its effect on heath vegetation. *Journal of Applied Ecology*, **24**, 163-175.

Marrs, R.H. (1993a) Soil fertility and nature conservation in Europe: Theoretical considerations and practical management solutions. *Advances in Ecological Research*, **24**, 242-300.

Marrs, R.H. (1993b) An assessment of change in *Calluna* heathlands in Breckland, Eastern England, between 1983 & 1991. *Biological Conservation*, **65**, 133-139.

Marrs, R.H., Hicks, M.J. & Fuller, R.M. (1986) Losses of lowland heath through succession at four sites in Breckland, East Anglia UK. *Biological Conservation*, **35**, 19-38.

Marrs, R.H. & Gough, M.W. (1989) Soil fertility - a potential problem for habitat restoration. *Biological Habitat Reconstruction* (ed G.P. Buckley) pp. 29-44, Belhaven Press, London.

Marrs, R.H., Lowday, J.E., Jarvis, L., Gough, M.W. & Rowland A.P. (1992) Control of bracken and the restoration of heathland IV. Effects of bracken control and heathland restoration treatments on nutrient distribution and soil chemistry. *Journal of Applied Ecology*, **29**, 218-225.

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

May, R.M. (1973) Stability in randomly fluctuating versus deterministic environments. *American Naturalist*, **107**, 621-650.

Miles, J. (1973) Natural recolonisation of experimentally bared soil in *Callunetum* in North-east Scotland. *Journal of Ecology*, **61**, 399-412.

Miles, J. (1979) *Vegetation Dynamics*. Chapman and Hall, London.

Miles, J. (1981a) *Effects of Birch on Moorlands*. Institute of Terrestrial Ecology, Cambridge.

Miles, J. (1981b) Problems in heathland and grassland dynamics. *Vegetatio*, **46/47**, 61-74.

Miles, J. (1985) The pedogenic effects of different species and vegetation types and the implications of succession. *Journal of Soil Science*, **36**, 571-584.

Miles, J. (1988) Vegetation and soil change in the Uplands. *Ecological Change in the Uplands,* eds M.B. Usher & D.B.A. Thompson, pp57-70. Blackwell Scientific Publications, Oxford.

Miles, J. & Young, W.F. (1980) The effects on heathland and moorland soils in Scotland and Northern England following colonization by Birch (*Betula spp*). *Bulletin Society d' Écology France*, **11**, 233-242.

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

Mitchell, R.J., Marrs, R.H, LeDuc, M.G. & Auld, M.H.D. (in prep) A study of the restoration of heathland on successional sites in Dorset, Southern England; Changes in vegetation and soil chemical properties. Submitted to *Journal of Applied Ecology*.

Mitchell, R.J., Marrs, R.H. & Auld, M.H.D. (in prep) A comparative study of the seedbanks of heathland and successional habitats in Dorset, Southern England. Submitted to *Journal of Ecology.*

Morrison, P. (1994) *Mammals, Reptiles & Amphibians of Britain and Europe*. Macmillian, London.

Moore, N.W. (1962) The heaths of Dorset and their conservation. *Journal of Ecology*, **50**, 369-391.

Muller, F.M. (1978) *Seedlings of the North-western European lowland. A flora of seedlings.* Dr W. Junk B.V. publishers, The Hague.

Nielsen, K.E, Dalsgaard, K. & Nørnberg, P. (1987a) Effects on soils of an oak invasion of a *Calluna* heath, Denmark. I Morphology and Chemistry. *Geoderma*, **41**, 79-95.

Nielsen, K.E, Dalsgaard, K. & Nørnberg, P. (1987b) Effects on soils of an oak invasion of a *Calluna* heath, Denmark. II Changes in organic matter and cellulose decomposition. *Geoderma*, **41**, 97-106.

Noble, I.R. & Slatyer, R.O. (1978) The effect of disturbance on plant succesion. *Proceedings of the Ecological Society of Australia*, **10,** 135-145.

Noble, I.R. & Slatyer, R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, **43**, 5-21.

Nolan, A.M., Aktinson, P.M. & Bullock, J.M. (1997) Patch based statistical modelling of heathland dynamics in Dorset, England. *Species dispersal and landuse processes. Proceedings of the sixth annual IALE (UK) conferance* (eds A. Cooper & J. Power), p193-201. IALE (UK).

Odum, E.P. (1969) The strategy of ecosystem development. *Science*, **164**, 262-269.

Økland, R.H. & Eilertsen, O. (1994) Canonical Correspondence Analysis with variation partitioning: some comments and an application. *Journal of Vegetation Science*, **5**, 117-126.

Owen, K.M., Marrs, R.H., Snow, C.S.R. & Evans C. (1996) Soil acidification and heathland establishment on former arable land. *Aspects of Applied Biology*, **44**, 385-392.

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

Palmer, M.W. (1993) Putting things in even better order: the advantages of Canonical Correspondence Analysis. *Ecology*, **74**, 2215-2230.

Pastor, J., Aber, J.D., McClaugherty, C.A. & Melillo, J.M. (1984) Above ground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology*, **65**, 256-268.

Perkins, J.W. (1977) *Geology explained in Dorset.* David & Charles, London.

Pickess, B., Burgess, N., & Evans, C. (1989) *Management Case Study heathland management at Arne Dorset.* RSPB Reserves Ecology Department, Sandy, England.

Pickess, B. & Auld, M. (1992) *Managment plan Arne reserve.* RSPB Reserves Ecology, Department, Sandy, England.

Pigott, C.D. (1970) Soil formation and development on the carboniferous limestone of Derbyshire. *Journal of Ecology*, **58**, 529-541.

Pimm, S.L. (1984) The complexity and stability of ecosystems. *Nature*, **307**, 321-326.

Putwain, P.D & Gillham, D.A. (1990) The significance of the dormant viable seedbank in the restoration of heathlands. *Biological Conservation*, **52**, 1-16.

Pywell, R.F. (1993) *The restoration of heathland on farmland in southern Britain.* Ph.D. thesis, University of Liverpool.

Pywell, R.F., Webb, N.R. & Putwain, P.D. (1994) Soil fertility and its implications for the restoration of heathland on farmland in Southern Britain. *Biological Conservation*, **70**, 169-181.

Pywell, R.F., Webb, N.R. & Putwain, P.D. (1995) A comparison of techniques for restoring heathland on abandoned farmland. *Journal of Applied Ecology*, **32**, 400-411.

Pywell, R.F., Putwain, P.D. & Webb, N.R. (1997) The decline of heathland seed populations following the conversion to agriculture. *Journal of Applied Ecology*, **34**, 949-960.

Rodwell, J.S. (1991) *British Plant Communities. Volume 2 Mires and Heaths.* Cambridge University Press, Cambridge.

SAS Institute Inc. (1988) The CANDISC procedure. *SAS/STAT User's Guide, Release 6.03 Edition.* pp. 173-188. SAS Institute Inc., Cary, NC.

Satchell, J.E. (1980a) Soil and vegetation changes in experimental birch plots on a *Calluna* podzol. *Soil Biology and Biochemistry*, **12,** 303-310.

Satchell, J.E. (1980b) Earth population of experimental birch plots on a *Calluna* podzol. *Soil Biology and Biochemistry*, **12**, 311-316.

Seagrief, S.C. (1959) Pollen diagrams from Southern England: Wareham, Dorset and Nursling, Hampshire. *New Phytologist*, **58**, 316-325.

Skeffington, R.A., & Bradshaw, A.D. (1980) Nitrogen fixation by plants grown on reclaimed china clay waste. *Journal of Applied Ecology*, **17**, 469-477.

Smith, J.E. (1978) *The moss flora of Britain and Ireland.* Cambridge University Press, Cambridge.

Smith, R.E.N., Webb, N.R. & Clarke, R.T. (1991) The establishment of heathland on old fields in Dorset England. *Biological Conservation*, **57**, 221-234.

Snow, C.S.R. (1995) *A study of the manipulation of soil chemical properties for the recreation of areas of conservation interest.* Ph.D. Thesis, University of Liverpool.

Snow, C.S.R. & Marrs, R.H. (1996) The effects of harvesting four crops under varying fertiliser regimes on nutrient off take and selected soil properties. *Aspects of Applied Biology*, **44**, 413-418.

Squires, R. (1991) Control of *Rhododendron ponticum* at Ynys-hir RSPB reserve Wales. *Proceedings of Heathland Conference II. History and management of southern lowland heaths.* (eds M.H.D. Auld, B.P. Pickess & N.D. Burgess) RSPB Southern Heathland Project. RSPB, Sandy, England

Stace, C. (1991) *New Flora of the British Isles.* St Edmundsbury Press Ltd, Bury St Edmunds, Suffolk.

Stieperaere, H. & Timmerman, C. (1983) Viable seeds in the soils of some parcels of reclaimed and unreclaimed heath in the Flemish district (Northern Belgium). *Bulletin de la Societe Royale de Botanique Belgique*, **116**, 62-73.

Summerhayes, V.S., Cole, L.W. & William, P.H. (1924) Studies on the Ecology of the English heaths I The vegetation of the unfelled portions of Oxshott Heath and Esher Common Surrey. *Journal of Ecology*, **12**, 287-306.

Taylor, C. (1970) *The making of the English Landscape: Dorset.* Hodder & Stoughton, London.

Ter Braak, C.J.F (1988) *CANOCO - a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correlation analysis, principal components analysis and redundancy analysis.* IW15-TNO, Wageningen, The Netherlands.

Ter Braak, C.J.F (1990) *Update notes: CANOCO version 3.10.* Agricultural Mathematics Group, Wageningen, The Netherlands.

Thomas, J. & Lewington, R. (1991) *The butterflies of Britain and Ireland.* Dorling Kindersley, London.

Thompson, K. & Grime, J.P. (1979) Seasonal variation in the seedbanks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, **67**, 893-921

Tilman, G.D. (1984) Plant dominance along an experimental nutrient gradient. *Ecology*, **65**, 1445-1453.

Tilman, D. & Downing, J.A. (1994) Biodiversity & stability in grassland. *Nature*, **367**, 363-365.

Traynor, C.H. (1995) *The management of heathland by turf cutting: historical perspective and application to conservation.* Ph.D. thesis, University of Liverpool

Unicam Ltd (1991) *Atomic absorption spectrometry. Methods manual.* Unicam Ltd, Cambridge.

Van Der Eerden, L.J., Dueck, TH.A., Berdowski, J.J.M., Greven, H. & Van Dobben, H.F. (1991) Influence of NH_3 and $(NH_4)_2SO_4$ on heathland vegetation. *Acta Botanica Neerlandica*, **40**, 281-296.

Webb, N.R. (1980) The Dorset Heathlands: Present status and conservation. *Bulletin* of *Ecology*, **11**, 659-664.

Webb, N.R. (1986) *Heathlands. A Natural History of Britain's Lowland Heaths.* Collins, London.

Webb, N.R (1990) Changes on the Heathlands of Dorset, England, between 1978 and 1987. *Biological Conservation*, **51**, 273-286.

Webb, N.R. & Haskins, L.E. (1980) An ecological survey of heathlands in the Poole Basin, Dorset, England in 1978. *Biological Conservation*, **17**, 281-296.

Webb, N.R. & Vermaat, A.H. (1990) Changes in vegetational diversity on remnant heathland fragments. *Biological Conservation*, **53**, 253-264.

Webster, J.R., Waide, J.B. & Pattern, B.C. (1975) Nutrient recycling and the stability of ecosystems. *Mineral Cycling in Southeastern Ecosystems* (eds F.G. Howell, J.B. Gentry & M.H. Smith), pp1-27. CONF 740513 National Technical Information Service, Springfield, VA.

Wedin, D.A. & Tilman, D. (1990) Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia,* **84**, 433-441.

Westman, W.E. (1978) Measuring the inertia and resilience of ecosystems. *Bioscience*, **28**, 705-710.

Williamson, M.H. (1987) Are communities ever stable? *Colonisation, Succession and Stability. The 26th Symposium of The British Ecological Society.* (eds A.J. Gray, M.J. Crawley, P.J. Edwards), pp353-371. Blackwell Scientific Publications, Oxford.

Woodrow, W., Symes, N. & Auld, M. (1996) *RSPB Dorset Heathland Project 1989-1995. A management case study.* RSPB, Sandy, England.

Woodrow, W., Symes, N., Auld, M. & Cadbury, J. (1996) Restoring Dorsets Heathland: The RSPB Dorset Heathland Project. *RSPB Conservation Review*, **10**, 69-81.