DOCTOR OF PHILOSOPHY

Vegetation succession following the clearance of Rhododendron in the Vale of Ffestiniog.

Hockley, T G.

Award date:
1989

Awarding institution:
Bangor University

Link to publication

VEGETATION SUCCESSION FOLLOWING THE CLEARANCE OF

RHODODENDRON IN THE VALE OF FFESTINIOG

A dissertation submitted in partial fulfilment of the requirements for the degree of Magister in Scienta in Environmental Forestry.

School of Agricultural and Forest Sciences
University College of North Wales
Bangor
Gwynedd
North Wales

T.G.HOCKLEY

October 1989

ABSTRACT

This study analyses vegetation succession following the clearance of Rhododendron in a sessile oakwood in North Wales. The Rhododendron has been cleared since 1984/5 and prior to clearance dominated the understorey.

The succession was analysed in relation to the number of years since clearance; method of clearance; density of the former Rhododendron cover, and vegetation adjoining the site. An experiment was undertaken in the University's nursery to assess the presence and viability of seed within the seedbank, and the ability of the soil to support germination. Over 50% of the samples were dominated by bryophytes (60%), with birch, bramble and Rhododendron seedlings each present at less than 10%.

There was a significant difference between the mean percentage crown cover of each TWINSPAN group; those groups with more light demanding species had a lower mean percentage crown cover than groups dominated by more shade tolerant species. Only bramble and birch germinated in soil collected from the two most recent years of clearance. Their presence is probably due to seed dispersed prior to clearance, and there is therefore no viable seed in the seedbank. Colonisation must therefore rely on immigration of seed.

There was no significant difference between the ability of soil recently infested by Rhododendron, or the ability of peat, to support germination of Betula pendula or Festuca ovina.

There is a significant difference between the frequency and abundance of vegetation and the year of clearance. With the

exception of one plot, frequency and abundance increased with the number of years since clearance.

Rhododendron seedlings are associated with a bryophyte cover. The site contains substantial Rhododendron coppice and seedlings, and continued eradication and containment programmes will be needed.

ACKNOWLEDGEMENTS

I am grateful to the many people who have provided their advice and support. Gordon Patterson of the Forestry Commission for his help in shaping the outline of this study, and to Doug Oliver and Wil Jones of the Nature Conservancy Council for giving their time to provide information and advice on the site.

At the University I am grateful to Tom Jenkins and Steve Jones for invaluable computer and statistical knowledge, and to my supervisor, Dr G.J Mayhead.

TABLE OF CONTENTS

		PAGE NUMBER
Declaration		i
Abstract		ii
Acknowledgements		iv
Table of contents		v
List of figures		vii
List of tables		viii
List of maps		viii
Appendices		ix
1.0	INTRODUCTION	1
2.0	OBJECTIVES	1
3.0	LITERATURE REVIEW	
3.1	Nomenclature	2
3.2	Introduction to Great Britain	2
3.3	Seed production and dispersal	4
3.4	Early life and germination	5
3.5	Competitive ability following establishment	9
3.5.1	Shade tolerance	9
3.5.2	Resistance to herbivores	10
3.5.3	Allelopathy	10
3.5.4	Mycorrhiza	11
3.5.5	Freedom from pests and diseases	12
3.6	Vegetative spread and longevity	13
3.7	Climatic conditions	14
3.8	Edaphic conditions	14
3.9	Resistance to herbicide	15
3.10	Associated fauna	16
4.0	SITE DESCRIPTION	
4.1	Introduction	18
4.2	_Rhododendron_ cover	21
4.3	Tree cover	21
4.4	Species composition	23
4.5	Adjacent vegetation	23
4.6	Geology	25

5.0 EXPERIMENTAL DESIGN AND COLLECTION OF DATA

5.1 Germination trials 26
5.2 Collection of vegetation succession data 28

5.2.1 Tree density and _Rhododendron_ cover 28
5.2.2 Vegetation survey 29
5.2.3 Adjacent vegetation 31

6.0 ANALYSIS OF DATA

6.1 Data analysis techniques 32
6.2 Data analysis 39

6.2.1 Vegetation associations 39
6.2.2 Crown cover and vegetation associations 46
6.2.3 Vegetation succession and year of clearance 50
6.2.4 Species composition within plots 53
6.2.5 Succession of _Rhododendron_ and oak 62

6.3 Germination trials 64

6.3.1 Germination of seed within the seedbank 64

6.3.2 Test sowings 67

7.0 CONCLUSIONS AND RECOMMENDATIONS

7.1 Vegetation associations 70
7.2 Vegetation and light intensity 70
7.3 Germination trials 70
7.4 Vegetation succession 71
7.5 Management implications 73
7.6 Further research 73

REFERENCES 74

LIST OF FIGURES

FIGURES		PAGE NUMBER
1	Tree species composition	24
2	Categories of Rhododendron density	30
3	TWINSPAN sample classification	36
4	TWINSPAN species classification	37
5	DECORANA sample ordination coded to accord with TWINSPAN groups	47
6	DECORANA species ordination	48
7	Mean and standard deviation of percentage crown cover for each TWINSPAN group	49
8	DECORANA sample ordination showing year of clearance only	51
9	Cumulative frequency and Domin values for each year	52
10	Species composition in plot 5	54
11	Species composition in plot 4	56
12	Species composition in plot 3	57
13	Species composition in plot 2	58
14	Species composition in plot 1	59
15	Summary of species composition between plots	60
16	Rhododendron seedling establishment	62

LIST OF TABLES

TABLE		PAGE NUMBER
1	Mean yield of <u>Festuca</u> <u>ovina</u> seedlings with and without the presence of <u>R.ponticum</u>	11
2	Site stand composition (dbh classes)	23
3	The Domin scale	29
4	TWINSPAN two way table	38
5	Distribution of quadrats between TWINSPAN groups	43
6	Summary of vegetation associations	44
7	One-way analysis of variance for the relationship between percentage mean crown cover and TWINSPAN groups	50
8	Analysis of variance for the regression between vegetation succession and year of clearance	52
9	Summary of species composition for each plot	61
10	Species germinating in seedtrays 1 - 10	64
11	Germination rates in seedtrays 1a - 10a & controls 1 - 5	67
12	One-way analysis of variance for test sowings	68

LIST OF MAPS

MAPS		PAGE NUMBER
1	Site location	19
2	Location and year of clearance of each plot	20
3	Adjacent vegetation and areas of each plot with scarce, or no, tree cover	22

APPENDICES

APPENDIX		PAGE NUMBER
I	Parasitic flora and fauna associated with R.ponticum	79
II	Bird species abundance following the removal of Rhododendron at Coombes Valley	80
III	Assessment of the quantity of seed per seedtray	81
IV	Species recorded at plot 1	82
V	Species recorded at plot 2	83
VI	Species recorded at plot 3	84
VII	Species recorded at site 4	85
VIII	Species recorded at site 5	86
IX	Species list and abbreviated names	87
X	Scheffey's test	90

1.0 INTRODUCTION

Rhododendron has colonised many areas to the exclusion of native vegetation. The freely draining, acid soils of Western Britain are particularly favourable to the plant, and in the Snowdonia National Park Rhododendron is found in an area of approximately $34km^2$ (Snowdonia National Park, 1987). No statutory powers of control exist, and the plant has joined the grey squirrel, Japanese knotweed and New Zealand willowherb as undesirable aliens (Simons, 1988).

The complete eradication of Rhododendron is dependent on substantial and sustained expenditure; containment is therefore seen as the only viable objective, with clearance undertaken in areas of prime importance only. Attempts to assess current annual expenditure on clearance and containment are hampered by the predominant reliance on voluntary labour, the availability of which is limited. An indication of expenditure can however be derived from the Forestry Commission budget of £6500 for clearance in 1989/90 in two forest districts of North Wales only, and the N.C.C budget for 1989/90 of approximately £3700, most of which will be spent in the Maentwrog area.

2.0 OBJECTIVES

The primary objective of the study was to analyse succession following the clearance of Rhododendron, thereby assessing the vegetation associations present in a given year of clearance. In addition the succession was related to the light intensity; method of clearance; density of the former Rhododendron cover and of the sessile oakwood; and the vegetation adjoining the site. The vegetation developing is dependent on the ability of the soil to support vegetation and available seed sources. These seed sources may either be seed alighting in the area for the first time, or seed that is stored in the seedbank. Germination trials were undertaken to assess the presence of viable seed in the seedbank, and the ability of the soil to support germination and growth.

3.0 **LITERATURE REVIEW**

3.1 Nomenclature

The full Latin name Rhododendron ponticum, with a sub-species qualification, is used where appropriate. The British feral form is referred to simply as Rhododendron.

3.2 Introduction to Great Britain

The genus Rhododendron, along with Erica, Calluna and Vaccinium, belong to the family Ericaceae (Clapham et al, 1981). The genus consists of more than 600 species concentrated in South East Asia, with a few representatives in America, Asia Minor and Iberia (Cross, 1975). Rhododendron was first introduced to Britain in 1763 with the first plant established at Kew in 1765 (Bean, 1976). These early introductions were dispatched from Gibraltar, and are likely to have been of the Iberian form from either Spain or Portugal (Shaw, 1984).

According to Flora Europea (Tutin et al, 1972), the Iberian form is of the sub specific status baeticum, the other sub species, ponticum, being naturally distributed in the Balkan Peninsular (Bulgaria, Turkey and the USSR) and Lebanon, a geographical separation of nearly 3000Km (Shaw, 1984). The distribution of R.ponticum is thought to be the result of Quaternary glaciation. Shaw (1984) quotes Jesson et al (1959), in referring to the fossil remains that have been recovered in various places in Europe, and that indicate a once continuous distribution. Whilst R.ponticum has been found in two sites of interglacial age in Ireland, no such finds have yet been made in Britain (Shaw, 1984).

Since its introduction Rhododendron has been widely planted for game cover and ornamental purposes. Before modern propagation techniques were developed, R.ponticum was commonly used as a rootstock for grafting ornamental varieties (Brown, 1953a); when planted out the rootstock often developed shoots, which in time overwhelmed the less robust scion.

Cross (1975) considers plants in Britain to predominantly resemble R.ponticum, whilst Shaw (1984) believes feral Rhododendrons in North Wales most closely resemble R.baeticum. A number of separate introductions have probably led to both sub species and sub specific hybrids being present (Shaw 1984).

Rhododendron is now widely naturalised in suitable areas, such as the free draining acid soils of Western Britain, and aerial photography and population studies in Snowdonia show that the species has become increasingly widely distributed in the last 15 to 20 years (Shaw, 1984). Rhododendron is estimated to be present in approximately 3,407ha or 1.6% of the National Park, with over 49.8% of conifer woodland, and 14.7% of broadleaved woodland infested (Snowdonia National Park, 1987).

3.3 Seed production and dispersal

In common with other ericaceous species Rhododendron seeds are among the smallest in the plant kingdom, the average weight of seed being assessed by Cross (1981) as 63 micrograms, and by Shaw (1984) as 50 micrograms, or 20 million /kg. Under British conditions Rhododendron flowers annually, with a single flower head (a raceme) containing 3000 to 7000 seeds. Given that Rhododendron is monoecious, and that there are several hundred flowers on a bush, the reproductive potential is high. Flowers on the raceme also open sequentially from top to bottom, reducing loss to high winds or frosts (Shaw, 1984). Bushes originating directly from seed do not usually flower until 10 or 12 years old, although coppice shoots may reproduce earlier. The flower buds are terminal, continued growth being through the activation of three or four lateral buds, resulting in an actively flowering bush quickly becoming bushy (Shaw, 1984). Nearly one year elapses between flowering and the release of seeds, the capsules opening in dry weather in the late winter and spring following flowering (Shaw, 1984). The seeds resemble flattened disks with frills of hairs at each end (Cross, 1975) which are estimated to have only a minor aerodynamic function (Brown, 1953a). Dispersal is mainly by wind, and adopting a sinking velocity of the seed in still air of approximately 1m/sec (Brown, 1953a), the theoretical dispersal distance in strong winds is up to 100 metres (Shaw, 1984). Given the turbulent air conditions found in mountainous regions, Shaw (1984) believes seed in Snowdonia can be carried far greater distances. Dispersal within woodlands is less effective; Brown (1953b) recorded seed dispersal of only 16.6 metres in open woodland.

3.4 Early life and germination

The ultimate success of dispersal is dependent on the seed alighting on a site suitable for germination, and receiving the conditions needed for subsequent growth. The probability of these criteria being met are extremely low, a problem countered by prolific seed production and tolerance of shade.

Rhododendron seeds will germinate in 5 - 6 days under favourable conditions, although unlike many other weed species the seeds deteriorate quickly. Under field conditions all seeds became non viable after 160 days (Cross, 1973). Even under ideal (artificial) conditions of low temperature and desiccation the seed does not store well, suffering approximately a 50% loss of viability in one year (Shaw, 1984).

Germination will occur on many substrates (Cross, 1975). A germination rate of 80% was recorded on a semi natural medium (horticultural peat, pH 4.0), of 60% on a mor humus of pH 4.4 from an oak / holly wood, and approximately 40% on a brown earth of pH 5.5.

Brown (1953a) recorded germination in less than 1% daylight, although fungal attack prevented accurate estimates of germination rates. Cross (1973) found that the shade cast by Rhododendron thickets (2% total light) reduced the rate and quantity of germination when compared with shade cast by an oak / holly canopy (9% total daylight). In one experiment the rate of germination after 49 days under a Rhododendron canopy was 17%, compared to 75% under an oak / holly canopy

(Cross, 1973). Germination only started to decline in levels of less than 5% full daylight (Cross, 1975). Therefore providing the seeds are not buried, the light in most woodlands is unlikely to restrict germination unless the canopy is very dense.

The effect of temperature on germination is not known (Cross, 1975), although there is no evidence that this is a limiting factor in Britain (Shaw, 1984). Moisture is more critical, short periods of desiccation (perhaps even measured in hours) can be lethal (Shaw, 1984).

The seedling stage is generally considered to be the most hazardous stage in the life of a plant (Cross, 1981), and this transition from dependence on seed reserves to independent assimilates is particularly critical for Rhododendron, which has little competitive ability in the seedling stage, and is readily smothered by low growing vegetation and drifting litter (Cross, 1981). The term "safe site", originally used by Harper et al (1965) is used to describe the conditions in which Rhododendron seeds can germinate and the seedlings develop. A safe site is essential as the cotyledon stage seedling of Rhododendron is only 2 - 5 mm across with a rudimentary root system, and even at the end of one growing season the seedlings may only consist of the cotyledons and one true leaf (Shaw, 1984). During this stage the plant is therefore very vulnerable to adverse conditions such as desiccation, frost heave, trampling, or smothering by the dead parts of other plants. It is only when the plants are 3 - 5 years old, and 5 - 10 cm in height, that their vulnerability declines.

The most favourable safe sites are thin bryophyte carpets, such as those formed by the pleurocarpus mosses (having lateral fructifications), such as Plagiothecium undulatum (Shaw, 1984). These maintain a relatively humid environment, and act as a protective cushion which lessens the physical impact of heavy drips from the canopy that can uproot exposed seedlings, or bury them with soil thrown up from the drip (Cross, 1981). Taller communities of acrocarpus mosses (having terminal fructifications), such as Polytrichum formosum do not provide such favourable sites as they tend to provide conditions similar to that of grass or a grass / herb sward (Shaw, 1984).

Inherently moist patches of bare mineral soil and humus can also provide safe sites (Cross, 1981). If not moist the dark surfaces of these substrates are subject to extremes of temperature and desiccation; they are often unstable and receive heavy drips from the canopy which can physically destroy the young seedlings. The tightly packed shoots of most Sphagnum spp provide a suitable habitat, although seedlings experience difficulty if they cannot quickly get their roots into the soil (Shaw, 1984).

A ground cover of litter or vegetation, like a thick bryophyte cover, also restricts establishment. This may be due to a combination of burial, drought, and the instability of the substrate. Even if germination does occur, the roots may fail to reach the soil and the seedlings subsequently die during a dry spell (Cross, 1981).

The importance of this bryophyte layer is demonstrated by a Rhododendron clearance in the Killarney oakwoods of Ireland, where for 5 years no Rhododendron seedlings appeared on the peaty humus exposed to the full sun until a 2 mm layer of mosses became established (Cross, 1981). Cross (1981) also studied the relationship between the depth of bryophyte cover and the number of R.ponticum seedlings and found that one year old plants occurred only in bryophyte carpets of 1cm depth or less, and that 2 - 3 year old plants were concentrated in carpets of a depth of less than 2.5 cm.

Factors favouring the development of bryophytes will consequently favour Rhododendron. Shaw (1984) divides these factors into two categories: static and active. Static factors such as high rainfall and humidity, steep slopes, rocks and shelter reflect local climate and topography. Active factors such as grazing, trampling, burning and other factors of disturbance are - in contrast to static factors - controllable. The role of disturbance is emphasised by the observations of Cross (1981) that the establishment of seedlings in the Killarney oakwoods was related to the distribution of loose boulders, rock outcrops and breaks in slope. The distribution also showed a concentration on slopes of between 10° and 50°, with a decrease in numbers of seedlings with increase in angle of slope. This is partly attributed to the tendency of seedlings to root on humus formed from bryophytes. The humus tends to be thicker at the base of slopes and therefore less subject to drought than soil at the top of slopes.

Cross (1981) describes an experiment in the Killarney oakwoods where areas were enclosed to reduce disturbance. It was observed that under a relatively thin canopy a thick herbaceous ground cover developed that had a smoothing effect, burying many of the surface irregularities and reducing the movement of air close to the ground. This in turn led to litter accumulating either in the vegetation itself or in the pockets formed for example between vegetation and the base of rock outcrops. Species such as Luzula sylvatica which spread vegetatively into thick bryophyte mats or rock outcrops and loose boulders contribute still further to this smoothing effect. The elimination of grazing therefore reduces the number of safe sites available.

3.5 Competitive ability following establishment

3.5.1 Shade tolerance

Prolific seed production and shade tolerance are the methods by which Rhododendron overcomes the difficulty of finding safe sites for germination and early growth. Once established, Rhododendron is remarkably shade tolerant, with a physiological compensation point of less than 2% full daylight, and with only 5 - 10% of full daylight required for satisfactory growth (Shaw, 1984). The seedlings have a low metabolic rate; they have the ability to modify specific leaf area in response to prevailing light levels (Shaw, 1984). Cross (1975) found an 89% increase in dry weight matter over the winter months for 5 year old Rhododendron seedlings growing in an oakwood. Although there was no change in size this reflects the advantage of being evergreen and possessing the ability to make use of improved light conditions when deciduous woodland is not in leaf. Dormancy of buds is broken by increased day length with shoot extension usually beginning in early May (Cross, 1975).

3.5.2 Resistance to herbivory

Cross (1975) quotes Forsyth (1954) who found that *R.ponticum* contains andromedo toxin, which is highly poisonous if ingested by mammals. Grazing animals therefore avoid browsing the plant, giving it a significant advantage over other woody plants, including spiny ones such as *Crataegus monogyna* and *Ilex aquifolium* (Shaw, 1984). Cross (1981) found no evidence of seedlings in the Killarney oakwoods being damaged or killed by animals, although some seedlings may have been eaten by slugs which are known to eat newly germinated seedlings (Cross, 1973).

Rotherham (1988) investigated the free phenol content of a range of *R.ponticum* tissues. The concentrations were generally higher in leaves than stems or roots. The highest concentrations were in new leaf (57.0% dry weight), new stem (22.0% dry weight), and adventitious roots (17.7% dry weight). High concentrations of these free phenols may offer resistance to attacks from both vertebrate and invertebrate herbivores (Rotherham, 1988).

3.5.3 Allelopathy

Rotherham (1988) conducted experiments into the allelopathic properties of *Rhododendron*. Under controlled laboratory conditions *R.ponticum* was able to suppress the growth of *Festuca ovina* seedlings, resulting in a decrease in dry weight and almost total inhibition of root growth. This suppression was independent of competition for water, nutrients, space, light or mycorrhizal infection, and applied to *Festuca ovina* grown either in soil with living *Rhododendron* plants, or in soil which has recently supported

Rhododendron (Table 1). This effect may be a result of toxic organic acids released from *Rhododendron* roots into the soil, these organic acids being either simple phenols or short chain aliphatics. Cross (1975) states that, in common with other ericaceous plants, *Rhododendron* has a deleterious effect on the soil mobilising cations either directly or indirectly by the production of polyphenols.

TABLE 1: MEAN YIELDS OF FESTUCA OVINA SEEDLINGS (MG DRY WEIGHT) AFTER 6 WEEKS GROWTH WITH AND WITHOUT THE PRESENCE OF RHODODENDRON (ROTHERHAM 1988)

Experimental conditions (m) = Mycorrhiza present (nm) = Mycorrhiza absent	Mean yields (mg) Added nutrient solution		Distilled deionized water	
	Root	Shoot	Root	Shoot
(i) *R.ponticum* present (m)	0.00	0.01	0.00	0.01
(ii) *R.ponticum* present (nm)	0.00	0.01	0.0001	0.03
(iii) *R.ponticum* harvested prior to treatment (m)	0.00	0.03	0.00	0.01
(iv) *R.ponticum* harvested prior to treatment (nm)	0.00	0.0	0.00	0.02
(v) Control (endophyte only	0.66	4.68	0.52	6.15
(vi) Control (no plant or fungus)	0.66	5.93	0.47	4.59

3.5.4 Mycorrhiza

Dramatic increases (184% dry matter production) in *Rhododendron* growth were achieved by mycorrhizal infection in soils of low nutrient status (Rotherham, 1988). Like other ericaceous plants *R.ponticum* has endotrophic mycorrhiza (Cross, 1975), forming such an extensive and efficient network that neighbouring plants are starved by the soaking up of nutrients around their roots (Simons, 1988). This ability to compete more effectively than competitors for restricted nutrient resources is

particularly important in the acidic soils that are typical of the areas invaded by Rhododendron (Rotherham, 1988).
The view of a competitive advantage given to Rhododendron by mycorrhizal infections is not universally held. Tester (1988) points out that mycorrhizas are found in most plants, including those commonly competing with Rhododendron such as ivy, oak and heather. Indeed the advantage afforded to mycorrhizal plants over plants not forming such associations is itself not absolute, as many weedy species invading disturbed land such as stinging nettles, goosefoot and dock are rarely affected by mycorrhizal fungi. Tester (1988) concludes that the ability of Rhododendron to compete so effectively with native flora is not even partly due to mycorrhizal associations.

3.5.5 Freedom from pests and diseases

Elton (1958) cites Rhododendron as an example of an invasive plant that may be in the process of being brought under control by the later introduction of animals and plants that feed on it. There is little evidence that this has occurred (Shaw, 1984), and due to its presence in Britain between the ice ages, Rotherham (1988) states that the species is already adapted to the pests and diseases found in Britain. Cross (1975) lists the parasitic flora and fauna associated with Rhododendron (Appendix I), although none of these have yet had any serious debilitating or control effect. Given the distribution and size of the genus it is likely that there are predators that could have a great impact on the species (Shaw, 1984). Any natural control mechanism is however likely to conflict with horticultural interests.

3.6 Vegetative spread and longevity

It is not known how long individual bushes of Rhododendron can live. Brown (1953a) reported stems of 60 years, whilst Cross (1975) states the greatest age to be at least 100 years. In mature bushes the age of the oldest stems is limited by mechanical weakness; they become top heavy and are blown over. The centres of the old bushes tend to die out, and the original root system may be replaced by younger, adventitious roots. With age, individual bushes become difficult to distinguish, and maximum age is not easily determined (Shaw, 1984).

Rhododendron is able to spread vegetatively; this is most common on the edge of thickets where unsupported branches become prostrate. Cross (1975) and Brown (1953a) state that adventitious buds are produced from the roots, whereas Shaw (1984) considers that it is often difficult to distinguish between root and stem, and it is from the stem, not the root, that new shoots develop. Many Rhododendron bushes have a length of procumbent stem or layered shoots at their base, whilst others have an accumulation of mosses around the base from which adventitious roots on the stem develop. In respect of the uprooting of bushes as a method of control, aside from ground disturbance creating safe sites, it seems not essential that all roots are removed so long as no piece of stem is left in the ground.

The ability to produce new shoots and coppice means that cutting as a means of control is ineffective, although repeated cutting may eventually lead to death by starvation. Fire has a similar effect to cutting. Normal grass or heather fires only kill young seedlings. Fire may even favour Rhododendron by destroying other vegetation cover and creating suitable habitats for seedlings (Shaw, 1984)

3.7 Climatic conditions

Despite its southern origin, the distribution of Rhododendron in Britain is unlikely to be limited by temperature, as it endures lower temperatures in Turkey and continental Russia than would be found in the British Isles (Tabbush, 1987). A combination of wind and low temperature probably limit its range in the mountains; in Snowdonia it has been found growing at just over 400m in fairly sheltered conditions, although it seems to produce little seed above approximately 300m (Shaw, 1984). In Ireland Rhododendron has been found growing up to 530m (Cross, 1975).

The ability to tolerate drought, a substantial problem especially during the early years of establishment, depends on the habitat to which it is adapted. Cross (1975) found plants growing in the normally very damp Killarney woods were badly affected by drought in 1972, whereas plants in open habitats in the same area were unaffected. Although able to grow on both north and south facing slopes, growth on south facing slopes tends to be less vigorous (Snowdonia National Park, 1987).

3.8 Edaphic conditions

Rhododendron is an extremely versatile species found growing on a wide range of soils with varying degrees of vigour, flowering in most situations (Shaw, 1984). Most soils supporting R.ponticum have a low cation exchange capacity and low levels of potassium (Cross, 1975). Optimum growth occurs on freely drained, acid soils that do not readily dry out in summer. Soils containing a high proportion of coarse particles are also favoured (Cross, 1975). Whilst growth is normally poor at a pH of greater than 5.0, Cross (1975) found Rhododendron growing in a range of soils between pH 3.3 and 6.4. At a pH of greater than 5.0, the plants show signs of mineral imbalance, with low levels of manganese in the foliage (Shaw, 1984). Rhododendron is tolerant of high levels of magnesium and as many alkaline soils contain high levels of this cation this may explain the presence of Rhododendron in such soils.

The root system forms a dense, compact mat, ramifying throughout the upper soil horizon. Although preferring deeper soils, a few centimetres of humus over rock is sufficient to support small, fertile bushes. In these situations the plant is highly vulnerable to drought, with death occurring in extreme cases (Shaw, 1984). Cross (1975) states that Rhododendron will not tolerate complete waterlogging of its roots, although it may grow in bogs where the ground is raised enough to avoid direct contact with the water table. Rhododendron has however been found growing directly in bogs, although the plants show premature loss of leaves and nutrient deficiency (Shaw, 1984). In such a situation the plants may form a thick layer of raw humus at the base to enable themselves to be raised above the water table.

3.9 Resistance to herbicides

The resistance of Rhododendron to herbicides may stem from the thick waxy cuticle on the upper surface of mature leaves, the under-side of the leaf being less well protected but less accessible. Immature leaves have a thinner cuticle and bushes are therefore often cut and allowed to regrow before being sprayed. There is also evidence that translocation of herbicide is poor compared with other weedy plants (Shaw, 1984). Chemicals designed to specifically control or eradicate Rhododendron are unlikely to be manufactured, as industrial companies tend to look for 50 million dollar markets (Snowdonia National Park, 1987).

3.10 Associated fauna

Rhododendron provides valuable cover for birds and animals, including blackcaps, chiffchaffs, finches, nightingales, thrushes, otters and badgers (Simons 1988). Despite the shelter afforded to these species, the diversity of bird species tends to be lower in mature oakwoods invaded by Rhododendron than in uninvaded woodlands. Hope Jones (1972) assessed the number of pairs of birds in Welsh woodlands as follows.

Vegetation	Bird density Pairs per sq km
Open ground	13
Low scrub	130
Medium scrub	178
High scrub	89
Mature oak with sheep	388
Mature oak with gaps and scrub	684
Mature oak with Rhododendron	161
Degenerate oak	67

Becker (1988) states that whilst Rhododendron may be used by mammals and birds for breeding sites, cover and roosts, this may be due to a lack of alternative vegetation. For most species the plant is of little value as a food source; it lacks a high population of insects and has toxic nectar and poisonous leaves.

Following Rhododendron clearance in 1977/8 at the Coombes Valley R.S.P.B reserve in Staffordshire, the diversity of bird species increased (Appendix II), although the overall number of birds using the area was not significantly different. The species that declined either had a notable association with Rhododendron, such as the blackcap and chiffchaff, or were species associated with areas of dense ground cover. Conversely, species showing an increase, or recorded for the first time tended to have a preference for open woodland (Becker, 1988).

4.0 SITE DESCRIPTION

4.1 Introduction

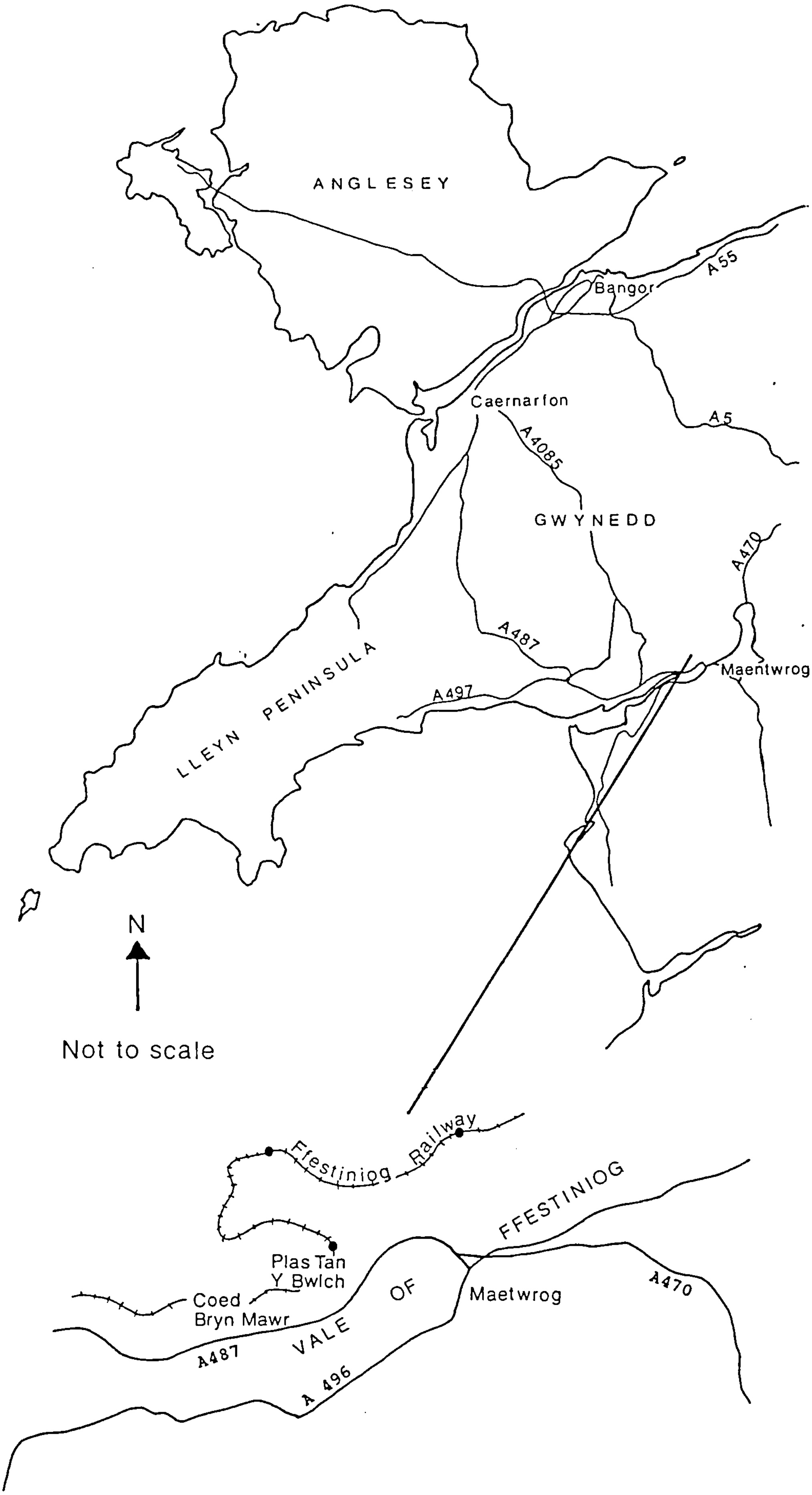
Coed Bryn Mawr (OS 124, Grid ref. 648404), is situated in the Vale of Ffestiniog in North Wales (Map 1). The vale is an important tourist attraction, especially during the summer months when the oakwoods are in leaf and the Rhododendrons in flower. The oakwoods are an intrinsic part of this landscape; their importance is highlighted by the Ffestiniog railway which runs along its northern boundary.

The entire site is approximately 3.87 hectares, forming a south facing slope 55 to 95 metres above sea level. The slope, whilst not uniform, is generally steep in the middle part of each plot, with more gentle slopes above and below. Rainfall is estimated at 1700mm per annum. There is no formal grazing pressure, although there are goats in the vicinity. These are only occasional visitors, and no evidence of grazing was found.

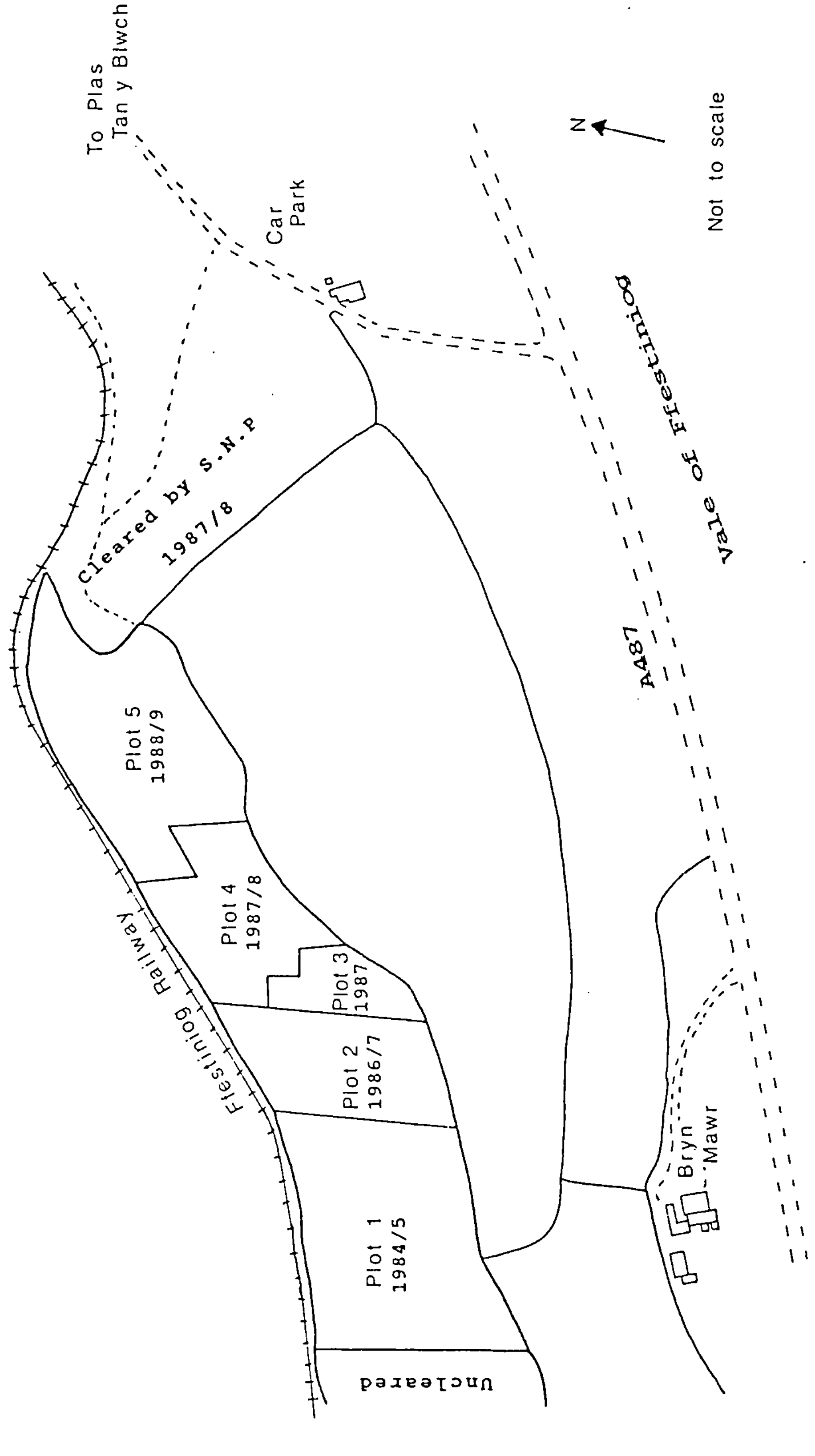
Within the wood five plots were defined according to their year of clearance (Map 2).

Plot 1. This is the earliest Rhododendron clearance comprising 1.1 hectares cleared pre-1986, predominantly during the winter of 1984/5. The southern part of this plot has no tree cover. Ammonium sulphamate was used in the initial year of clearance only as there was concern that herbicide might enter the Bryn Mawr water supply. Stumps were cross cut before being treated. Regrowth has been partly removed three times a year for the last three years, although with limited success.

MAP 1 : SITE LOCATION



MAP 2 : LOCATION AND YEAR OF CLEARANCE OF EACH PLOT



Plot 2. 0.86 hectares cleared in 1986/7. The Rhododendron was first cut and burnt, followed by brush treatment of stumps with a 50% solution of glyphosate, water, and a chemical dye to show which stumps were treated. Spraying is intended this year.

Plot 3. 0.43 hectares cleared in 1987; the method of clearance was as for plot 2.

Plot 4. 0.58 hectares cleared for approximately £2500 in 1987/8. The method of clearance was as for plot 2.

Plot 5. 0.88 hectares cleared for approximately £3000 in the winter of 1988/9. The method of clearance was as for plot 2.

4.2 Rhododendron cover

A former Rhododendron cover throughout the site of 75 - 100% was derived from measurement of stumps, and confirmed by the N.C.C warden.

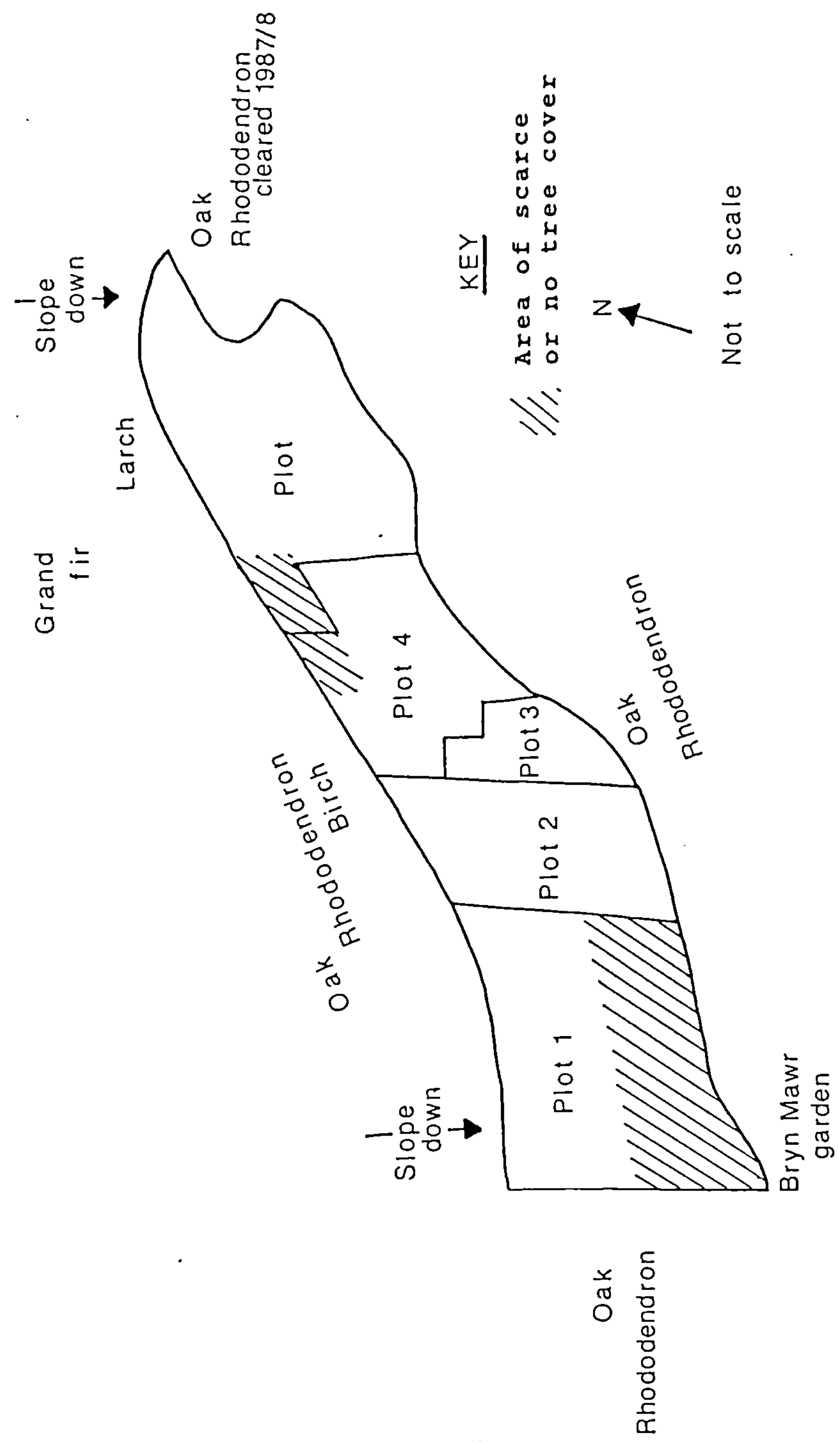
4.3 Tree cover

Basal areas per hectare were derived for the wooded areas of each plot. The areas with scarce, or no tree cover are illustrated in Map 3.

Plot	Basal area
Plot 1	42.28 m^2/ha
Plot 2	31.82 m^2/ha
Plot 3	27.30 m^2/ha
Plot 4	30.03 m^2/ha
Plot 5	32.45 m^2/ha

This gave an average basal area for the site as a whole of 32.78 m^2/ha.

MAP 3 : ADJACENT VEGETATION AND AREAS OF EACH PLOT WITH SCARCE OR NO TREE COVER



4.4 Species composition

The wood is a predominantly mature sessile oakwood with some Betula pubescens (Figure 1). The mature Pseudotsuga menziesii, Tilia cordata and Fraxinus excelsior were recorded in plot 5 which appeared more diverse in species than the other plots. Areas in plots 1, 4 and 5 with scarce, or no tree cover are shown at Map 3.

Table 2 shows the stand composition for the site. The dbh classes 21 - 30cm, 31 - 40cm and 41 - 50cm each comprise approximately 23 - 24% of the stand, with 13% of the stand in the dbh range 11 - 20cm. The structure appears sufficiently diverse to allow regeneration with the majority of the stand capable of producing seed.

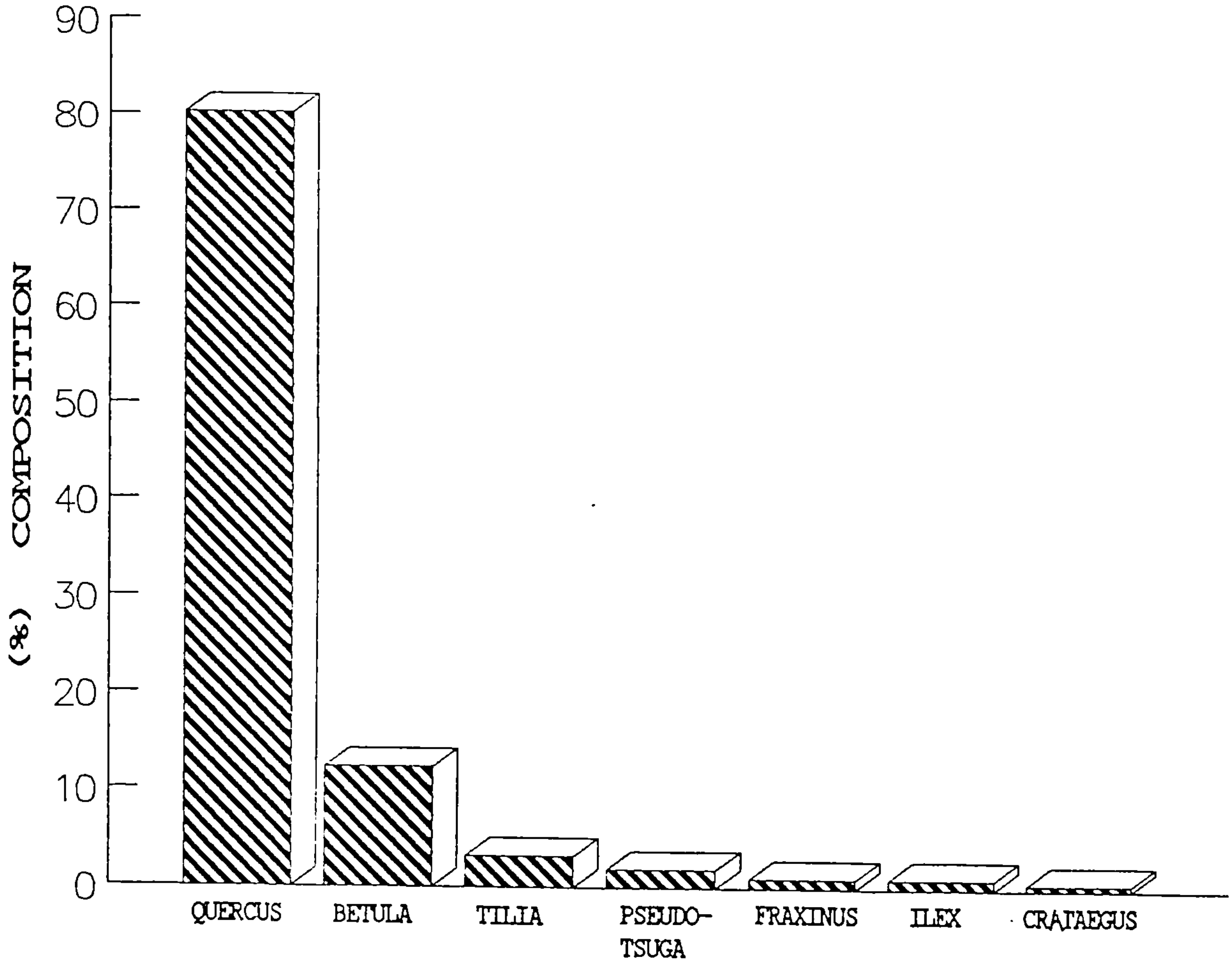
TABLE 2 : SITE STAND COMPOSITION (DBH CLASSES)

DBH Class (cm)	Number of trees	%
7 - 10	8	3.9
11 - 20	28	13.4
21 - 30	48	23.0
31 - 40	50	23.8
41 - 50	49	23.4
51 - 60	12	5.6
61 - 70	8	3.9
71 - 80	1	0.5
81 - 90	2	1.0
91 - 100	2	1.0
100 - 111	1	0.5
	---	---
	209	100

4.5 Adjacent vegetation

The vegetation adjoining the site (Map 3), is predominantly sessile oak with birch and impregnable Rhododendron, reminiscent of the infestation that occurred within Coed Bryn Mawr before clearance. To the east is the National Park's Plas Tan y blwch Estate, the area adjoining the wood also being predominantly sessile oakwood (Domin score 9).

FIGURE 1 : TREE SPECIES COMPOSITION FOR THE SITE



This is the only adjoining area in which the <u>Rhododendron</u> has been cleared. The clearance was undertaken in 1986. Birch and ash (Domin scores 3 and 5 respectively), are also present.

To the North of plot 5 is a larch plantation, running along approximately 50% of the boundary to the plot. Beyond this a plantation of grand fir extends along the boundaries of both plots 4 and 5.

Immediately to the south of plot 1 is Bryn Mawr garden. The species present include sycamore, oak, ash, wild cherry, holly, hawthorn, giant sequoia and <u>Cryptomeria japonica</u>.

4.6 <u>Geology</u>

A management report for the Maentwrog National Nature Reserve (Howells 1967), gives details of the geology of the reserve which covered an area extending east from Coed Bryn Mawr. The geology of the Maentwrog National Nature Reserve, and Coed Bryn Mawr appears similar, although no independent analysis was undertaken for Coed Bryn Mawr. The area has a shale rock outcrop running east to west, dividing Coed Bryn Mawr along its long axis. The soil is largely shallow brown earth, with a transition to brown podzolic soil formed from frost shattered shale. The pH in the surface horizon ranges from 4.0 to 4.6.

5.0 EXPERIMENTAL DESIGN AND COLLECTION OF DATA

5.1 Germination trials

Twenty soil samples were collected in early May from 10 locations, 5 from plot 5 (cleared in winter 1988/9) and 5 from plot 4 (cleared in winter 1987/8). Only a limited number of trials could be undertaken in the time available and the location of samples was therefore subjective. Samples 1/1a to 6/6a were in an area dominated before clearance by dense Rhododendron thickets and would show the latent effects, if any, of the Rhododendron infestation. The area was sparsely populated with trees and samples 7/7a to 10/10a were chosen as a contrast, being within the mature, predominantly oak canopy. All samples were within an area of 75-100% former Rhododendron cover.

Twigs, branches and leaf litter were removed before the samples were collected. The top 5cm layer of soil was cut to the size of a seedtray (185mm x 270mm) to give approximately equal quantities of soil in each sample.

The samples were taken to the University's Nant Porth Nursery, and treated with the aim of ensuring early and maximum germination. A small quantity of Moist Irish Shamrock peat was placed on the base of each seedtray to prevent excessive moisture loss, and the soil samples were scattered on top of the peat. Three separate treatments were then undertaken as described below.

i) Germination of seed within the seedbank

One seedtray from each sample plot was covered with a thin layer of horticultural gravel (2-3 mm grain size, neutral pH). This had a similar function to the layer of peat in preventing excessive moisture loss and in view of the exceptionally hot weather proved valuable.

ii) Trial sowings

The remaining seedtrays were sown with *Festuca ovina* and *Betula pendula* seed, each species being sown into separate halves of the seedtrays. *Betula pendula* seed (Kincardine Forest provenance, 1987, E.Scotland), was obtained from the Forestry Commission Seed Branch, no *Betula pubescens* being available at the time. For each seedtray 0.5g of *Betula pendula* seed was stratified for three weeks, being mixed with moist Irish Shamrock peat and placed in plastic bags in a refrigerator kept at between 2° and 5° C.

In order to sow similar quantities of *Betula* and *Festuca* seeds, a number of samples of both seed were counted (Appendix III). The average number of *Betula* seeds stratified and sown, and therefore the number of *Festuca* seeds sown, was 2157. In retrospect this proved too many, and it would have been prudent to have initially measured a smaller quantity of *Betula* seeds.

The seed once scattered in the seedtrays was covered with a thin layer of horticultural gravel.

iii) Control sowings

To provide a control for the trial sowings, *Festuca* and *Betula* seed stratified as above were sown into separate halves of a seedtray filled with moist Irish Shamrock peat. In common with the other experiments the seeds were then covered with a thin layer of horticultural gravel.

All seedtrays were placed on a bench over three layers of capillary matting, intended to provide a moisture retaining surface. The seedtrays were watered as required.

During the stages of abundant germination (weeks 2 to 5), the seeds germinating in the test sowing experiment were counted and removed twice a week. As the rate of germination declined (by week 6), this was reduced to once a week. Germination was very limited in the experiments designed to assess the viable seedbank, and the majority of seedlings were left in the seedtrays throughout the experiment.

Although the method described above allowed comparison of germination rates between treatments, a measure of dry weight (combined with a smaller number of seeds sown), may have provided a better comparison of the ability of the soil to support growth beyond germination. A measure of dry weight would therefore be recommended in future experiments.

5.2 Collection of vegetation succession data

5.2.1 Tree density and Rhododendron cover

To assess tree basal area and Rhododendron cover nineteen 20 x 20m quadrats were surveyed, four in plots 1, 2, 4 and 5, and three in the smaller plot 3. This gave an area surveyed of 0.76ha, equivalent to approximately 19.7% of the site. The nineteen quadrats were placed randomly; the areas of scarce tree cover in plots 1, 4 and 5 were ignored. The species and diameter at breast height (dbh), of each tree in the quadrats was recorded, and a basal area derived for plots 1 to 5 and for the site as a whole.

It had been intended to assess Rhododendron density by recording stump diameter within each quadrat. This proved impracticable for several reasons. Stumps cut close to the ground were buried under litter, smaller ones being easily missed, whilst others were destroyed where bonfires had been sited. Mature bushes with large stools but few stems also made accurate measurement difficult.

As an alternative the strategy adopted by the R.S.P.B (Becker 1988) was used (Figure 2). Three categories of density are specified, with the corresponding cover, height, root ball and trunk diameter identified. This method allowed a number of stumps to be measured and a classification derived.

5.2.2 Vegetation survey

The vegetation was surveyed in mid July, using 35 randomly placed 1 x 1m quadrats in each plot. Whilst most individual grasses were identified, sedges were recorded as Carex spp and bryophytes as bryophyte spp. Abundance for each species was assessed using the Domin scale (Table 3).

TABLE 3 THE DOMIN SCALE

Cover	Domin scale
Cover > 100%	10
Cover > 75%	9
Cover 51 - 75%	8
Cover 34 - 50%	7
Cover 25 - 33%	6
Abundant, cover approximately 20 %	5
Abundant, cover approximately 5%	4
Scattered, cover small	3
Very scattered, cover small	2
Scarce, cover small	1
Isolated, cover small	X

An assessment of mean percentage crown cover was made at the centre of each quadrat using a spherical densiometer (Mayhead 1969). Four readings were taken for each quadrat (north, south, east and west) and the average taken as the mean percentage crown cover. The data for each plot is shown at Appendix IV to VIII.

FIGURE 2 : CATEGORIES OF RHODODENDRON DENSITY

FEATURES OF *RHODODENDRON*	LIGHT (Pioneer stage)	MODERATE (Building stage)	DENSE (Mature and degenerating)
Cover	1 - 34.9%	35 - 74.9%	75 - 100%
Height	<1 metre	1 - 1.9 metres	2 - 4 metres
Root ball diameter	10 - 19cm	20 - 59cm	60 - 200cm
Trunk diameter	1 - 3.9cm	4 - 19cm	20 - 60cm

5.2.3 Adjacent vegetation

Adjacent vegetation was assessed visually from the perimeter of the site and by access to adjacent areas where possible. Only species in the shrub and canopy layer were recorded.

6.0 **ANALYSIS OF DATA**

6.1 Data analysis techniques

Multivariate techniques of classification and ordination, followed by statistical analyses were undertaken. The VESPAN package (Malloch, 1988) was produced for the N.C.C, and specifically designed to handle and analyse vegetation data. Within VESPAN the programmes RECORD, PREPARE, TWINSPAN and DECORANA were used.

Data is entered using RECORD, which allows simultaneous checking of data for accuracy. *Rhododendron* coppice and seedlings were entered using separate codes, as were *Quercus petraea* seedlings and stumps. PREPARE converts the data from RECORD into a form acceptable for the TWINSPAN and DECORANA programmes, and also allows amalgamation of species - such as *Rhododendron* coppice and seedling to *Rhododendron* species. Whilst the amalgamation of grasses and of *Rhododendron* coppice and seedling was tried, in the final analysis no amalgamations were used as given the small number of species recorded the result was more comprehensive.

TWINSPAN produces a dichotomy based on the principal axes of an ordination, giving two groups of samples which are themselves re-ordinated and re-divided. This continues until the number of divisions requested is reached. Each division is the result of a three stage analysis.

i) Primary ordination. Species indicative of a group of samples, known as differential species, are identified.

ii) Refined ordination. Each of these differential species is assigned a value of +1, and the cumulative score for each sample is derived. The samples are divided at an appropriate point and depending on whether they have a score greater or less than a critical value are assigned to the positive or negative group, thereby producing a dichotomy.

iii) Indicator ordination. With the exception of borderline cases, it is the refined ordination that is used to determine the dichotomy. By using the differential species that are most characteristic of a division, the indicator ordination provides a simple criterion for re-identification of the groups, and using this assigns borderline cases to the positive or negative side of the dichotomy.

The dichotomy not only relies on frequency, but by the use of pseudospecies takes account of quantitative data. Using the Domin scale to record abundance results in four pseudospecies levels being used.

Pseudospecies level	Domin scale
1	> 0
2	> 2
3	> 4
4	> 7

As only 31 species were recorded, three levels of division were used giving eight sample classifications (Figure 3). A fourth or fifth division would result in 16 or 32 classifications respectively, and to achieve this with so few species TWINSPAN would divide groups into artificial associations using poor indicator species. Whilst this study aims to analyse the vegetation that succeeds following the clearance of *Rhododendron*, this species has not been omitted from the analysis as it is an integral part of the vegetation, and its presence may ultimately dictate future species composition. Species names are shortened to eight letters in the TWINSPAN output, the abbreviated names being shown at Appendix IX. <u>Rhododendron</u> seedling is abbreviated to RHOD PONS, and coppice to RHOD PONC. Likewise <u>Quercus petraea</u> seedling becomes QUER PETS, and the tree stump QUER PETT.

Having ordinated the samples, TWINSPAN then ordinates and divides the species, using the sample classification as a basis (Figure 4).

The final output from TWINSPAN is an ordered two way table (Table 4) combining the sample and species divisions. The samples are arranged from left to right in the order of the sample division with the species being arranged from top to bottom in the order of the species division. The sample and species groups are shown in binary coding along the bottom and right hand margin of the table. The table can be used as a visual illustration of the homogeneity of samples within each group. If a fourth or fifth division had been requested, a further 8 or 24 groups would be created, and the homogeneity of the associations lost.

DECORANA is also an ordination technique, using the same input from PREPARE as TWINSPAN. Down-weighting of rare species is possible whereby any species that has a frequency in the data of less than 20% of that of the commonest species is down-weighted in proportion to its frequency. Species such as <u>Umbilicus</u> <u>rupestris</u> (occurring only once), whilst still retained in the analysis is therefore given less weight than the frequently occurring species. DECORANA produces axes of ordination for both samples and species: the final output is a two dimensional scatter diagram in which similar entities are located close together and dissimilar entities far apart. Environmental gradients can usually be associated with the axes. An eigenvalue is calculated for each axis and where this is much less than that of axis 1 the axis is unlikely to be of much significance. For both the sample and species ordination only the first two axes were of significance.

VESPAN ordinates quadrats according to the vegetation parameters defined. No measure of bare ground was made, and consequently where a quadrat has no vegetation it is not included in either the TWINSPAN or DECORANA ordinations. Their are 6 quadrats with no vegetation, 1 in plot 2, 4 in plot 4 and 1 in plot 5.

Statistical analyses were then undertaken to assess the relationship between crown cover and vegetation parameters, and vegetation and the number of years since clearance. Statistical analyses were also used for the germination trials to assess germination rates between different treatments.

FIGURE 3 : TWINSPAN SAMPLE CLASSIFICATION

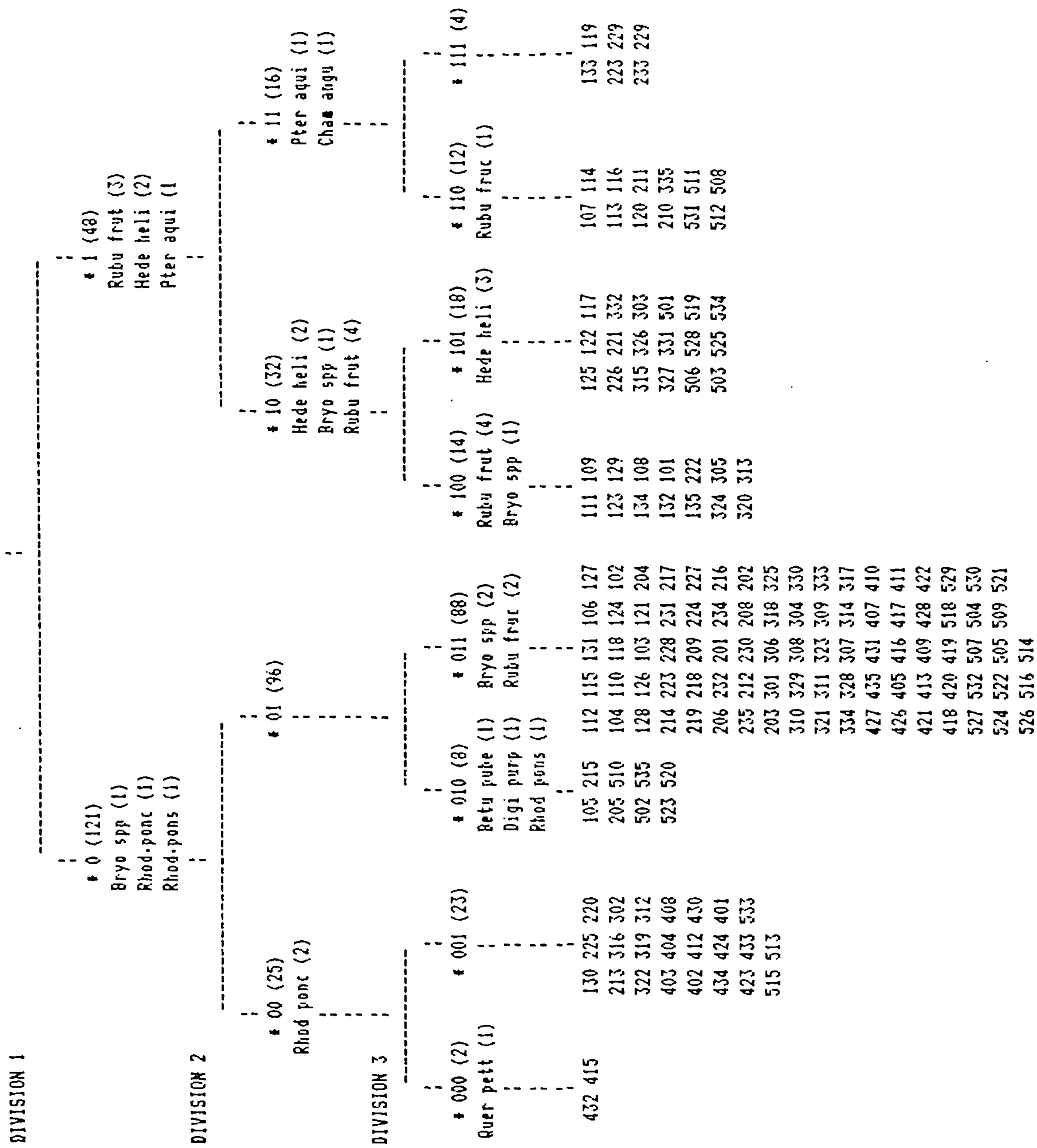


FIGURE 4 : TWINSPAN SPECIES CLASSIFICATION

```
                          Negative (-ve)       N  = 31       Positive (+ve)
                                                  |
LEVEL 1                                           |
                                ---------------------------------------------
                                |                                            |
                              * 0 (16)                                     * 1 (15)
                                |                                            |
LEVEL 2                         |                                            |
                 -------------------------------          ---------------------------------
                 |                             |           |                               |
               * 00 (13)                   * 01 (3)     * 10 (2)                        * 11 (13)
                 |                         Desc flex    Rume acet                          |
                 |                         Epil mont    Quer pets                          |
                 |                         Care spp                                        |
LEVEL 3          |                                                                         |
        ----------------------------                              ----------------------------
        |                          |                              |                           |
      * 000 (12)                 * 001 (2)                      * 110 (8)                   * 111 (5)
        |                          |                              |                           |
  Athy fili  Betu pube         Junc effu                  Digi purp  Dryo dila          Agro capi
  Bryo spp   Call vulg         Care spp                   Dryo fili  Hede heli          Cham angu
  Hier pill  Holc lana                                    Hyac nons  Rubu frut          Prun vulg
  Ilex aqui  Quer pett                                    Sorb aucu  Tili cord          Pter aqui
  Rhod ponc  Rhod pons                                                                  Teuc scor
  Ulex euro  Umbi rupe
```

TABLE 4 : TWINSPAN TWO WAY TABLE

```
Species    Samples, relative numbers.
           Entries in the table are the pseudospecies levels not quantitative values.
           44 12223333344444444444555 12255555 1111111111111122222222222222222222222333333333333333333334444444444444444455555555555555 11111111123333 111223333335555555 111112235555 1122
           31 32211021100001332023311 01010322 1130201120220201223111022030313130000012120032120332011233010111210221212122300322002211 10223030322021 221223120230021023 011121133110 3122
           25 05036229234822044133353 55502530 2516740842863144381798947621465208231685098401139348747751705671139828096897274042591664 19394821524503 527612563711689354 743601051128 3939

Athy fili  -- -2--------------------- -------- ---------------1-----------------------3------------------------------------------------ -------------- ------------------ ------------ ----  000
Call vulg  -- ----------------------- -------- -------------1-------2------------------------------------------------------------------ -------------- ------------------ ------------ ----  000
Holc lana  -- ----------------------- -------- 3------------------2-------------------------1--2--------------------------------------- -------------- ------------------ ------------ ----  000
Ilex aqui  -- ----------------------- -------- -------------------------------------------------------------------------1-------------- -------------- ------------------ ------------ ----  000
Hier pilo  -- ----------------------- -------- ---------------------------------2------------------------------------------------------ -------------- ------------------ ------------ ----  000
Quer pett  33 ----------------------- -------- ---------------------------------------------------------------------------------------- -------------- ------------------ ------------ ----  000
Umbi rupe  -- ----------------------- -------- -----------------------------------------1---------------------------------------------- -------------- ------------------ ------------ ----  000
Betu pube  -- ---------3------11---12 11211122 1-2----------------1--11--2-2213-1---1-------------1-------------------------11-1112221- ---1--12-1---- ------------11-1-- 2----------- ----  000
Ulex euro  -- ----------------------- -------- -------------1-------------------------------------------------------------------------- -------------- ------------------ ------------ ----  000
Rhod pont  3- 33322232323213333333323 1-1----- ------1------------1-1-----------------2-----------------------------1-----1------------ -------------- -1-------3-------- ------------ ----  000
Rhod pons  -- -2---------1---1--1---- -1------ 1--11---11------1-----221-21--22212--1----11-------1------------------------------------ -------------- 1-1--------------- ------------ ----  000
Bryo spp   -3 44343433222211343421--2 3-21--11 4424323343322214233344444344343442322423444424322243322233442213423343332133333232233321 333--32-23331- -----3-----21---2- 3------3---- 1---  000
Junc effu  -- ----------------------- -------- -------------2----3-------------1----2-------------------------------------------------- -------1------ ------------------ ------------ ----  001
Care spp   -- ----1------------------ -------1 -211---------------1--1-------1--1-----1-----1--1------1---------------------1---------- -1-----1-2---- ------------------ ------------ ----  001
Desc flex  -- -----------1----------- -------- ---------------------------------3------------------------------------------------------ -------------- ------------------ 2----------- ----  01
Epil mont  -- ----------------------- -------- ------------------------------2--2----3------------1---3-------------------------------- -12----------- ------------------ ---3-------- 1---  01
Rume acet  -- ----------------------- -------- 2-------------------2--------3---------------------------------------------------------- ----2---12---- ------------------ ------------ ----  10
Quer pets  -- ------1---------------- -------- -1-----------------------------------2-1-------11------11-----------1------------------- -------------- -1--1------------3 -----1------ 1---  10
Digi purp  -- ----------------------- 12------ -------------2-------------------------------------------------------------------------- -----11------1 --------2--------- -3---------- ----  110
Dryo dila  -- ----------------------- -------- ---------------------------------------------------------------------------------------- ---------2---- ------------------ ------------ ----  110
Dryo fili  -- ----------------------- -------- -----------------------------------------2---------------------------------------------- ----------3--- ----------3------- ------------ ----  110
Hyac nons  -- ----------------------- -------- ---------------------------------------------------------------------------------------- -------------- -----------------2 ------------ ----  110
Hede heli  -- ----------------------- -------- ---------------------------------------1-11-------1-----------------1------2------------ ----------232- 444433423443444333 ------1----- -2--  110
Sorb aucu  -- ----------------------- -------- ---------------------------------------------------------------------------------------- --------1----- ------------------ ------------ ----  110
Rubu frut  -- ----------------------- ---1---1 33--1-1--22-------322-------2--3----22-------1--1------1-----------------------------1-- 4334444444-444 -3234----34----1-- 313333343334 ----  110
Tili cord  -- ----------------------- -------- ---------------------------------------------------------------------------------------- -------------- ------2----------- ------------ ----  110
Agro capi  -- ----------------------- -------- --1------------------------------------------------------------------------------------- --------1----- ------------------ 22--2------- ----  111
Epil angu  -- ----------------------- -------- -------------1-------------------------------2------------------------------------------ -------------- ------------------ 23------2222 ----  111
Prun vulg  -- ----------------------- -------- ---------------------------------------------------------------------------------------- -------------- ------------------ ------------ -1--  111
Pter aqui  -- ----------------------- -------- ------2----------------------------------------------------------------------------------- -------------- ----2------------- ------434444 3244  111
Teuc scor  -- ----------------------- -------- ---------------------------------------------------------------------------------------- -------------- ------------------ ------------ -3--  111

           00 00000000000000000000000 00000000 0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000 11111111111111 111111111111111111 111111111111 1111
           00 00000000000000000000000 11111111 1111111111111111111111111111111111111111111111111111111111111111111111111111111111111111 00000000000000 000000000000000000 111111111111 1111
           00 11111111111111111111111 00000000 1111111111111111111111111111111111111111111111111111111111111111111111111111111111111111 00000000000000 111111111111111111 000000000000 1111
```

6.2 Data analysis

6.2.1 Vegetation associations

The TWINSPAN stand classification (Figure 3), and species classification (Figure 4) can be read in conjunction, since species occurring on the left hand side of Figure 3 will occur on the left hand side of Figure 4. Given the relatively small data set however, Figure 3 alone provides sufficient information.

The first division uses Rhododendron coppice, seedling, and bryophytes as the basis of the negative division, whilst bramble, ivy and bracken form the basis of the positive division. This concurs with the literature reviewed (section 3.4), in that the Rhododendron seedling is associated with the most favourable safe site of a low level of bryophytes (pseudospecies level 1). In contrast the dense vegetation on the positive side of the division provides far fewer safe sites.

The negative group is then divided at level 2 by Rhododendron coppice (pseudospecies level 2). The positive group is divided on the negative side by ivy (pseudospecies level 2), bryophytes (pseudospecies level 1), and bramble (pseudospecies level 4), whilst the positive group is characterised by bracken (pseudospecies level 1), and rosebay willowherb (pseudospecies level 1).

The structure and abundance of vegetation within each TWINSPAN group can be derived by accumulating the Domin score of each species in each group, and converting this score to a percentage. The Domin score is used for this purpose as the TWINSPAN dichotomy is itself derived from quantitative data.

I) Group *000

Number of quadrats : 2

Species present	% Domin
Quer pett (stump)	50
Bryo spp	27
Rhod ponc (coppice)	23

TWINSPAN has separated the two quadrats which partly fell on mature oak stumps; the remaining ground was covered by bryophytes and Rhododendron coppice.

II) Group *001

Number of quadrats : 23

Species present	% Domin
Bryo spp	46
Rhod ponc (coppice)	44
Betu pube	5

Species occurring at 2-3% : Rhod pons (seedling)
Species occurring at 1-2% : Athy fili
Species occurring at <1% : Care spp; Desc flex; Quer pets

The group can be classified as dominated by **bryophytes** and **Rhododendron coppice.**

III) Group *010

Number of quadrats : 8

Species present	% Domin
Betu pube	38
Bryo spp	31
Digi purp	12
Rhod ponc (coppice)	7
Rubu frut	7

Species occurring at 2-3% : Care spp; Rhod pons (seedling)

Dominated by **Betula pubescens** and **bryophytes**, with **Digitalis purpurea, Rubus fruticosus,** and **Rhododendron coppice** also present.

IV) Group *011

Number of quadrats : 88

Species	% Domin
Bryo spp	60
Betu pube	7
Rubu frut	7
Rhod pons (seedling)	5

Species occurring at 2-3% : Care spp; Hede heli; Epil mont; Rhod ponc (coppice).
Species occurring at 1-2% : Holc lana; Junc effu; Quer pets; Rume acet.
Species occurring at <1% : Agro capi; Athy fili; Call vulg; Cham angu; Desc flex; Digi purp; Dryo dili; Hier pill; Pter aqui; Umbi rupe; Ulex euro.

Dominated by **bryophytes** , with **Betula pubescens, Rubus fruticosus** and **Rhododendron seedlings** also present.

V) Group *100

Number of quadrats : 14

Species	% Domin
Rubu frut	50
Bryo spp	23
Hede heli	6

Species occurring at 4-5% : Rume acet.
Species occurring at 3-4% : Betu pube.
Species occurring at 2-3% : Care spp; Dryo fili; Epil mont.
Species occurring at 1-2% : Digi purp; Dryo dili.
Species occurring at <1% : Agro capi; Cham angu; Junc effu; Sorb auc.

The group can be classified as **Rubus fruticosus** and **bryophytes**, with to a lesser extent **Hedera helix**.

VI) Group *101

Number of quadrats : 18

Species	% Domin
Hede heli	61
Rubu frut	14
Bryo spp	6

Species occurring at 3-4% : Quer pets.
Species occurring at 2-3% : Dryo fili; Rhod ponc (coppice).
Species occurring at 1-2% : Betu pube; Digi purp; Frax exce; Hyac nons; Pter aqui; Rhod pons (seedling).
Species occurring at <1% : Care spp.

Dominated by **Hedera helix**, with **Rubus fruticosus** and **bryophytes.**

VII) Group *110

Number of quadrats : 12

Species	% Domin
Rubu frut	38
Pter aqui	26
Cham angu	10
Agro capi	6
Bryo spp	6

Species occurring at 4-5% : Digi purp; Epil mont.
Species occurring at 2-3% : Desc flex.
Species occurring at 1-2% : Betu pube; Hede heli; Quer pets.

Dominated by **Rubus fruticosus** and **Pteridium aquilinum,** with a substantial presence of **Chamaenerion angustifolium, Agrostis capillaris** and **bryophytes**.

VIII) Group *111

Number of quadrats : 4

Species	% Domin
Pter aqui	65
Teuc scor	15
Hede heli	6

Species occurring at 4-5% : Bryo spp; Prun vulg.
Species occurring at 2-3% : Epil mont; Quer pets.

Although dominated by **Pteridium aquilinum**, the proportion of **Teucrium scorodonia** is misleading as this TWINSPAN group comprises only four quadrats, in which this species occurs only once.

The distribution of quadrats between TWINSPAN groups is shown in Table 5, and the vegetation associations summarised in Table 6.

TABLE 5: DISTRIBUTION OF QUADRATS BETWEEN TWINSPAN GROUPS

Plot	TWINSPAN stand group							
	Negative (-ve)				Positive (+ve)			
	*000	*001	*010	*011	*100	*101	*110	*111
1	-	1	1	14	9	3	5	2
2	-	3	2	22	1	2	2	2
3	-	5	-	19	4	6	-	-
4	2	11	-	18	-	-	-	-
5	-	3	5	15	-	7	4	-
Total	2	23	8	88	14	18	11	4

Over 50% of the quadrats fall into group *011, the association dominated by 60% bryophytes with birch, bramble, and Rhododendron seedlings. This is therefore the predominant association for the site. Of the 88 quadrats in this group the individual plots are represented as follows, each plot having a greater proportion of its quadrats within this vegetation association than any other association.

Group *001 Plot	Number of quadrats
1	14
2	22
3	19
4	18
5	15

The second most frequent association is group *001, with approximately 13% of the quadrats. This is the bryophyte (46%) and Rhododendron coppice (44%) association, with birch (5%). The occurrence of individual plots within the group is in contrast to group *011 not evenly distributed, plot 4 being the only plot substantially present.

TABLE 6 : SUMMARY OF VEGETATION ASSOCIATIONS

% Domin	TWINSPAN groups (number of quadrats)							
	*000 (2)	*001 (23)	*010 (8)	*011 (88)	*100 (14)	*101 (18)	*110 (12)	*111 (4)
> 61	-- --	-- --	-- --	-- --	-- --	-- --	-- --	Pter aqui
51.0 - 60.9	-- --	-- --	-- --	Bryo spp	-- --	Hede heli	-- --	-- --
41.0 - 50.9	Quer pett	Bryo spp Rhod ponc	-- --	-- --	Rubu frut	-- --	-- --	-- --
31.0 - 40.9	-- --	-- --	Betu pube Bryo spp	-- --	-- --	-- --	Rubu frut	-- --
21.0 - 30.9	Bryo spp Rhod ponc	-- --	-- --	-- --	Bryo spp	-- --	Pter aqui	-- --
11.0 - 20.9	-- --	-- --	Digi purp	-- --	-- --	Rubu frut	-- --	Teuc scor
5.0 - 10.9	-- --	Betu pube	Rubu frut Rhod ponc	Betu pube Rhod pons Rubu frut	Hede heli	Bryo spp	Cham angu Agro capi Bryo spp	Hede heli

Group *011 Plot	Number of quadrats
1	1
2	3
3	5
4	11
5	3

The only other association on the negative side of the dichotomy with several quadrats is group *010, again with byrophytes substantially present (38%), and also birch (31%). There are only 8 quadrats within this group, 5 from plot 5, 2 from plot 2 and 1 from plot 1.

Three of the associations on the positive side of the dichotomy comprise over 25% of the quadrats. Group *100, the bramble (50%) and birch (23%) association, principally contains plots 1 (9 quadrats) and 3 (4 quadrats). Group *110 is also a bramble association (38%) with bracken (26%), mainly consisting of plots 1 (5 quadrats) and 5 (4 quadrats). Group *101 whilst having a substantial presence of bramble (14%), is dominated by ivy (61%), with the principal plots being plots 3 (5 quadrats) and 5 (7 quadrats).

Of the quadrats from plot 5 that are on the positive side of the dichotomy, all 4 in group *110 are clustered in the northern (upslope) part of the plot and may be a result of disturbance associated with the railway line. The 7 quadrats in group *101 comprise 4 whose vegetation may also be a result of disturbance, and 3 in a small pocket that may have been unaffected by Rhododendron, as indicated by the presence of ivy. Disturbance may therefore account for plot 5 having a more diverse and abundant species composition than plot 4. Plot 4 may also have suffered from a particularly low mean monthly rainfall in June 1988, when only 27.4mm of rainfall was recorded at Porthmadog (approximately 8km to the west), and 32.0mm at Blaeneau Ffestiniog (approximately 6km to the north east).

The principal associations are on the negative side dominated by bryophytes and Rhododendron coppice, and on the positive side by bramble, ivy, bracken and bryophytes. The diversity of associations within plots also decreases from plots 1 and 2, the most diverse, to plots 3, 4 and 5, plot 4 being the least diverse.

6.2.2 Crown cover and vegetation associations

Further interpretation of the ordination of the TWINSPAN groups can be derived from Figure 5 where the DECORANA sample ordination has been coded to accord with the TWINSPAN groups. Comparing this to the DECORANA species ordination (Figure 6), shows the correlation of species to TWINSPAN groups, with for example group *110 in a corresponding position to the light demanding species bracken and rosebay willowherb, whilst group *101 corresponds with ivy, a more shade tolerant species.

The mean and standard deviation for the percentage absence of crown cover for each TWINSPAN group is shown in Figure 7. Despite the high standard deviation from the mean of most groups, there appears to be a trend between crown cover and vegetation, with the TWINSPAN groups containing light-demanding species such as bracken, rosebay willowherb and foxglove having a greater percentage absence of crown cover than groups dominated by more shade tolerant species such as ivy, Rhododendron and bryophytes.

FIGURE 5 : <u>DECORANA SAMPLE ORDINATION CODED TO ACCORD WITH TWINSPAN GROUPS</u>

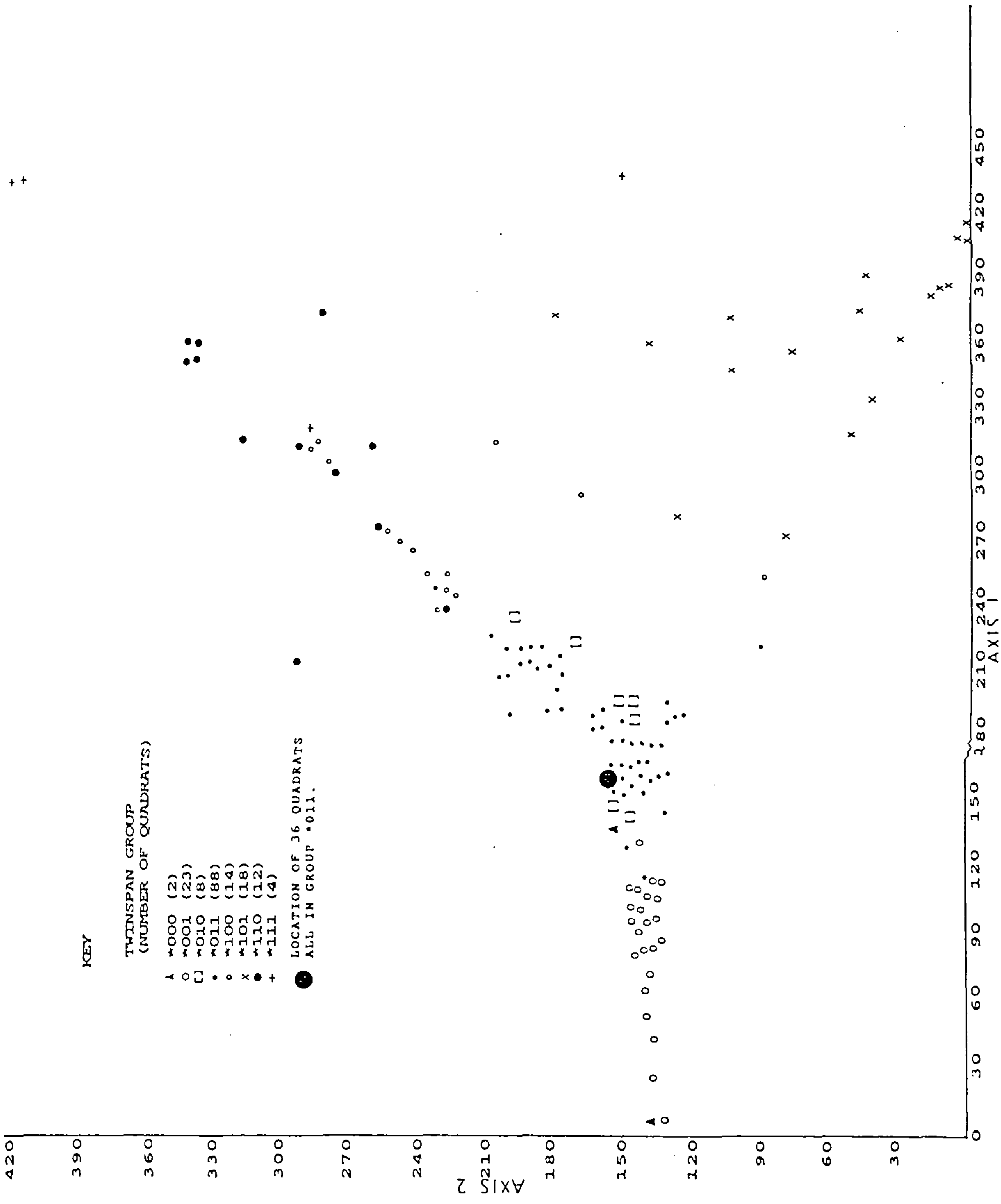


FIGURE 6 : <u>DECORANA SPECIES ORDINATION</u>

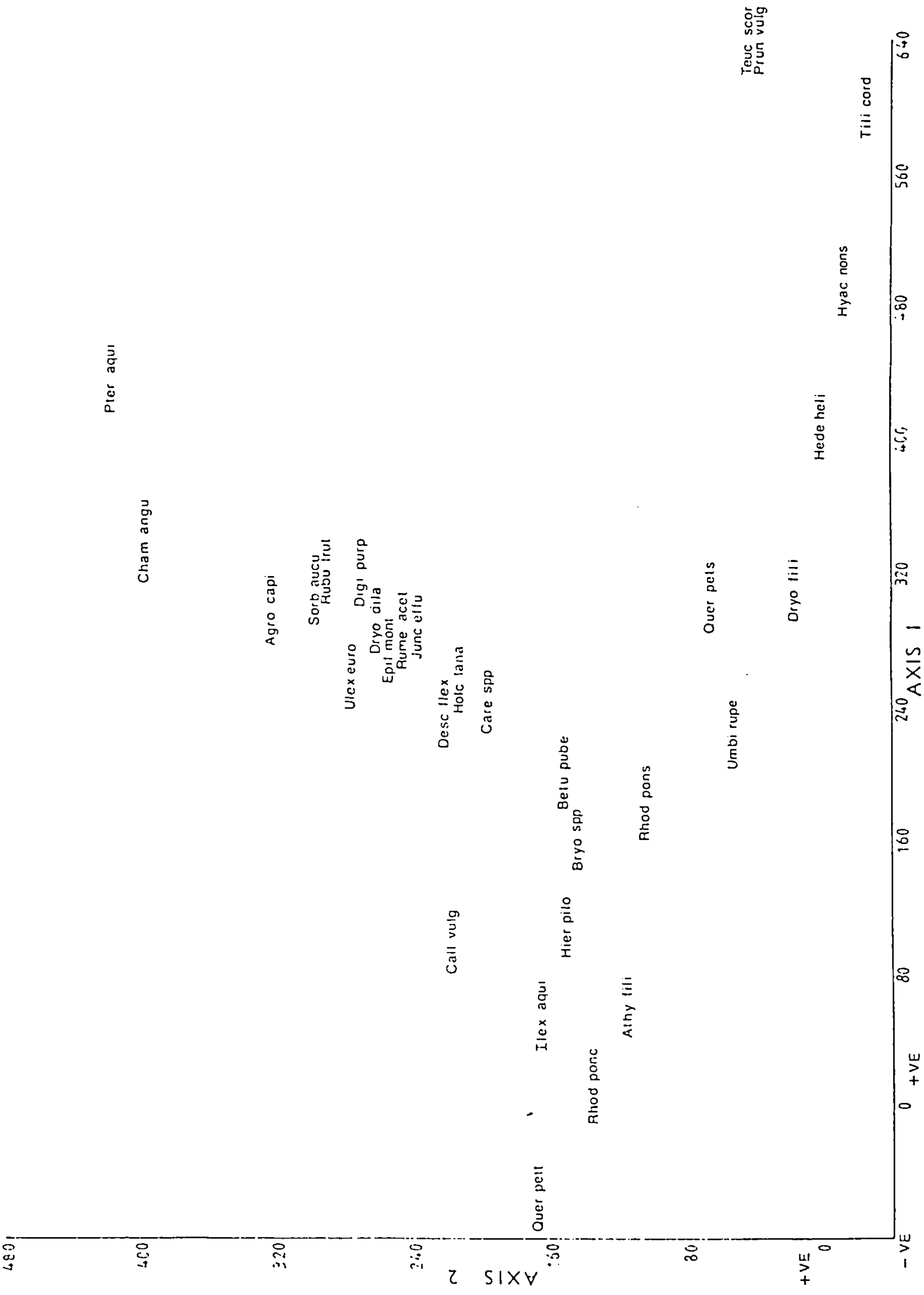
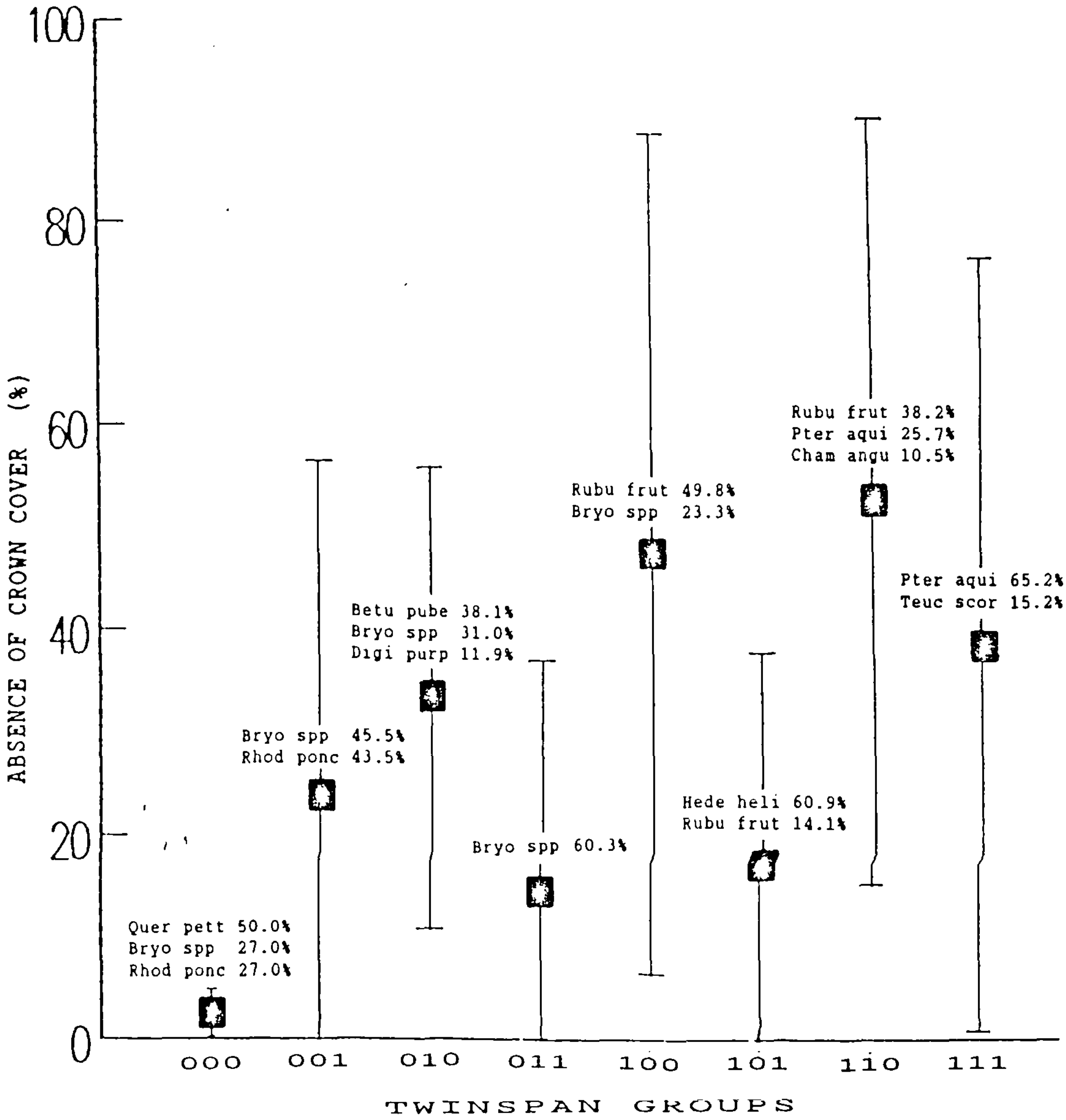


FIGURE 7 : MEAN AND STANDARD DEVIATION OF THE ABSENCE OF CROWN COVER FOR EACH TWINSPAN GROUP



This relationship was statistically analysed using a one-way analysis of variance (Table 7), which identified a significant variation in crown cover between the TWINSPAN groups, with a probability of the variation occuring by chance of less than 0.001%.

TABLE 7 ANALYSIS OF VARIANCE FOR LIGHT INTENSITY BETWEEN TWINSPAN GROUPS

SOURCE	D.F	S.S	M.S	F	P
FACTOR	7	28563	4080	5.36	0.000
ERROR	161	122670	762		
TOTAL	168	151232			

A Scheffy's test was undertaken to produce further analysis (Appendix X) which identifies two principal differences, between groups *011 and *100, and *011 and *110. Group *001 has a low mean percentage crown cover, whilst groups *100 and *110 have the two highest mean percentage crown covers.

6.2.3 Vegetation succession and year of clearance

The Decorana stand ordination (Figure 8), with the year of clearance only shown, illustrates quadrats of the same year of clearance tending to cluster or ordinate in a similar direction, indicating that there is a correlation between the year of clearance and vegetation that succeeds. A comparison of the cumulative frequency and Domin values of all species in each plot (Figure 9), gives a further illustration of this trend, with the abundance of vegetation increasing as the number of years since clearance increases.

FIGURE 8 : DECORANA SAMPLE ORDINATION SHOWING YEAR OF CLEARANCE ONLY

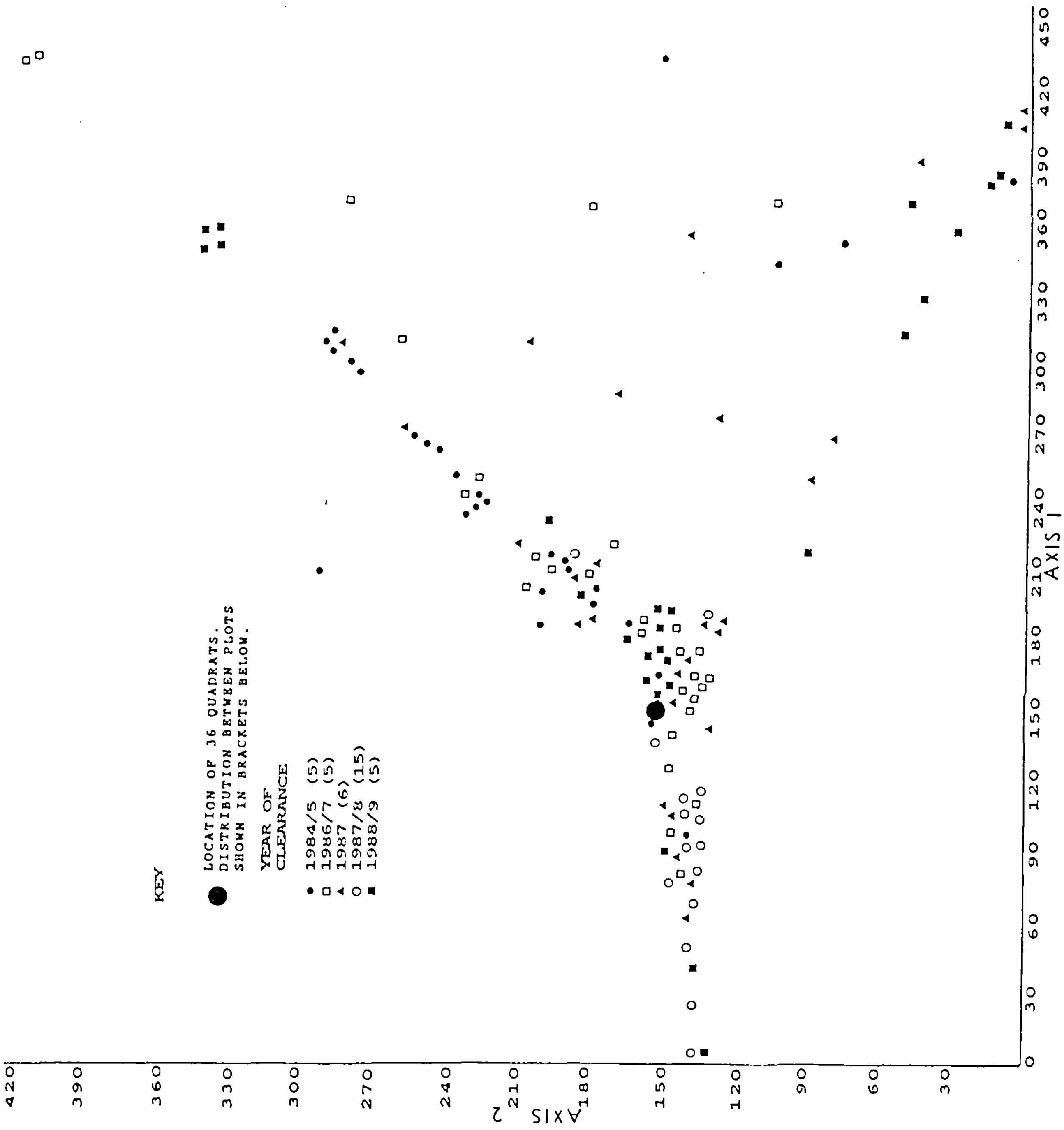
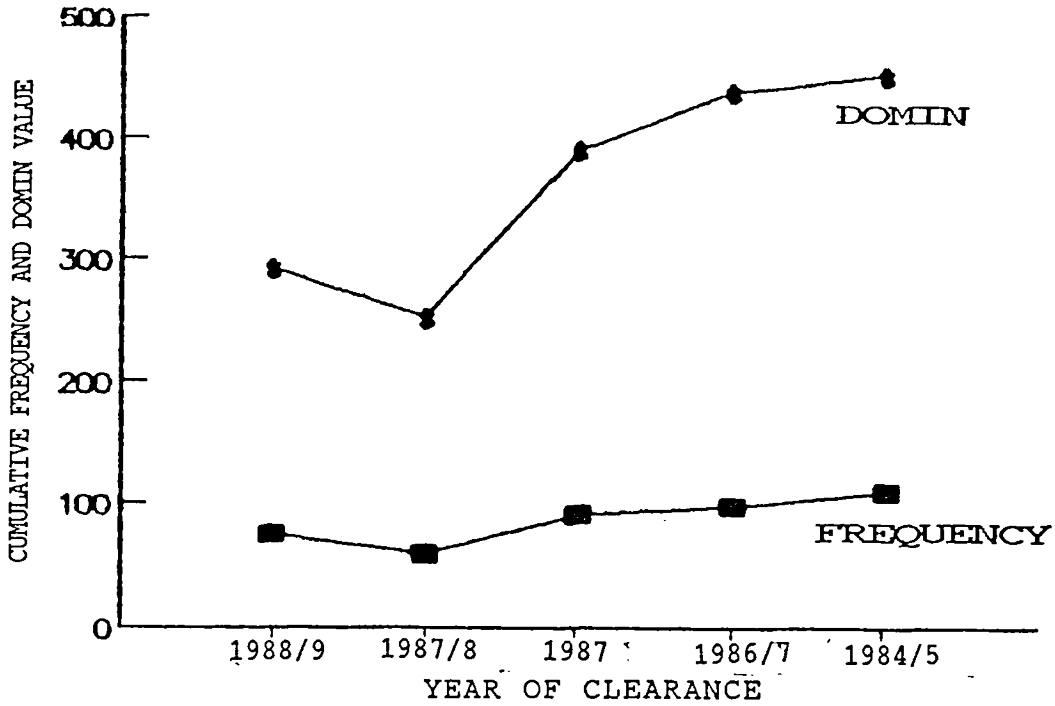


FIGURE 9 CUMULATIVE FREQUENCY AND DOMIN VALUE FOR EACH PLOT



To gain a more precise analyse of this relationship a regression analysis was undertaken using frequency data.

TABLE 8 : ANALYSIS OF VARIANCE FOR THE REGRESSION BETWEEN VEGETATION SUCCESSION AND YEAR OF CLEARANCE

The regression equation is $Y = 3.82 - 0.335\ F$
Y = Year
F = Frequency (number of species in each quadrat)

Analysis of variance

SOURCE	D.F	S.S	M.S	F	P
REGRESSION	1	35.197	35.197	19.34	0.000
ERROR	173	314.803	1.820		
TOTAL	174	350.000			

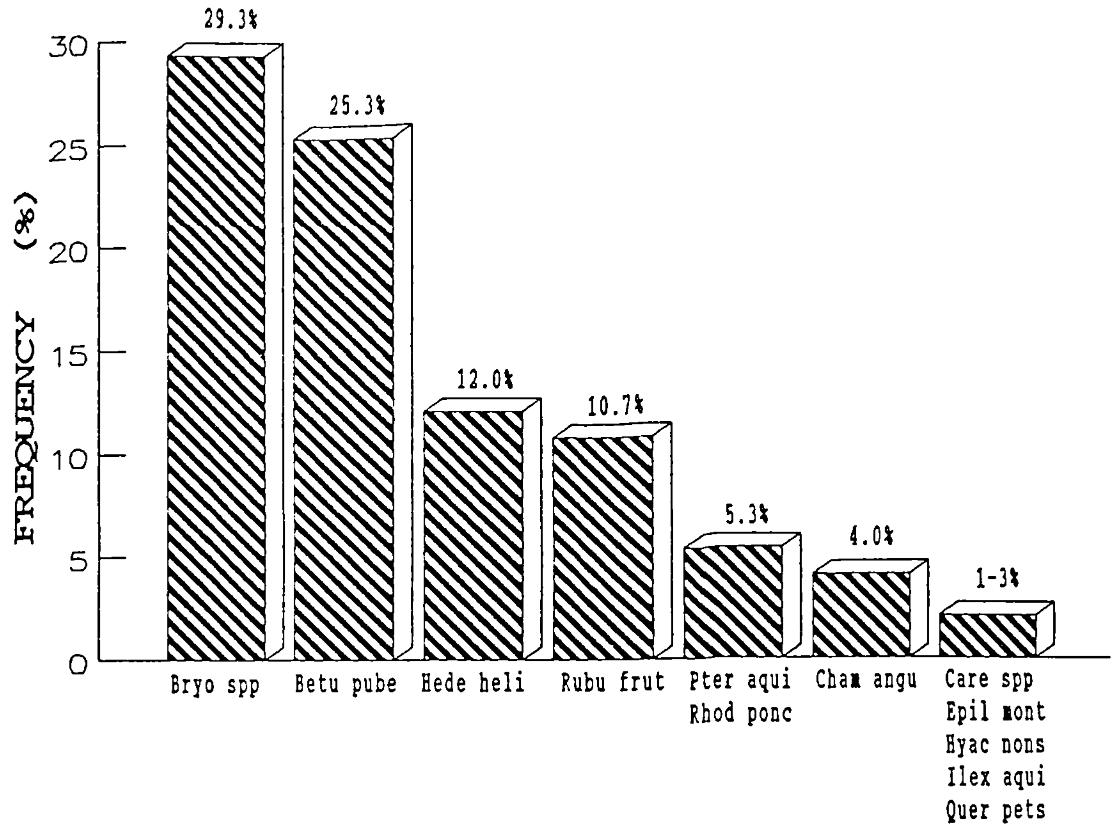
The regression indicates a significant negative correlation between the year of clearance and the mean number of species within a quadrat, with a probability of the relationship occurring by chance of less than 0.001%. The frequency of species increases as the number of years since clearance increases. The regression was also undertaken using the Domin data, and transformed frequency and Domin data. All regressions produced significant negative correlations, the most significant correlation being derived from the untransformed Domin data.

6.2.4 Species composition within plots

Having established that the abundance of vegetation is correlated to the year of clearance the structure of the vegetation in the different years is of interest. By calculating the percentage frequency of each species in each year, these characteristics can be derived. For ease of interpretation the analysis is set out using the most recent year of clearance as the base year.

I) FIGURE 10 : SPECIES COMPOSITION IN PLOT 5

Cleared in 1988/9

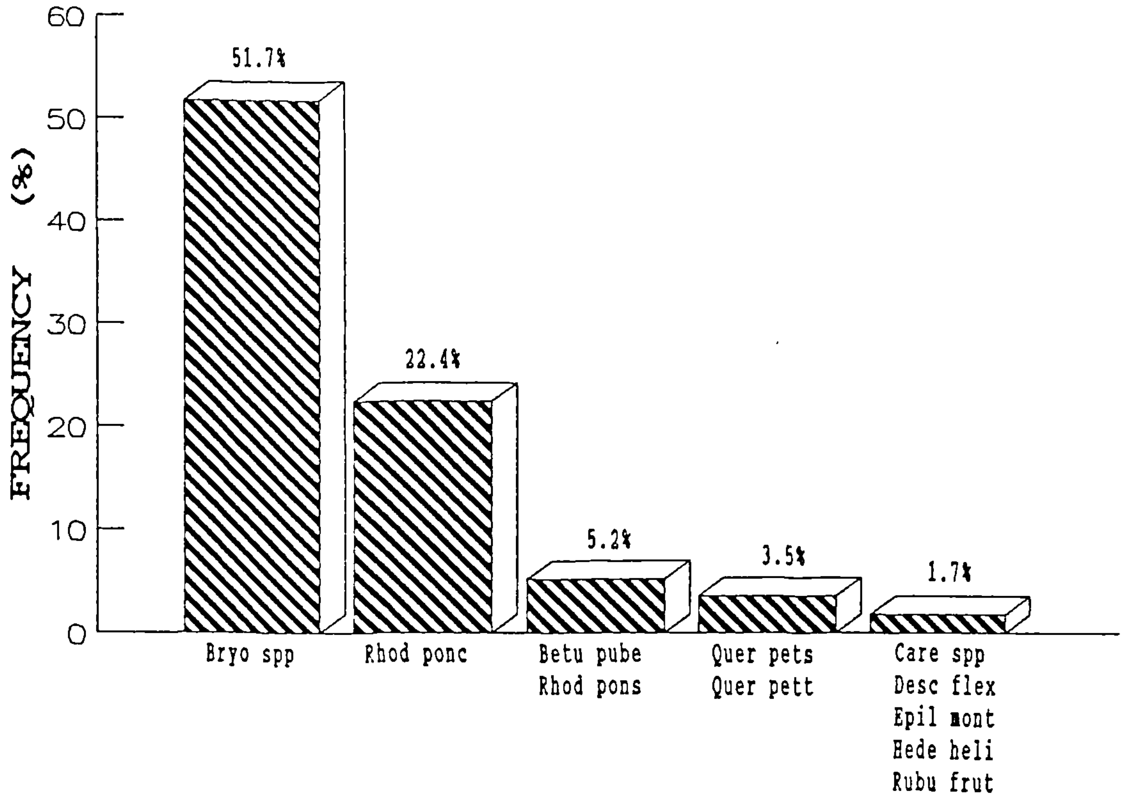


The dominant species are *bryophytes and birch seedlings.* Although ivy and bracken are also present (12% and 10.7% respectively), their presence is entirely restricted to the northern (upslope) part of the plot, close to the railway line. Bracken, rosebay willowherb, broadleaved willowherb and bluebell are also restricted to this location. Maintenance of the railway line, including the replacement of all sleepers in the last 20 years, has inevitably led to disturbance along the northern boundary of the site; the vegetation adjoining the railway now reflects that disturbance. Without the species resulting from that disturbance the diversity of vegetation within the plot would be substantially reduced.

Whilst the colonisation by bryophytes and birch is limited to the area cleared in 1988, their rapid invasion is significant. The difficulty experienced by Rhododendron in finding safe sites for establishment is shown by this being the only plot in which no Rhododendron seedlings were recorded.

II) FIGURE 11: SPECIES COMPOSITION IN PLOT 4

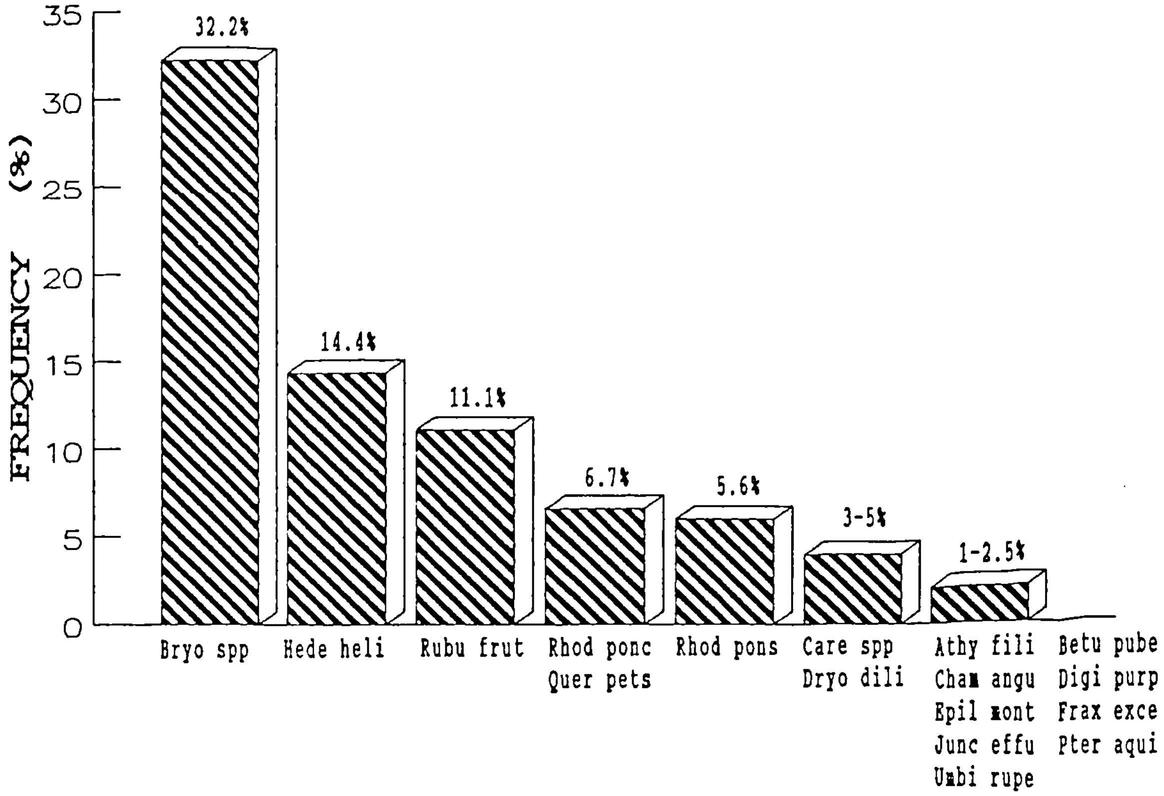
Cleared in 1987/8



Whilst bryophytes have succeeded to a frequency of over 50%, the presence of Rhododendron coppice (22.4%) highlights the limited success of the initial clearance. For the first time Rhododendron seedlings are beginning to establish as safe sites are generated. Grasses and sedges (Carex spp and wavy hair grass) are beginning to colonise.

III) FIGURE 12: SPECIES COMPOSITION IN PLOT 3

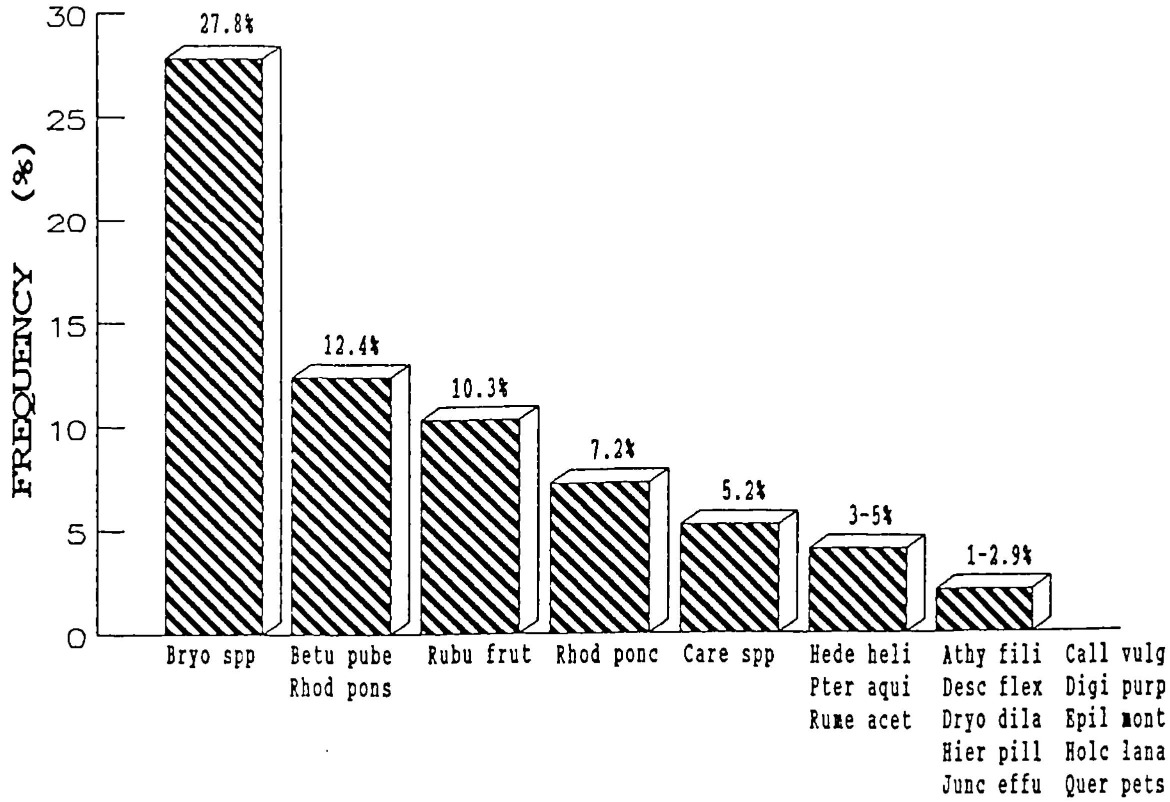
Cleared in 1987



Although bryophytes (32.2%) are the most frequently occurring species, ivy and bramble are present at 14.4% and 11.1% respectively. The substantial presence of ivy and bramble may in part be due to a small area of vegetation in the centre of the plot with little former Rhododendron cover, and to the vegetation recorded in the quadrats in the northern (upslope) boundary of the plot. Rhododendron coppice and seedling are present at a frequency of 6.7% and 5.6% respectively. The number of flowering plants has increased.

IV) FIGURE 13: SPECIES COMPOSITION IN PLOT 2

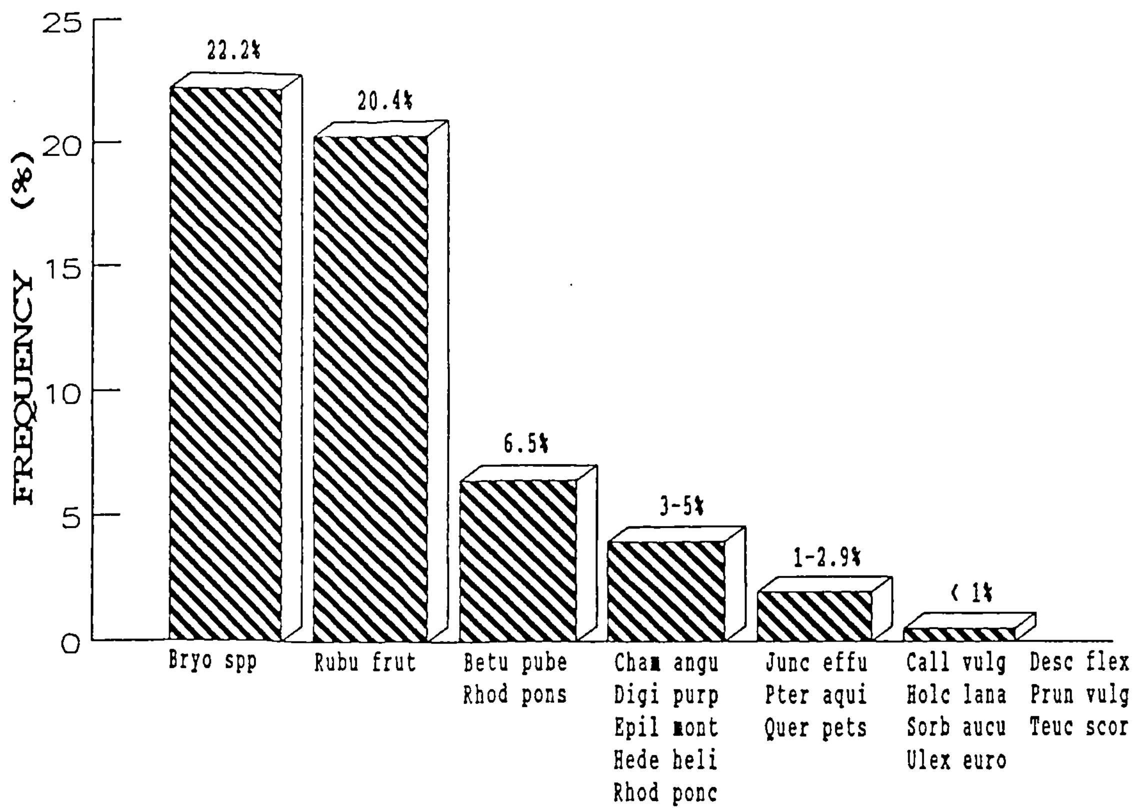
Cleared in 1986



The plot has a greater diversity of species than the previous plots, with bryophytes (27.8%), still the most frequently occurring species. There is a considerable presence of Rhododendron seedling (12.4%), birch (12.4%), bramble (10.3%), and Rhododendron coppice (7.2%).

V) FIGURE 14 : SPECIES COMPOSITION IN PLOT 1

Cleared in 1984/5

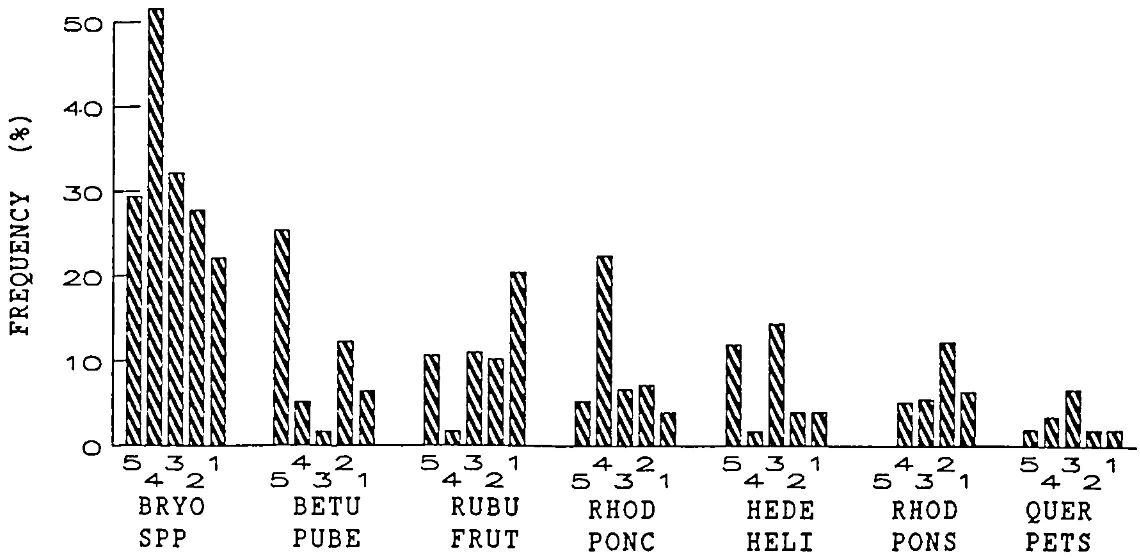


The plot is dominated by bryophytes (22.2%) and bramble (20.4%), although the major part of this bramble is found in the southern part of the plot which is devoid of trees (Map 3). Rhododendron seedling and birch both occur in 6.5% of the quadrats. The grasses and flowering plants are more frequent and diverse than in other years.

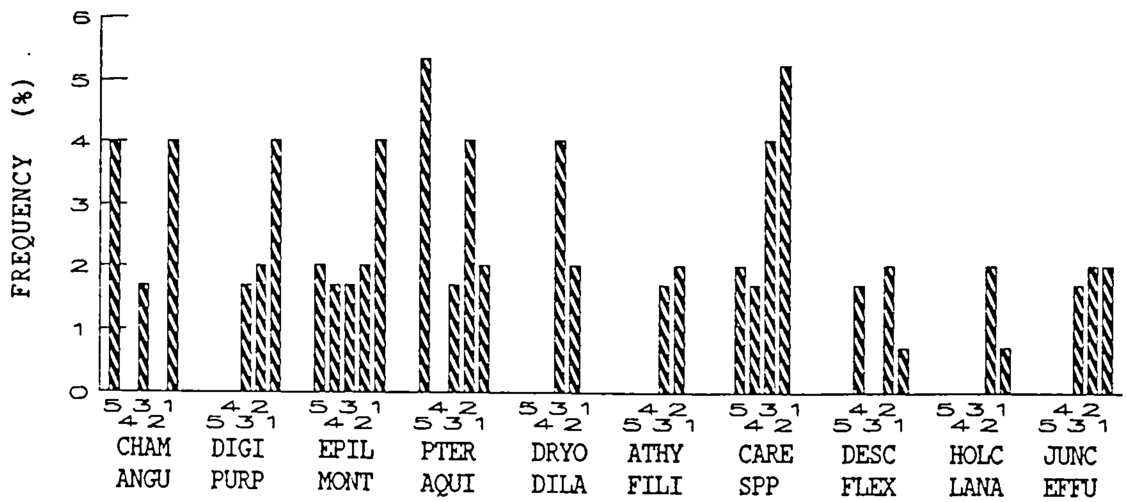
A summary of the species composition for each plot is shown at Figure 15 and Table 9.

FIGURE 15 : SUMMARY OF SPECIES COMPOSITION BETWEEN PLOTS

i) Frequently occurring species



ii) Epilobiums, ferns and grasses



iii) Species occurring in 1 or 2 plots only

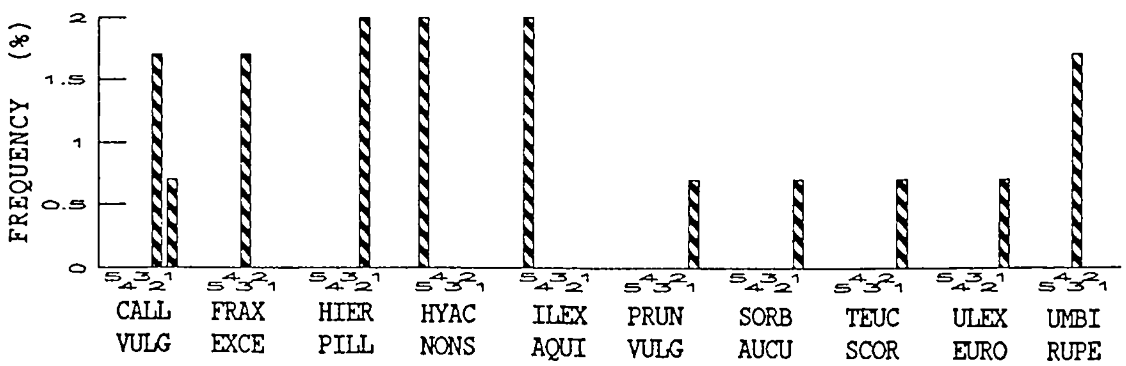


TABLE 9 : SUMMARY OF SPECIES COMPOSITION FOR EACH PLOT

% Frequency	Plot number 5	4	3	2	1
> 51	-- --	Bryo spp	-- --	-- --	-- --
30.0 - 34.9	-- --	-- --	Bryo spp	-- --	-- --
25.0 - 29.9	Bryo spp Betu pube	-- --	-- --	Bryo spp	-- --
20.0 - 24.9	-- --	Rhod ponc	-- --	-- --	Bryo spp Rubu frut
15.0 - 29.9	-- --	-- --	-- --	-- --	-- --
10.9 - 14.9	Hede heli Rubu frut	-- --	Hede heli Rubu frut	Betu pube Rhod pons Rubu frut	-- --
5.0 - 9.9	Pter aqui Rhod ponc	Betu pube Rhod pons	Rhod ponc Rhod pons Quer pets	Care spp Rhod ponc	Betu pube Rhod pons
3.0 - 4.9	Cham angu	Quer pets Quer pett	Care spp Dryo dila	Hede heli Pter aqui Rume acet	Cham angu Digi purp Epil mont Hede heli Rhod ponc
< 3	Care spp Epil mont Hyac nons Ilex aqui Quer pets	Care spp Desc flex Epil mont Hede heli Rubu frut	Athy fili Betu pube Cham angu Digi purp Epil mont Frax exce Junc effu Pter aqui Umbi rupe	Athy fili Call vulg Desc flex Digi purp Dryo dila Epil mont Hier pill Holc lana Junc effu Quer pets	Call vulg Desc flex Holc lana Prun vulg Sorb aucu Teuc scor Ulex euro

6.2.5 Succession of *Rhododendron* and oak

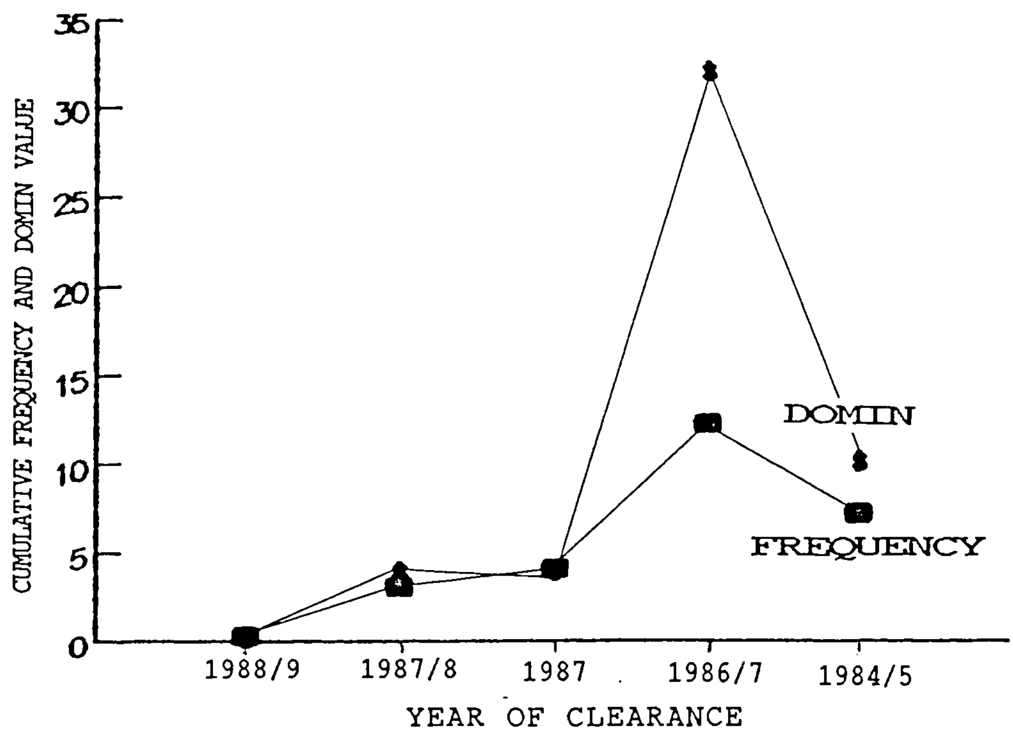
The succession of *Rhododendron* and oak seedlings is of particular importance, the former undesirable and the latter essential if the characteristics of the woodland are to be maintained in the long term. Statistical analysis of the succession of these species is however complicated by their low frequency of occurrence; in each plot the majority of the quadrats have neither seedling. This was less a reflection of quadrat size (1 x 1m) than their low occurrence.

Simple analysis is possible by plotting the cumulative frequency and Domin value for each plot.

i) *Rhododendron* seedlings

Year of Clearance	Plot	Frequency	Domin value
1988/9	5	0	0
1987/8	4	3	4
1987	3	4	4
1986/7	2	12	32
1984/5	1	7	10

FIGURE 16 RHODODENDRON SEEDLING ESTABLISHMENT



The establishment of Rhododendron appears to conform with the literature reviewed (section 3.4). No seedlings are able to establish until a suitable site such as a thin bryophyte carpet appears. As time since clearance passes so the number of suitable sites increases. A point should be reached where the grass and herb sward prevents further Rhododendron seeds establishing, and for this particular site this point may have been reached at plot 1, where the lack of tree cover in the southern part of the plot has allowed a considerable grass and herb sward cover to develop. At this point however the Rhododendron seedlings that are already established may begin to grow through the sward despite its presence (section 3.5.1).

ii) Oak seedlings

Year of clearance	Plot	Frequency Number of quadrats	Domin value
1988/9	5	1	5
1987/8	4	2	2
1987	3	6	8
1986/7	2	2	3
1984/5	1	3	3

No significant trend in the establishment of oak seedlings is evident; indeed with the exception of plot 2 there is little variation in frequency, which is low in all plots. The stand composition (section 4.4) should ensure sufficient seed production for natural regeneration, and the low frequencies are not at present cause for concern, especially as establishing a trend over such a short time period is complicated by irregular mast years.

6.3 Germination trials

The germination trials were allowed to continue until the last week of August, by which time the seedtrays had been in the polytunnel for 15 weeks.

6.3.1 Germination of seed within the seedbank

TABLE 10 SPECIES RECORDED IN SEEDTRAYS 1-10

Sample number	Seedlings recorded	Number of individuals
1988 / 4	*Betula* spp	1
1988 / 5	-- --	
1988 / 6	-- --	
1988 / 7	*Betula* spp	3
	Rubus fruticosus	3
1988 / 8	*Betula* spp	2
1989 / 1	*Betula* spp	2
1989 / 2	*Betula* spp	13
	Rubus fruticosus	2
1989 / 3	*Betula* spp	2
1989 / 9	*Betula* spp	18
	Rubus fruticosus	1
1989 / 10	*Betula* spp	5

Only two species, birch and bramble, germinated in these trials. Where the seedlings were not too numerous within an individual seedtray they were not removed but allowed to grow. The seedlings developed strongly, reaching up to 40cm in height whilst in the polytunnel; they showed no signs of inhibited growth.

The presence of seed in the soil seedbank depends on many factors, including seed production, dispersal, longevity, dormancy and viability, vulnerability to parasites, and possibly the time necessary to move through the litter layer to the mineral soil (Brown and Oosterhuis, 1981). The apparent lack of a diverse and abundant seedbank at Coed Bryn Mawr may therefore reflect a failure to meet the requirements of one or more of these factors.

The lack of germination can be contrasted with other seedbank experiments. Abdy (pers.comm, 1989) undertook germination trials in the polytunnel at the same time as the Coed Bryn Mawr experiment, and using similar techniques obtained large numbers of seedlings from second rotation Sitka spruce sites at Clocaenog Forest in North Wales. Hill and Stevens (1981) recorded 13 species from a clearfelled Douglas fir plantation at Gwydyr forest in North Wales. The Douglas fir had been planted by the Forestry Commission in 1927, and at the time of felling there was virtually no ground cover. The 13 species recorded were all present in the 0-5cm soil layer.

Marks (1974) states that seed survives in quantity in soil for up to 50 years, after which there is a rapid decline in viability. Hill and Stevens (1981) substantiate this by referring to Peter (1893, 1894), who states that in plantations established for over 100 years, the flora of the previous *land use is largely eliminated. That* *Rhododendron* has dominated the understorey of the wood for perhaps over 100 years (no planting records exist), may have led to the exhaustion of viable seed in the seedbank, which would account for the germination of only two species.

Birch seed is short lived (Hill and Stevens, 1981), and although birch was one of the 13 species recorded by Hill and Stevens (1981) in Gwydyr forest, its presence was attributed to contamination during collection. Granstrom and Fries (1985) found that viability of *Betula pubescens* in forest soil declined to 6% of the original within one year, and to 1.5% of the original by the third year. The birch that germinated from the soil collected at Coed Bryn Mawr is almost certainly from seed dispersed subsequent to the Rhododendron clearance.

Bramble is able to remain viable in the seedbank far longer than birch, although Marks (1974) states that substantial viability of the species may last only 50 years. The presence of bramble may therefore also be due to immigration of seed.

The Rhododendron may have been so impregnable that wind dispersal was inhibited, and the reduced fauna (particularly birds) using the wood since infestation would severely reduce potential dispersal by this source.

These inhibitions to the creation of a viable seedbank are in addition to any allelopathic inhibition to germination caused by the plant itself. Brown and Oosterhuis (1981) cite Howard and Ashton (1976) who state that whilst the processes of seed penetrating mineral soil are not well understood, burial by earthworms, ants and invertebrates is a more likely mechanism than the pure accumulation of litter and formation of a fermentation layer which may eventually become part of the mineral soil. Ground up Rhododendron leaves, when added to peaty soil, reduced the number of earthworms (Lumbricus rubellins) present (Doekson, in Cross, 1975). The same may be true of Coed Bryn Mawr, in which case another factor necessary in the formation of a viable seedbank is not satisfied.

It may be concluded that the colonisation of a cleared area will therefore not be from the seedbank, but by immigration. For seeds that are not wind dispersed, effective dispersal will be dependent on chance and may be slow, and consequently not be capable of large scale colonisation. However wind-borne seed such as birch, rosebay willowherb, Epilobium spp and Compositae are capable of invading in appreciable numbers, and if conditions allow these will therefore be the species most likely to colonise cleared areas (Hill & Stevens, 1981).

6.3.2 Test sowings

TABLE 11 GERMINATION RATES IN SEEDTRAYS 1A-10A AND CONTROLS 1-5

Sample number		Number of seedlings: Festuca	Betula
1988 / 4a		809	324
1988 / 5a		409	128
1988 / 6a		336	0
1988 / 7a		921	213
1988 / 8a		920	290
	Total	3395	955
	Mean	679	191
1989 / 1a		769	166
1989 / 2a		848	70
1989 / 3a		506	67
1989 / 9a		816	189
1989 / 10a		539	15
	Total	3478	507
	Mean	696	101
Control 1		833	92
Control 2		889	154
Control 3		939	70
Control 4		468	13
Control 5		710	115
	Total	3839	444
	Mean	768	89

A one-way analysis of variance was undertaken for the test sowings in order to test for significant differences between the mean germination rates of the three treatments.

TABLE 12 ONE WAY ANALYSIS OF VARIANCE FOR TEST SOWINGS

I) *Festuca* germination

SOURCE	DF	SS	MS	F	P
FACTOR	2	22360	11180	0.24	0.793
ERROR	12	568887	47407		
TOTAL	14	591247			

II) *Betula* germination

SOURCE	DF	SS	MS	F	P
FACTOR	2	31053	15526	1.85	0.200
ERROR	12	100952	8413		
TOTAL	14	132005			

For both species there are no significant differences between the means of samples, and germination rates in this experiment cannot be attributed to year of clearance, or any latent inhibition to germination.

The mean germination of *Festuca* seedlings per half tray in all experiments was 716, a germination rate of approximately 33%. For the *Betula* seed this was approximately 127 seeds, or just under 6%. Although the germination of *Betula* was less than the average expected, namely 26% (Gordon and Rowe, 1982), as there was no significant difference between the mean germination rates for treatments, this cannot be attributed to any inhibiting factor within the soil. The germination of *Betula* seeds was more erratic than of the *Festuca*, varying from 0 to 324 per half tray.

Assuming that colonisation is dependent on immigration, then the ability of the soil to support germination and growth of the seed alighting on its surface is critical. From this experiment it appears that there is no significant difference in this ability between soil recently supporting dense *Rhododenron* thickets, and the test substrate of peat.

The conditions for germination created in the polytunnel are however not a replicate of conditions found in the wood itself. If this were the case the result of the germination trials (Table 10) would suggest that after a short time any cleared site would be substantially invaded by birch, with a presence of bramble.

The vegetation recorded in the quadrats shows that such an infestation has not occurred, and field conditions must therefore be different from conditions created in the polytunnel. These differences may include an allelopathic inhibition to growth, and differences in temperature, water and light.

Rotherham (1988) showed the inhibition of Festuca ovina shoot and root growth to be associated with a presence or recent presence of Rhododendron. However as Newman (1978) states, although an allelopathic substance may be present in a plant and released to the outside environment, it is difficult to know the concentrations of the active substance that reaches the receiver plant. Whilst the germination of seeds in a petri dish has therefore been shown to be restricted, the chemical change undergone by the inhibiting substance in the soil are complex and rapid (Newman, 1978), and the effects in the field may be very different.

7.0 CONCLUSIONS AND RECOMMENDATIONS

7.1 Vegetation associations

Over 50% of the site (88 quadrats) is dominated by bryophytes (60%), with birch, bramble and *Rhododendron* seedlings each present at less than 10%. If *Rhododendron* coppice and foxglove (the presence of foxglove is probably due to disturbance in plot 5) are included, over 68% of the quadrats are accounted for. The remaining 32% of the quadrats are contained in groups dominated by bramble, ivy or bracken. The diversity of associations within each plot varies from plot 1 (cleared in 1984/5) and plot 2 (cleared in 1986/7), the most diverse, to plots 3 (cleared in 1987), 4 (cleared in 1987/8) and 5 (cleared in 1988/9).

7.2 Vegetation and light intensity

There is a significant difference between the mean percentage crown cover of each TWINSPAN group. Groups with a high mean percentage crown cover are dominated by shade tolerant species such as bryophytes and ivy, whilst the groups with lower mean percentage crown cover contain more light demanding species such as bracken and foxglove.

7.3 Germination trials

Very little viable seed appears to be present in the seedbank. Although both birch and bramble germinated in soil collected from the site, their presence may be due to seed dispersed subsequent to clearance. In the absence of a viable seedbank colonisation of the site is dependent on immigration of seed; wind dispersed seeds will be able to colonise more rapidly than seed dispersed by other mechanisms. The conditions in the nursery are not replicated in the field, and consequently an infestation by birch, with substantial bramble is not seen.

The germination in the polytunnel of birch and Festuca ovina seed was erratic but there was no significant difference between the ability of soil recently infested by Rhododendron, or the ability of peat, to support germination. Whilst allelopathy seems to account for inhibition of growth under laboratory conditions (Rotherham, 1988), no inhibiting agent appears to be present in the soil collected from Coed Bryn Mawr. A significant time lapse will usually occur between Rhododendron clearance and the dispersal and germination of seed; it may therefore be that any allelopathic agent has by this time undergone such changes whilst in the soil that any inhibition to growth is substantially reduced.

7.4 Vegetation succession

i) Vegetation and year of clearance

There is a significant difference between the frequency and abundance of vegetation in each plot. With the exception of the area cleared in 1987/8 (plot 4), both frequency and abundance increase with the number of years since clearance. The vegetation within each plot reflects the many factors of succession including the dispersal of seed and ability of the soil to support germination and growth. These factors are in turn affected by extraneous factors such as year of clearance and disturbance.

Bryophytes dominate each plot, with wind dispersed seeds accounting for an increasing diversity and abundance of grasses and flowering plants as the number of years since clearance increases. The wind dispersed flora plays a dominant role from plot 3 (cleared in 1987), increasing in dominance in plots 2 and 1 (cleared in 1986/7 and 1984/5 respectively). By plot 1 a grass / herb sward has developed which prevents the establishment of *Rhododendron* seedlings and allows forest trees such as oak to establish. If the *Rhododendron* already established in this sward is suppressed (either by the vegetation itself or a control programme), clearance would appear successful. However the site being exposed to prolific seed sources will always be vulnerable to *Rhododendron* re-infestation, as disturbance creates fresh sites for establishment. Until more effective measures of initial control are found continued repeated eradication treatments will therefore be necessary.

ii) *Rhododendron*

The high frequency of *Rhododendron* coppice in plot 4 (cleared 1987/8) reflects the limited success of the initial clearance, and the need for subsequent treatments. The establishment of *Rhododendron* seedlings is shown by TWINSPAN to be strongly associated with the development of a bryophyte cover, and the site therefore provides plenty of opportunity for *Rhododendron* to re-invade, particularly when the wood is surrounded by seed sources. Despite the site being south facing (section 3.7) *Rhododendron* seedlings have a substantial presence in all plots with the exception of plot 5 (cleared in 1988/9) in which no suitable sites for germination have yet developed.

iii) Oak

The presence of oak shows no trend of increasing as the number of years since clearance increases. The present low frequency and abundance of oak is not yet cause for concern, as the stand composition should provide sufficient seed to ensure natural regeneration when site conditions are suitable.

7.5 Management implications

The aim of Rhododendron clearance within an oakwood of conservation interest is to end the domination of the understorey by Rhododendron, and to allow the native flora and fauna to re-colonise the wood. This aim is achieved as within five years of clearance the frequency and abundance of vegetation increases significantly; indeed within three years of clearance this increase is apparent.

The expenditure required for the initial clearance and for repeated control measures is substantial. Until more cost effective methods of control are developed, the availability of adequate funds to continue present control programmes will be essential.

7.6 Further research

Further succession studies are necessary to monitor the vegetation composition that results from complete removal of the understorey within an oakwood, and to assess the future inputs needed to prevent infestation reoccurring. Further research into the allelopathy that persists in the field, and into improved eradication and control measures are also needed.

REFERENCES

BEAN, W.J. (1976). Trees and shrubs hardy in the British Isles. Vol III : 741 - 744.

BECKER, D. (1988). Management techniques. Control and removal of Rhododendron ponticum on R.S.P.B reserves in England and Wales. 45pp.

BROWN, J.M.B. (1953a). The Rhododendron problem in the woodlands of Southern England. Quarterly Journal of Forestry. (47). 239 - 253.

BROWN, A.H, & OOSTERHUIS, L. (1981). The role of buried seed in coppicewoods. Biological conservation 21. 19 - 38.

CHAMBERLAIN, D.F, COPPINS, B.J, & GREGORY, N.M. (1985). Proceedings of the second international Rhododendron conference. Notes from the Royal Botanic Gardens, Edinburgh. 43 (1).

CLAPHAM, A.R, TUTIN, T.G, & WARBERG, E.F. (1981). Excursion flora of the British Isles. Third edition. Cambridge University Press. 586pp.

COLLINS. (1984). Guide to the grasses, sedges, rushes and ferns of Britain and Northern Ireland. 272pp.

CROSS, J.R. (1973). The ecology and control of Rhododendron ponticum L. Unpublished Ph.D thesis. University of Dublin.

CROSS, J.R. (1975). Biological flora of the British Isles, Rhododendron ponticum L. Journal of Ecology 69, 345 - 364.

CROSS, J.R. (1981). The establishment of Rhododendron ponticum in the Killarney oakwoods. Journal of Ecology 69, 807 - 824.

COX, P, & HUTCHINSON, P. (1963). Rhododendrons in North East Turkey. Rhododendron yearbook. London 17. 64 - 67.

ELTON, C.S. (1958). The ecology of invasions by animals and plants. Methuen, London.

FISHER, SIR R.A, & YATES, F. (1963). Statistical tables for biological, agricultural and medical research.

FULLER, R.M, & BOORMAN, L.A. (1977). The spread and development of Rhododendron ponticum on dunes at Winterton, Norfolk, in comparison with invasions by Hippophae rhamnoides at Saltfleetberry, Lincolnshire. Biological Conservation 12. 83 - 84.

FORESTRY COMMISSION. Booklet number 39. Forest mensuration handbook. HMSO, London. 274pp.

GORDON, A.G, & ROWE, D.C.F. (1982). Seed manual for ornamental trees and shrubs. Forestry Commission Bulletin 59. 33 - 47 & 121.

GRANSTROM, A, & FRIES, C. (1985). Depletion of viable seeds of Betula pubescens and Betula verrucosa sown onto some North Swedish forest soils. Canadian Journal of Forest Research 15. 1176 - 1180.

HARPER, J.L, WILLIAMS, J.T & SAGAR G.R. (1965). The behaviour of seeds in soil I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. Journal of Ecology 53, 273 - 286.

HILL, M.O. (1979b). DECORANA, A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Section of Ecology and Systematics, Cornell University, Ithaca, New York.

HILL, M.O, & STEVENS, P.A. (1981). The density of viable seed in soil of forest plantations in upland Britain. Journal of Ecology 69. 693 - 709.

HOPE JONES, P. (1972). Succession in breeding bird populations of sample Welsh oakwoods. British Birds. Vol 65 (7). 291 - 299.

HOWELLS, G. (1967). Coedydd Maentwrog National Nature Reserve management plan. N.C.C unpublished document.

JONES, E.W. (1959). Biological flora of the British Isles, Quercus L. Journal of Ecology 47. 169 - 222.

KELLY, D.L. (1981). The native forest vegetation of Killarney, South West Ireland : an ecological account. Journal of ecology 69, 437 - 472.

KERSHAW, K.A. (1973). Quantitative and Dynamic plant ecology. 308pp

MALLOCH, A.J.C. (1988). VESPAN II. A computer package to handle and analyse multivariate species data and handle and display species distribution data. University of Lancaster. 54pp.

MARKS, P.L. (1974). The role of pin cherry (Prunus pensylvanica L) in the maintenance of stability in Northern Hardwood Ecosystems. Ecological monographs 44. 73 - 88.

MAYHEAD, G.J. (1969). A brief comparison of two light regime assessment techniques. Commonwealth Forestry Review, 48 (4). 350 - 354.

MITCHELL, A. (1984). A field guide to the trees of Britain and Northern Europe. Collins, London. 416pp.

NEWMAN, E.I. (1978). Allelopathy or accident ? (in) Harbone, J.B. (Ed). Biochemical aspects of plant and animal coevolution. Academic press. 327 - 341.

PETERKEN, G.F, & JONES, E.W. (1987). Forty years of change in Lady Park Wood : The old growth stands. Journal of Ecology 75. 477 - 512.

PETERKEN, G.F, & JONES, E.W. (1989). Forty years of change in Lady Park Wood : The young growth stands. Journal of Ecology 77. 401 - 429.

PETERKEN, G.F, & LLOYD, P.S. (1967). Biological flora of the British Isles. Ilex aquifolium L. Journal of Ecology 55. 841 - 858.

ROSE, F. (1981). The wild flower key. British Isles and North West Europe. Warne, London. 480pp.

ROTHERHAM, I.D. (1986). The introduction, spread and current distribution of Rhododendron ponticum in the Peak district and Sheffield area. Naturalist 111. 61 - 67.

ROTHERHAM, I.D. (1986). Rhododendron ponticum L in the Sheffield area. The Sorby Record, number 24. 19 - 28.

ROTHERHAM, I.D. (1988). Aspects of the ecology of Rhododendron ponticum with reference to its competitive and invasive properties. Aspects of Applied Biology 16. 327 - 335.

SHAW, M.W. (1984). Rhododendron ponticum - ecological reasons for the success of an alien species in Britain and features that may assist in its control. Aspects of Applied Biology 5. 231 - 242.

SIMONS, P. (1988). The day of the Rhododendron. New Scientist number 1620, 50 - 55.

SNOWDONIA NATIONAL PARK. (1987). The spread of Rhododendron ponticum. A national problem. Report of the discussion conference held in Snowdonia. 53pp.

TABBUSH, P.M & WILLIAMSON, D.R. (1987). Rhododendron ponticum as a forest weed. Forestry Commission bulletin 73.

TESTER, M. (1988). Putting down roots. New Scientist number 1624, 94.

TUTIN, T.G, HEYWOOD, V.H, BURGES, N.A, MOORE, D.M, VALENTINE, D.H, WALTERS, S.M, & WEBB, D.A. (1972). Flora Europaea, Vol III. Cambridge University Press.

Appendix I PARASITIC FLORA AND FAUNA ASSOCIATED WITH RHODODENDRON PONTICUM.

I) Animal feeders or parasites

Hemiptera :*Stephanitis rhododendri* Horv
Dicyphus rhododendri Dolling
*Graphocephala coccinea*Forster
Dialeurodes chittendeni Laing
Masonaphis lambersi McGillivray

Coleoptera :*Melolontha melolontha*L
Otiorhynchus sulcatus F
Otiorhynchus singularis L

II) Plant parasites

Armillaria mellea (Vahl ex Fr) Kummer	
Botrytis cinerea Pers. ex Fr.	Leaf blast
Cercospora handelii Bub.	Leaf spot
Chrysomyxa rhododendri de Bary	Root rot
*Colletotrichum*sp.	Leaf spot
Cylindrocarpon destructans (Zins) Scholten	Root rot
Echidnodes aulographoides (Bomm., Rouss & Sacc.) Robertson	Twig blight
Exobasidium vaccinii (Fuckel) Woron.	Bud - gall
Lophodermium rhododendri Chev.	Leaf spot
Mycosphaerella rhodoendri Lindau	Leaf spot
Phomopsi ericaceana Fairm.	Stem rot of young trees
Phytophthora cactorum (Lebert & Cohn) Schroet.	Stem rot
P.cinnamoni Rands	Wilt
P.citricola Sawada	Root rot and ariel lesions
P.cryptogea Pethybr. & Laff	Etiolation and death
Pycnostysanus azalaea (Peck) Mason	Bud blast
Rhizoctonia solani DC. ex Fr.	Necrosis of scion leaves

APPENDIX II BIRD SPECIES ABUNDANCE FOLLOWING THE REMOVAL OF RHODODENDRON AT COOMBES VALLEY.

Source : Becker (1988)

I) New records

Acanthis flammea	Redpoll
Accipiter nisus	Sparrowhawk
Certhia familiaris	Treecreeper
Columba oenas	Stock dove
Dendrocopos major	Great spotted woodpecker
Dendrocopos minor	Lesser spotted woodpecker
Muscicapa striata	Spotted flycatcher
Parus ater	Coal tit
Scolopax rusticola	Woodcock
Sitta europaea	Nuthatch
Sylvia curruca	Lesser whitethroat

II) Species showing an increase

Ficedula hypoleuca	Pied flycatcher
Fringilla coelebs	Chaffinch
Parus caeruleus	Blue tit
Parus major	Great tit
Phoenicurus phoenicurus	Redstart
Phylloscopus sibilatrix	Wood warbler

III) Species showing a decrease

Garrulus glandarius	Jay
Phylloscopus collybita	Chiffchaff
Sylvia atricapilla	Blackcap
Turdus merula	Blackbird
Turdus philomelos	Song thrush

IV) Species showing no change

Aegithalos caudatus	Long tailed tit
Columba palumbus	Woodpigeon
Corvus corone	Carrion crow
Erithacus rubecula	Robin
Parus palustris	Marsh tit
Picus viridis	Green woodpecker
Prunella modularis	Dunnock
Sitta europaea	Nuthatch
Strix aluco	Tawny owl
Sturnus vulgaris	Starling
Sylvia borin	Garden warbler
Troglodytes troglodytes	Wren
Turdus viscivorus	Mistle thrush

APPENDIX III ASSESSMENT OF THE QUANTITY OF SEED PER SEEDTRAY

I) The seed in eight petri dishes, each containing 0.5 grams of *Betula pubescens* seed was counted.

Petri dish	Number of seeds (X)	$(X-\bar{X})$	$(X-\bar{X})^2$
1	2199	42	1764
2	2305	148	21904
3	1981	-176	30976
4	2227	70	4900
5	2197	40	1600
6	2000	-157	24649
7	2109	-48	2304
8	2238	81	6561
Total	17256		94478
X =	2157		

This adequately satisfies the required number of counts needed to produce an accurate mean, according to the formulae :-

$$N = \frac{t^2 \quad cv^2}{e^2}$$

N = The number of petri dishes required to be counted
t = T table factor at N - 1 degrees of freedom
cv = Coefficient of variation
e = Percentage accuracy reuired

Adopting a 95% probability level, and 5% accuracy required, eight counts were shown to be sufficient :-

$$N = \frac{(1.895^2) * (5.04^2)}{5^2} = 3.65$$

II) Five samples of 2157 *Festuca* seed were counted into separate petri dishes, and an average weight of seed derived. The remaining quantities of seed were weighed accordingly.

APPENDIX IV : SPECIES RECORDED AT PLOT 1 - CLEARED 1984/5

QUAD NUMB	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
PERC LIGH	100	2	2	3	5	3	94	96	8	2	94	68	14	100	0	19	7	4	3	100	100	42	2	4	5	3	10	2	49	3	100	100	8	94	30
NUMB SPEC	4	3	1	1	4	3	6	3	4	4	2	6	1	4	4	2	3	1	4	2	6	4	3	1	2	1	3	3	2	2	4	4	4	2	5
BETU PUBE	4	-	-	-	X	-	3	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	3	X	-	-	-
QUER PETS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	X	-	-
SORB AUCU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X
CALL VULG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CHAM ANGU	-	-	-	-	-	-	4	X	-	-	-	-	-	5	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DIGI PURP	-	-	-	-	1	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	2	-	-	-
EPIL MONT	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	6	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	X	-	-
HEDE HELI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-	3	-	-	9	-	-	9	-	-	-	-	-	-	-	-	-	-
PRUN VULG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RHOD PONS	-	2	-	-	-	1	-	-	-	-	-	1	-	-	-	-	2	-	-	-	-	-	-	-	X	-	1	2	-	-	-	-	-	-	-
RHOD PONC	-	-	-	-	1	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	5	-	-	-	-	-
RUBU FRUT	8	4	-	-	-	-	5	8	6	1	8	5	7	2	5	5	3	-	-	7	-	5	6	-	-	-	2	3	10	-	-	9	-	8	9
RUME ACET	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	2
TEUC SCOR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ULEX EURO	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AGRO CAPI	-	-	-	-	-	-	4	-	-	-	-	-	-	3	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2
CARE SPP	2	-	-	-	-	2	-	-	1	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
DESC FLEX	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HOLC LANA	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
JUNC EFFU	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BRYO SPP	-	6	3	4	5	9	5	7	5	7	5	9	-	-	9	-	-	7	-	-	4	-	6	8	-	4	5	6	-	8	4	4	2	-	4
PTER AQUI	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-

APPENDIX V : SPECIES RECORDED AT PLOT 2 - CLEARED 1986/7

QUAD NUMB	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232	233	234	235
PERC LIGH	35	11	3	2	41	5	3	45	11	8	3	3	19	2	16	33	14	15	16	4	4	54	1	15	2	11	17	3	71	40	2	8	71	8	76
NUMB SPEC	3	3	1	1	3	1	-	6	3	3	2	5	2	2	3	3	5	3	4	2	4	6	1	3	4	2	3	2	1	3	3	2	1	2	5
BETU PUBE	3	2	-	-	4	-	-	-	-	-	-	2	-	-	2	3	-	-	2	-	-	1	-	2	-	-	2	-	-	5	-	-	-	-	4
QUER PETS	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CALL VULG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DIGI PURP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EPIL MONT	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
HEDE HELI	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	8	-	-	-	-	-	-	-	-	-
HIER PILL	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RHOD PONS	2	4	-	-	-	-	-	2	4	-	-	3	-	-	1	-	-	-	-	-	-	-	-	3	3	-	2	X	-	3	-	-	-	-	4
RHOD PONC	-	-	-	-	2	-	-	-	-	-	-	-	4	-	-	-	1	2	-	5	-	-	-	-	5	-	-	-	-	-	-	3	-	-	-
RUBU FRUT	-	-	-	-	-	-	-	-	-	5	5	5	-	-	-	-	4	-	4	-	8	8	-	-	-	5	-	-	-	-	7	-	-	3	-
RUME ACET	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	4	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
CARE SPP	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	2	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	2
DESC FLEX	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HOLC LANA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
JUNC EFFU	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-
BRYO SPP	8	7	3	2	4	6	-	4	9	-	-	9	9	8	-	8	6	9	8	5	-	5	4	8	8	-	8	5	-	9	6	8	-	5	6
ATHY FILI	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-
DRYO DILA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
PTER AQUI	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	10	-	-	-	10	-	-

APPENDIX VI : SPECIES RECORDED AT PLOT 3 - CLEARED 1987

QUAD NUMB	301	302	303	304	305	306	307	308	309	310	311	312	313	314	315	316	317	318	319	320	321	322	323	324	325	326	327	328	329	330	331	332	333	334	335
PERC LIGH	6	2	10	2	12	1	4	4	3	2	5	5	15	4	6	4	10	3	2	6	5	5	10	3	6	9	5	2	4	11	1	6	2	4	12
NUMB SPEC	2	2	2	2	3	5	1	3	4	1	2	2	2	1	2	3	2	3	2	3	5	3	2	3	6	1	3	4	4	1	3	2	1	2	3
BETU PUBE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-
FRAX EXCE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
QUER PETS	-	-	-	-	-	3	-	-	-	-	X	-	-	-	-	-	X	-	-	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-
CHAM ANGU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DIGI PURP	-	-	4	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EPIL MONT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
HEDE HELI	-	-	5	-	5	-	-	1	-	-	-	-	-	-	9	-	-	-	-	3	-	-	-	4	1	4	9	-	X	-	9	5	-	X	-
RHOD PONS	-	-	-	X	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-
RHOD PONC	-	4	-	-	-	-	-	-	-	-	-	5	-	-	-	4	-	-	4	-	-	7	-	-	3	-	5	-	-	-	-	-	-	-	-
RUBU FRUT	3	-	-	-	8	4	-	-	X	-	-	-	10	-	-	-	-	-	-	9	X	-	-	-	-	-	7	-	-	-	9	-	-	-	8
UMBI RUPE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
CARE SPP	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-	-	-	X	-	-	-	1	-	-	-	-	-	-	-	-	-	-
HOLC LANA	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
JUNC EFFU	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BRYO SPP	4	8	-	9	6	9	7	8	3	5	7	3	-	3	-	7	4	3	5	2	9	6	3	7	7	-	-	6	9	4	-	6	3	8	6
ATHY FILI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-
DRYO FILI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	3	-	5	-	-	-	-
PTER AQUI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5

APPENDIX VII : SPECIES RECORDED AT PLOT 4 - CLEARED 1987/8

QUAD NUMB	401	402	403	404	405	406	407	408	409	410	411	412	413	414	415	416	417	418	419	420	421	422	423	424	425	426	427	428	429	430	431	432	433	434	435
PERC LIGH	31	2	100	100	3	2	5	100	3	5	2	2	15	3	3	2	2	6	7	3	2	8	51	5	2	2	100	4	5	5	4	2	41	9	2
NUMB SPEC	3	2	3	2	1	-	1	4	1	1	1	2	1	-	2	1	1	2	1	1	1	3	3	3	-	1	5	1	-	2	1	2	2	3	1
BETU PUBE	1	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
QUER PETS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	X	-	-	-	-	-	-	-	-
QUER PETT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-
EPIL MONT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-
HEDE HELI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-
RHOD PONS	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-
RHOD PONC	5	1	4	6	-	-	-	3	-	-	-	7	-	-	-	-	-	2	-	-	-	-	5	5	-	-	-	-	-	5	-	6	5	5	-
RUBU FRUT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
CARE SPP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
DESC FLEX	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BRYO SPP	8	1	3	4	4	-	9	3	6	8	5	1	3	-	7	3	2	5	5	6	8	9	4	7	-	4	4	5	-	7	7	-	2	8	5

APPENDIX VIII : SPECIES RECORDED AT PLOT 5 - CLEARED 1988/9

QUAD NUMB	501	502	503	504	505	506	507	508	509	510	511	512	513	514	515	516	517	518
PERC LIGH	35	75	14	39	6	13	33	20	5	35	77	71	15	72	34	28	68	11
NUMB SPEC	2	1	3	2	2	3	3	3	2	3	3	3	3	1	2	2	-	3
BETU PUBE	-	X	1	1	2	1	1	-	3	1	-	-	3	-	X	1	-	-
ILEX AQUI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X
QUER PETS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CHAM ANGU	-	-	-	-	-	-	-	4	-	-	4	3	-	-	-	-	-	-
EPIL MONT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HEDE HELI	7	-	7	-	-	8	-	-	-	-	-	-	-	-	-	-	-	8
HYAC NONS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RHOD PONC	-	-	-	-	-	-	-	-	-	-	-	-	5	-	4	-	-	-
RUBU FRUT	-	-	X	-	-	-	-	8	-	X	7	7	-	-	-	-	-	-
CARE SPP	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
BRYO SPP	3	-	-	5	4	1	7	-	5	2	-	-	3	X	-	3	-	2
PTER AQUI	-	-	-	-	-	-	-	9	-	-	9	9	-	-	-	-	-	-

QUAD NUMB	519	520	521	522	523	524	525	526	527	528	529	530	531	532	533	534	535
PERC LIGH	8	49	22	7	34	63	2	4	2	48	4	28	53	14	4	80	12
NUMB SPEC	1	4	2	2	2	2	2	3	3	2	1	1	3	1	1	3	1
BETU PUBE	-	3	3	1	3	1	-	3	-	X	-	-	-	-	-	-	X
ILEX AQUI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
QUER PETS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-
CHAM ANGU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EPIL MONT	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
HEDE HELI	8	-	-	-	-	-	7	-	4	9	-	-	-	-	-	5	-
HYAC NONS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-
RHOD PONC	-	-	-	-	-	-	-	-	2	-	-	-	-	-	5	-	-
RUBU FRUT	-	2	-	-	-	-	-	X	-	-	-	-	7	-	-	-	-
CARE SPP	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BRYO SPP	-	X	7	3	1	5	4	7	5	-	5	3	-	7	-	-	-
PTER AQUI	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-

APPENDIX IX SPECIES LIST AND ABBREVIATED NAMES

BOTANICAL NAME	VESPAN CODE	COMMON NAME
TREES		
Betula pubescens	Betu pube	White birch
Crataegus monogyna		Hawthorn
ILex aquifolium	Ilex aqui	Holly
Pseudotsuga menziessi		Douglas fir
Quercus petraea		Sessile oak
(Seedling)	Quer pets	
(stump)	Quer pett	
Salix caprea		Goat willow
Sorbus aucuparia	Sorb aucu	Rowan
Tilia x europaea	Tili cord	Common lime
FLOWERING PLANTS		
Buddleja davidii		Buddlea
Calluna vulgaris	Call vull	Heather
Chamaenerion angustifolium	Cham angu	Rosebay Willowherb
Circaea lutetiana		Enchanters Nightshade
Digitalis purpurea	Digi purp	Foxglove
Epilobium montanum	Epil mont	Broadleaved Willowherb
Fragaria vesca		Wild strawberry
Geranium robertianum		Herb Robert
Hedera helix	Hede heli	Ivy
Hieracium pilosella		Hawkweed
Hyacinthoides nonscriptus	Hyac nons	Bluebell
Hypericum androsaemum		Tutsan
Hypochoeris glabra		Smooth cats-ear

BOTANICAL NAME	VESPAN CODE	COMMON NAME
Lysimachia nemorum		Yellow Pimpernel
Oenothera biennis		Common evening primrose
Oxalis acetosella		Wood sorrel
Potentilla sterilis		Barren strawberry
Prunella Vulgaris	Prun vulg	Selfheal
Ranunculus spp		Buttercup
Rhododendron ponticum		Rhododendron
(Seedling)	Rhod pons	
(Coppice)	Rhod ponc	
Rubus fruticosus	Rubu frut	Bramble
Rubus idaeus		Raspberry
Rumex acetosella	Rume acet	Sheeps sorrel
Senecio jacobaea		Common Ragwort
Solidago virgaurea		Goldenrod
Taraxacum officinale		Dandelion
Teucrium scorodonia	Teuc scor	Woodsage
Umbilicus rupestris	Umbi rupe	Wall pennywort
Veronica officinalis		Heath speedwell
Ulex europaeus	Ulex euro	Gorse
GRASSES		
Agrostis capillaris	Agro capi	Common bent
Anthoxanthum odoratum		Sweet vernal grass
Carex binervis		Green ribbed sedge
Carex demissa		Common yellow sedge
Carex pallescens		Pale sedge
Deschampsia flexuosa	Desc flex	Wavy hair grass
Holcus lanatus	Holc lana	Yorkshire fog
Juncus articulatus		Jointed rush
Juncus effusus	Junc effu	Soft rush

BOTANICAL NAME	VESPAN CODE	COMMON NAME
BRYOPHYTES		
Atrichum undulatum		
Bryophyte spp	Bryo spp	
Campylopus introflexus		
Dicranum majus		
Funaria hygrometrica		
Hypnum cupressiforme		
Isothecium myosuroides		
Leucobryum glaucum		Cushion moss
Mnium hornum		
Polytrichum spp		
PTERIDOPHYTES		
Athyrium filix - femina	Athy fili	Lady fern
Dryopteris dilatata	Dryo dili	Broad buckler fern
Dryopteris filix - mas	Dryo fili	Male fern
Pteridium aquilinum	Pter acqu	Bracken

APPENDIX X SCHEFFEY'S TEST - following a one way analysis of variance to assess the relationship between TWINSPAN groups and light intensity.

ROW	TWINSPAN	GROUP	DIFFMEAN	SE	LOW_CI	UPP_CI
1	*000	*001	-21.20	20.3502	-98.606	56.2061
2	*000	*010	-30.88	21.8232	-113.889	52.1288
3	*000	*011	-11.92	19.7398	-87.004	63.1643
4	*000	*100	-44.86	20.8669	-124.232	34.5116
5	*000	*101	-14.50	20.5751	-92.761	63.7615
6	*000	*110	-50.08	21.0832	-130.274	30.1142
7	*000	*111	-35.75	23.9061	-126.682	55.1816
8	*001	*010	-9.68	11.3305	-52.778	33.4179
9	*001	*011	9.28	6.4645	-15.309	33.8690
10	*001	*100	-23.66	9.3573	-59.252	11.9324
11	*001	*101	6.70	8.6870	-26.343	39.7427
12	*001	*110	-28.88	9.8301	-66.271	8.5107
13	*001	*111	-14.55	14.9543	-71.432	42.3317
14	*010	*011	18.96	10.1936	-19.813	57.7334
15	*010	*100	-13.98	12.2343	-60.516	32.5557
16	*010	*101	16.38	11.7296	-28.236	60.9959
17	*010	*110	-19.20	12.5996	-67.125	28.7252
18	*010	*111	-4.87	16.9041	-69.168	59.4284
19	***011**	***10**	**-32.94**	**7.9428**	**-63.152**	**-2.7280**
20	*011	*101	-2.58	7.1409	-29.742	24.5819
21	***011**	***110**	**-38.16**	**8.4947**	**-70.471**	**-5.8489**
22	*011	*111	-23.83	14.1124	-77.509	29.8493
23	*100	*101	30.36	9.8368	-7.056	67.7761
24	*100	*110	-5.22	10.8595	-46.526	36.0863
25	*100	*111	9.11	15.6502	-50.419	68.6387
26	*101	*110	-35.58	10.2875	-74.711	3.5507