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Restoration of Native Woodland in Former Conifer Plantations

George Francis Smith

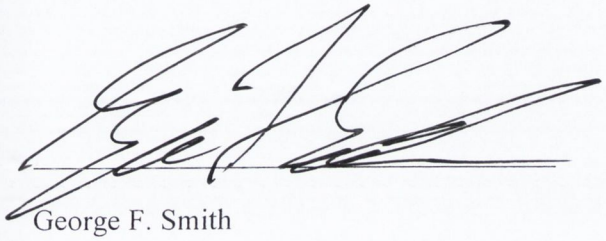
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George F. Smith

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Abbreviations

1. General abbreviations:

ANOVA-	analysis of variance
asl-	above sea level
Ca-	calcium
CCA-	canonical correspondence analysis
DCA-	detrended correspondence analysis
K-	potassium
MANOVA-	multivariate analysis of variance
Mg-	magnesium
Mn-	manganese
MRBP-	blocked multi-response permutation procedure
N-	nitrogen
NGO-	non-governmental organisation
NHA-	National Heritage Area
NMS-	non-metric multidimensional scaling
NVC-	[British] National Vegetation Classification
NWS-	Native Woodland Scheme
P-	phosphorus
PCA-	principal components analysis
pers. comm.-	personal communication
pers. obs.-	personal observation
SAC-	Special Area of Conservation
SER-	Society for Ecological Restoration
se-	standard error
sp.-	species (singular)
spp.-	species (plural)
ssp.-	subspecies
TWINSPAN-	two-way indicator species analysis

2. Common names will be used for most tree species, following Webb (1996) for European trees and Little (1953) for North American trees; the scientific name of each species will also be indicated when it first appears in text. For convenience, common and scientific names of trees are listed below. When referring to trees planted in the course of this study, "oak" and "birch" will indicate *Quercus petraea* and *Betula pubescens*, respectively. Other species may be

referred to by generic name only, such as *Calluna* for *Calluna vulgaris* and *Rhododendron* for *Rhododendron ponticum*, where such usage is customary and unambiguous. When first appearing in text, the full species name will be used.

alder-	*Alnus glutinosa*
ash-	*Fraxinus excelsior*
beech-	*Fagus sylvatica*
Douglas-fir-	*Pseudotsuga menziesii*
downy birch-	*Betula pubescens*
eared willow-	*Salix aurita*
hawthorn-	*Crataegus monogyna*
hemlock-	*Tsuga heterophylla*
holly-	*Ilex aquifolium*
Japanese larch-	*Larix kaempferi*
lodgepole pine-	*Pinus contorta*
noble fir-	*Abies procera*
Norway spruce-	*Picea abies*
pedunculate oak-	*Quercus robur*
rowan-	*Sorbus aucuparia*
sally-	*Salix cinerea* ssp. *oleifolia*
Scots pine-	*Pinus sylvestris*
sessile oak-	*Quercus petraea*
Sitka spruce-	*Picea sitchensis*
sycamore-	*Acer pseudoplatanus*
yew-	*Taxus baccata*

3. Compass directions are often abbreviated as N = north, NE = northeast, E = east, etc.

"The trees were the worst loss and damage, for at Sharkey's bidding they had been cut down recklessly far and wide over the Shire; and Sam grieved over this more than anything else. For one thing, this hurt would take long to heal, and only his great-grandchildren, he thought, would see the Shire as it ought to be... So Sam planted saplings in all the places where specially beautiful or beloved trees had been destroyed... [and] spring surpassed his wildest hopes."

J.R.R. Tolkien
The Return of the King

Abstract

The majority of Irish forests are plantations of exotic conifer species, with semi-natural woodlands occupying less than 1% of Ireland. Recent land-use changes, in particular the expansion of National Parks and Nature Reserves, provide opportunities for the restoration of native woodlands to areas formerly occupied by conifer plantations. Woodland restoration, however, has received little research attention in Ireland. The main objectives of this project are: i) to determine in what situations natural succession will be sufficient to establish native woodlands, and ii) to identify where more intensive management options, such as tree planting, will be successful.

Twenty-one pairs of 400m^2 permanent plots were established in or near the Wicklow Mountains and Killarney National Parks. One plot of each pair was fenced to exclude large herbivores. In each plot, vegetation was surveyed in eleven 1m^2 quadrats, and the growth and survival of 72 planted sessile oaks (*Quercus petraea*) and downy birches (*Betula pubescens*) and also of naturally regenerating trees was measured annually over three years.

Vegetation development was slow over the first few years after felling, but older clearfelled sites developed fairly stable heath vegetation. Acid grassland developed on clearfells with better soils, while rush-dominated communities occurred on wet soils. Early vegetation development was strongly influenced by the soil seed bank, but large herbivores appeared to have little effect.

Survival and growth of planted trees was significantly reduced by large herbivores in all years. Sites with greater soil moisture experienced greater survival of planted trees in the first year; transplantation shock (exacerbated by late planting in some sites) also reduced first-year survival, especially of birch. Browsing by hares was a significant impediment to planted tree establishment, but the importance of hares declined in the second and third years. In most sites, vegetation competition was not an important factor in tree growth and survival; low vegetation cover was in fact associated with higher oak mortality. Overall, establishment of trees by planting in conifer clearfells was successful, with 83% survival of oak and 61% survival of birch in fenced plots over the three years.

Regeneration of the wind-dispersed species birch, sally (*Salix cinerea*) and Sitka spruce (*Picea sitchensis*) was strongly limited by availability of seed sources. Regeneration of these species was favoured in sites with high covers of bare soil or needle litter and low vegetation cover. Sitka spruce regeneration was also favoured by higher soil moisture. The bird-dispersed species rowan (*Sorbus aucuparia*) and holly (*Ilex aquifolium*) were able to regenerate in low densities in most sites. *Rhododendron ponticum* invasion was very high in

Killarney, but not Wicklow. Other species, including oak and conifers other than Sitka spruce, regenerated rarely in clearfells.

It is concluded that those attempting the restoration of woodlands on conifer clearfells should delay management, except for herbivore control, so that vegetation and tree regeneration can be assessed. Better vegetation development may also improve planted tree establishment by shading the soil. Woodland restoration will be most feasible near (within approximately 250 m of) existing woodlands, where dispersal of native tree species and woodland understorey flora will be facilitated. Conifer felling brash may have a small positive effect on the regeneration of trees and shade-tolerant understorey species, and should be retained on-site. Because the greatest risk of high densities of Sitka spruce regeneration occurs when a stand is felled after significant seed dispersal, spruce plantations should be felled in summer before cones ripen.

Table of Contents

Chapter 1: Introduction **1**
1.1 Background 1
1.2 Objectives 2

Chapter 2: Restoration Ecology **6**
2.1 Defining Restoration Ecology 6
2.2 Ethics of Restoration Ecology 7
2.3 Restoration as a Test of Ecological Theory 9
2.4 Applied Restoration Ecology 10

Chapter 3: Forest Restoration and Creation **12**
3.1 Present Study in Context 12
3.2 Forest Restoration Practice 12
3.3 Restoring Native Woodlands after Conifer Clearance in Ireland and Britain 14
3.3.1 Conifer Clearfells 14
3.3.2 Woodland Restoration 15
3.4 Irish Upland Oakwoods 17
3.4.1 Composition 17
3.4.2 Disturbance 18

Chapter 4: Study Sites and Design of Permanent Plots **22**
4.1 Study Locations 22
4.2 Study Sites 22
4.3 Permanent Plot Study Design 24
4.4 Environmental Data Collection 27
4.4.1 Soils 27
4.4.2 Brash 29
4.4.3 Other Site Variables 30

Chapter 5: Vegetation Study: Methods **31**
5.1 Vegetation Sampling 31
5.2 Seed Bank Sampling 31
5.3 Data Analysis 32
5.3.1 Data Handling 32
5.3.2 Species Richness 34
5.3.3 Vegetation Types 34
5.3.4 Vegetation – Environment Relationships 35
5.3.5 Succession 37

Chapter 6: Vegetation Study: Results **39**
6.1 Species Richness 39
6.2 Vegetation Types 39
6.2.2 Pteridium – Agrostis Type 41
6.2.3 Calluna – Galium Type 42
6.2.4 Low Calluna – Erica Type 42
6.2.5 Digitalis – Juncus Type 42
6.2.6 High Calluna – Erica Type 43
6.3 Seed Bank 43
6.4 Vegetation – Environment Relationships 44
6.5 Vegetation Succession 47
6.5.1 Experimental Treatments 49
6.5.2 Ordination 51
6.6 Soil Replacement Quadrats 61

Chapter 7: Vegetation Study: Discussion **64**
7.1 Vegetation Development on Conifer Clearfells 64
7.1.1 Initial Conditions *64*
7.1.2 Successional Trajectories *66*
7.1.3 Brash *72*
7.1.4 Grazing *73*
7.1.5 Rate of Succession *74*
7.1.6 Patterns of Species Richness *74*
7.2 Restoration of Woodland Flora 75

Chapter 8: Planted Tree Study: Methods **77**
8.1 Tree Planting 77
8.2 Birch Seed Experiment 79
8.3 Field Sampling 79
8.4 Data Analysis 80
8.4.1 Data Handling *80*
8.4.2 Experimental Treatments *80*
8.4.3 Environmental Factors *81*
8.4.4 Other Statistical Testing *83*

Chapter 9: Planted Tree Study: Results **84**
9.1 Experimental Treatments 84
9.1.1 Mortality *84*
9.1.2 Growth *86*
9.2 Provenance 88
9.3 Small Mammal Browsing 90
9.4 Other Seedling Damage and Disease Symptoms 91
9.5 Environmental Factors 93
9.5.1 Exclosed Oak CCA *93*
9.5.2 Exclosed Birch CCA *98*

Chapter 10: Planted Tree Study: Discussion **102**
10.1 Herbivory 102
10.1.1 Exclosure of Large Herbivores *102*
10.1.2 Hare Browsing *103*
10.1.3 Comparison of Oak and Birch *105*
10.1.4 Insect Herbivory *105*
10.2 Vegetation Effects on Planted Trees 106
10.3 Environmental Factors 107
10.3.1 Oak *107*
10.3.2 Birch *109*
10.4 Provenance of Oak 110

Chapter 11: Natural Tree Regeneration Study: Methods **111**
11.1 Field Sampling 111
11.1.1 Regenerating Trees *111*
11.1.2 Seed Sources *112*
11.1.3 Sitka Spruce Regeneration Transects *113*
11.2 Data Analysis 113
11.2.1 Data Handling *113*
11.2.2 Exclosure *114*
11.2.3 Small Mammal Damage *115*
11.2.4 Environmental Factors *115*
11.2.5 Sitka Spruce Regeneration *117*

Chapter 12: Natural Tree Regeneration Study: Results 119
12.1 Study Sites 119
12.2 Exclosure 123
12.2.1 Seedling Densities 123
12.2.2 Sapling Recruitment and Growth 124
12.3 Small Mammal Damage 127
12.4 Environmental Factors 128
12.5 Sitka Spruce Regeneration 134
12.5.1 Effects of Site and Environment on Invasion 134
12.5.2 Size Class Distributions 136
12.5.3 Direction of Seed Sources 145
12.5.4 Sitka Spruce Regeneration Transects 148
12.6 Soil Replacement Quadrats 148

Chapter 13: Natural Tree Regeneration Study: Discussion 150
13.1 Herbivory 150
13.1.1 Large Herbivores and Exclosure 150
13.1.2 Hares 151
13.2 Dispersal 152
13.3 Site Factors 154
13.3.1 Rowan 154
13.3.2 Holly 154
13.3.3 Birch and Sally 154
13.4 Sitka Spruce Regeneration 155
13.4.1 Dispersal 155
13.4.2 Site Conditions 156

Chapter 14: Conclusions and Recommendations 160
14.1 Conclusions 160
14.2 Recommendations 162

Literature Cited 167

Appendix 1: Soil Chemical and Physical Data 182

Appendix 2: Species List 184

Appendix 3: Plot Photographs 187

Appendix 4: Species Codes 204

List of Tables

Table 4.1 Permanent plot locations and site data..... 22
Table 4.2 Soil chemical data means by plot location..... 28

Table 5.1 Environmental variables used in 1999 vegetation cover CCA..... 36

Table 6.1 Percent cover and frequency of species in six vegetation types..... 41
Table 6.2 Site and forestry data for six vegetation types..... 41
Table 6.3 Soil seed bank results..... 43
Table 6.4 Change in species cover between 1999 and 2001 by conifer felling years... 48
Table 6.5 ANOVA of the effects of experimental treatments on succession rate..... 49
Table 6.6 ANOVA of treatments and vegetation type on succession rate..... 50
Table 6.7 Percent cover of species emerging in soil replacement quadrats..... 63

Table 8.1 Environmental variables used in planted tree CCAs..... 82

Table 9.1 Mean percent mortality of planted oak and birch..... 84
Table 9.2 Odds ratios for planted tree survival in exclosed / unexclosed plots..... 85
Table 9.3 Odds ratios for planted tree survival in weeded / non-weeded plots..... 85
Table 9.4 Planted oak and birch growth means in exclosed / unexclosed plots 86
Table 9.5 MANOVA tables: overall significance of treatments on tree growth 87
Table 9.6 ANOVA tables of experimental treatments on planted tree growth 88
Table 9.7 Percent mortality by provenance of oak planted in Wicklow..... 89
Table 9.8 Percent mortality of oak and birch browsed by small mammals..... 90
Table 9.9 Growth means of oak and birch browsed by small mammals..... 91
Table 9.10 Percent occurrence of small mammal herbivory by vegetation type..... 91
Table 9.11 Numbers of live planted trees showing disturbance symptoms..... 92
Table 9.12 Oak performance CCA: environment - fitted scores correlations..... 95
Table 9.13 Birch performance CCA: environment - fitted scores correlations..... 99

Table 11.1 Sitka spruce regeneration transect details..... 113
Table 11.2 Environmental variables used in naturally regenerating tree CCAs..... 116

Table 12.1 Densities of common natural tree regeneration: seedlings..... 119
Table 12.2 Densities of common natural tree regeneration: saplings..... 119
Table 12.3 Total numbers of less commonly occurring natural tree regeneration.... 119
Table 12.4 Seed source abundances in the six study sites..... 120-122
Table 12.5 Density of naturally regenerating native tree species: seedlings..... 123
Table 12.6 Density of Sitka spruce and *Rhododendron* seedlings: non-weeded..... 124
Table 12.7 Density of Sitka spruce and *Rhododendron* seedlings: weeded subplots... 124
Table 12.8 Density and recruitment native tree species: saplings..... 125
Table 12.9 Density and recruitment of Sitka spruce and *Rhododendron* saplings..... 125
Table 12.10 Native and Sitka spruce sapling growth in exclosed / unexclosed plots.... 126
Table 12.11 Native and Sitka spruce sapling mortality in exclosed / unexclosed plots.. 127
Table 12.12 Growth of birch and rowan saplings browsed by small herbivores..... 128
Table 12.13 Logistic regression of Sitka spruce invasion on environmental factors..... 135
Table 12.14 Numbers of tree seedlings in soil replacement quadrats..... 149

List of Figures

Figure 4.1 Location of permanent study sites..... **22**
Figure 4.2 Locations of Looscaunagh permanent plots in Killarney National Park..... **22**
Figure 4.3 Locations of Muckross Forest permanent plots in Killarney National Park.. **22**
Figure 4.4 Locations of Wicklow permanent plots..... **22**
Figure 4.5 Fraughan Rock Glen study site.....**23**
Figure 4.6 Sample plot map..... **26**
Figure 4.7 Exclosed and unexclosed plot pair, showing soil sampling points..... **27**

Figure 6.1 Linear regressions of species richness..... **40**
Figure 6.2 Flexible-beta clustering of vegetation data..... **41**
Figure 6.3 Correlation biplot of 1999 vegetation data CCA..... **45-46**
Figure 6.4 Mean distances between years of quadrats in six vegetation types..... **51**
Figure 6.5 NMS ordination of species cover data: subplots..... **52**
Figure 6.6 NMS ordination of species cover data: vegetation types..... **54**
Figure 6.7 NMS ordination of species cover data: *Agrostis – Galium*..... **55**
Figure 6.8 NMS ordination of species cover data: *Pteridium – Agrostis*..... **56**
Figure 6.9 NMS ordination of species cover data: *Calluna – Galium*..... **57**
Figure 6.10 NMS ordination of species cover data: Low *Calluna – Erica*..... **58**
Figure 6.11 NMS ordination of species cover data: High *Calluna – Erica*..... **59**
Figure 6.12 NMS ordination of species cover data: *Digitalis – Juncus*..... **60**

Figure 7.1 Possible successional pathways for clearfelled conifer plantations..... **67**

Figure 9.1 Histogram of oak height growth 1999-2000 by provenance..... **89**
Figure 9.2 Histogram of oak height growth 2000-2001 by provenance..... **89**
Figure 9.3 Histogram of oak diameter growth 1999-2000 by provenance..... **89**
Figure 9.4 Histogram of oak diameter growth 2000-2001 by provenance..... **89**
Figure 9.5 Correlation biplot of planted oak performance CCA..... **96-97**
Figure 9.6 Correlation biplot of planted birch performance CCA..... **100**

Figure 10.1 Oak in unexclosed plot (#17U) protected by dense brash..... **109**

Figure 12.1 Correlation biplot of naturally regenerating tree CCA..... **130-133**
Figure 12.2 Percentage invasion of Sitka spruce by soil type..... **136**
Figure 12.3 Sitka spruce size distributions in Muckross Forest (felled 1988)..... **137**
Figure 12.4 Sitka spruce size distributions in Glendalough (felled 1991/93)..... **138**
Figure 12.5 Sitka spruce size distributions in Benleagh (felled 1993)..... **139**
Figure 12.6 Sitka spruce size distributions in Looscaunagh (felled 1994)..... **140**
Figure 12.7 Sitka spruce size distributions in Glendalough (felled 1995)..... **141**
Figure 12.8 Sitka spruce size distributions in Glenmalure (felled 1997)..... **142**
Figure 12.9 Sitka spruce size distributions in Glenmalure (felled 1998)..... **143**
Figure 12.10 Radar diagrams of the Sitka spruce seed source index..... **146-147**
Figure 12.11 Sitka spruce transects from plantation edges: west vs. east..... **148**
Figure 12.12 Sitka spruce transects from plantation edges: 1998 vs. 2000 felling..... **148**

Appendix 3
Figure 1 Plot 3E in 1999 and 2001..... **188**
Figure 2 Plot 3U in 1999 and 2001..... **189**
Figure 3 Plot 6E in 1999 and 2001..... **190**
Figure 4 Plot 6U in 1999 and 2001..... **191**
Figure 5 Plot 9E in 1999 and 2001..... **192**
Figure 6 Plot 9U in 1999 and 2001..... **193**

Figure 7 Plot 11E in 1999 and 2001 ..... **194**
Figure 8 Plot 11U in 1999 and 2001 ..... **195**
Figure 9 Plot 12E in 1999 and 2001 ..... **196**
Figure 10 Plot 12U in 1999 and 2001 ..... **197**
Figure 11 Plot 15E in 1999 and 2001 ..... **198**
Figure 12 Plot 15U in 1999 and 2001 ..... **199**
Figure 13 Plot 19E in 1999 and 2001 ..... **200**
Figure 14 Plot 19U in 1999 and 2001 ..... **201**
Figure 15 Plot 22E in 1999 and 2001 ..... **202**
Figure 16 Plot 22U in 1999 and 2001 ..... **203**

CHAPTER 1

INTRODUCTION

1.1 Background

The vast majority of the Irish landscape was once covered in forests of elm and oak, with alder prominent in areas of wetter soil and pine and birch abundant in mountainous areas (Mitchell & Ryan, 1997). Irish forests first developed about 10,000 years ago, following the end of the last glaciation, but changed in composition over time in response to changing climatic conditions and other events, such as the elm decline. The greatest changes in forest cover, however, occurred after the arrival of Neolithic farmers in Ireland approximately 6,000 years ago (Mitchell & Ryan, 1997). These peoples began forest clearance for agriculture, a process which was continued by successive groups of invaders until only 1.5% of the island of Ireland was forested by the early 20th century (Neeson, 1991). Since then, forest cover has increased, reaching 9.4% in the Republic in 2000 (Forest Service, 2001a), mostly as a result of state-sponsored and grant-aided private afforestation. Non-native conifer species, primarily Sitka spruce (*Picea sitchensis*), comprise 87.1% of total forest cover, while broadleaved species account for 12.9%, including recent plantings and plantations of exotic broadleaves (Forest Service, 2001a). At present, semi-natural woodlands occupy less than 1% of the Irish landscape (Cross, 1998).

Ireland has recently expanded its network of National Parks and Nature Reserves, and continues to add to some existing protected areas, such as the Wicklow Mountains National Park. Much of the newly required land, particularly in mountainous regions and the west, is or was recently occupied by conifer plantations. These exotic species are frequently removed to improve the conservation value of such areas. In addition, the coniferisation of semi-natural woodlands, such as Brackloon Wood, Co. Mayo and the oak woodlands of the Vale of Clara, Co. Wicklow, carried out prior to the 1970s, is now being reversed. If conifer plantations are simply felled and abandoned, they may undergo natural succession to heathland, scrub or even woodland. Several factors, however, including soil alteration during silviculture, invasion by exotic species, and overgrazing, may interfere with the development of plant communities of high conservation and aesthetic value. Some form of management will probably be necessary to enhance many clearfelled sites. One ambitious management option for conifer clearfells is the restoration of native woodlands. Woodland restoration would provide valuable habitats and redress the paucity of native woodland cover in Ireland. In addition, recent changes in forestry policy, particularly the Native Woodland Scheme

(NWS) (Forest Service, 2001b), may provide further opportunities to restore native woodlands to former conifer plantations on private or semi-state lands.

To date, there has been very little experience in establishing native woodlands on clearfelled conifer sites; no such research has been conducted in Ireland, and very little in Britain (see section 3.3.2). Difficulties likely to be encountered include those common to any forest restoration effort and some unique to the former plantation situation. The former conifer crop and attendant silvicultural and harvesting practices alter vegetation development in ways that may affect woodland restoration (Rodwell & Patterson, 1994; Olsson & Staaf, 1995; Wallace & Good, 1995; Bergquist *et al.*, 1999). Browsing by deer, sheep, hares, and more locally feral goats is a well-known obstacle to tree regeneration in deciduous woodlands (Mitchell & Kirby, 1990; Gill, 1992b), and is likely to be a problem in most conifer clearfells as well. The brash remaining from the felling operation may affect establishment and growth of woody and herbaceous species and may also influence the behaviour of grazing mammals (Grisez, 1960). Many conifer plantations are located long distances from existing broadleaved woodlands or other significant native tree populations. In these situations, planting may well be necessary to achieve tree cover. Clearfelled sites are likely to provide opportunities for the invasion of exotic species, particularly conifers such as Sitka spruce (McNeill & Thompson, 1982; Clarke, 1992; von Ow *et al.*, 1996; Dagg, 1998), and also *Rhododendron ponticum*. These and other factors have received little formal research attention, yet research is essential if success is to be achieved while using resources efficiently.

To put the present study into context, the discipline of restoration ecology will be reviewed in Chapter 2. To address the more practical considerations raised above, forest restoration practice and conifer clearfell conditions in Ireland and Britain are discussed in Chapter 3. The ecology of Irish upland oakwoods, the most appropriate type of woodland to restore to the sites used in this study, will be briefly discussed in Chapter 3.

1.2 Objectives

The main objectives of this research were twofold: i) to determine in what situations natural succession will be sufficient to establish native woodlands, and ii) to identify where more intensive management options, such as tree planting, will be successful. To achieve these objectives, three related studies were conducted: vegetation succession on clearfells, the growth and survival of trees planted in conifer clearfells, and the invasion of naturally regenerating tree species, including non-native species. In addition to the short-term results presented in this thesis, these studies may be regarded as the start of long-term experiments.

Three main factors that could potentially influence natural succession or planted tree survival were investigated using a factorial experimental design. To test whether or not large herbivore grazing hinders natural succession to woodland (objective i) or reduces the growth and survival of planted trees (objective ii), paired exclosures and unexclosed control plots were used. A vegetation control treatment was used in half of each fenced and unfenced plot: potentially competing vegetation was removed from around planted trees and exotic woody species, such as regenerating conifers, were cut (objective ii). Lastly, two different planting mixtures were tested (objective ii).

Because of the lack of research on woodland restoration, a broad approach was taken by choosing study sites that differed in several environmental and management variables. The permanent plots used in this study were placed in or near the Wicklow Mountains National Park in the east of the country and Killarney National Park in the more oceanic southwest. The two main study locations were chosen to represent both ends of the continental – oceanic climatic gradient in Ireland. In addition, three different types of parent material underlie the study sites. The plots were established in former clearfells of Sitka spruce, lodgepole pine (*Pinus contorta*) and Japanese larch (*Larix kaempferi*) that were felled between 1988 and 1998. Soil, topography, brash, distance to native woodland cover and other factors also varied among the plots. The placement, design, geography, geology, soils and climate of the plots are described in further detail in Chapter 4.

The vegetation succession study (Chapters 5-7) focuses on the development of different vegetation communities over time. Changes over the study period 1999 – 2001 were recorded and analysed. In addition, a chronosequence approach was employed by investigating stands felled at different times. Both of these approaches have been widely used in the study of succession (Begon *et al.*, 1990); a chronosequence was in fact used in the pioneering paper on ecological succession: Cowles' study on the Lake Michigan dune systems (1899). The use of a chronosequence permits the investigator to study change over periods of time that exceed the duration of a research project. Chronosequence studies, however, are often subject to confounding site influences that are independent of time. In this study, time since felling was confounded with such site differences as former conifer crop, climate and parent material, which necessarily warrants caution in the interpretation of some results.

Several biotic and abiotic factors potentially affecting succession to woodland or other communities were investigated to achieve objective (i). The effects of grazing were examined using the exclosure treatment discussed above. A particular question I attempted to address

was whether grazing slowed or deflected the trajectory of succession (sensu Gibson & Brown, 1992). The effects of soil, climate and other site variables discussed above on vegetation composition and change were investigated. The influence of the soil seed bank on succession, which I expected to be strong in more recently felled stands, was assessed using a greenhouse experiment. The effectiveness of a soil replacement trial in introducing woodland understorey species and the success of experimental bird perches in introducing bird-disseminated species were also evaluated (objective ii).

The planted tree study (Chapters 8-10) assesses the survival and growth of sessile oak (*Quercus petraea*) and downy birch (*Betula pubescens*) planted in the clearfelled study sites (objective ii). The large herbivore exclusion treatment was used to test the hypothesis that browsing pressure is too high to permit growth and survival of planted trees. The vegetation control treatment was used to test the importance of competition to planted tree performance. The effects of vegetation composition on planted tree growth and survival were also assessed using vegetation types defined in the vegetation succession study. The planting mixture treatments used were pure oak and mixed oak and birch, designed to test if birch would play the role of a nurse tree or a competitor. The effects of other biotic and abiotic factors varying by site, including small mammal herbivory, disease, soil and climate, were also studied.

The natural tree regeneration study (Chapters 11-13) investigates patterns of regeneration of native tree species (objective i). The impact of grazing on natural regeneration was examined using the exclosure treatment. The effects of site and environmental factors, including small mammal herbivory, vegetation competition, soil and climate, on tree regeneration and growth were also studied. Because conifer plantations in the Irish uplands are frequently isolated from native woodlands, special attention was paid to dispersal and the abundances of native trees in the landscape required to achieve adequate tree regeneration. Another question addressed was whether the regeneration of wind-disseminated species was more dependent on proximity to seed sources than was the regeneration of animal-disseminated species. Because invasion by non-native conifers and *Rhododendron* may interfere with conservation goals and thus require control, the effects of the above treatments, biotic and abiotic factors on the regeneration of exotic woody species, particularly Sitka spruce, was also studied (objective ii). In addition, the vegetation control treatment (removal of exotic woody species) was used to assess annual rates of invasion by such species as conifers, beech (*Fagus sylvatica*) and *Rhododendron*.

In Chapter 14, the conclusions derived from these three related studies are considered together and in the context of the two main objectives of this research, and recommendations will be made on how best to restore native woodlands to the sites of former conifer plantations.

CHAPTER 2

RESTORATION ECOLOGY

2.1 Defining Restoration Ecology

Restoration ecology can be loosely defined as the application of ecological principles to the restoration of natural systems. The practice of ecological restoration has been defined by the Society for Ecological Restoration (SER) as "... the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER, 2002). As a self-aware branch of science, restoration ecology is quite young: SER, the major professional society concerned with restoration ecology, was founded as recently as 1988. The first efforts to recreate natural communities using ecological principles, however, were conducted in 1935 by Aldo Leopold. He attempted to restore midwestern American prairies that had largely vanished because of modern agriculture and bison extirpation (Jordan *et al.*, 1987). Since Leopold's path-breaking work, however, rehabilitation of damaged ecosystems, particularly industrial sites, has been dominated by civil engineers and landscape architects relying on agricultural techniques rather than ecological theory (Clark, 1997). Their goals are often establishment of any vegetation cover rather than the reestablishment of the pre-existing natural community. The use of such terms as "rehabilitation", "restoration", and "reclamation" interchangeably when referring to projects with divergent goals has created confusion in the past about what exactly is ecological restoration. The definitions below (after Bradshaw, 1997) have found wide acceptance amongst practitioners:

Restoration- Returning a damaged ecosystem to its former, undamaged state. The goal is the recreation of an ecosystem similar to a specified reference ecosystem that existed previously or exists nearby the particular site.

Rehabilitation- Any improvement of a degraded site. Most projects whose goal is restoration actually achieve rehabilitation.

Remediation- Similar to *rehabilitation*, but in this case the focus is on repairing processes rather than achieving a specified endpoint.

Reclamation- Bringing degraded land back to a "useful" state. This may involve *replacement*, the substitution of a new ecosystem where strict restoration may not feasible or desirable.

Mitigation- Moderating or compensating for an ecological loss. Note that *mitigation* is a planning term which may involve restoration, but is more likely to comprise *rehabilitation* or habitat *creation* on a different site (Clark, 1997).

From the above, it is clear that restoration *sensu stricto* is one goal in a continuum from rehabilitative management, such as *Rhododendron* clearance, to the creation or replacement of new ecosystems on intensely disturbed sites, including land under agriculture for many years (Rodwell & Patterson, 1994; Bradshaw, 1997; Stanturf *et al.*, 2001). The particular objectives of the restoration (*sensu lato*) work are often strongly influenced by practical and socio-political considerations (Gilbert & Anderson, 1998; Stanturf *et al.*, 2001). Another important factor is the choice of the reference ecosystem to which the restored ecosystem will be compared. The principles and practice of restoration were largely developed in North America where the goal is usually the return of habitats to conditions that existed prior to European colonisation (Stanturf *et al.*, 2001). Because of the long development of "natural" habitats under human management, in Europe the goal generally is the establishment of conditions that existed prior to twentieth-century intensive agriculture, industry, and land-use change (Gilbert & Anderson, 1998). With greater understanding of the role of Native Americans in altering their environment (Stanturf *et al.*, 2001), restoration approaches have become more similar between the continents (Gilbert & Anderson, 1998).

2.2 Ethics of Restoration Ecology

Restoration or creation of new habitats involves tinkering with nature, an activity loaded with ethical considerations. Jordan (1994a) and some other practitioners of ecological restoration justify their activities by proposing a new restorationist paradigm to govern the relationship between humans and nature. Under the traditional utilitarian viewpoint, exploitation of the environment solely for human gain is morally acceptable. Conservationists disagree and seek to preserve natural areas from the destructive effects of human interference. Restorationists hold that humans can have a beneficial influence on the environment. According to restorationists, both the utilitarian and the conservationist paradigms are flawed because they suffer from human-nature dualism (Jordan, 1994a). The separation of humans from nature in the utilitarian position leads to the degradation of ecosystems. The conservationist idealisation of nature as "untrammelled by man" (U.S. Wilderness Act, 1964 cited in Jordan, 1994a) produces an inherently negative and alienating relationship. Restoration provides the basis for a healthy relationship between nature and culture by viewing humans as active participants in the biotic community.

Conservationist critics of the restorationist ethic deny that they view humans as somehow apart from nature, but only seek to reduce harmful environmental impacts of human activities (Kane, 1994). Many are wary of some of the more forceful assertions of restorationists, such as "the fate and well-being of the biosphere depend ultimately on us" (Jordan, 1994a) and that humans are "the lords of creation" (Turner, 1985). Such perspectives suit better the utilitarian philosophy than an understanding of humans as part of a community. Assertions of dominance and desire to control negate the possibility of the freedom and independence of the other members of the community. Thus, while conservationists view humans as part of nature, they recognize and value the independence or otherness of nature. Natural ecosystems have evolved independently for hundreds or thousands of years. Human influence interferes with the evolutionary processes and breaks the continuity between the ancestral environment and the present (Elliot, 1997; Gilbert & Anderson, 1998). In other words, the "naturalness" of an environment has inherent value that human intervention reduces (Elliot, 1997). In contrast, the restorationist viewpoint holds that no part of the environment should be excluded *a priori* from human intervention (Kane, 1994).

The difference in how different parties value naturalness has practical importance in what Elliot (1997) calls the "replacement thesis". This proposes that an ecosystem can be destroyed for commercial purposes and then restored or replaced intact. The replacement thesis has been invoked by developers or governments to defend habitat destruction for mining or road construction. In south London, 8.3 ha of ancient oak woodland was to be destroyed for this purpose and replaced by 10.2 ha of new forest planted on adjacent farmland. During a public inquiry, the British Department of Transportation argued that the loss of value was temporary and that habitat creation would completely replace the forest's value (Gilbert & Anderson, 1998). In Ireland, the National Roads Authority claimed that the destruction of part of the ancient, semi-natural oak woodland in the Glen of the Downs Nature Reserve caused by a road-widening scheme would be "more than replaced" by new planting on an adjacent site (McDonald, 1997). Opponents of the replacement thesis argue that because naturalness has intrinsic value, mitigation is inadequate compensation for habitat destruction. Such artificial habitats have been likened to faked art by several critics (Elliot, 1997; Gilbert & Anderson, 1998). In Britain the replacement thesis failed to convince the authorities, whereas it may have contributed to the going-ahead of the road scheme in the Glen of the Downs.

Except for their most extreme advocates, supporters of the conservationist and restorationist viewpoints agree with each other much more than with those who consider nature of little

importance. In general, conservationists accept that human activity can add to the value of ecosystems, for example by increasing species diversity (Elliot, 1997). Restored ecosystems are preferable to damaged ones, and given time to develop naturally after human intervention has stopped, they can approximate the value of the original ecosystem (Elliot, 1997). For their part, restoration ecologists generally agree that natural habitats should be preserved and disagree with the replacement thesis (Jordan, 1994b; Gilbert & Anderson, 1998).

Perhaps the most interesting aspect of the restorationist perspective on the human-nature relationship is the potential for restoration activities to take on a dimension of ritual healing. Jordan (1994b) pointed out that ritual has long served as a medium for human communication with the unknown, including nature. Western science has destroyed ritual and objectified nature, leading to its destruction. The symbolic healing involved in restoration projects has the potential to lead to healthier relationships with the environment. These arguments, however, have received little support from Jordan's critics (e.g. Kirby, 1994). An exception is Higgs (1997), who recognises the redemptive potential of restoration activities. He argues that good restoration projects encompass cultural, aesthetic, and moral aspects in addition to the scientific elements. It is perhaps this redemptive or ritual quality of restoration activity that accounts for the success of such practical environmental organisations as Groundwork and Conservation Volunteers of Ireland.

2.3 Restoration as a Test of Ecological Theory

Although restoration ecology is more often seen as purely applied ecology, many have pointed out that it can be an effective tool for ecological research. In fact, Leopold's original prairie restoration efforts were focused on research rather than habitat reconstruction for conservation (Jordan *et al.*, 1987). Bradshaw (1987) views restoration ecology as an "acid test" of ecological theory. He states that there is "no more direct test of knowledge of ecosystem function than when components are restored to see if structure and function are the same" as the reference ecosystem. Jordan (1987) compares the information gained from reconstructing ecosystems to that gained by an engineer rebuilding an object. For example, the importance of fire in maintaining prairie ecosystems was only discovered after several failed restoration attempts (Jordan *et al.*, 1987). Similarly, the failure of natural dispersal to bring in desired species has revealed the absence of key dispersal agents (Ashby, 1987). Gaps in knowledge of the site requirements of species can be identified (Stanturf *et al.*, 2001). Restoration ecology has the potential to answer other questions, ranging from the specific, such as how forests attain layered canopy structures (Ashby, 1987), to the theoretical, such as

what are the links between the community composition of a site and ecosystem processes such as nutrient cycling (Webb, 1997).

Because restoration attempts are essentially experiments in assembling communities (Lockwood & Pimm, 1999), they can test theories of succession. Restoration experiments have tested models of succession, both supporting and refuting the classical facilitation model in different cases (Ashby, 1987). Following a review of 87 projects, Lockwood and Pimm (1999) suggest that the original species composition of an ecosystem may only be achieved when historical pathways of secondary succession are used. This observation supports the facilitation model and implies that the number of possible pathways to a given persistent community is limited.

2.4 Applied Restoration Ecology

Just as restoration ecology can inform ecological theory, the reverse is necessary for successful outcomes. Modern ecology has rejected the notion that nature is static and operates in closed systems, the so-called "balance of nature." The current paradigm accepts that natural systems are constantly in a state of flux, subject to disturbances and external processes. Restoration of an ecosystem, therefore, is an attempt to hit a moving target. This acknowledgement leads to three implications: 1) restoration ecology should focus on restoring ecosystem processes rather than ecosystem structure, 2) no single example of a reference ecosystem can be used as a model, and 3) restoration should be seen as an ongoing process rather than a single discrete event (Pickett & Parker, 1994; Bradshaw, 1997; Parker & Pickett, 1997).

The goals of a particular project can be divided into the reestablishment of: 1) ecosystem processes, such as nutrient flux, productivity, and disturbance regimes, and 2) community structure, the abundance and distribution of species (Lenz & Haber, 1992; Bradshaw, 1997; Parker & Pickett, 1997; Lockwood & Pimm, 1999). Restoration of processes is the more important of the two, because ecosystem function is essential for the immigration and persistence of the desired species (Lenz & Haber, 1992; Bradshaw, 1997). In general, ecosystem functions can be achieved and maintained using a broad array of species, such that the processes operating in a particular site are largely independent of specific species composition (Lockwood & Pimm, 1999). For example, the light regime required by woodland herbs can be provided by a broad array of deciduous tree species, including exotics. In fact, processes are often easier to achieve than structure (Lockwood & Pimm, 1999).

Forests may require close to 500 years to achieve an uneven age structure (Bradshaw, 1997), although ecosystem functions depending on a forest canopy can be established much earlier.

Given that communities are dynamic entities, replicating a particular set of species in specified abundances may be not only an unattainable, but also an inappropriate goal. Long term environmental change may prevent exact replication of past conditions (Urbanska *et al.*, 1997; Stanturf *et al.*, 2001). Therefore, selecting one ecosystem state fixed in time and space as a reference for restoration efforts is a "trap" (Pickett & Parker, 1994). Many examples of a broader habitat type must be used to develop a framework for a particular site. Higgs (1997) warns, however, that "ecological fidelity" must be adhered to. He cautions that economic imperatives of efficiency of time and money must not be allowed to lead to "reverse adaptation", where the focus of the restoration effort shifts from replication of the target habitat to creation of something natural-seeming but affordable. This is especially a threat given our cultural shift to preferring a hyperreal, "Disney-type" idealisation to the real thing (Higgs, 1997).

A process-oriented view of ecological restoration suggests that the restoration activity itself cannot be viewed as a discrete event, but as an intervention in ongoing ecosystem development (Pickett & Parker, 1994). In this way, restoration is akin to managing succession (Parker & Pickett, 1997) and is most successful when the basic principles of natural succession are used to inform the restoration effort (Bradshaw, 1987; Lockwood & Pimm, 1999). The process view will facilitate restoration of both ecosystem structure and function. In our consumer-oriented society where quick results are demanded, long-term approaches to restoration will be resisted, however (Higgs, 1997). To justify the expense implicit in the long-term view of restoration and to ensure a more successful outcome adequate assessment of practices is needed (Pickett & Parker, 1994; Michener, 1997).

CHAPTER 3

FOREST RESTORATION AND CREATION

3.1 Present Study in Context

The research project summarised in this thesis is a study of the feasibility of and factors affecting the restoration of native woodlands to sites occupied by felled conifer plantations. In the present study, "restoration" is used in the looser sense of the term, because semi-natural woodland was not the immediate precursor vegetation to the conifer plantations (based on inspection of first- and second-edition Ordnance Survey maps). Establishment of a semi-natural community on sites where the community was not previously present or has been absent for a long period of time is often termed habitat "creation," but such activities fall under the general umbrella of ecological restoration (section 2.1). The most appropriate target community to be restored in this study is acidophilous oak woodland, because of the soil and climatic conditions present. Oak woodland currently exists in similar situations within a maximum of two miles of the study sites. It is likely that acid oakwoods occupied these sites prior to their destruction hundreds or perhaps thousands of years ago. In the higher elevation sites, Scots pine – birch woodland may have comprised the original forests, but no semi-natural examples of such woodlands currently exist in Ireland. The relative abundances of pine and oak in primeval montane forests was dependent on elevation (Mitchell, 2000), and so the transition between oak forest and pine forest would have been ecotonal in nature, rather than a separation of discrete communities. Irish upland oakwoods are discussed in more detail in section 3.4 below.

3.2 Forest Restoration Practice

Restoration of forest or woodland (the terms are used here interchangeably) ecosystems differs in scale, both time and physical dimensions, from most other types of restoration (Ashby, 1987). This is largely because of the great size and long lives of trees, the dominant organisms in forests. Restoration of tree cover is usually the primary goal in forest restoration because it is a prerequisite for repairing many other facets of forest structure and function (Howell, 1986; Stanturf *et al.*, 2001). For example, many forest understorey species require the shade and higher humidity provided by a canopy in order to outcompete species of open habitats. The choice of which tree species to plant or to encourage to regenerate depends on the site environment (Howell, 1986).

The strategy normally employed in Ireland and Britain is to choose the type of native woodland most appropriate for the site as the reference ecosystem. The Native Woodland Scheme (NWS) recently launched by the Forest Service grant-aids the management, restoration and creation of semi-natural woodlands (Forest Service, 2001b). Under this scheme, the appropriate woodland type is chosen according to soils and the distribution of native woodlands in Ireland, with guidance from a woodland classification scheme by Cross (2002). Britain's Forestry Commission provides guidance (Rodwell & Patterson, 1994) on selection of suitable woodland types and prescribes species to be introduced or encouraged using the British National Vegetation Classification as a model (Rodwell, 1991a). The selection of the target habitat is based on the climate and soils on the site and may be facilitated by the presence of indicator species for particular woodland types. Rodwell and Patterson (1994) provide lists of species found in "optimal precursor vegetation" for each NVC woodland type. In Ireland, long periods of cloud cover allow the survival of many typical woodland species outside the woodland canopy, thus facilitating the matching of woodland type to the site.

The task of establishing tree cover is aided by practices well-established by foresters, but in some aspects, the goals and methods of forest restoration differs from standard forestry practice. Ground preparation and weed control may need to be carried out on many sites, and fencing to exclude livestock and/or deer is virtually a prerequisite in Ireland (Forest Service, 2000a). Eradication of invasive exotic species almost always has high priority. The choices of tree regeneration methods include planting seed, bare-rooted transplants, and seedlings in biodegradable containers (Evans, 1984), but natural regeneration is preferred in establishing Irish and British native woodlands (Rodwell & Patterson, 1994; Forest Service, 2001b). Natural regeneration can be encouraged by such practices as scarifying and herbicide use (Rodwell & Patterson, 1994). In North America, provision of bird perches to facilitate seed dispersal has been found to encourage regeneration of trees and forest shrubs (McClanahan & Wolfe, 1993). Natural regeneration permits a natural forest structure to develop and allows for the preservation of local (presumably native) genetic diversity. Where planting is necessary, local provenances are preferred or required in Ireland and Britain (Soutar & Peterken, 1989; Rodwell & Patterson, 1994; Forest Service, 2000b; Forest Service, 2000a; Forest Service, 2001b; Sackville Hamilton, 2001). For example, in the NWS, planting stock used in or adjacent to "SACs, NHAs, Nature Reserves, National Parks, and known ancient woodlands must originate from seed collected from within or nearby these areas" (Forest Service, 2001b).

Current best practice encourages attention to the spatial and structural aspects of forest restoration. During planting, provision of open spaces is encouraged, particularly where valuable open habitats already exist (Rodwell & Patterson, 1994). Where timber production is also an objective, trees will likely be planted in rows, but Rodwell and Patterson (1994) provide advice on varying spacing and planting in clumps. The restored or new forest should fit well in the landscape. In the NWS, planting above the natural treeline is not permitted (Forest Service, 2001b) (despite the lack of a good understanding of where the treeline should be!). The planting of understorey species, such as hazel and hawthorn, is strongly recommended in Britain and Ireland, and is grant-aided under the NWS.

Quite often, no provisions are made for restoring the forest field layer apart from encouraging natural regeneration, such as by thinning. Because many typical Irish and British woodland plants are poor dispersers (Peterken & Game, 1984; Usher *et al.*, 1992), active restoration efforts may be required in isolated sites. Usually, attempts to reintroduce woodland field layers are delayed until the tree canopy is closed (Buckley & Knight, 1989; Cohn & Packham, 1993; Rodwell & Patterson, 1994). Sowing seed tends to be the most successful for edge or gap species, whereas many woodland herbs that usually regenerate vegetatively are better established as containerised plants (Buckley & Knight, 1989; Francis *et al.*, 1992; Cohn & Packham, 1993). Transferring woodland soil has also had some success in restoring woodland flora (Buckley & Knight, 1989; Helliwell *et al.*, 1996).

3.3 Restoring Native Woodlands after Conifer Clearance in Ireland and Britain

3.3.1 Conifer Clearfells

Conifer clearfell sites differ in several ways from woodlands or other habitats used for forest restoration and creation. The initial conditions for restoration on clearfell sites are strongly influenced by the species and management of the former conifer crop. Sitka spruce plantations cast a very dense shade, eliminating nearly all vascular plant cover on canopy closure (Hill & Jones, 1978; Hill, 1979; Wallace & Good, 1995; Fahy & Gormally, 1998; Ferris *et al.*, 2000). A few species, however, can survive as depauperate individuals (Hill & Jones, 1978). Of course, under canopy gaps or near the plantation edge more plants may persist. Species that cast less shade than spruces, such as pine (*Pinus* spp.) and larch (*Larix* spp.), do not have such a severe effect on the understory, and may support substantial plant cover (Hill, 1979; Ferris *et al.*, 2000). Understorey communities of these plantations may be similar to those developing under semi-natural Scots pine (*Pinus sylvestris*) forests.

Conifer plantations are well-known for increasing soil acidity, promoting podzolisation, and formation of deep mor-humus and litter layers (Page, 1968; Miles, 1978; Hornung, 1985; Miles, 1985). The impact of plantations on soils varies widely by crop species and initial soil conditions (Stone, 1975; Hornung, 1985). Felling conifer plantations likewise has profound effects on soil properties. Soil pH has been found to increase following clearfelling through release of cations from brash and decomposition of humic compounds (Nykvist & Rosén, 1985).

The removal of the conifer crop represents the removal of a significant proportion of the nutrients of a site (Hornung, 1985; Goulding & Stevens, 1988). In addition to the boles, felling brash represents a sizeable source of nutrients. If left on site, nutrients retained in brash are gradually released into the soil on decay. Conifer leaf litter both on the felled branches and in the soil litter layer represents a larger fraction of nutrients than in the twigs and branches (Fahey *et al.*, 1991; Hyvönen *et al.*, 2000). Because conifer needles are more readily decomposed, they provide an initial pulse of nutrients to developing vegetation (Titus & Malcolm, 1999), whereas woody debris releases nutrients more slowly with increasing diameter (Fahey *et al.*, 1991). In fact, decay of woody debris may *reduce* soil nutrient availability over time. After the more nutrient-rich parts of the debris are consumed and the C / N ratio increases, decomposing fungi and microbes may require additional nutrients from the soil to meet their demands (Brady & Weil, 2002). The spatial arrangement of brash left on site may be important: windrowing brash has been found to decrease foliar nutrient concentrations of Sitka spruce seedlings planted between brash rows relative to seedlings adjacent to rows (Hendrick, 1979). Brash may also exert a physical effect on the site by deterring browsing of regenerating trees (Grisez, 1960) or by inhibiting vegetation development (Rodwell & Patterson, 1994).

Decay of conifer needles (Titus & Malcolm, 1999) and woody brash (Fahey *et al.*, 1991) releases N, P, and Ca relatively slowly. Leaching is a more important process for Mg, which is released more quickly than mass is lost from brash. K is leached the fastest, such that it may be lost from soils with poor cation exchange capacities before significant uptake by vegetation has occurred (Goulding & Stevens, 1988; Titus & Malcolm, 1999).

3.3.2 Woodland Restoration

There has been some experience in Ireland or Britain of restoring native woodlands on sites of felled plantations of exotic conifers. Most has been in semi-natural woodlands that have been

underplanted with conifers or have had pockets of them planted in formerly open areas. Recently, efforts have been made to remove the conifers and allow woodland to regenerate on the site, for example in the Vale of Clara Nature Reserve in Co. Wicklow (pers. obs.), managed by Dúchas, and in ancient woodlands in Britain, under the auspices of English Nature, the Woodland Trust and Coed Cymru (Kirby & May, 1989; Radford, 1998, J. Healey, pers. comm.). In most cases, especially where native woodland cover is relatively extensive and close by, the conifers are felled, but nothing else is done to encourage woodland development.

Very little information is available about more intensive restoration practices in Ireland and Britain. I am aware of only one other study (Palmer *et al.*, 2001) researching restoration feasibility and methods. Palmer *et al.* (2001) studied the effects of exclosure and conifer brash cover on a former Sitka spruce stand in an Atlantic oakwood in western Scotland. They found higher survival of planted oak seedlings (10-15 cm tall) inside exclosures. Although brash protected the seedlings from browsing by deer and sheep, seedling survival under the brash was reduced. Palmer *et al.* (2001) attributed this result to lower light levels under the brash piles and herbivory by voles.

Despite the lack of empirical work, Rodwell and Patterson (1994) provide guidance on the establishment of woodlands on clearfelled conifer stands. Similarly, Humphrey and Nixon (1999) discuss the planning and restoration of upland oakwoods in Britain. Both caution against damaging the site with heavy machinery during harvesting and recommend minimising the amount of ground covered with dense brash which may impede natural regeneration of native trees. Lighter brash cover, however, may provide shelter for any shade-tolerant woodland plants that may be present (Humphrey & Nixon, 1999). Rodwell and Patterson (1994) and Humphrey and Nixon (1999) recommend felling during periods of poor conifer seed production in order to minimise conifer regeneration.

No accounts of native woodland restoration on former conifer sites in Ireland have been published, but I am aware of a small number of projects of varying size. In Killarney National Park, a former Sitka spruce stand in the Muckross Forest area (adjacent to one of the sites in this study) was planted with sessile oak. Prior to planting, brash was piled and burned (P. O'Sullivan, pers. comm.). In Glencree, Co. Wicklow, Crann (an NGO) and Coillte (the semi-state forestry company) have planted sessile oak of French and Irish provenances on a large former Sitka spruce stand (the Oak Glen project; T. O'Regan, pers. comm.). The trees were pit planted at standard stocking rates and fertilised with rock phosphate, and brash was burned prior to planting. Selective herbicides have been applied on an as-needed basis.

The most comprehensive woodland restoration in Ireland is that of Brackloon Wood, Co. Mayo (J. Hawe, pers. comm.). The wood was planted in the 1950s and 1960s with 54 ha of conifers, mostly Sitka spruce, adjacent to small stands of remnant oak woodland totalling around 20 ha. To date, nearly all conifers and other non-native species, including sycamore (*Acer pseudoplatanus*), beech (*Fagus sylvatica*), northern red oak (*Quercus rubra*), and a small amount of *Rhododendron*, have been removed. Veteran individuals of non-native broadleaved trees and Scots pine stands have been left. Regeneration operations have been dictated by the size and location of felling coupes. Natural regeneration is being relied upon to restore woodland cover over most of the wood. Planting efforts have largely focused on reducing the fragmentation of the remnant oak stands. Several ground preparation, planting and after-care methods have been used to permit comparisons of their success. Although large herbivores are not a major problem, herbivory by hares has been severe, particularly in more open sites. Planted trees are being protected by tubes, which also protect them from smothering vegetation and facilitate their location for later treatments.

3.4 Irish Upland Oakwoods

3.4.1 Composition

Because coniferous plantations in Ireland are primarily situated in upland areas with acidic soils of low nutrient status and cool, wet climates, the most appropriate target community for woodland restoration is generally acidophilous oak woodland. This type of woodland is referable to the phytosociological association Blechno-Quercetum petraeae, which occurs on siliceous parent materials, often in hilly or mountainous terrain (Kelly & Moore, 1975). These woodlands are classified as oak-birch-holly woodland (WN1) in the Irish habitat classification scheme (Fossit, 2000). The high conservation value of upland acid oakwoods in Ireland is recognized by inclusion of "old sessile oak woods with *Ilex* and *Blechnum* in the British Isles" (code 91A0) in Annex 1 of the EU Habitats Directive (European Commission, 1999).

The dominant tree species of upland oakwoods in Ireland is sessile oak. Downy birch, and rowan (*Sorbus aucuparia*) are usually abundant, as is holly (*Ilex aquifolium*), which often forms a dense understorey in woodlands with higher rainfall (Kelly & Moore, 1975; Kelly, 1981). Characteristic species of the field layer include *Blechnum spicant, Luzula sylvatica, Vaccinium myrtillus, Lonicera periclymenum* and *Pteridium aquilinum.* Species typical of heath or acid grassland, such as *Calluna vulgaris, Agrostis canina, Agrostis capillaris, Holcus mollis* and *Carex pilulifera*, may be frequently found together with other characteristic

woodland plants, such as *Hedera helix, Oxalis acetosella* and *Rubus fruticosus* (Kelly & Moore, 1975).

Two counties host the best and most extensive acidophilous oakwoods in Ireland: Co. Kerry, most notably in the Killarney area, and Co. Wicklow, especially in the vicinity of the Avonmore River and its tributaries (Kelly, 1981; Cabot, 1999). Western woodlands in general and the Killarney woodlands in particular are characterised by higher precipitation than Wicklow oakwoods, which results in a much higher diversity and luxuriance of bryophytes. These bryophyte-rich communities have been referred by Kelly (1975) to a scapanietosum subassociation of the Blechno-Quercetum, differentiated by such moss, liverwort, and filmy fern species as *Scapania gracilis, Plagiochila spinulosa* and *Hymenophyllum tunbrigense*. *Saxifraga spathularis* is also a differential species of the subassociation. Greater rainfall in the Killarney woodlands also permits better development of the vascular and bryophyte epiphytic flora (Kelly & Moore, 1975; Kelly, 1981). Wicklow oakwoods are generally referable to a typicum subassociation, which is more bryophyte and species-poor. *Deschampsia flexuosa* is usually more abundant in these drier woodlands (Kelly & Moore, 1975). In more base-rich sites throughout the country, a coryletosum subassociation has been found that has floristic affinities with pedunculate oak-ash-hazel woodland (Kelly & Moore, 1975).

3.4.2 Disturbance

No Irish woodlands can be considered to have escaped the direct or indirect effects of human interference. Management and clearance of upland oakwoods for timber, charcoal, and bark for leather tanning has been documented in many places (e.g. Mitchell, 1988; Little *et al.*, 1996). Some Wicklow oakwoods, and probably others, have been managed in the past as coppice woodland (Nairn & Crawley, 1998). Other past and present anthropogenic disturbances in sessile oakwoods include high levels of grazing by wild and domestic animals (Kelly, 1975) and invasion by exotic species (Cross, 1982).

This human interference has resulted in woodlands with tree species compositions quite different than in the original, natural forests. For example, palynological data from Derrycunihy Wood in Killarney show that the forest that stood there c.5000 years ago was much more diverse and less dominated by oak (Mitchell, 1988). Because of the commercial value of oak, the present-day dominance of oak in Derrycunihy Wood in particular and upland Irish woodlands in general is at least in part due to management (Mitchell, 2000), as also occurred in Britain (Rackham, 1976). Selective felling and the planting of woodlands

with non-local and possibly foreign provenances have probably altered the genetic diversity of sessile oak populations (Joyce *et al.*, 1998). *Quercus* plants were imported from England in the 18th century, and there are records of planting non-local and foreign *Quercus robur* in many estate woods (McCracken, 1971). Recently, Kelleher (2001) detected a sessile oak with a chloroplast DNA haplotype unlike any others he found in Ireland from a population in west Kerry, which he suggested was of planted origin. Planting of foreign oak provenances continues in Ireland to this day. Nearly absent from Irish oakwoods is Scots pine, which was an important canopy species in prehistoric times, particularly at higher elevations, (Mitchell, 1988; Little *et al.*, 1996; Mitchell, 2000) but declined dramatically and probably became extinct in the first millennium AD (Bradshaw & Browne, 1987). There is some documentary evidence of uncertain quality (the putative pines are referred to as "fir trees") that pine persisted as late as the sixteenth century (Fitzpatrick, 1966), but if so, then it must have been at low numbers and was ecologically unimportant (Bradshaw & Browne, 1987).

The flora of Irish woodlands is impoverished relative to Britain and continental Europe: many species that are relatively abundant elsewhere are either rare or absent from Ireland. While some may have never reached Ireland following the last glaciation (cf. Webb, 1983), it is likely that many have been driven to extinction by widespread woodland clearance (Praeger, 1934). Woodland herbs absent from Ireland that occur in acidophilous woodlands in Britain include: *Linnaea borealis, Trientalis europaea, Corallorhiza trifida, Goodyera repens, Maianthemum bifolium,* and *Ruscus aculeatus* (Praeger, 1934). Local extinctions due to anthropogenic disturbances can account for much of the paucity of species in many sessile oakwoods. Certain plants are considered "old forest species" because they have persisted in woodlands that have not been felled for many years, including the grasses *Milium effusum* and *Festuca altissima*, the saprophyte *Monotropa hypopitys*, *Pyrola minor* and *P. media* (Praeger, 1934). It is likely that they were more widespread in the original upland oakwoods. Similarly, fauna characteristic of woodlands, such as woodpeckers, capercaillie and goshawks, have also become extinct in Ireland, most likely due to forest clearance and fragmentation (Cabot, 1999). The extinction of the wolf was a crucial loss to the woodland fauna, given the very high numbers of deer and other herbivores present in many modern Irish woodlands.

On the other hand, several exotic species have become established in and around upland oakwoods in Ireland; many of these are relatively innocuous, but several have profound ecological impacts. *Rhododendron* is highly invasive in the wetter oakwoods of the west (Kelly & Moore, 1975; Cross, 1981; Kelly, 1981; Cross, 1982), while *Prunus laurocerasus* is more invasive in the east (pers. obs.). These evergreen species form dense understoreys in

woodlands, thus eliminating field layer species and preventing tree regeneration. Many woodlands have been planted with exotic trees, including broadleaves like beech and sycamore, and conifers such as Norway spruce (*Picea abies*), hemlock (*Tsuga heterophylla*) and western red-cedar (*Thuja plicata*). Beech, sycamore and hemlock are quite shade-tolerant and frequently regenerate under woodland canopies (pers. obs.).

Although Irish woodland communities may have developed in the presence of large herbivores, it is widely accepted that the large numbers of grazing animals present in many Irish woodlands today prevent tree regeneration and reduce field layer diversity (Hester *et al.*, 1998). Results from experimental deer exclosures have shown that the grazing levels currently experienced in many sessile oak woodlands severely reduces the height of the shrub and field layers, prevents adequate regeneration of native tree species, and reduces species richness (Kelly, 1975; Kelly, 1981; Kelly, 2000; pers. obs. of exclosures in Wicklow established by M. Neff in the 1970s). Under severe grazing, the woodland understorey becomes dominated by less palatable species, such as *Agrostis capillaris*, *Pteridium aquilinum* and the exotic *Rhododendron*, while more grazing-sensitive species, like *Dryopteris aemula*, are restricted to sites beyond the reach of herbivores, such as the root plates of windthrown trees (Kelly, 1975; Cross, 1982; Kelly, 2000).

In addition to influencing the species composition of Irish upland oakwoods, anthropogenic disturbance has undoubtedly had profound effects on their structure, although these are more difficult to identify with confidence. Because most woodlands have been at least partially cleared within the past few centuries, the canopy trees are often the result of only one or a few regeneration episodes, and thus exhibit fairly uniform age and size structures. For example, Glaisín na Marbh oakwood in Killarney experienced a main phase of regeneration in the 1830s, followed by two further episodes in the 1880s and the 1910s which were confined to separate areas around the periphery of the young woodland (O'Sullivan, 1991). High grazing pressure and the inability of oak to regenerate under closed canopies (Shaw, 1974) limit the establishment of new oak cohorts, and thus reinforce the evenness of the age and size structures of present-day oak woodlands. Is an even-aged structure natural for acidophilous woodlands in Ireland? Even-agedness is characteristic of forests that experience large, intense disturbances at intervals within the lifetime of the dominant trees. Such forests include the conifer forests of western North America, which regenerate after fires (Johnson & Fryer, 1989), and forests that experience relatively frequent severe windstorms, such as hurricanes (Foster, 1988). In most northern temperate forests, smaller-scale disturbances dominate: the windthrow of single trees or small groups, which allows the regeneration of trees in canopy gaps (Runkle, 1985; Frelich & Lorimer, 1991; Frelich & Graumlich, 1994).

This disturbance and regeneration regime facilitates the development of uneven age distributions, often with a characteristic "inverse-J" shape when tree density is plotted against age (Hett & Loucks, 1976). Because the disturbance regime of present-day Irish woodlands is characterized by small gaps averaging 96 m^2 (Higgins, 2001), more uneven size and age structures of canopy trees are likely to be the natural situation. However, severe windstorms capable of creating large blowdowns occur at more irregular intervals, but well within the lifespan of most tree species (Higgins, 2001). The disturbances created by these storms may have been more important for regeneration in truly natural woodlands, which therefore would develop broadly even-aged patches several thousand square meters in size. Many North American temperate old-growth forests are in fact complex mosaics of larger even-aged patches interspersed with uneven-aged stands maintained by gap regeneration (Foster, 1988; Frelich & Lorimer, 1991). The persistence of species characteristic of open habitats, such as grasslands, during the millennia when Ireland was supposedly swathed in forest implies that significant open areas must have existed in primeval Irish woodlands.

In conclusion, the composition and structure of present-day upland oakwoods in Ireland has been dramatically altered from truly natural conditions. Although the species composition of natural woodlands can be elucidated to some degree using paleoecological methods, relative abundances are more difficult to determine, particularly for woodland herbs, ferns and bryophytes. Other aspects of structure and spatial distribution of species remain poorly known and may be unknowable. Therefore, no individual woodland can serve as a model community for woodland restoration, and more abstract conceptions of upland acid oakwoods, informed by best scientific understanding and adapted to local conditions, must suffice.

CHAPTER 4

STUDY SITES AND DESIGN OF PERMANENT PLOTS

4.1 Study Locations

As stated in the introduction (section 1.2), sites were chosen to encompass a broad range of environmental conditions so as to increase the applicability of this study. The majority of the research was conducted in a set of 21 pairs of 20 m × 20 m permanent plots established in the area of the Wicklow Mountains National Park (latitude 53°1′N, longitude 6°20′W) and in Killarney National Park, Co. Kerry (latitude 52°1′N, longitude 9°30′W) (Fig. 4.1). The locations were chosen to represent both ends of the main climatic gradient in Ireland. In Killarney, three plot pairs were located northeast of Looscaunagh Lough at the southwest edge of the National Park (Fig. 4.2). Three more pairs of plots were placed in an area of plantations known as Muckross Forest on the lower north slopes of Mangerton Mountain (Fig. 4.3). Four plot pairs were located in Glendalough, Co. Wicklow on the north face of Derrybawn Mountain (Fig. 4.4). These plots are in the Wicklow Mountains National Park and, as in Killarney, the land is owned and managed by Dúchas, The Heritage Service. The remaining eleven plot pairs were established in the Glenmalure Forest in Co. Wicklow (Fig. 4.4). This forest is owned by Coillte Teo., the semi-state forestry company, but is due to become part of the Wicklow Mountains National Park. Within Glenmalure, six pairs were placed in Fraughan Rock Glen (nos. 12, 14-17, and 20) (Fig. 4.5). Three plot pairs were placed at lower elevations and closer to Baravore Ford and the Avonbeg River (nos. 18, 19 and 21). The last two pairs were at higher elevations on the northeast flank of Benleagh Mountain (nos. 13 and 22). The elevation ranges at which the plots were located are shown in Table 4.1.

The study sites were chosen as representative of recently felled sites across a range of geographical, altitudinal and edaphic conditions. Sites under active vegetation management, such as tree planting, were avoided. The sites contained a mixture of clearfelled patches, intact and remnant conifer stands, forest roads, rock outcrops, streams and sometimes patches or woodlands of native species (Fig. 4.5).

4.2 Study Sites

The study sites chosen for permanent plots encompass two different climatic regimes, three bedrock types, and several soil types and silvicultural regimes. The climate of Killarney is

Figure 4.1. Location of permanent study sites. NP = National Park.

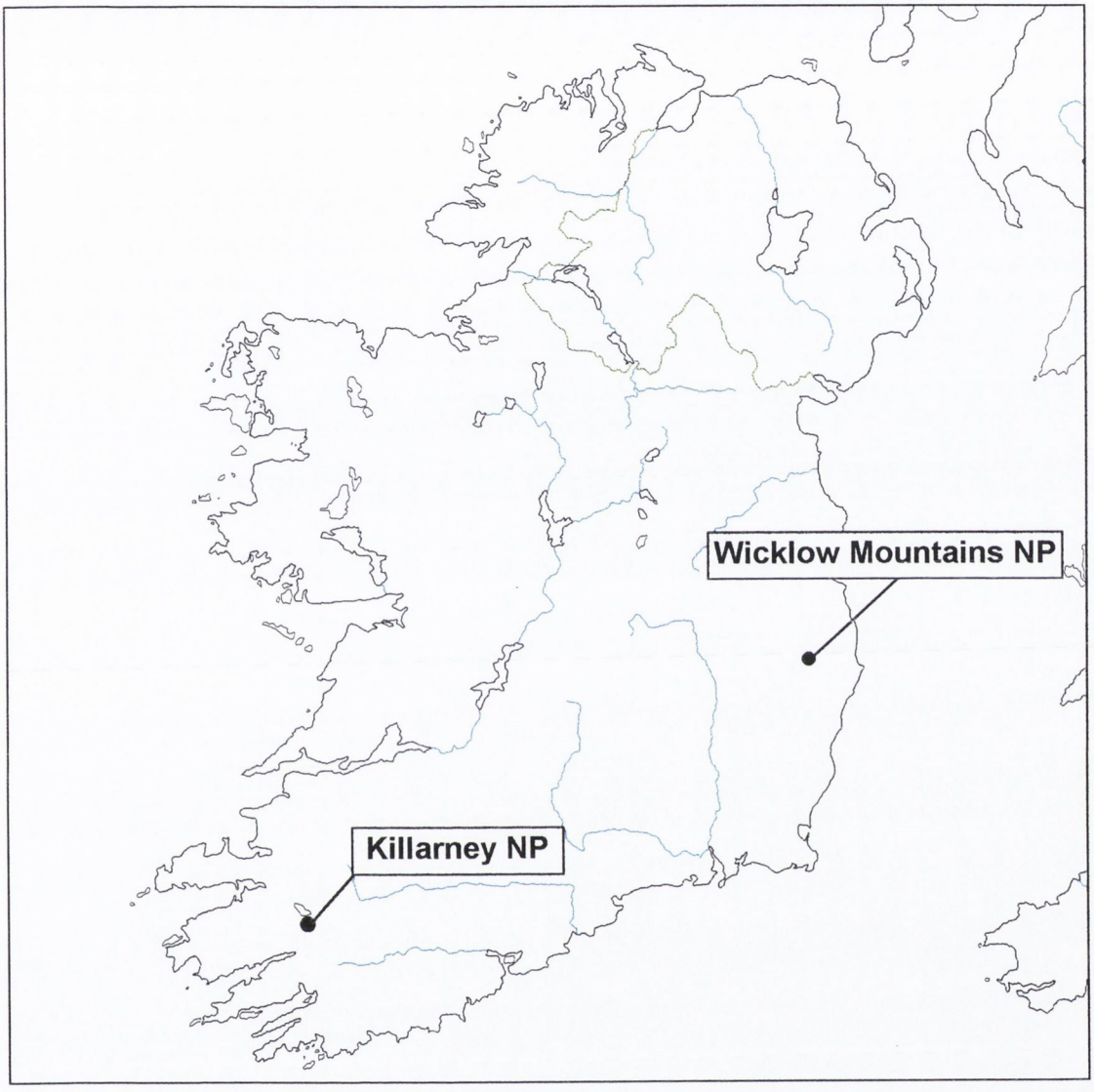


Figure 4.2. Locations and identification numbers of Looscaunagh permanent plots in Killarney National Park. Map is from the Ordnance Survey National Park Series (1:25,000). Note that there is no plot pair 2.

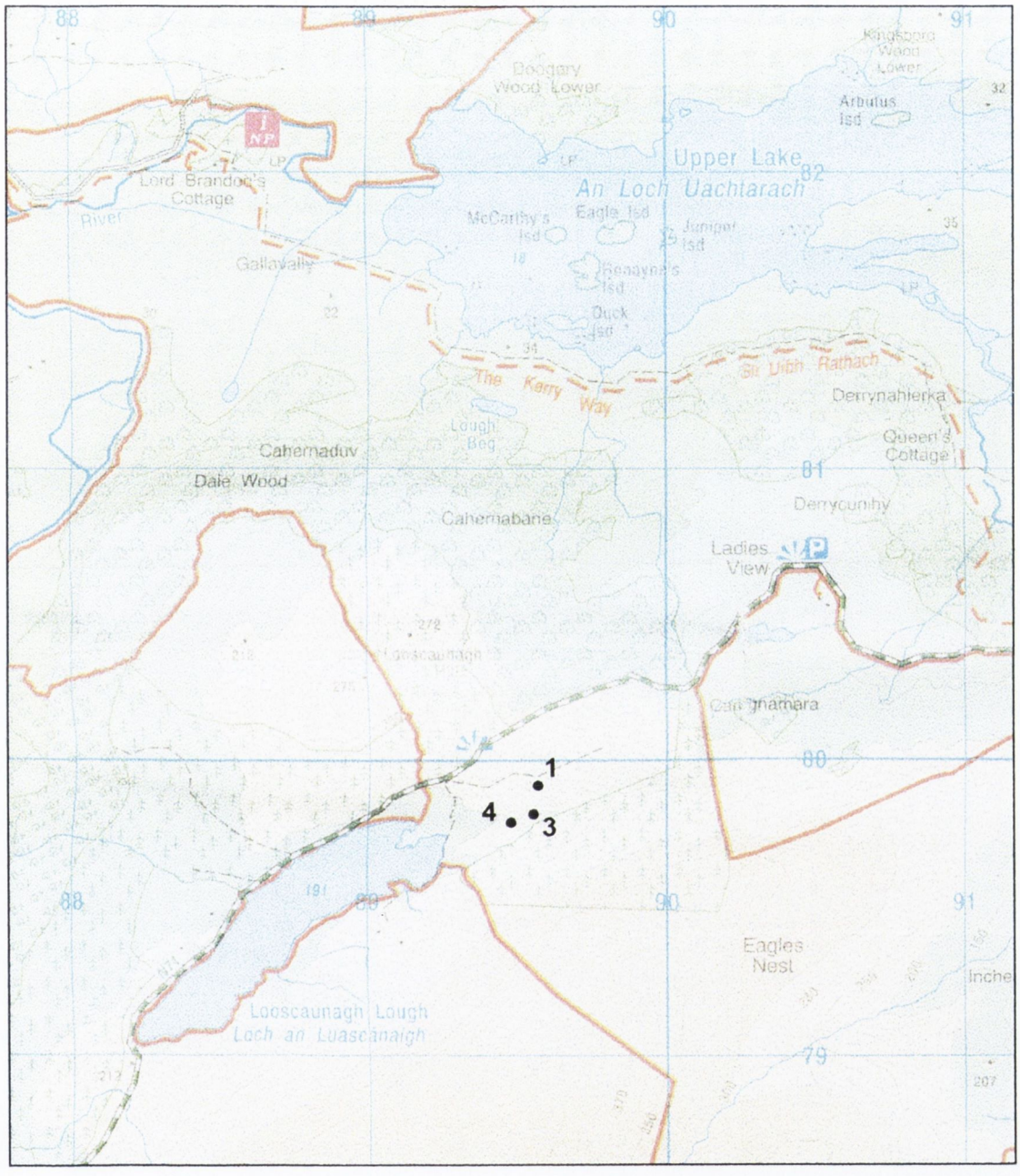


Figure 4.3. Locations and identification numbers of Muckross Forest permanent plots in Killarney National Park. Map is from the Ordnance Survey National Park Series (1:25,000). Note that these plots are located approximately 9 km northeast of the Looscaunagh plots.

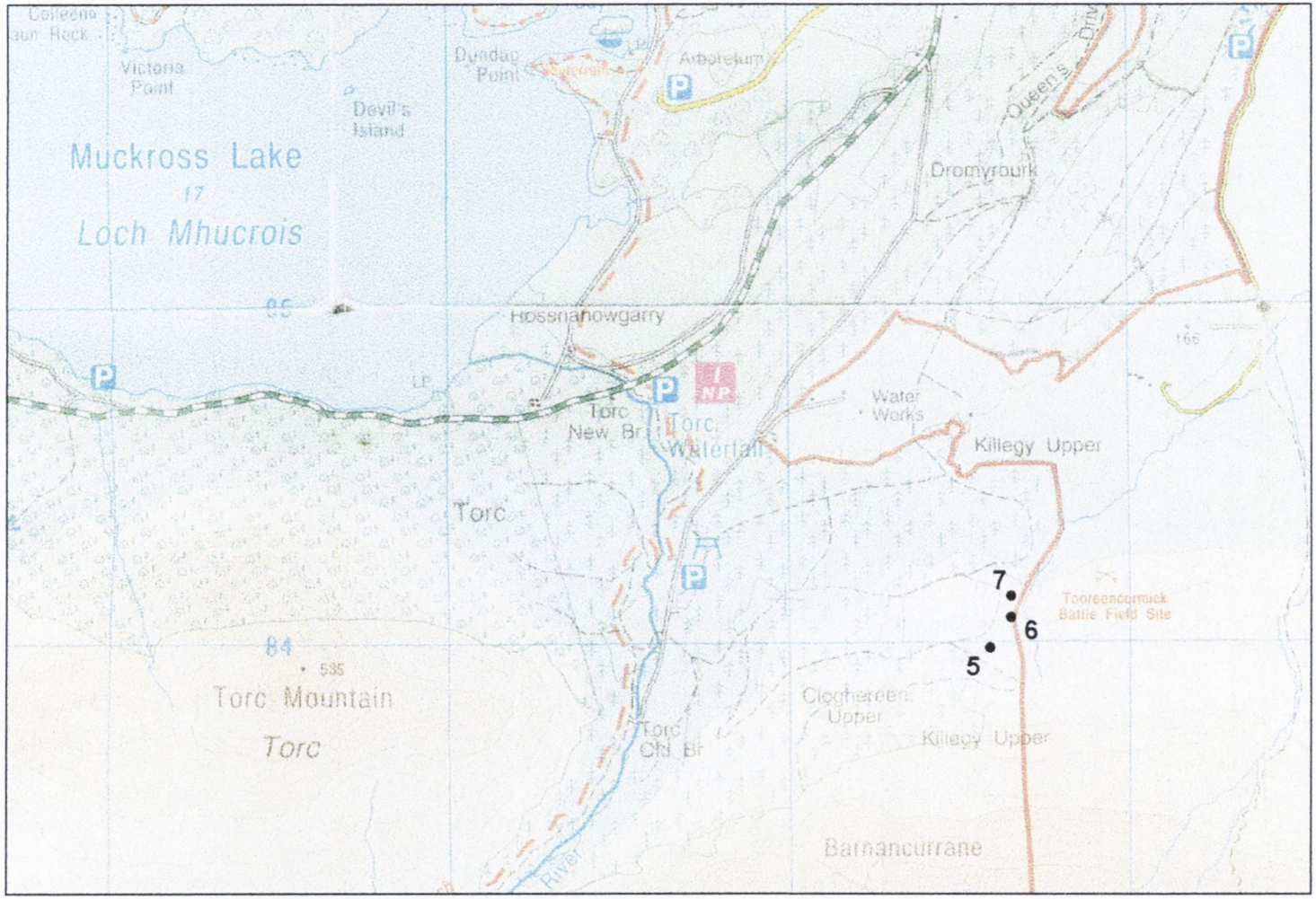


Figure 4.4. Locations and identification numbers of Wicklow permanent plots. Map is from the Ordnance Survey Discovery Series (1:50,000) sheet 56.

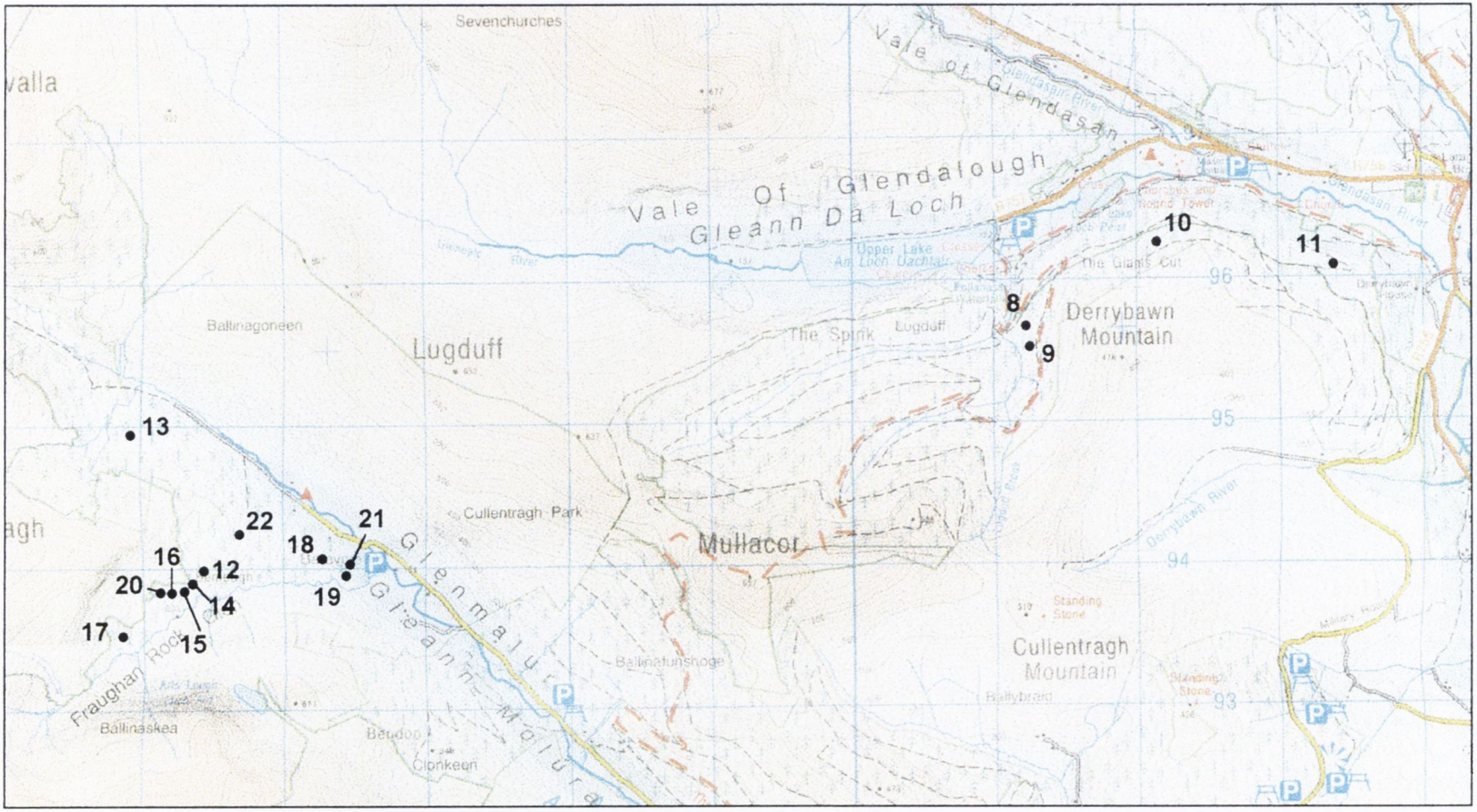


Table 4.1. Permanent plot locations, elevation range of plots, mean 1999-2001 temperatures for January and July, mean annual (1999-2000) rainfall, mean monthly rainfall from May to August in 1999-2001 (growing season), soil types, geology, former conifer crop species, and years when conifer planting and clearfelling took place. Numbers in parentheses indicate the number of plots in each category. Climate data are extrapolated from local Met Éireann weather stations (see text for details). The conifer species are spruce: *Picea sitchensis*, pine: *Pinus contorta*, and larch: *Larix kaempferi*.

Location	Site	No. of Plots	Elevation Range (m)	Mean Jan Temp (°C)	Mean July Temp (°C)	Mean Annual Rainfall (mm)	Mean Monthly Growing Season Rainfall (mm)
Killarney	***Muckross Forest***	6	240-255	5.1	15.1	2284	109.3
	Looscaunagh	6	215-240	4.9	14.9	2324	112.6
Wicklow	***Glendalough***	8	220-285	4.6	15.2	1847	85.1
	Glenmalure- *Baravore*	6	160-225	4.9	15.6	1748	76.9
	Glenmalure- *Fraughan Rock Glen*	12	320-350	4.1	14.7	1966	95.0
	Glenmalure- *Benleagh*	4	350-380	3.9	14.6	2003	98.1

Table 4.1 cont'd.

Location	Site	No. of Plots	Soil Types	Geology	Former Crop	Planting Year	Felling Years
Killarney	***Muckross Forest***	6	podzol	Devonian Old Red Sandstone	spruce	1935	1988
	Looscaunagh	6	blanket peat	Devonian Old Red Sandstone	spruce	1962	1994
Wicklow	***Glendalough***	8	brown earth (6), brown podzolic (1), peaty gley (1)	Ordovician schist and phyllite	larch (4), spruce (2), spruce / pine (2)	1939 (4), 1954 (2), 1960 (2)	1991 (4), 1993 (2), 1995 (2)
	Glenmalure- *Baravore*	6	brown earth (4), peaty podzol (2)	Granite	spruce	1952	1998
	Glenmalure- *Fraughan Rock Glen*	12	peaty podzol (8), podzol (4)	Granite	spruce (6), pine (6)	1952 (4) [1], 1951 (8)	1998 (6), 1997 (6)
	Glenmalure- *Benleagh*	4	peaty podzol	Granite	spruce	1952	1993 (2), 1998 (2)

[1] Four spruce plots were planted in 1952 and two in 1951; all six pine plots were planted in 1951.

Figure 4.5. Fraughan Rock Glen study site. From left to right, plot numbers 20, 16 and 15 were in a former lodgepole pine stand, and numbers 14 and 12 were in a former Sitka spruce stand. Note the heavier brash in the former lodgepole pine stand.



extremely oceanic, with over 200 rain days per year and mild temperatures year-round, accumulating 2500-3000 degree days per year in the lowlands (Mitchell & Ryan, 1997). The central Wicklow Mountains are slightly more continental, receiving 150-200 rain days per year and generally not exceeding 2000 degree-days per year (Mitchell & Ryan, 1997).

Meteorological data from January 1999 to September 2001 were obtained from Met Éireann to provide more accurate estimates of climate. Monthly mean temperature data were from weather stations in Glenealy, Co. Wicklow (122 m asl) and Muckross House, Killarney, Co. Kerry (58 m asl). Temperatures were corrected for site elevation using the accepted lapse-rate of a 0.6 °C decrease per 100 m elevation increase (Keane, 1986). A comparison of mean January temperatures (averaged over 1999-2001) shows that the Killarney sites experienced warmer winters than the Wicklow sites (Table 4.1). Mean July temperatures varied more by elevation than geographical location, however. Data for frost-free days (not shown), could not be corrected for elevation, and therefore provided a poorer indication of on-site conditions. It may be worth noting, however, that neither of the weather stations experienced frosts between May and September during 1999-2001.

Rain gauges at Glenmacnass, Co. Wicklow (238 m asl) and Muckross House, Killarney, Co. Kerry (58 m asl) provided estimates of differences in precipitation between the sites. In Ireland, precipitation increases with elevation: mountainous regions generally receive more than 2000 mm per year, and mean annual precipitation exceeding 3000 mm per year occurs in

some western and southwestern mountain areas (Rohan, 1986). Greater rates of increase with elevation are observed on windward slopes than on lee slopes, but in complex mountain ranges, such as Wicklow, the effects of orography on precipitation are also complex. As a rule of thumb, however, annual precipitation increases between 100 mm and 200 mm for every 100 m increase in elevation in Ireland (Keane, 1986). Precipitation values for the study sites were therefore extrapolated from the rain gauge data using a 150 mm precipitation per 100 m elevation correction (Table 4.1). The Killarney sites experienced greater amounts of annual rainfall and rainfall during the May to August growing season than the Wicklow sites during the course of this study.

The study sites in Killarney overlay Devonian Old Red Sandstone (Table 4.1) (Geological Survey of Ireland, 1995). The granite of the central Wicklow massif forms the bedrock in Glenmalure, while Glendalough lies in a geologically complex zone of metamorphic rock bordering the granitic areas (Table 4.1) (Geological Survey of Ireland, 1995). All of these parent materials give rise to acidic soils, which are discussed in greater detail below.

The limited availability of clear-felled areas prevented balanced sampling across felling year, former conifer crop, and site (Table 4.1). Most of the plots were located in former plantations of Sitka spruce felled between 1988 and 1998. Six plots in Fraughan Rock Glen were established in lodgepole pine (*Pinus contorta*) stands felled in 1997. Four Glendalough plots were in Japanese larch (*Larix kaempferi*) stands felled in 1991, and two were in a mixed stand of lodgepole pine and Sitka spruce (50:50) felled in 1993. In Glenmalure, stands were felled by chainsaw and removed to the roadside by skyline cables. In some of the other study sites, the presence of brash mats suggests that conifers were felled using harvesters or by chainsaw with tractor extraction. Photographs of plots in Appendix 3 show the variation among study sites in former crop, felling year and other variables.

4.3 Permanent Plot Study Design

The forty-two 20 × 20 m permanent plots were marked with aluminium stakes in December 1998 to February 1999. Because woodland development requires longer than the three year timeframe of this study, the locations of the plots were marked and recorded as precisely as possible to facilitate later resampling. The location of a plot within a given clearfell was determined randomly where possible, within certain constraints. Areas with numerous boulders, extremely wet areas (with high covers of *Sphagnum*), and positions near the former plantation edge were avoided when placing plots. This was done to avoid areas that may have been influenced by edge effects, such as increased light levels, while the conifers were

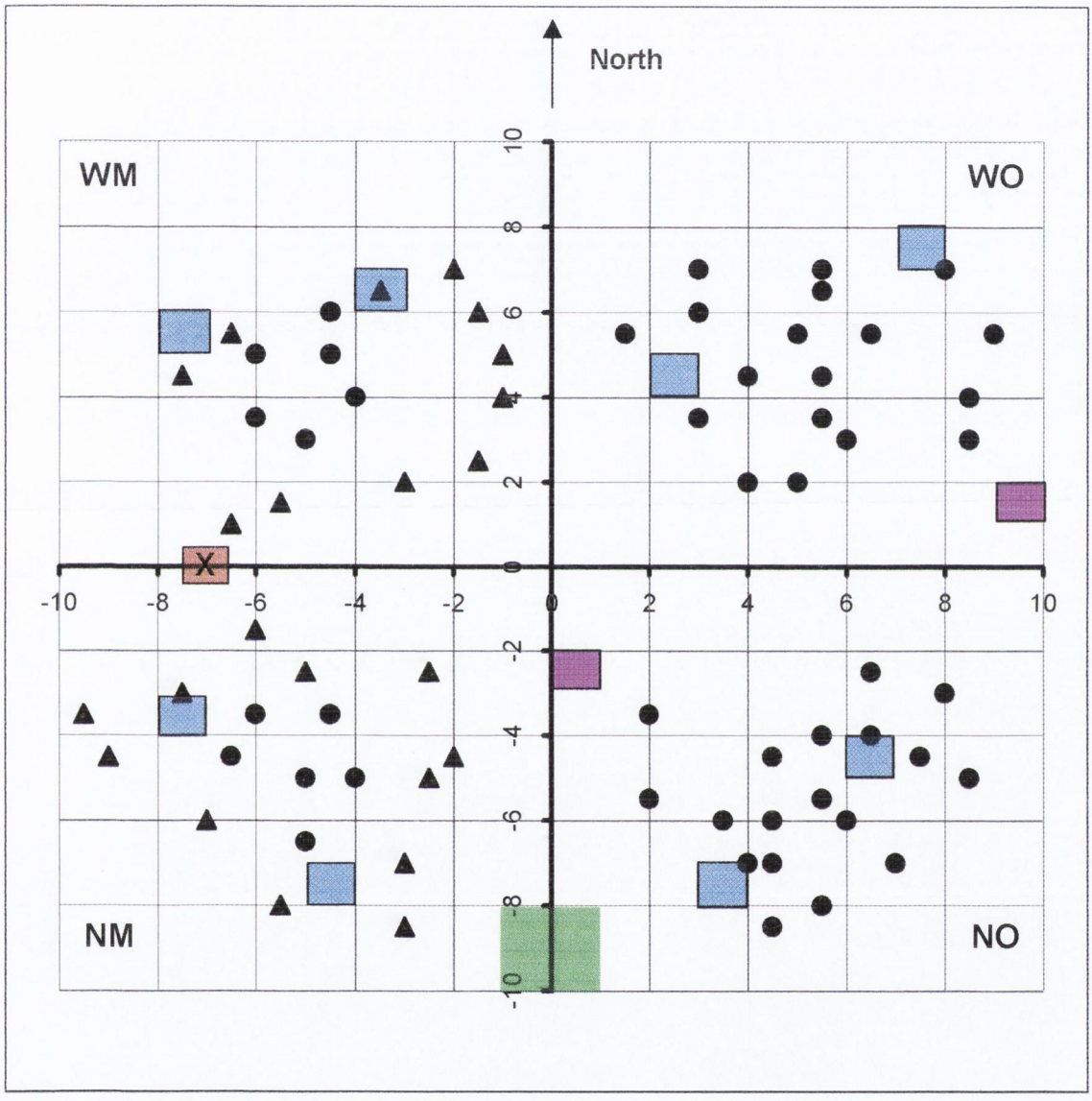
present. Some clearfell areas meeting these criteria were too small to permit random placement.

Three experimental treatments, each with two levels, were applied to the plots in a 3-way factorial design: large herbivore exclosure, tree species planting mixture, and weeding. Plots were established in pairs, one of which was later fenced, leaving the other as an unfenced control. The fences were double strands of sheep wire high enough to exclude deer and other large herbivores. No break-ins occurred during the study. Rabbit fencing was not used. There was a gap of 1-3 m between a fence and the edge of an adjacent unexclosed plot to reduce edge effects, such as the tendency of deer to create paths around exclosures. The remaining two treatments were allocated to the four 10 × 10 m quarters (referred to as "subplots" from this point forward) of each fenced and unfenced plot (Fig. 4.6). Two randomly selected subplots were planted with 18 sessile oak bare-rooted transplants; the other two subplots were planted with 6 oak and 12 downy birch bare-rooted transplants (see section 8.1). The planted trees in one randomly chosen subplot of each planting mix were manually weeded. All vegetation (except naturally regenerating tree seedlings) in an approximately 75 cm diameter circle around each tree was uprooted annually by hand or with the aid of a weeding fork. In addition, all exotic species (most commonly Sitka spruce and *Rhododendron*) were removed from each weeded subplot. Weeding in 1999 and 2001 coincided with vegetation sampling (summer); in 2000 weeding took place in April and May. Within each of the subplots, planted and naturally regenerating trees were monitored annually (see sections 8.3, 11.1.1) and other vegetation was sampled in 1999 and 2001 (see section 5.1).

Ancillary experiments and trials were also carried out in the permanent plots. Wooden, T-shaped bird-perches about 2 m tall were erected in both fenced and unfenced plots to test if these would encourage the colonisation and spread of bird-disseminated species such as rowan and bramble (*Rubus fruticosus* agg.). The perches were placed on the line dividing two randomly chosen subplots (Fig. 4.6). Distance away from plot centre was determined randomly where the terrain permitted.

A small-scale soil replacement trial was conducted in late March, 2000, in five fenced plots: two in the Muckross Forest site, two in Fraughan Rock Glen, and one in Glendalough. Soil was removed to a depth of 10 cm from a randomly chosen 1 × 1 m square in an area where no trees were planted. The soil was replaced with an identical volume (1 m × 1 m × 10 cm) of soil from a nearby oak woodland. Live plants were removed before the soil was translocated.

Figure 4.6. Sample plot map (from plot 20E (exclosed)). Grid scale is 2 m. Circles indicate planted oaks and triangles indicate planted birch. Treatment combinations are as follows: W = weeded, N = not weeded; M = mixed birch/oak, O = pure oak. Position of the bird perch is indicated with an X. The positions of vegetation quadrats are shown: blue = planted, purple = unplanted, and red = bird perch. Green indicates the area sown with birch seed.



The soil donor site in Killarney was an oak woodland with a dense holly understorey in the Muckross House area. There was little vegetation to remove from the donor soil, but nearby species included *Luzula sylvatica*, *Vaccinium myrtillus*, and *Anemone nemorosa*. As an organic layer comprised most of the top 10 cm, little mineral soil was translocated. The donor site for the three Wicklow plots was an open, relatively young oak woodland on the eastern side of Derrybawn Mountain in Glendalough. The soil was a brown earth supporting abundances of

Luzula sylvatica, *Rubus fruticosus* agg., *Lonicera periclymenum*, *Blechnum spicant*, *Vaccinium myrtillus*, *Oxalis acetosella*, and *Hyacinthoides non-scripta*.

4.4 Environmental Data Collection

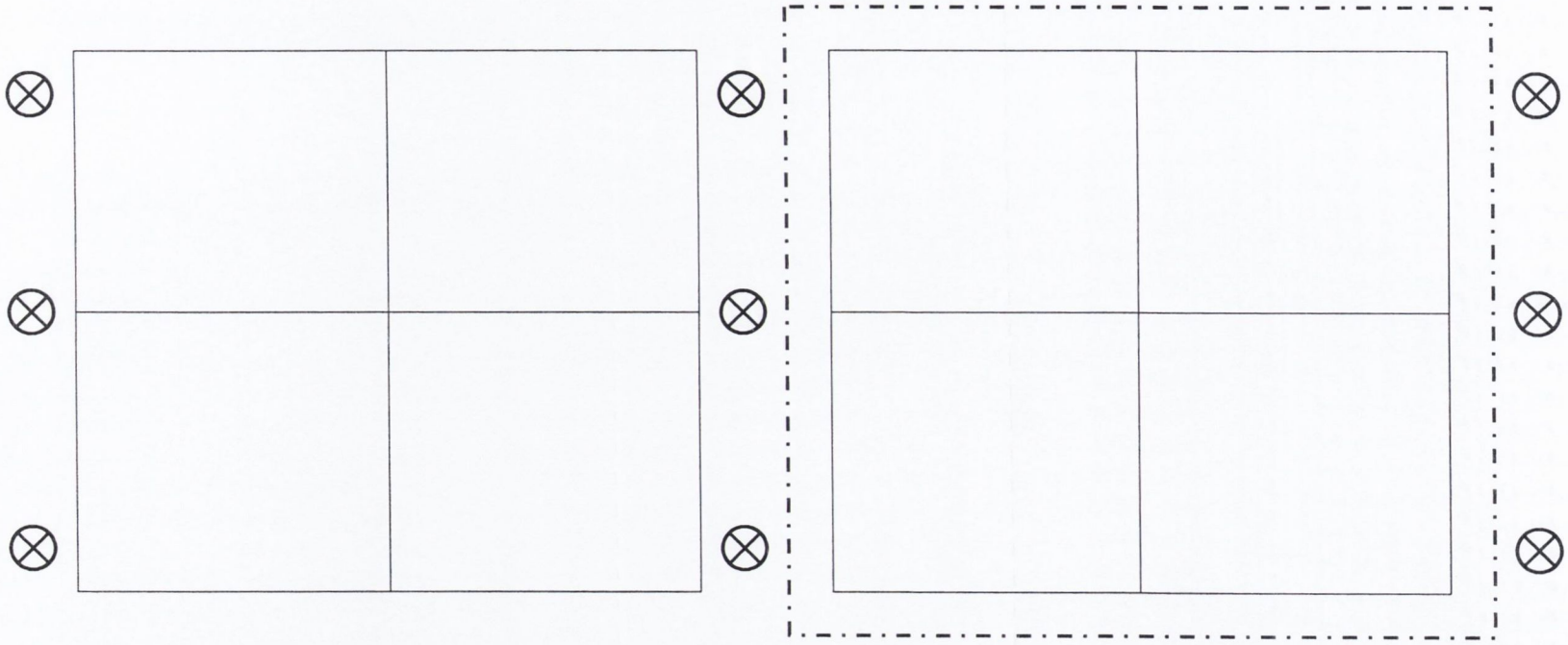
4.4.1 Soils

A small soil pit 30-50 cm deep was dug between each pair of plots. Soils were identified according to the Irish Great Soil Groups (Gardiner & Radford, 1980). Peaty podzols were most common, with podzols and brown earths the next most abundant soil types (Table 4.1). All study sites had been drained and mounded prior to planting the conifer crop. Depths of the organic and/or A-layers, humus type, and presence of gleying were noted. The texture of mineral layers was assessed by hand (Trudgill, 1989). Soil depth was measured at nine points per fenced/unfenced pair of plots: three points between the plots and three on either side (Fig. 4.7). Soil sampling points were moved parallel to the plot as necessary to avoid boulders, stumps, hollows, drains, and similar topographic irregularities. At each point a stiff wire was pushed into the soil five times within a small area and the median depth recorded.

Soil was collected for chemical analyses at the 21 pairs of plots with a steel tube 3.5 cm diameter at the points where soil depth was measured (Fig. 4.7). The top 10 cm of soil, including humus but not litter, was sampled at each point and bulked in the field. In three plot pairs, however, there was a second vegetation community present that was quite different from the dominant vegetation. In a plot pair in Glendalough (#11), *Agrostis* species and other grasses dominated two subplots, in contrast to the more heterogeneous *Calluna* and *Juncus effusus* dominated vegetation in the other six subplots. In this plot pair, a separate bulked sample (of six subsamples) was collected from the *Agrostis* subplots, in addition to the sample from the majority community. In two neighbouring Looscaunagh plot pairs (#3 and #4), a total of three subplots were primarily dominated by *Molinia*, in contrast to the surrounding *Juncus* and *Digitalis* dominated vegetation. An additional bulked sample (of six subsamples) was collected from the *Molinia* subplots in these plots. Thus, a total of 23 soil samples were collected and analysed.

Soil pH of each sample was determined with a glass electrode on field moist soil on return to the lab. Soil samples were then air-dried and passed through a 2 mm sieve to remove stones and large plant remains prior to further chemical analysis. Chemical analysis was conducted on two replicates of each soil sample in the laboratory of the Centre for the Environment, TCD.

Figure 4.7. Exclosed and unexclosed plot pair, divided into subplots, showing soil sampling points: ⊗. The heavy dashed line indicates the fence. Soil sampling points were moved as necessary to avoid topographic irregularities, such as boulders.



A summary of the results by sites is presented in Table 4.2 and detailed results are given in Appendix 1. Soil chemical results are expressed in a concentration per unit of soil volume basis. This is appropriate in plant ecology research because plant roots interact with the soil matrix spatially, rather than with soil mass. In addition, results presented in terms of soil volume may readily be converted to an area basis to facilitate comparison with other studies (Boone *et al.*, 1999).

Exchangeable Ca^{2+}, K^{+}, Mg^{2+} and Mn^{2+} were extracted in a solution of 0.5 *M* ammonium acetate and 1.2 *M* acetic acid solution according to the methods of Nykvist and Rosén (1985). The pH of the extracting agent was 4.2. Although a solution of neutral pH is typically used for comparability, I believed that a more acidic extraction medium would better reflect availability of exchangeable cations in the field. With decreasing pH, availability of Ca^{2+}, K^{+} and Mg^{2+} decreases, while Mn^{2+} availability increases (Waring & Schelsinger, 1985). A subsample of 4 g of soil was added to approximately 90 ml of extracting agent, and was then shaken for 90 min. Samples were then filtered, made up to 125 ml volume, and cation concentrations measured using a Perkin-Elmer 3100 atomic absorption spectrophotometer with an acetylene and air flame.

Total organic carbon and nitrogen were measured using a Leco CNS elemental analyser. Any inorganic carbon was first removed by treatment with sulphurous acid. Organic content was also estimated using the loss-on-ignition method. Because many of the soil samples were highly organic, the furnace temperature was slowly increased to 550°C over three hours; 550°C was then maintained for five hours before cooling the samples in a dessicator and weighing. Because bulk density is difficult to measure directly, loss-on-ignition data were used to estimate soil bulk density, by applying the equation provided by Jeffrey (1970). The relationship between soil organic matter and bulk density has been established and verified empirically several times (Grigal *et al.*, 1999). Soil samples for loss-on-ignition were not replicated.

Total phosphorus was analysed using spectrophotometry after nitric acid digestion. Data are expressed as mg P/L soil to enable comparison between sites of differing soil bulk density. As stated above, this approach also enables data to be expressed on an areal basis. Total phosphorus was chosen over other forms of P because it is easier to measure than many other forms, and also provides an approximation of general soil fertility (Jeffrey, 1987). Following the standard laboratory protocols employed in the TCD Centre for the Environment, 0.5 g soil was added to a small amount of 69% nitric acid and boiled at 170°C for 150 min; after cooling, the digestion was filtered and made up to 50 ml with distilled water. Then 100 µl of

Table 4.2. Soil chemical data means (± se) by plot location. Cation data are for exchangeable cations extracted in an agent of pH 4.2. N is the number of bulked samples.

Location	Site	N	Bulk Density (g/ml)	pH	Total C (%)	Total N (%)	C/N Ratio	Loss-on Ignition (%)	Total P (mg/L)	Ca^{2+} (mg/L)	K^{+} (mg/L)	Mg^{2+} (mg/L)	Mn^{2+} (mg/L)
Killarney	***Muckross Forest***	3	0.292 ± 0.037	4.29 ± 0.05	27.6 ± 4.1	1.060 ± 0.138	26.05 ± 1.84	57.7 ± 7.0	153.8 ± 29.1	263.1 ± 20.0	67.6 ± 2.51	157.8 ± 9.4	56.68 ± 23.34
	Looscaunagh	4	0.187 ± 0.025	4.25 ± 0.05	44.4 ± 2.7	2.091 ± 0.115	21.21 ± 0.26	81.8 ± 6.5	67.3 ± 7.9	163.0 ± 10.8	41.52 ± 3.71	130.0 ± 7.3	8.62 ± 1.79
Wicklow	***Glendalough***	5	0.452 ± 0.048	4.84 ± 0.11	16.6 ± 2.2	0.905 ± 0.082	17.8 ± 0.93	34.8 ± 5.6	201.3 ± 19.6	29.1 ± 5.7	73.76 ± 7.05	51.4 ± 5.5	56.08 ± 9.50
	Glenmalure- *Baravore*	3	0.469 ± 0.108	4.29 ± 0.10	16.0 ± 4.1	0.882 ± 0.192	19.29 ± 0.66	32.7 ± 12.6	179.5 ± 22.8	50.1 ± 15.6	32.86 ± 3.78	69.3 ± 18.3	24.11 ± 6.10
	Glenmalure- *Fraughan Rock Glen*	6	0.331 ± 0.078	4.41 ± 0.11	30.2 ± 4.8	1.311 ± 0.176	21.92 ± 1.00	57.9 ± 12.3	140.1 ± 27.2	71.3 ± 12.5	28.42 ± 1.28	56.0 ± 4.0	26.54 ± 8.20
	Glenmalure- *Benleagh*	2	0.388 ± 0.103	4.47 ± 0.28	20.8 ± 5.0	0.987 ± 0.243	21.08 ± 0.65	43.5 ± 14.7	199.3 ± 48.3	108.8 ± 45.8	42.98 ± 1.96	79.4 ± 8.7	11.15 ± 2.02

filtrate was added to 5 ml distilled water and 1 ml of a mixed reagent containing 17.5 ml 3.6N H_2SO_4, 25 ml antimony stock solution, 25 ml molybdate stock solution, and 0.2 g ascorbic acid per 100 ml. The samples were mixed well and then left for at least 15 min to allow the colour reaction to develop. Total P concentration was then calculated by measuring absorbency at 882 nm on a Shimadzu UV-1601 spectrophotometer. When the results were inspected, however, a large number of the replicate samples from the same plot pair showed dramatically different P concentrations. Centre for the Environment staff (Dr. Norman Allott and Dr. Louise Scally, pers. comm.) recommended microwave digestion as an alternative method. The required instrument, however, was not functional, and subsequent delays in acquiring parts and servicing took more than three months. Because of time constraints, it was reluctantly decided to pursue reanalysis no further. Mean total P results are shown in Table 4.2 and Appendix 1, but not used in subsequent investigations. It is worth noting, however, that mean total P in the Looscaunagh site falls within the 50-75 mg/L range that Jeffrey (1987) suggests may be capable of supporting low-productivity scrub or perhaps birch or Scots pine woodland.

Time since felling was positively correlated with mean available Ca^{2+} (Pearson's $r = 0.60$, $P = 0.003$), Mg^{2+} ($r = 0.75$, $P < 0.0001$), and K^+ ($r = 0.54$, $P = 0.009$) concentrations in the top 10 cm of the soil in the 23 samples. Soil type and parent material were also important factors affecting cation availability. Available Ca^{2+} and Mg^{2+} concentrations were greater in soils with higher C/N ratios and higher organic content, most likely because of increased cation exchange sites (Table 4.2). K^+ concentrations, on the other hand, were generally higher in more mineral soils, including brown earths, brown podzolics and podzols. Available Mn^{2+} was also generally higher in more mineral-rich soils, but concentrations were especially high in two of the wetter plots.

4.4.2 Brash

When felling a conifer crop, there is normally a large amount of branches and abandoned timber left on site. This felling brash can potentially influence vegetation development on a site by retaining and releasing nutrients through slow decay and altering regeneration microsites (Fahey *et al.*, 1991; Rodwell & Patterson, 1994). Brash characteristics were assessed by measuring brash height at 14 points at 1 m intervals between the plot centre and each of the four corners, yielding a total of 56 measurements per 400 m^2 plot. In addition, brash density was estimated at each point on a subjective scale: 0- none, 1- light, 2- medium, and 3- dense. More recently felled stands tended to have more brash; brash was also denser in

the former lodgepole pine plots, in part because pine tends to branch more heavily than spruce (c.f. plot photos in Appendix 3).

4.4.3 Other Site Variables

At each plot, elevation to the nearest 5 m was measured using an altimeter, slope in degrees was measured with a clinometer, and aspect in degrees was recorded using a compass. Site exposure was estimated using the distance-limited topex method of Quine and White (1998). From the centre of each plot, the vertical angles to the horizon were measured with a clinometer at the eight major compass points and then summed. High topex values therefore reflect more sheltered conditions. To allow for the negligible shelter caused by distant landscape features, a maximum distance of 500 m was used. If the object creating the horizon (e.g. a mountain or plantation) was more than 500 m distant at a given point, the angle to the highest point within 500 m was recorded.

CHAPTER 5

VEGETATION STUDY: METHODS

5.1 Vegetation Sampling

Lists of all vascular plant species present in each permanent plot were compiled in the late summer / early autumn of 1999 and 2001. Quantitative sampling was conducted at the same time. In eleven 1 × 1 m quadrats per plot, percent cover (nearest 5%) of each species was recorded (Fig. 4.6); the sum of individual species cover percentages could exceed 100% (Kent & Coker, 1992). Two quadrats were sampled within each subplot so that all combinations of planting mix and weeding treatments were equally represented. The quadrats were randomly located inside the 8 m diameter area within the subplot where tree seedlings were planted (see section 8.1). Two additional quadrats were randomly placed in each plot outside the planted area to investigate the effect of tree growth on vegetation development (Fig. 4.6). The last quadrat was placed under the bird perch to detect possible increases in bird-disseminated species (Fig. 4.6). The same quadrats sampled in 1999 were resampled in 2001. The quadrats were not permanently marked, but the location of the southwest corner of each one was measured, recorded and remeasured on resampling as precisely as possible.

Percentage ground cover was estimated to the nearest 5% in the same 1 × 1 m quadrats as the vegetation. Percent cover was estimated for all field layer species combined, all woody species, bare soil, bryophytes, bare rock, plant litter (mostly conifer leaf litter), brash, and wood. Field layer species included herbaceous species and dwarf shrubs; cover could not exceed 100% in a quadrat, regardless of vegetation layering. Woody species included tree seedlings and large shrubs, including *Rubus*, but not dwarf shrubs like *Calluna*. Brash was defined for cover purposes as woody debris less than 5 cm diameter. Wood was defined as stumps and logs greater than 5 cm diameter.

Vegetation and ground cover in the six soil replacement quadrats (see section 4.3) were recorded in 2001.

5.2 Seed Bank Sampling

Soil seed bank samples were collected with a 3.5 cm diameter soil corer to a depth of 10 cm and included the litter and bryophyte layers. Killarney plots were sampled on 14-15 March, 1999, and Wicklow plots were sampled on 23-24 March, 1999. Sampling was conducted at this time

to take advantage of the natural period of chilling that may be required to break dormancy for some species. Eleven samples were collected at regular intervals around the edges and between each fenced/unfenced pair of plots and bulked in the field. Bulked seed bank samples were used in order to characterise the soil seed bank over the whole plot area, rather than at discrete points. The samples were stored in a dark cold room at 4°C until they were moved into a greenhouse on 15 April, 1999. The samples were worked through a coarse sieve to remove stones, roots, and coarse plant debris and then placed in 355 x 215 x 60 mm seed trays (1 tray per plot pair) over a 50/50 mixture of sand and peat. The seed trays, including two controls containing only sand and peat, were randomly arranged in a heated greenhouse and watered daily.

Germinal seedlings emerging from each seed tray were tallied by species and removed. Csapody (1968) and Chancellor (1966) provided assistance in germinal identification. Where seedlings could not be readily identified, they were repotted and grown on until an identification could be made. Seed trays were monitored until the end of November 1999, when emergence had virtually ceased. The greenhouse germination method may not detect all species present in the soil seed bank, particularly species with additional requirements for breaking dormancy (Roberts, 1981) or those where only a brief interval separates a chilling period and the onset of germination, such as *Hyacinthoides non-scripta* and *Viola riviniana* (Thompson & Grime, 1979). Nevertheless, this method is commonly used for seed bank sampling (Roberts, 1981), because it is much less time consuming and more feasible for small seeded species than the alternative method of directly sorting seeds from soil and testing for viability.

5.3 Data Analysis

5.3.1 Data Handling

Nomenclature follows Stace (1997). In 1999, it was frequently difficult to identify plants in the vegetation samples with certainty. Many were severely grazed and lacked flowers, fruits, or other features which would facilitate identification. The small size and poor condition of young specimens in recently felled plots also made identification problematic. To investigate vegetation change from 1999 to 2001, it was necessary to reconcile species identifications made to generic level in 1999 with identifications to species level in 2001. There were also cases of doubtful identifications made in 1999. The two datasets were reconciled as follows:

1. *Carex* sp.: In 1999, sedges were mostly recorded as *Carex* sp. In 2001, four species were confidently identified: *C. binervis, C. pilulifera, C. echinata,* and *C. panicea.* In a given quadrat where *Carex* sp. was recorded in 1999 and only one species was recorded in 2001, the 1999 record was changed to the same species as in 2001. Where more than one species occurred in a quadrat in 2001, 1999 cover values were assigned

proportionately to each species. Where no *Carex* species was present in a quadrat in 2001, the 1999 record was assigned to the most frequent species in the plot. These amendments probably result in an underestimate of change in *Carex* species over the two years.

2. *Deschampsia caespitosa*: This species was recorded in several plots in 1999, but recorded only once in 2001. It may have been confused in 1999 with *Agrostis canina*, because of its long ligule. Because most 1999 identifications were probably in error, *Deschampsia caespitosa* was not included in data analyses.
3. *Festuca* sp.: In one quadrat, *Festuca* sp. was recorded in 1999. Since the only species of *Festuca* found were *F. ovina* and, more rarely, *F. vivipara*, this record was amended to *Festuca ovina*.
4. *Epilobium* sp.: All 1999 records of *Epilobium* sp. were changed to *Chamerion angustifolium*, the only related species found in a quadrat in 2001.
5. *Juncus tenuis*: This species was not recorded in 2001, but was confused with *J. squarrosus* in 1999. According to the floras of Cos. Wicklow and Kerry (Scully, 1916; Brunker, 1950), *J. tenuis* in these counties has a limited, mainly lowland roadside, distribution. *J. tenuis* records were changed to *J. squarrosus*.
6. *Luzula* sp.: Species of *Luzula* were recorded as *Luzula* sp. or *L. sylvatica* in 1999. *Luzula* sp. records were treated as for *Carex* sp. above. This resulted in changing the 1999 data to *L. multiflora* in all but one quadrat, which was changed to *L. sylvatica*.
7. *Ulex gallii*: In two plot pairs (nos. 19 and 21) where this species was recorded in 1999, only *Ulex europaeus* was recorded in 2001. The 1999 records in these plots were changed to agree with the 2001 data.

Prior to analysis of the vegetation quadrat data, species occurring in less than ten (1%) of the quadrats in both years combined were removed from the data set to reduce the influence of rare species. The omitted taxa (and number of quadrats in which they appeared) included: *Abies procera* (1), *Aira praecox* (2), *Carex panicea* (1), *Cirsium palustre* (4), *Danthonia decumbens* (5), *Eriophorum angustifolium* (4), *Juncus conglomeratus* (9), *Nardus stricta* (2), *Pinus sylvestris* (4), *Polygala serpyllifolia* (2), *Polypodium vulgare* (7), *Salix cinerea* (7), *Salix* sp. (3), *Viola palustris* (1), and *Viola* sp. (4). Records of *Festuca vivipara* (3) were added to *Festuca ovina* (as *F. ovina* agg. (Stace, 1997)). These rare species deletions were not made when investigating species richness patterns among plots (section 6.1).

Except where otherwise noted, vegetation data were analysed using PC-ORD (McCune & Mefford, 1997).

5.3.2 Species Richness

Before patterns in species richness could be investigated, the plot species lists in Appendix 2 were adjusted according to the guidelines in the above section to permit comparisons between years. Also, records of *Salix* × *multinervis* in 2001 were combined with *Salix cinerea* into "*Salix* sp.", as only the genus was recorded in 1999. To correct for exotic species that were removed by weeding treatments (see section 4.3), exotics present in a plot in 1999 were also considered present in 2001. Taxa unidentified in 1999 and taxa appearing only in soil replacement quadrats (see section 4.3) were not included in species richness analyses.

After inspection for normality, paired t-tests were used to detect significant differences in species richness between plots in 1999 and 2001 and between exclosed and unexclosed plot pairs. Paired t-tests are appropriate to measure change over one time interval, as they are frequently used in "before-and-after treatment" experiments (Sokal & Rohlf, 1995). Simple linear regression equations were constructed to investigate the relationships between species richness in 1999 and 2001 and the number of years since felling of the conifer crop. These analyses were performed using SPSS (1999).

5.3.3 Vegetation Types

Each 10 × 10 m subplot was assigned to a vegetation type defined by the results of a flexible-beta clustering. Species cover data in the two quadrats (excluding bird perch and unplanted quadrats) in each subplot were averaged to provide mean subplot species covers. Only 1999 data were used. Flexible-beta clustering is a hierarchical agglomerative clustering technique (Legendre & Legendre, 1998). This method was chosen over other clustering methods, such as TWINSPAN, because the resulting hierarchical structure might provide information about successional relationships. The β variable was set to $\beta = -0.5$ after experimentation, because it dilated the clustering space of the "noisy" vegetation data, and Bray-Curtis distance was the distance coefficient used. The resulting clusters were plotted in reduced space using non-metric multidimensional scaling (NMS) ordination.

Prior to clustering, outlying subplots were identified. The distances of six subplots were more than two standard deviations from the mean Bray-Curtis distance. Three were removed from the data set: subplots 4E2, 5E2 and 5E3. Subplot 4E2 was dominated by a *Molinia* sward and subplots 5E2 and 5E3 were dominated by dense *Luzula sylvatica*. Three others were retained despite being statistical outliers, because their species compositions were more similar to the remainder of the subplots. Subplot 21E1 was also omitted because no vegetation occurred in the quadrats in 1999.

5.3.4 Vegetation – Environment Relationships

The effects of the environment on vegetation composition in 1999 were assessed using canonical correspondence analysis (CCA) (ter Braak, 1986). CCA is a form of direct gradient analysis, in which a correspondence analysis ordination of a data matrix (usually species data) is constrained to be maximally related to a second matrix (usually environmental data). As with the cluster analysis above, species abundance data from the two quadrats in the planted area of each subplot were averaged to obtain mean percent cover data for each subplot.

The environmental variables included in the second matrix of the CCAs were also expressed at the subplot scale and are shown in Table 5.1. I attempted to be parsimonious in selection of environmental variables to reduce correlations among them. Since CCA involves a multiple regression on ordination axes, strong correlations among explanatory variables (i.e. multicollinearity) may distort the model (McCune & Mefford, 1997; Legendre & Legendre, 1998). Prior to analysis, Spearman rank correlation coefficients among the environmental variables were examined. Depth of the soil organic layer and C/N ratio were not included in the CCAs because they were highly correlated with several other variables. Available Mg^{2+} was also omitted because of a very high correlation with Ca^{2+}. Percent cover of brash was used although it was highly correlated with brash height, because I considered that brash cover has implications for vegetation establishment and growth that are not adequately represented by height.

Many environmental variables had to be recoded or otherwise transformed before CCA. An index of the ability of soils to hold water was constructed by ranking soil textures assessed in the field: loamy sands ranked lowest while clay loams ranked second-highest. Organic soils, such as blanket peats or the O layer of peaty podzols were then assigned the highest rank. The water-holding capacity index was then applied separately to the dominant soil layers in the upper 15 cm and the lower 15 cm of the top 30 cm of the soil profile. Upper soil water-holding capacity index (henceforth referred to as "upper soil index") applied to the A or E_A layer in the case of mineral soils, and the O layer in the case of peaty soils (such as peaty podzols). Lower soil water-holding capacity index (henceforth referred to as "lower soil index") applied to the B layer in the case of mineral soils, the top mineral layer for peaty soils, and the lower part of the O layer for blanket peats. Plot aspect was transformed from degrees to a linear scale ranging from 0 (SW aspect) to 2 (NE aspect), according to the formula: $A' = \cos(45\text{-}A) + 1$, where A is the aspect in degrees and A' is the transformed aspect (Beers *et al.*, 1966). Precipitation and

Table 5.1. Environmental variables used in 1999 vegetation cover CCA and their degrees of precision. For further explanations, see text.

Variables	Type	Variables	Type
Soil Variables:		***Site Variables:***	
Gleying	presence/absence	Slope (%)	quantitative
Soil Depth (cm)	quantitative	Aspect	quantitative
K^+ (mg/L)	quantitative	Precipitation (mm)	quantitative
Ca^{2+} (mg/L)	quantitative	Temperature (°C)	quantitative
Mn^{2+} (mg/L)	quantitative	Topex	quantitative
Organic Content (%)	quantitative	SW Exposure	quantitative
pH	quantitative	Brash Height	quantitative
Upper Soil Index	ranks (1-6)	Felling Year	quantitative
Lower Soil Index	ranks (1-7)	Sitka Spruce Site	presence/absence
Peat	presence/absence		
Podzol	presence/absence	***Ground Cover (%):***	
Brown Earth	presence/absence	Brash	quantitative
Brown Podzolic	presence/absence	Litter	quantitative
Peaty Gley	presence/absence	Wood	quantitative
		Bryophytes	quantitative
		Bare Soil	quantitative
		Rock	quantitative

temperature were expressed as annual means (averaged over 1999 and 2000). The southwest topex value was used in addition to the total topex value to determine if exposure in the direction of the prevailing winds had a distinct effect compared with overall site exposure. Soil types were coded as 0/1 dummy variables, with the most common type, peaty podzols, treated as the default (i.e. 0 values for all the other soil types). Unlike the planted tree performance CCAs (section 8.4.3), soil type was used because it has implications for germination and establishment that may not be accounted for by the other soil variables. Former conifer crop was indicated by coding 1 for Sitka spruce stands and 0 for larch and lodgepole pine.

Prior to CCA, chi-square distances among the subplots were computed to identify outliers which may distort the ordination. Seven subplots had chi-square distances more than two standard deviations from the mean; these were not used in the ordination. One subplot, 21E1, was also omitted because no vegetation occurred in the quadrats in 1999. Because inclusion of noisy or irrelevant environmental variables can influence the results of CCA (McCune, 1997), the CCA was performed twice. The first CCA used all the environmental variables in Table 5.1, and the final CCA was conducted after removing variables that had correlations between -0.2 and 0.2 with the first three canonical axes. This procedure did not radically change the

ordination, but had the benefit of removing the least relevant variables which might otherwise interfere with interpretation.

5.3.5 Succession

Blocked multi-response permutation procedures (MRBP) (McCune & Mefford, 1997) were used to test for differences in vegetation between sample years, between quadrats in areas not planted with tree seedlings ("unplanted quadrats") and those in planted areas ("planted quadrats"), and also used to test the effect of bird perches on vegetation development. Multi-response permutation procedures test differences in distance coefficients calculated for species data among *a priori* groups or treatments by permutation. (In this study, the distance measure used was rank-transformed Euclidean distance.) The technique is therefore analogous to multivariate analysis-of-variance, but does not require the assumption of a multivariate normal distribution in the data. The blocked variant, MRBP, is applicable to the situation where sample units are paired across groups. In addition to the P-value obtained by permutation, MRBP also provides a statistic, A, which indicates the magnitude of the differences between groups. A approaches 1 when the distances within groups are smaller than distances between groups, A = 0 when the distances among and within groups are equal, and A < 0 when the distances within groups are larger than distances between groups. In ecological research, values of A from 0-0.1 are common (McCune & Mefford, 1997).

To test for differences between species cover in 1999 and 2001, mean subplot species cover percentages were used in the MRBP, as in the vegetation type clustering and CCA above. To investigate differences between unplanted and planted quadrats, mean cover in the two unplanted quadrats was computed at the plot scale. Mean cover in planted quadrats was calculated by plot, using data from the four quadrats in the two non-weeded subplots (Fig 4.5). Species cover under bird perches was also compared with mean plot data from the four non-weeded, planted quadrats. Unplanted and bird perch MRBPs were conducted separately for 1999 and 2001 data. Percent cover of *Betula pubescens* and *Quercus petraea* (the two species planted) were omitted from the unplanted and bird perch MRBPs. Differences in percent cover of the bird-disseminated species *Hedera helix, Ilex aquifolium, Rubus fruticosus* agg., *Sorbus aucuparia,* and *Vaccinium myrtillus* were also tested using Mann-Whitney U non-parametric tests (Sokal & Rohlf, 1995), using SPSS (1999). The resulting P-values were corrected to control the experimentwise error rate using Hochberg's (1988) procedure. This procedure is more powerful than the traditional Bonferroni correction (Legendre & Legendre, 1998).

The effects of exclosure, weeding, and tree planting mixture on vegetation succession could not be tested with MRBPs because of the factorial design of the treatments. Instead, Bray-Curtis distance coefficients between sample years were calculated for each quadrat. Bray-Curtis distance was more appropriate for the vegetation data than most other distance coefficients (Legendre & Legendre, 1998) and was relatively easy to calculate. The Bray-Curtis distance coefficients were averaged by subplot, square-root transformed to improve normality and then tested by ANOVA. A randomized complete block design, with the 21 plot pairs as blocks, was used to partition the variation due to differences among plots. The effects of weeding, planting mixture and exclosure were analysed using a 3-way factorial ANOVA with interaction terms included.

Investigation and testing of Bray-Curtis distances between quadrats reveal the magnitude, but not the direction of vegetation change over the two year interval. To better understand how vegetation has changed, a non-metric multidimensional scaling (NMS) ordination was conducted on a Bray-Curtis distance matrix computed on mean species cover data for subplots. Subplots 4E2, 5E2, 5E3 and 21E1 were omitted as detailed in section 5.3.3. Both 1999 and 2001 subplot means were used in the same ordination. NMS ordination was used rather than more conventional eigenanalysis techniques such as PCA and DCA because it has been found to be better at recovering complex gradients (Minchin, 1987; Legendre & Legendre, 1998).

CHAPTER 6

VEGETATION STUDY: RESULTS

6.1 Species Richness

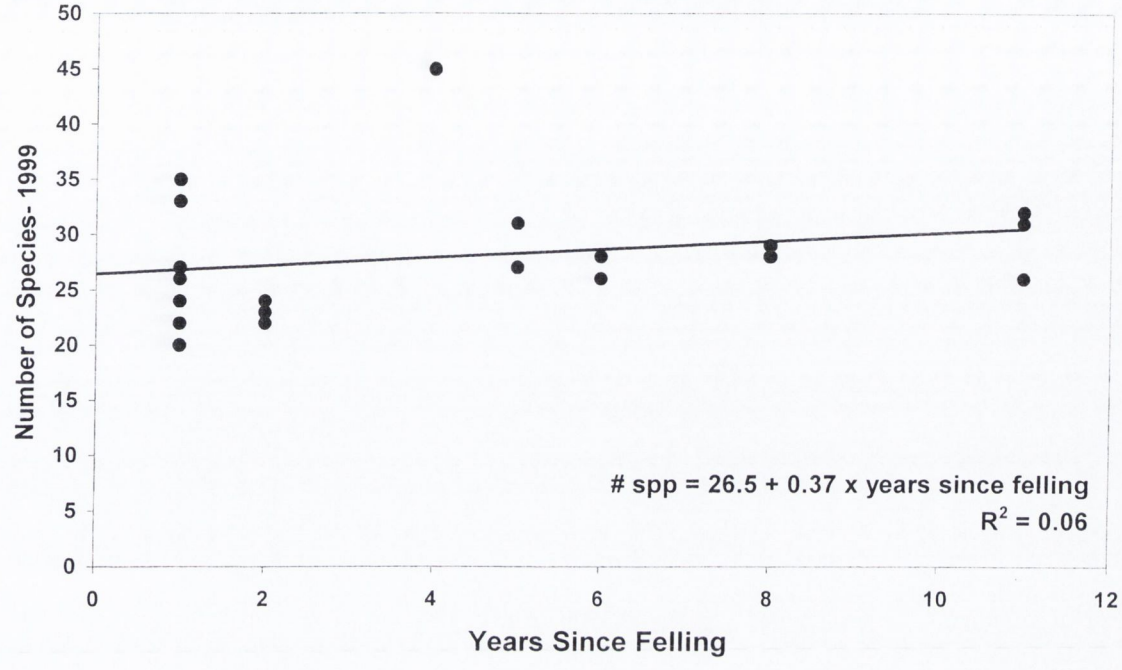
A total of 63 taxa were recorded in 1999 and 72 in 2001 (Appendix 2) in vegetation sampling quadrats and in plots outside quadrats (section 5.1). Because species were only recorded during the summer, a few vernal species which may have been present, particularly in plots near existing semi-natural woodland, would have been overlooked (Kirby *et al.*, 1986). The species lists in Appendix 2 should therefore not be regarded as comprehensive. After adjustments for comparison detailed in section 5.3.1, in 1999 the mean species richness per plot pair was 28.1. This increased significantly ($P = 0.027$, paired t-test) to a mean 30.5 species per plot pair in 2001. Exclosure did not significantly affect species richness: paired t-tests found no significant differences in mean number of species between exclosed and unexclosed pairs of plots in either year. Although species richness in both 1999 and 2001 increased with the number of years since the felling of the conifer crop, these relationships were not significant (Fig. 6.1). However, the intercepts of the linear regression equations were remarkably similar. Clearfelled sites quickly became occupied (whether by immigrating or persisting under the canopy and after felling) by an average of approximately 26 species (Fig. 6.1).

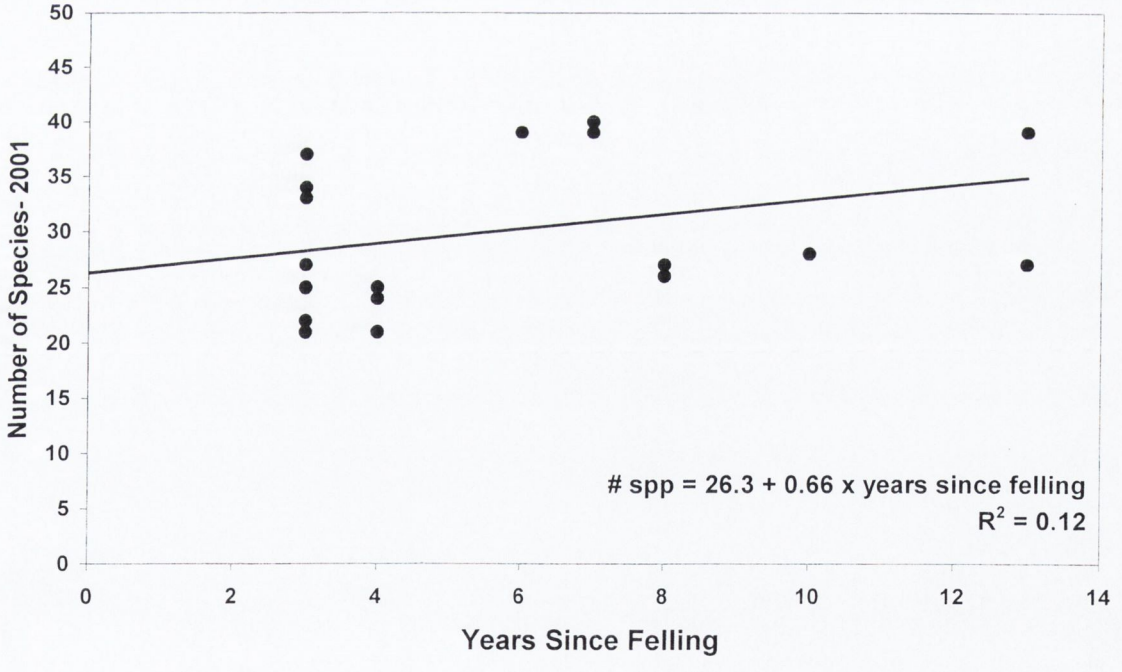
6.2 Vegetation Types

Flexible-beta clustering results were plotted as a dendrogram, and species compositions of the clusters formed at several hierarchical levels were inspected to define a small number of vegetation types. The six-cluster stage was chosen to represent vegetation types. The five-cluster solution combined subplots dominated by *Agrostis capillaris* with another cluster with high covers and frequencies of *Pteridium* and *Agrostis capillaris* (Fig. 6.2). I considered it desirable to retain the *Pteridium – Agrostis* vegetation type to be able to investigate the effects of dense *Pteridium* on tree seedlings and vegetation development. Seven or more vegetation types were not chosen because additional clusters appeared to reflect differences in microsite and colonisation more than ecological differences at a larger scale (Fig. 6.2). The clusters were plotted on an NMS ordination, and showed a reasonable degree of separation. Examples of each of the vegetation types are shown in the photographs of plots in Appendix 3.

In many cases, subplots in the same plot were assigned to different vegetation types. Vegetation heterogeneity at this scale often reflected the dominance of gregarious species such as *Pteridium*

Figure 6.1. Linear regressions of species richness in 1999 (P = 0.294) and 2001 (P = 0.126) on number of years since felling of the conifer crop. Linear regression equations and R^2 values are shown.





aquilinum, Calluna vulgaris, and *Agrostis capillaris* (cf. removal of subplots prior to analysis, section 5.3.3). In some cases, vegetation differences appeared linked to changes in small-scale topography or the presence of flushes. In plots where topography was relatively homogeneous and vegetation cover was not dominated by large patch-forming species, such as in early-successional vegetation, the subplots were more likely to be assigned to the same vegetation type.

6.2.1 Agrostis – Galium *Type*

The *Agrostis – Galium* vegetation type is characterised by high cover and frequency of *Agrostis capillaris* and relatively high frequency and cover of *Galium saxatile* (Table 6.1). Species with the next highest covers include *Holcus mollis*, *Pteridium aquilinum*, and *Calluna vulgaris*. Species with high frequency include *Calluna*, *Holcus mollis*, and *Potentilla erecta*. Overall cover of the field layer is high (Table 6.2). As will be discussed at greater length in section 7.1.2, this vegetation type is referable to the Achilleo – Festucetum tenuifoliae phytosociological association (White & Doyle, 1982). Together with the *Pteridium – Agrostis* type below, this vegetation type is the most different from the others, i.e. *Agrostis* dominated subplots combined with the others in the last clustering step (Fig. 6.2).

The *Agrostis – Galium* type was most common in the Glendalough plots (Table 6.2). It is a late to mid-successional vegetation type, compared with the other five types. Most of the subplots assigned to *Agrostis – Galium* were felled in 1995 or earlier. Former larch stands frequently developed this vegetation type, probably before the crop was felled. Japanese larch casts a light shade, and stands of larch (and also Scots pine) remaining in and around the study sites had well-developed grassland swards below them. *Agrostis – Galium* vegetation develops most frequently on better soils, such as brown earths and brown podzolics.

6.2.2 Pteridium – Agrostis *Type*

Subplots in the *Pteridium – Agrostis* type have high covers of *Pteridium*, and relatively high covers and frequencies of *Agrostis capillaris*, *Galium saxatile*, and *Holcus mollis* (Table 6.1). Mean cover of herbs and small shrubs is very high (Table 6.2). These subplots generally occur in the same plots as *Agrostis – Galium* subplots, and differ from them primarily in the relative abundances of *Agrostis* and *Pteridium*. Accordingly, the *Pteridium – Agrostis* type is also referable to the Achilleo – Festucetum tenuifoliae association (White & Doyle, 1982). This vegetation type, however, is more species-poor than the *Agrostis – Galium* type (Table 6.1).

Figure 6.2. (Overleaf) Last eight clusters formed by flexible-beta clustering ($\beta = -0.5$) of 1999 vegetation data means by subplot. Lengths of the lines connecting clusters do not indicate degree of cluster separation. Clusters used as vegetation types indicated with solid borders; clusters combined to form vegetation types indicated with dashed borders. Cluster names indicate the species with the highest covers and/or frequencies. The number of subplots in each cluster is shown. Following the names of the eponymous species are the number of subplots in which they occur and their mean percent cover.

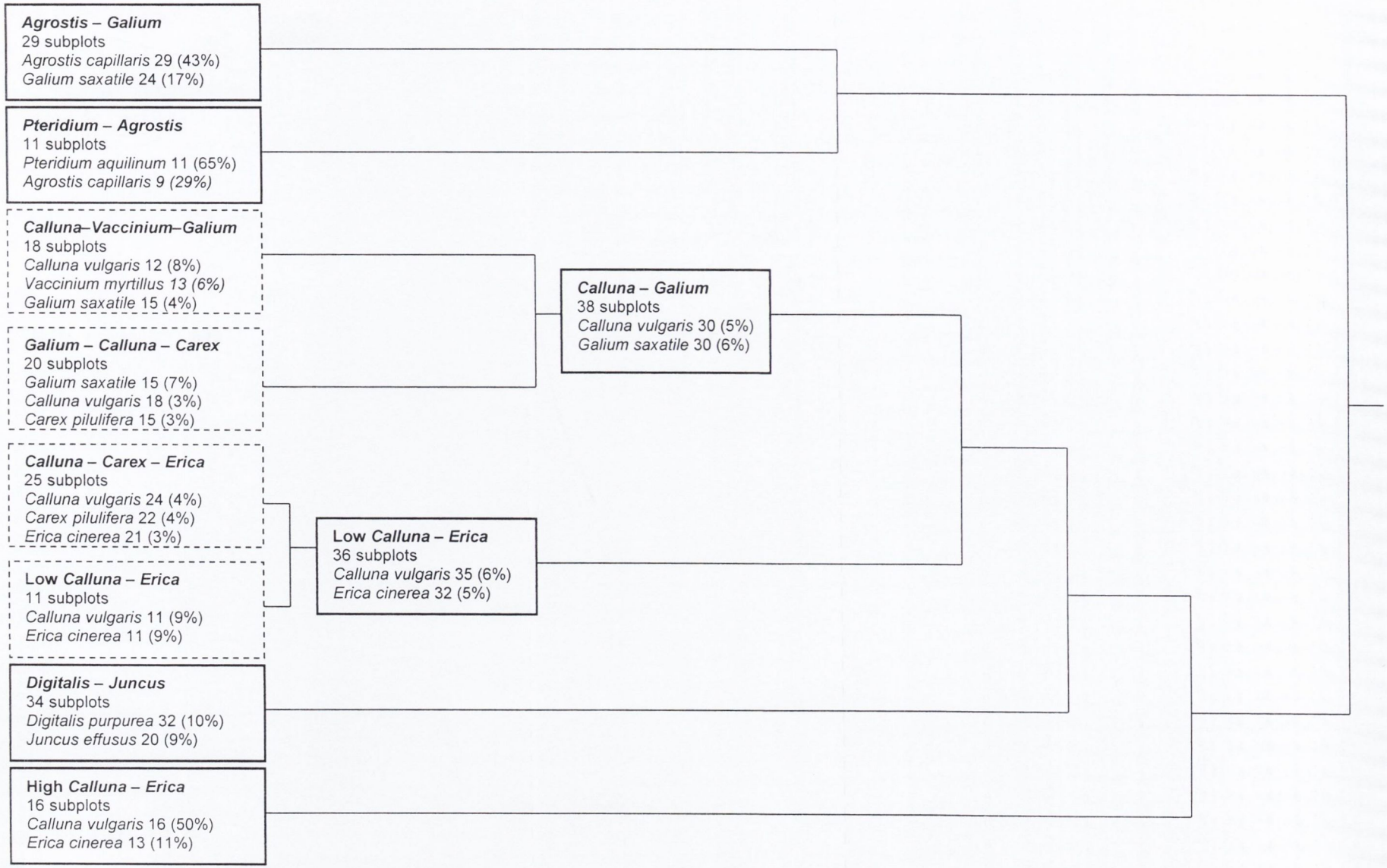

Agrostis – Galium
29 subplots
Agrostis capillaris 29 (43%)
Galium saxatile 24 (17%)
Pteridium – Agrostis
11 subplots
Pteridium aquilinum 11 (65%)
Agrostis capillaris 9 (29%)
Calluna–Vaccinium–Galium
18 subplots
Calluna vulgaris 12 (8%)
Vaccinium myrtillus 13 (6%)
Galium saxatile 15 (4%)
Galium – Calluna – Carex
20 subplots
Galium saxatile 15 (7%)
Calluna vulgaris 18 (3%)
Carex pilulifera 15 (3%)
Calluna – Galium
38 subplots
Calluna vulgaris 30 (5%)
Galium saxatile 30 (6%)
Calluna – Carex – Erica
25 subplots
Calluna vulgaris 24 (4%)
Carex pilulifera 22 (4%)
Erica cinerea 21 (3%)
Low Calluna – Erica
11 subplots
Calluna vulgaris 11 (9%)
Erica cinerea 11 (9%)
Low Calluna – Erica
36 subplots
Calluna vulgaris 35 (6%)
Erica cinerea 32 (5%)
Digitalis – Juncus
34 subplots
Digitalis purpurea 32 (10%)
Juncus effusus 20 (9%)
High Calluna – Erica
16 subplots
Calluna vulgaris 16 (50%)
Erica cinerea 13 (11%)

Table 6.1. Mean percent cover and frequency of vascular plant species in six vegetation types identified in felled conifer plantations. The number of subplots in each vegetation type (n) is also shown. The vegetation types were identified using flexible-beta agglomerative clustering.

	Agrostis - Galium (n = 29)		*Calluna - Galium* (n = 38)		Low *Calluna - Erica* (n = 36)		High *Calluna - Erica* (n = 16)		*Digitalis - Juncus* (n= 34)		*Pteridium - Agrostis* (n = 11)	
Species	**Cover (%)**	**Freq**	**Cover (%)**	**Freq**	**Cover (%)**	**Freq**	**Cover (%)**	**Freq**	**Cover (%)**	**Freq**	**Cover (%)**	**Freq**
Agrostis canina	1.5	5	0.4	1	0.2	3	0.2	1	0.4	2	3.0	1
Agrostis capillaris	43.4	29	1.2	19	2.4	18	4.2	9	3.5	23	29.3	9
Anthoxanthum odoratum	4.2	7	0.1	1	-	-	-	-	-	-	8.4	5
Betula pubescens	0.9	7	0.1	3	0.3	5	0.9	4	0.7	9	1.1	5
Blechnum spicant	1.2	7	0.1	3	-	-	2.7	10	0.7	8	0.5	2
Calluna vulgaris	5.3	17	2.7	30	5.8	35	50.2	16	4.0	28	2.7	5
Carex binervis	0.3	2	0.3	7	1.5	15	1.1	5	0.1	1	0.5	2
Carex echinata	-	-	0.0	1	0.2	2	-	-	1.7	16	-	-
Carex pilulifera	3.0	13	0.8	17	3.9	28	2.3	7	0.7	9	0.5	2
Chamerion angustifolium	-	-	0.0	1	0.3	3	-	-	0.4	4	-	-
Deschampsia flexuosa	1.1	5	0.2	3	0.1	2	2.0	7	-	-	7.3	3
Digitalis purpurea	2.0	9	0.5	8	0.5	7	1.3	5	10.2	32	1.8	2
Dryopteris affinis	-	-	0.1	2	0.1	2	3.4	8	-	-	-	-
Dryopteris dilatata	1.2	8	1.4	25	1.3	14	3.6	15	3.2	27	0.7	2
Erica cinerea	2.5	13	0.2	6	4.8	32	11.4	13	0.5	7	0.7	3
Erica tetralix	-	-	-	-	-	-	0.2	1	0.1	1	-	-
Festuca ovina	1.9	7	0.2	3	0.2	3	-	-	0.1	1	11.6	4
Galium saxatile	16.8	24	2.8	30	1.7	12	0.3	2	0.4	5	14.3	11
Hedera helix	-	-	-	-	-	-	0.6	4	-	-	-	-
Holcus lanatus	0.3	4	-	-	-	-	-	-	-	-	0.2	1
Holcus mollis	9.8	16	0.0	1	-	-	-	-	0.1	1	14.1	7
Hypericum pulchrum	-	-	0.0	1	0.1	1	-	-	-	-	0.2	1
Ilex aquifolium	0.2	2	0.1	2	0.3	2	-	-	0.5	5	-	-
Juncus bulbosus	0.1	1	0.1	3	0.6	7	0.3	2	3.9	20	0.2	1
Juncus effusus	1.1	3	0.5	9	0.4	5	0.2	1	8.5	20	0.9	2
Juncus squarrosus	1.0	3	0.5	4	0.4	5	1.1	3	3.7	15	-	-
Luzula multiflora	0.1	1	0.0	1	0.3	4	-	-	0.1	2	0.2	1

Table 6.1. Cont'd

	Agrostis - Galium (n = 29)		*Calluna - Galium* (n = 38)		*Low Calluna - Erica* (n = 36)		*High Calluna - Erica* (n = 16)		*Digitalis - Juncus* (n = 34)		*Pteridium - Agrostis* (n = 11)	
Species	**Cover (%)**	**Freq**	**Cover (%)**	**Freq**	**Cover (%)**	**Freq**	**Cover (%)**	**Freq**	**Cover (%)**	**Freq**	**Cover (%)**	**Freq**
Luzula sylvatica	0.9	4	0.5	3	0.1	1	0.5	3	-	-	-	-
Molinia caerulea	0.7	2	0.5	2	0.7	9	0.2	1	1.3	8	-	-
Oxalis acetosella	1.0	11	0.4	3	-	-	0.3	1	-	-	1.6	6
Picea sitchensis	1.6	5	1.7	8	0.3	5	0.5	2	0.3	4	-	-
Potentilla erecta	2.0	15	0.4	5	0.6	8	0.2	1	1.0	9	2.3	4
Pteridium aquilinum	8.2	11	0.9	2	-	-	2.7	5	-	-	64.8	11
Quercus petraea	1.2	10	1.1	13	1.5	16	1.4	9	1.6	17	1.6	6
Rhododendron ponticum	0.2	2	0.1	1	-	-	1.4	5	-	-	-	-
Rubus fruticosus agg.	2.9	8	2.0	9	0.8	10	4.5	11	0.4	5	-	-
Rumex acetosella	0.1	1	-	-	-	-	-	-	2.3	10	-	-
Sorbus aucuparia	0.2	2	0.1	2	-	-	2.0	9	0.2	3	0.2	1
Ulex europaeus	-	-	-	-	0.3	3	-	-	-	-	-	-
Ulex gallii	0.2	1	-	-	-	-	-	-	1.2	11	-	-
Vaccinium myrtillus	0.8	9	3.5	22	2.2	17	2.2	10	0.8	9	-	-

Table 6.2. Location, felling year, former crop, soil type, and ground cover for six vegetation types. The number of subplots in each vegetation type is shown for location, felling year, former crop and soil type. Mean (± se) percent ground cover data are presented.

		Agrostis – Galium (n = 29)	*Pteridium - Agrostis* (n = 11)	High *Calluna - Erica* (n = 16)	Low *Calluna - Erica* (n = 36)	*Calluna - Galium* (n = 38)	*Digitalis - Juncus* (n = 34)
Location	**Muckross Forest**	4	1	14	0	3	0
	Looscaunagh	1	1	0	0	0	21
	Glendalough	21	9	0	0	2	0
	Glenmalure- *Baravore*	1	0	0	13	5	4
	Glenmalure- *Fraughan Rock Glen*	2	0	1	21	15	9
	Glenmalure- *Benleagh*	0	0	1	2	13	0
Felling Year	**1988 - 1991**	11	10	14	0	3	0
	1993 - 1995	15	1	1	0	9	21
	1997 - 1998	3	0	1	36	26	13
Former Crop	**Sitka spruce**	12 [1]	2	15	21	35	31
	Lodgepole pine	2 [1]	0	1	15	3	3
	Japanese larch	8	9	0	0	0	0
Soil Type	**Peat**	1	1	0	0	0	21
	Podzol	1	1	14	6	10	0
	Brown Earth	8	9	0	5	5	4
	Brown Podzolic	10	0	0	0	0	0
	Peaty Gley	4	0	0	0	2	0
	Peaty Podzol	5	0	2	25	21	9

[1] An additional eight plot quarters in the *Agrostis - Galium* vegetation type were formerly under a mix of Sitka spruce and lodgepole pine.

Table 6.2 cont'd.

		Agrostis – Galium (n = 29)	*Pteridium - Agrostis* (n = 11)	High *Calluna - Erica* (n = 16)	Low *Calluna - Erica* (n = 36)	*Calluna - Galium* (n = 38)	*Digitalis - Juncus* (n = 34)
Ground Cover (%)	**Herbs**	78.1 (± 3.4)	92.0 (± 1.5)	69.1 (± 3.6)	14.1 (± 1.5)	21.9 (± 3.1)	31.0 (± 3.5)
	Woody Plants	4.6 (± 1.4)	2.7 (± 0.6)	8.0 (± 1.4)	3.2 (± 0.4)	5.3 (± 1.3)	3.2 (± 0.4)
	Soil	2.1 (± 0.6)	0.9 (± 0.5)	3.8 (± 0.8)	13.3 (± 2.7)	5.5 (± 1.3)	5.4 (± 1.2)
	Litter	5.8 (± 1.5)	14.3 (± 3.1)	5.0 (± 1.2)	28.9 (± 2.6)	18.4 (± 3.6)	14.1 (± 3.6)
	Brash	8.8 (± 2.0)	2.3 (± 0.8)	9.5 (± 1.2)	35.0 (± 2.8)	34.9 (± 3.2)	27.7 (± 3.4)
	Wood	4.0 (± 0.9)	3.2 (± 1.4)	6.6 (± 1.2)	11.0 (± 1.3)	14.2 (± 1.5)	11.3 (± 1.4)
	Rock	2.7 (± 0.8)	2.5 (± 1.8)	3.9 (± 1.7)	3.3 (± 0.9)	4.7 (± 1.3)	3.4 (± 1.1)
	Moss	13.5 (± 1.6)	15.2 (± 3.0)	18.4 (± 2.7)	17.6 (± 2.3)	27.6 (± 2.9)	39.5 (± 3.8)

Pteridium – Agrostis is a late-successional vegetation type, developing most frequently under former larch stands on brown earth soils in Glendalough (Table 6.2).

6.2.3 Calluna – Galium *Type*

The *Calluna – Galium* vegetation type has very low covers of all species (Tables 6.1, 6.2). In addition to the eponymous species, *Dryopteris dilatata*, *Vaccinium myrtillus*, *Agrostis capillaris* and *Carex pilulifera* are fairly frequent. *Vaccinium* is also the species with the highest mean cover in this vegetation type. The cluster representing this type was formed at the six-cluster stage by fusing a mainly *Calluna – Vaccinium* cluster with a *Galium – Calluna – Carex* cluster (Fig. 6.2). The botanical differences between these two clusters were small and did not appear to reflect environmental differences between the subplots.

The *Calluna – Galium* type was most frequent in Glenmalure plots formerly occupied by Sitka spruce (Table 6.2). This type is early successional, although it includes poorly developed vegetation in stands felled for a longer period of time. Cover of brash and coarse woody debris (i.e. logs and stumps) is high. Because of its early successional status, the *Calluna – Galium* type cannot be referred to any phytosociological association. Likely successional pathways will be discussed in section 7.1.2.

6.2.4 *Low* Calluna – Erica *Type*

This vegetation type also has low mean covers of all species, the highest being *Calluna* and *Erica cinerea* (Tables 6.1, 6.2). *Carex pilulifera* is also frequent. The Low *Calluna – Erica* type differs from the *Calluna – Galium* type primarily in the greater abundance of *Erica* and the lower abundance of *Galium* (Table 6.1). *Carex binervis*, *Carex pilulifera*, and *Molinia caerulea* are also more frequent in this type, and *Dryopteris dilatata* is less frequent.

The Low *Calluna – Erica* vegetation type occurred only in recently felled stands in Glenmalure (Table 6.2). The lower elevation Baravore plots and the former lodgepole pine stands in Fraughan Rock Glen were likely to develop this type of vegetation. Low *Calluna – Erica* vegetation often occurred on peaty podzols. This vegetation type was also characterised by relatively high cover of bare soil, needle litter and brash. As another early successional vegetation type, parallels with phytosociological associations could not be drawn.

6.2.5 Digitalis – Juncus *Type*

The *Digitalis – Juncus* type has mean species covers slightly higher than the previous two types (Table 6.2). *Digitalis purpurea* and *Juncus effusus* have the highest mean covers, while

Digitalis, *Calluna*, and *Dryopteris dilatata* are the most frequent (Table 6.1). This vegetation type also has higher frequencies of the other *Juncus* species, *Rumex acetosella*, and *Ulex gallii* than in the other types. The *Digitalis – Juncus* type seems most similar to the *Calluna – Galium* and Low *Calluna – Erica* types; they are combined at the three-cluster stage (Fig. 6.2). The wet character of the vegetation is also shown by high cover of bryophytes (Table 6.2). *Polytrichum commune* and *Sphagnum* species were commonly encountered in *Digitalis – Juncus* subplots.

This vegetation type is characteristic of the blanket peats in the Looscaunagh site (Table 6.2). *Digitalis*- and *Juncus*-dominated vegetation also occurred in Glenmalure on brown earths and peaty podzols. The *Digitalis – Juncus* type is early to mid-successional, and so felling debris and stumps have had less time for decay. This vegetation type may perhaps be successional to the Narthecio – Ericetum tetralicis wet heath association (Moore, 1968; White & Doyle, 1982), as will be discussed in section 7.1.2.

6.2.6 High Calluna – Erica *Type*

The vegetation of these subplots is dominated by *Calluna*, with *Erica cinerea* the next most abundant species. This vegetation type differs from the Low *Calluna-Erica* type in the greater cover and height of *Calluna* and *Erica cinerea*. Other commonly occurring species include *Dryopteris dilatata*, *Rubus fruticosus* agg., *Vaccinium myrtillus* and *Blechnum spicant* (Table 6.1). This is also the only vegetation type in which *Hedera helix* appears. Overall vegetation cover is high (Table 6.2). This type is referable to the Calluno – Ericetum cinereae association (White & Doyle, 1982).

The High *Calluna-Erica* type is late successional, and was found most often in the Muckross Forest plots (Table 6.2). This site was a former Sitka spruce stand on podzol soils. Woody plants like tree seedlings, *Rubus* and *Hedera* have had more time to establish in the High *Calluna – Erica* type than in other vegetation types.

6.3 Seed Bank

Seedlings of *Calluna vulgaris*, *Erica cinerea* and *Carex* species emerged in the seed bank soil trays of every plot (Table 6.3). Tree species were not well represented in the soil or litter seed banks; *Betula pubescens* was the only species to emerge, and it appeared in only two seed trays. No ferns emerged in the seed trays. Abundances of some species in the seed trays of the most recently (1998) felled stands corresponded well with their abundances in the field in 1999. For example, *Erica cinerea* was more abundant in 1998 felled stands where Low *Calluna-Erica* was the dominant vegetation type than in stands with other vegetation types (Table 6.3). Similarly,

Table 6.3. Soil seed bank composition: density (numbers / 100 cm^2 of soil sampled) of seedlings emerging from seed trays for each plot and two control trays (C1 and C2). Also presented are the year of felling and the dominant vegetation types for each plot. Vegetation type abbreviations are: Agr-Gal- *Agrostis-Galium* , Cal-Gal- *Calluna-Galium* , Dig-Jun- *Digitalis-Juncus* , HCal-Eri- High *Calluna-Erica* , LCal-Eri- Low *Calluna-Erica* , Pte-Agr- *Pteridium-Agrostis* . Species obviously seeding in from the greenhouse environment (e.g. *Antirrhinum*) are not presented.

Plot	Fell Year	Dominant Vegetation Type	*Agrostis capillaris*	*Agrostis canina*	*Anthoxanthum odoratum*	*Betula pubescens*	*Calluna vulgaris*	*Carex species*	*Cirsium palustre*	*Digitalis purpurea*	*Erica cinerea*	*Erica tetralix*	*Galium saxatile*	*Holcus lanatus*	*Holcus mollis*	*Hypericum pulchrum*	*Juncus bulbosus*	*Juncus effusus*	*Juncus squarrosus*	*Luzula* species	*Molinia caerulea*	*Potentilla erecta*	*Rubus fruticosus*	*Rumex acetosella*	*Senecio* species	*Stellaria media*	*Ulex gallii*	*Vaccinium myrtillus*	*Viola* species
5	1988	Agr-Gal[1]	111	2	2	-	178	38	-	327	5	1	2	1	2	-	97	224	-	4	-	-	-	-	-	-	-	-	-
6	1988	HCal-Eri	50	-	-	1	381	8	-	372	58	1	-	-	-	-	15	8	-	-	-	-	-	-	-	-	-	-	-
7	1988	HCal-Eri	21	3	-	-	144	8	-	153	43	-	1	-	3	-	28	38	1	-	-	-	1	-	-	-	-	-	-
8	1991	Agr-Gal	139	6	-	-	3	7	-	37	4	-	10	8	-	-	7	52	-	1	1	-	-	-	-	-	-	-	1
9	1991	Pte-Agr	73	12	-	-	3	4	-	-	10	-	22	-	-	4	4	5	-	4	1	-	-	-	-	-	-	1	-
10	1993	Agr-Gal	146	3	-	-	29	6	1	-	11	-	7	-	5	1	6	10	1	-	2	1	-	-	-	-	-	-	-
22	1993	Cal-Gal	1	-	-	-	51	1	-	20	3	1	10	-	-	-	3	11	11	-	-	-	-	-	-	1	-	-	-
1	1994	Dig-Jun	3	-	-	-	57	1	-	141	12	8	-	-	-	-	56	33	-	-	-	1	1	14	-	1	3	-	-
3	1994	Dig-Jun	10	-	-	-	128	2	-	44	18	-	-	-	-	-	15	8	-	-	1	-	1	-	-	2	4	-	-
4	1994	Dig-Jun	-	-	-	-	102	7	-	10	2	22	-	2	-	-	57	32	-	-	-	-	-	-	-	-	4	-	-
11	1995	Agr-Gal	87	5	-	-	94	2	-	47	13	15	5	-	-	-	39	12	-	2	-	-	-	-	-	-	-	-	-
15	1997	LCal-Eri	1	-	-	-	127	10	-	-	157	-	-	-	-	-	-	2	8	-	-	1	-	-	-	-	-	-	-
16	1997	LCal-Eri	-	-	-	-	114	11	-	-	101	-	-	-	-	-	2	-	1	-	1	2	3	-	-	-	-	1	-
20	1997	LCal-Eri	1	-	-	-	180	21	-	-	148	-	-	-	-	-	16	4	8	1	-	6	2	-	-	-	-	3	-

[1] In plot pair 5, three plot quarters were assigned to the *Agrostis-Galium* type, three plot quarters were assigned to the *Calluna-Galium* type, and two plot quarters were dominated by *Luzula sylvatica* and were omitted from the vegetation clustering (see section 5.3.3).

Table 6.3 cont'd.

Plot	Fell Year	Dominant Vegetation Type	*Agrostis capillaris*	*Agrostis canina*	*Anthoxanthum odoratum*	*Betula pubescens*	*Calluna vulgaris*	*Carex species*	*Cirsium palustre*	*Digitalis purpurea*	*Erica cinerea*	*Erica tetralix*	*Galium saxatile*	*Holcus lanatus*	*Holcus mollis*	*Hypericum pulchrum*	*Juncus bulbosus*	*Juncus effusus*	*Juncus squarrosus*	*Luzula* species	*Molinia caerula*	*Potentilla erecta*	*Rubus fruticosus*	*Rumex acetosella*	*Senecio* species	*Stellaria media*	*Ulex gallii*	*Vaccinium myrtillus*	*Viola* species
12	1998	Cal-Gal	2	-	-	-	32	6	-	-	19	-	5	-	-	1	6	10	-	-	-	4	-	-	-	-	-	5	-
13	1998	Cal-Gal	1	1	-	-	49	3	-	-	1	-	-	-	-	-	7	47	4	-	-	-	-	-	1	-	-	-	-
14	1998	Cal-Gal	4	-	-	-	19	5	-	-	6	-	13	-	-	-	-	1	-	-	-	1	-	-	-	-	-	1	-
17	1998	Dig-Jun	-	-	-	-	20	3	-	15	8	-	-	-	-	-	90	30	3	1	-	6	-	-	-	-	-	2	-
18	1998	Dig-Jun	5	-	-	-	36	1	-	36	2	-	1	-	-	-	1	54	1	-	-	-	6	-	-	-	-	1	-
19	1998	LCal-Eri	-	1	-	25	98	2	-	-	37	6	-	-	-	-	5	2	-	-	1	-	-	-	1	-	-	-	-
21	1998	LCal-Eri	10	11	-	-	33	1	-	-	94	-	-	-	-	2	10	5	-	1	-	1	2	-	-	-	-	-	1
C1			-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	3	-	-	-
C2			-	-	-	-	2	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Digitalis purpurea, *Juncus effusus*, and *Juncus bulbosus* were generally more abundant in sites dominated by the *Digitalis-Juncus* type. *Galium saxatile*, *Luzula* species, *Juncus squarrosus*, and *Vaccinium myrtillus* were frequent in quadrats, but were not well represented in the seed banks of many of the most recently felled plots (Table 6.3). In earlier felled plots, the seed bank populations of many species reflected their abundances in the field, for example *Agrostis capillaris*, *Calluna vulgaris*, and *Erica cinerea*. Likewise, *Digitalis purpurea*, *Juncus effusus*, and *Juncus bulbosus* were well represented in the seed bank where they were abundant in the field (i.e. plot pairs 1, 3, 4), but these species also sustained seed bank populations in plots where 1999 field abundances were relatively low (e.g. plot pairs 6-8) (Table 6.3).

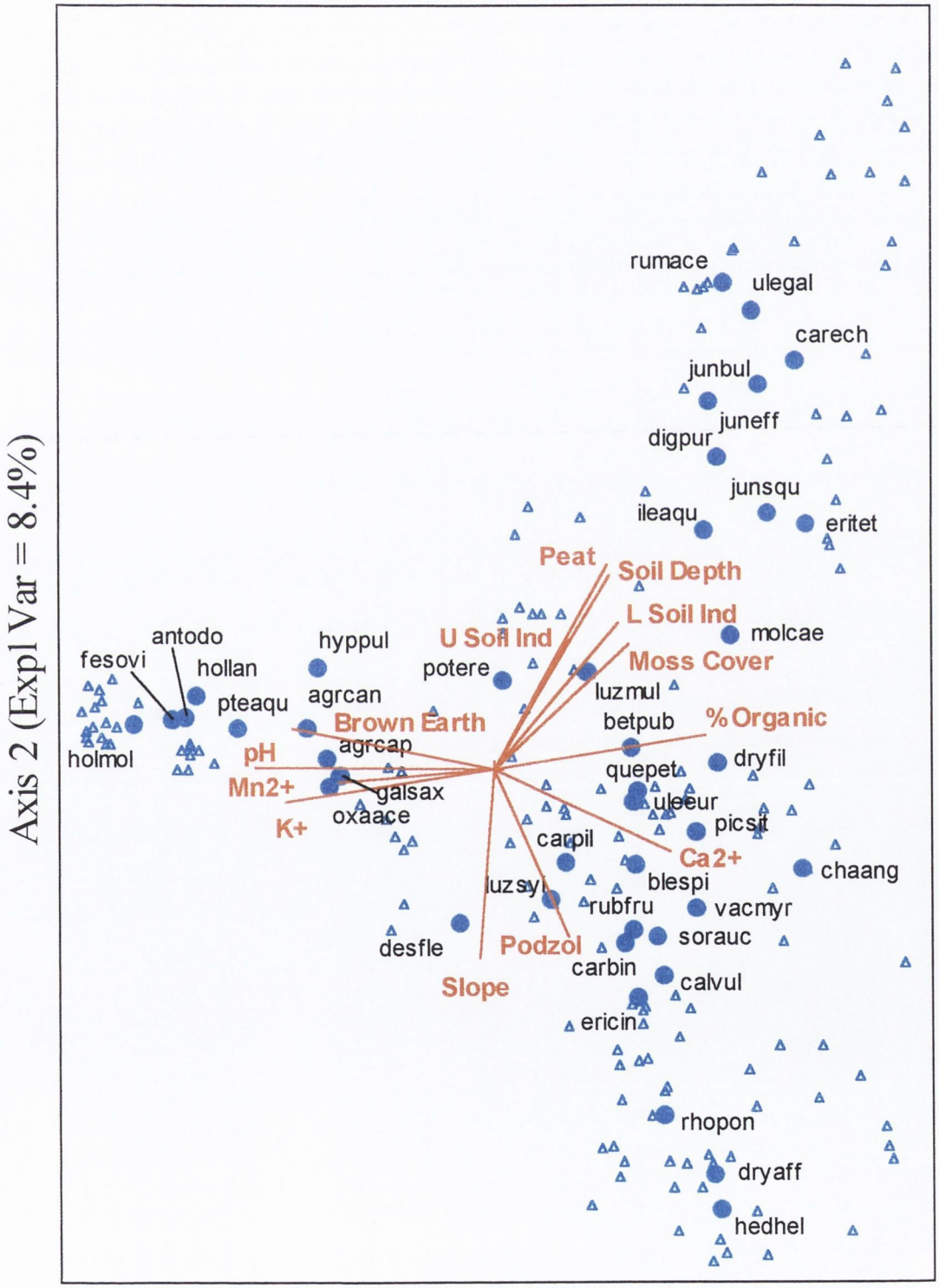
6.4 Vegetation – Environment Relationships

The preliminary canonical correspondence analysis (CCA) resulted in three variables with correlations between 0.2 and –0.2 with the first three ordination axes: aspect, percent cover of litter, and percent cover of rock. These were removed prior to the final analysis. The first three canonical axes of the final CCA explained only 24.7% of the total variance (4.56) in the species data. The weakness of the relationship between vegetation and the observed environmental variables is not surprising, considering that the majority of the sites were in a very early stage of successional development. It is likely that vegetation patterns were strongly influenced by biotic factors such as dispersal and seed bank composition and abiotic factors at a spatial scale smaller than was investigated.

The first eigenvalue of Axis 1 accounted for 11.8% of the variance in the species data (λ_1 = 0.540) and the correlation between axis 1 site scores and scores derived solely from the species data (known as the species-environment correlation) was 0.926. Axis 2 explained 8.4% of the variance (λ_2 = 0.384) and had a species-environment correlation of 0.923; Axis 3 explained 4.4% of the variance (λ_3 = 0.202) and had a species-environment correlation of 0.882. All eigenvalues and species-environment correlations were significant, according to Monte Carlo permutation tests with 99 randomised runs (P = 0.01).

Axis 1 mirrors the final step of the vegetation type clustering, separating grasses and *Pteridium* from mainly heathland species (Fig. 6.3a). *Oxalis acetosella*, which often occurred under *Pteridium*, was also ordinated with the acid grassland species. The grassland species on the left of the biplot are favoured by more mineral-rich (K^+ and Mn^{2+}) brown earth soils with lower organic content ("% Organic" in Fig. 6.3), and slightly higher pH. The heath species to the right are associated primarily with podzolized soils with higher organic content and greater availability of Ca^{2+} (and Mg^{2+}).

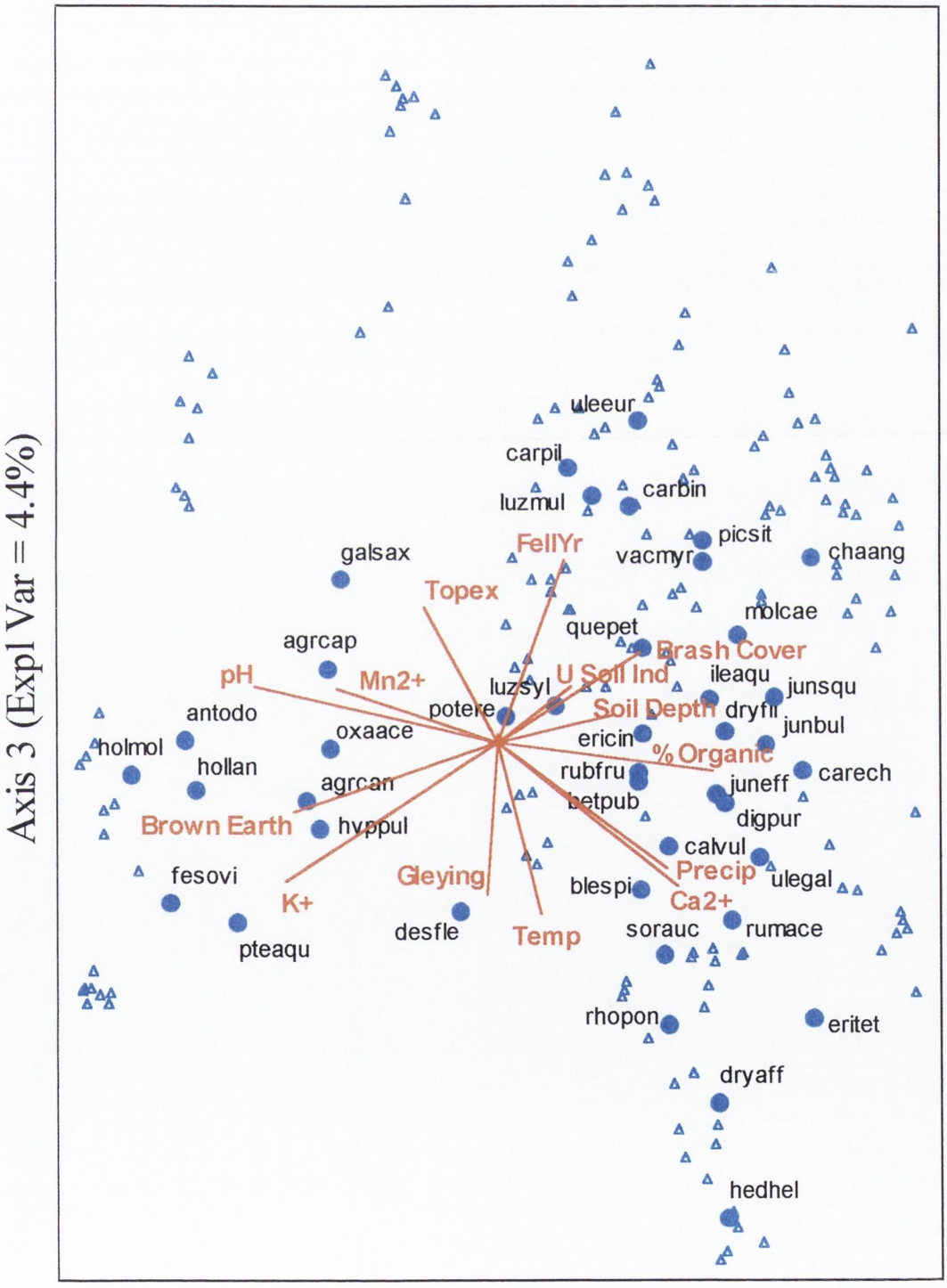
Figure 6.3a. Correlation biplot of axes 1 and 2 of the CCA of 1999 vegetation data subplot means with twenty-eight site and soil variables (abbreviations explained in text). Ordination of the subplots are indicated with triangles. Environmental variables with $R^2 < 0.2$ for any axis are not shown. Correlations between environmental variables and species are reflected by the angles between their vectors. The percent variance explained ($\lambda_i / \lambda_{sum}$) by each axis is shown. See Appendix 4 for definitions of species codes.



Axis 2 (Expl Var = 8.4%)

Axis 1 (Expl Var = 11.8%)

Figure 6.3b. Correlation biplot of axes 1 and 3 of the CCA of 1999 vegetation data subplot means with twenty-eight site and soil variables (abbreviations explained in text). Ordination of the subplots are indicated with triangles. Environmental variables with $R^2 < 0.2$ for any axis are not shown. Correlations between environmental variables and species are reflected by the angles between their vectors. The percent variance explained (λ_i / λ_{sum}) by each axis is shown. See Appendix 4 for definitions of species codes.



Axis 2 separated the non-grassland species on the right of the ordination into (i) species typical of the *Digitalis – Juncus* vegetation type towards the upper right and (ii) heathland species more characteristic of drier conditions in the lower right (Fig. 6.3a). The species in the upper right are associated with deeper soils and several soil variables that indicate moister conditions, such as the upper and lower soil layer indices of water-holding capacity ("U Soil Ind" and "L Soil Ind" respectively in Fig. 6.3), peat soils, shallower slope, and higher bryophyte cover ("Moss Cover"). Species in the lower right of the ordination are associated with podzol soils on steeper slopes. *Rhododendron, Dryopteris affinis*, and *Hedera helix* in the extreme lower right are much more abundant in the Muckross Forest plots which are also characterised by relatively shallow, stony soils.

Axis 3 contrasts species characteristic of more recent clearfells, such as *Carex pilulifera, Carex binervis, Luzula multiflora* and *Galium saxatile*, with slower developing species, including *Pteridium,* and certain woody plants like *Hedera helix* (Fig. 6.3b). The year in which the stand was felled ("FellYr" in Fig. 6.3b) is well correlated with Axis 3 ($r = 0.65$). Species more associated with sheltered sites (i.e. higher topex) occur towards the top of Axis 3. Presence of gleying and mean annual precipitation ("Precip") and temperature ("Temp") were negatively correlated with Axis 3. Several species that were much more abundant in the Killarney plots, which are warmer, wetter, and were felled earlier on average than Wicklow plots, are grouped at the bottom right of Axes 1 and 3 (Fig. 6.3b). These were *Hedera helix*, *Dryopteris affinis, Erica tetralix, Rhododendron* and, to a lesser extent, *Sorbus aucuparia* and *Rumex acetosella.*

6.5 Vegetation Succession

A blocked multiple-response permutation procedure (MRBP) (McCune & Mefford, 1997) found that vegetation composition changed significantly between the two years ($P < 0.0001$). The value of the A-statistic ($A = 0.007$), however, indicated that the vegetation differences between 1999 and 2001 were small relative to the between-sample heterogeneity within each year. Most species in the most recently felled stands increased in cover over the interval (Table 6.4). Notable exceptions were *Digitalis purpurea, Chamerion angustifolium,* and (mostly planted) *Quercus petraea.* Many species that increased in the recently-felled stands decreased over 1999-2001 in plots felled in 1995 or earlier (Table 6.4). These include *Agrostis capillaris, Galium saxatile, Holcus mollis, Juncus effusus, Juncus squarrosus,* and *Rubus fruticosus*. Note, however, that for many species, the interval of mean change in cover plus or minus standard error includes zero (Table 6.4).

Table 6.4. Change in mean percent cover (± se) between 1999 and 2001 of vascular plant species in exclosed and unexclosed plots by conifer felling years. The number of subplots (n) in which the species occurs in 1999 or 2001, whichever is greater, is shown.

	1988-1991		1993-1995		1997-1998	
	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n
Agrostis canina	2.2 ± 1.6	22	1.7 ± 1.8	21	6.1 ± 1.0	38
Agrostis capillaris	-20.2 ± 2.8	31	-9.9 ± 2.2	39	2.7 ± 1.0	57
Anthoxanthum odoratum	1.3 ± 2.9	18	1.7 ± 2.9	9	1.8 ± 2.0	7
Betula pubescens	1.7 ± 0.8	18	1.1 ± 0.4	23	3.2 ± 0.6	23
Blechnum spicant	-0.5 ± 0.6	20	0.3 ± 0.6	28	2.0 ± 0.3	11
Calluna vulgaris	-4.5 ± 2.4	30	2.9 ± 1.3	43	4.5 ± 0.8	72
Carex binervis	0.0 ± 0.8	12	0.4 ± 1.0	6	1.5 ± 0.3	29
Carex echinata	2.5	1	5.2 ± 1.8	27	1.1 ± 0.5	7
Carex pilulifera	-0.2 ± 0.7	14	-2.3 ± 2.4	15	0.9 ± 0.5	66
Chamerion angustifolium	-	0	2.5	1	-0.2 ± 0.8	13
Deschampsia flexuosa	-2.0 ± 1.9	24	2.5 ± 2.9	3	2.3 ± 1.0	10
Digitalis purpurea	-3.0 ± 0.7	14	-4.9 ± 1.0	33	-0.8 ± 1.1	40
Dryopteris affinis	-2.8 ± 1.5	9	2.9 ± 0.4	12	0.8 ± 0.8	6
Dryopteris dilatata	-0.1 ± 0.4	23	-0.7 ± 0.5	34	2.3 ± 0.3	56
Erica cinerea	-0.6 ± 1.8	20	0.3 ± 0.5	22	4.6 ± 0.8	58
Erica tetralix	2.5	1	3.5 ± 0.9	13	2.5 ± 0.0	2
Festuca ovina	-2.5 ± 3.5	13	1.4 ± 1.2	7	-0.9 ± 0.8	8
Galium saxatile	-7.2 ± 1.7	29	-2.1 ± 2.0	27	4.4 ± 1.4	44
Hedera helix	1.7 ± 0.5	6	-	0	-	0
Holcus lanatus	1.7 ± 1.9	6	2.5 ± 0.6	6	-2.5	1
Holcus mollis	-15.5 ± 4.6	15	-4.1 ± 3.5	14	1.3 ± 1.3	2
Hypericum pulchrum	1.3 ± 1.3	2	-	0	0.6 ± 1.2	4
Ilex aquifolium	-0.8 ± 1.7	3	-1.1 ± 0.9	7	2.5 ± 1.8	6
Juncus bulbosus	-2.5 ± 0.0	2	-4.4 ± 1.3	21	-0.1 ± 1.2	18
Juncus effusus	-3.2 ± 1.5	7	-4.9 ± 2.5	31	3.2 ± 1.0	22
Juncus squarrosus	-1.7 ± 0.8	3	-6.6 ± 1.7	23	2.3 ± 1.2	21
Luzula multiflora	2.9 ± 1.6	6	2.5 ± 0.7	11	1.5 ± 0.5	15
Luzula sylvatica	0.2 ± 3.7	14	-2.5	1	0.0	1
Molinia caerulea	2.5	1	1.8 ± 0.7	28	2.8 ± 0.7	20
Oxalis acetosella	0.6 ± 0.5	21	-1.0 ± 1.0	5	2.5 ± 0.0	2
Picea sitchensis	-12.5 ± 10.0	2	0.0 ± 4.0	13	0.0 ± 0.6	16
Potentilla erecta	0.2 ± 0.6	15	0.9 ± 0.5	29	1.8 ± 0.3	37
Pteridium aquilinum	7.6 ± 3.7	23	-8.8 ± 10.4	4	12.5 ± 12.5	3
Quercus petraea	-0.2 ± 0.5	22	-1.3 ± 0.4	30	-0.3 ± 0.5	37
Rhododendron ponticum	-1.8 ± 0.9	10	-	0	-	0
Rubus fruticosus agg.	-1.1 ± 0.9	14	-0.2 ± 2.5	12	3.3 ± 1.2	23
Rumex acetosella	-	0	-2.7 ± 2.0	12	1.0 ± 1.5	5
Sorbus aucuparia	0.5 ± 0.5	16	-0.4 ± 1.0	6	0.0 ± 1.4	4
Ulex europaeus	-	0	-	0	3.0 ± 2.0	5
Ulex gallii	-	0	2.3 ± 1.2	15	-	0
Vaccinium myrtillus	-0.4 ± 0.6	14	1.1 ± 1.2	16	2.0 ± 0.4	64

6.5.1 Experimental Treatments

The composition of vegetation in unplanted areas of the plots was not significantly different from the composition in planted, non-weeded plot areas in 1999 ($P = 0.19$) or 2001 ($P = 0.69$), according to MRBPs. Bird perches also did not have a significant effect on overall vegetation composition in 1999 ($P = 0.22$) or 2001 ($P = 0.63$). Mann-Whitney U tests also failed to find significant differences in cover of bird-disseminated species between bird perch quadrats and quadrats in non-weeded subplots.

The weeding treatment significantly affected rate of vegetation change between 1999 and 2001, measured as the mean Bray-Curtis distance between years for the two quadrats in each suplot, but, surprisingly, exclosure did not (Table 6.5). Planting mixture was nearly a significant factor at the $\alpha = 0.05$ level. The weeding treatment increased vegetation change relative to unweeded plots by directly removing vegetation, including exotics, and providing bare areas for new colonisation. Quadrats in mixed subplots changed more than quadrats in pure oak subplots over the two years, most likely because birch experienced both higher growth and higher mortality rates than oak (see section 9.1).

Table 6.5. Three-way ANOVA with randomised complete blocks of the effects of weeding, planting mix, and exclosure treatments on vegetation succession from 1999-2001. Rate of vegetation succession was measured as the mean Bray-Curtis distance between sample years for the two quadrats in each subplot; values were square root transformed prior to testing.

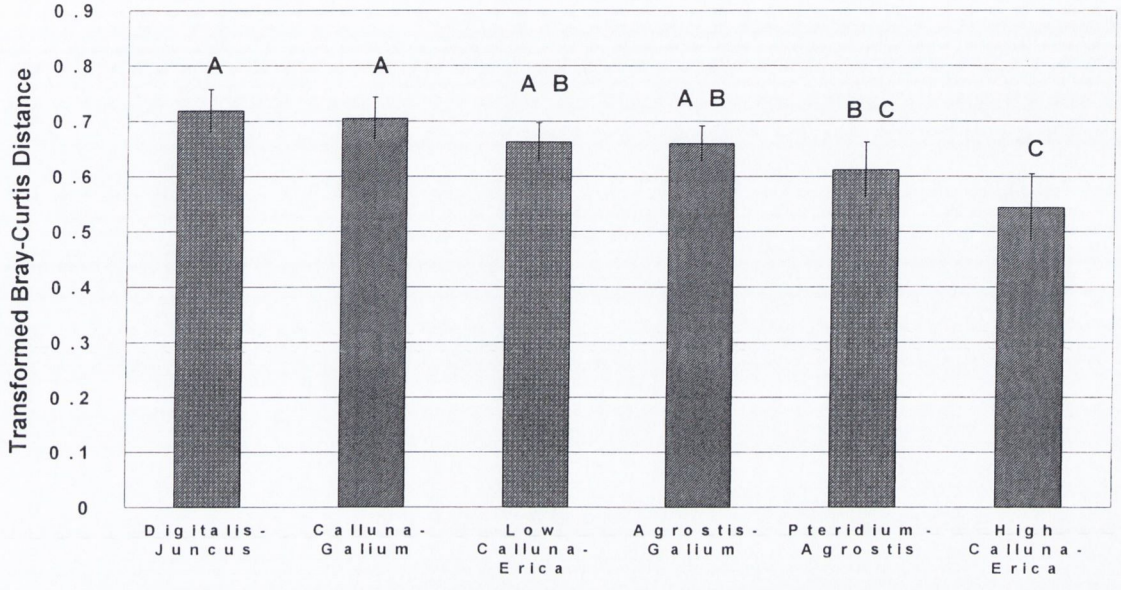
Source	df	Mean Square	F	P
Intercept	1	74.713	6533	≤ 0.0001
Exclosure (E)	1	0.018	1.60	0.207
Weeding (W)	1	0.062	5.43	0.021
Plant Mix (PM)	1	0.044	3.83	0.052
$E \times W$	1	0.002	0.15	0.700
$E \times PM$	1	0.005	0.40	0.529
$W \times PM$	1	0.003	0.28	0.595
$E \times W \times PM$	1	0.006	0.49	0.483
Plot (blocks)	20	0.035		
Error	140	0.011		

When the experimental treatments were tested with vegetation type and second-order interactions in the model, significant differences in the rate of vegetation change were found among vegetation type and weeding (Table 6.6). Exclosure and planting mix were not significant factors in this model. The later successional vegetation types generally had lower mean Bray-Curtis distances between sample years than the other vegetation types, as demonstrated by Tukey's HSD post-hoc tests (Sokal & Rohlf, 1995) (Fig. 6.4). The *Pteridium-Agrostis* and High *Calluna-Erica* vegetation types changed significantly less than the *Digitalis – Juncus* and *Calluna – Galium* types.

Table 6.6. Four-way ANOVA with second-order interactions of the effects of weeding, planting mix, exclosure treatments and vegetation type on vegetation succession from 1999-2001. Rate of vegetation succession was measured as the mean Bray-Curtis distance between sample years for the two quadrats in each subplot; values were square root transformed prior to testing.

Source	df	Mean Square	F	P
Intercept	1	51.86	4569	≤ 0.0001
Vegetation Type (VT)	5	0.0760	6.70	≤ 0.0001
Exclosure (E)	1	0.0032	0.28	0.598
Weeding (W)	1	0.0835	7.36	0.008
Plant Mix (PM)	1	0.0140	1.24	0.268
VT × E	5	0.0018	0.16	0.977
VT × W	5	0.0055	0.48	0.790
VT × PM	5	0.0029	0.26	0.935
E × W	1	0.0040	0.36	0.553
E × PM	1	0.0130	1.15	0.286
W × PM	1	0.0029	0.25	0.617
Error	137	0.0113		

Figure 6.4. Mean distances between years (1999 and 2001) in the six vegetation types. The distance metric used was square-root transformed Bray-Curtis distance coefficient. The distance coefficients of the vegetation types labelled with the same letter are not significantly different ($\alpha = 0.05$) according to Tukey's HSD post-hoc tests. Error bars show 95% confidence intervals.

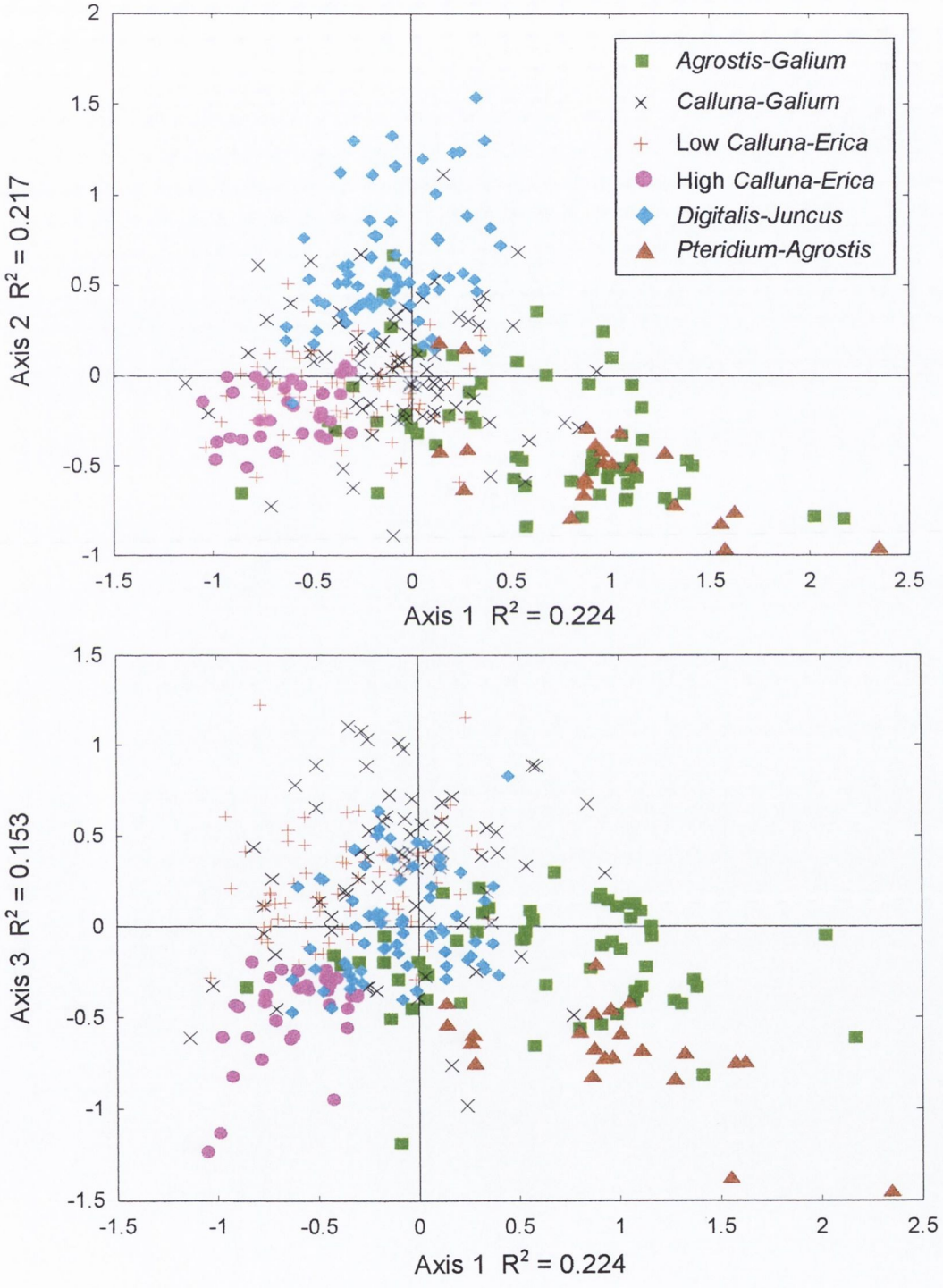


6.5.2 Ordination

To better understand the direction of vegetation change, an NMS ordination was conducted on mean species cover data for subplots in both 1999 and 2001. Twenty runs with real data and thirty runs with randomised data indicated that a three-dimensional ordination was most suitable. Monte Carlo tests showed that stress (Legendre & Legendre, 1998) in the preliminary runs was significantly ($P = 0.0323$) lower than would be expected by chance. The best three-dimensional solution was then used as the starting position for the final ordination.

As with the CCA above, the first ordination axis reflects the transition from heath communities on the left to grass-dominated communities (Fig. 6.5). Species positively correlated with Axis 1 include *Agrostis capillaris* ($r = 0.67$), *Galium saxatile* ($r = 0.59$), *Pteridium aquilinum* ($r = 0.56$) and *Holcus mollis* ($r = 0.55$). *Calluna vulgaris* and *Erica cinerea* were negatively correlated with Axis 1 ($r = -0.51$ and -0.42, respectively). Axis 2 describes a continuum from grass-dominated communities at the bottom to communities characteristic of wetter, peaty sites dominated by *Digitalis* and rushes. Species positively correlated with the second axis include *Digitalis purpurea* ($r = 0.59$), *Dryopteris dilatata* ($r = 0.44$), *Juncus effusus* ($r = 0.40$), *Carex*

Figure 6.5. NMS ordination of 1999 and 2001 species cover data in subplots. R^2 values between ordination distances and distances in the original data matrix are shown for each axis. Ordination stress is 19.31. Note that the vegetation types were defined using 1999 data only.



echinata (r = 0.38) and *Juncus bulbosus* (r = 0.36). *Galium saxatile* (r = -0.46), *Pteridium aquilinum* (r = -0.41), *Agrostis capillaris* (r = -0.38) and *Holcus mollis* (r = -0.36) are negatively correlated with Axis 2. The third ordination axis is the weakest, but best distinguishes open, recently established vegetation from more developed communities. *Carex pilulifera* (r = 0.23), *Carex binervis* (r = 0.14) and *Chamerion angustifolium* (r = 0.12) have the highest positive correlations with Axis 3. The strongest negative correlations with Axis 3 are demonstrated by *Pteridium aquilinum* (r = -0.53), *Calluna vulgaris* (r = -0.39), *Oxalis acetosella*, *Holcus mollis* and *Betula pubescens* (r = -0.28 for the last three species).

Because plotting all 328 subplots (21 plot pairs × 8 subplots × 2 years less 8 omitted subplots (section 5.3.5)) on one ordination diagram is inevitably cluttered, the centroids for each combination of vegetation type and year are shown in Fig. 6.6. Successional trajectories for the subplot vegetation data in each vegetation type are shown in Figs. 6.7-6.12 (note that these figures are different plots of the same NMS ordination).

The *Agrostis-Galium* and *Pteridium-Agrostis* vegetation types shifted to the left on Axis 1 between 1999 and 2001, an apparent decrease in the grassland character of these communities (Figs. 6.6-6.8). This is primarily due to large decreases in percent cover of *Agrostis capillaris* and *Holcus mollis*. The weeding treatments may account for a large part of the decrease. They appeared (visually) to have a more persistent effect in the *Agrostis – Galium* vegetation type than in many others. Observer error in vegetation recording between 1999 and 2001 may also account for part of the decrease. Because of the difficulty in accurately estimating percent cover (Stampfli, 1991), point quadrat sampling is generally recommended in grasslands. In the *Agrostis-Galium* type, cover of *Pteridium aquilinum* increased by an average of 14%, and so in this case *Agrostis* may be declining in response to expanding *Pteridium*. Both of these vegetation types moved very little along Axis 3 (Figs. 6.6-6.8).

The centroids of the early successional *Calluna-Galium* and Low *Calluna-Erica* vegetation types moved little along the heath-grassland axis (Axis 1) or the wet-dry axis (Axis 2) (Fig. 6.6). Inspection of the succession vectors shows that individual subplots in fact moved considerable distances in ordination space (Figs. 6.9, 6.10). Changes along Axes 1 and 2 in the *Calluna-Galium* type appear particularly chaotic, suggesting that this group is not homogeneous. Most appear to move towards the "heath" end of Axis 1 and the "rushy" end of Axis 2. Both vegetation types experienced a general increase in vegetation cover, reflected in movement downward on Axis 3 towards more late successional species (Figs. 6.6, 6.9, 6.10). Again, the Low *Calluna-Erica* type appears to be a more homogeneous grouping, whereas *Calluna-Galium* plots may eventually develop into a wider range of vegetation communities.

Figure 6.6. NMS ordination of 1999 and 2001 species cover data in subplots. Shown are centroids of the data points in each vegetation type and in each year. Hollow symbols are 1999 data and filled symbols are 2001 data. Also plotted are species scores calculated by weighted averaging. See Appendix 3 for species code definitions. Note that not all species are labeled.

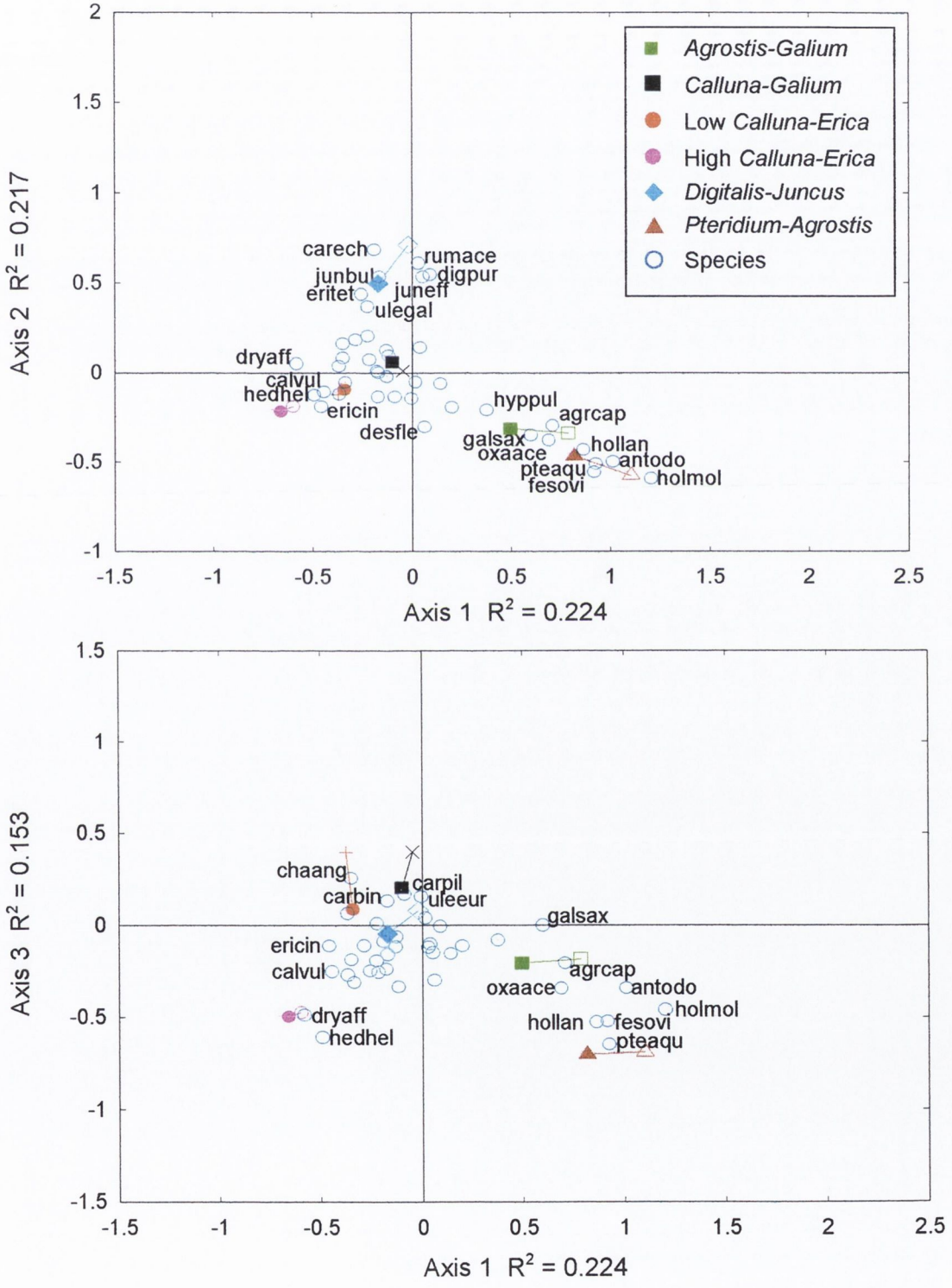


Figure 6.7. NMS ordination of 1999 and 2001 species cover data: subplots in the *Agrostis-Galium* vegetation type only are plotted. Samples from the two years from the same subplot are connected by a line.

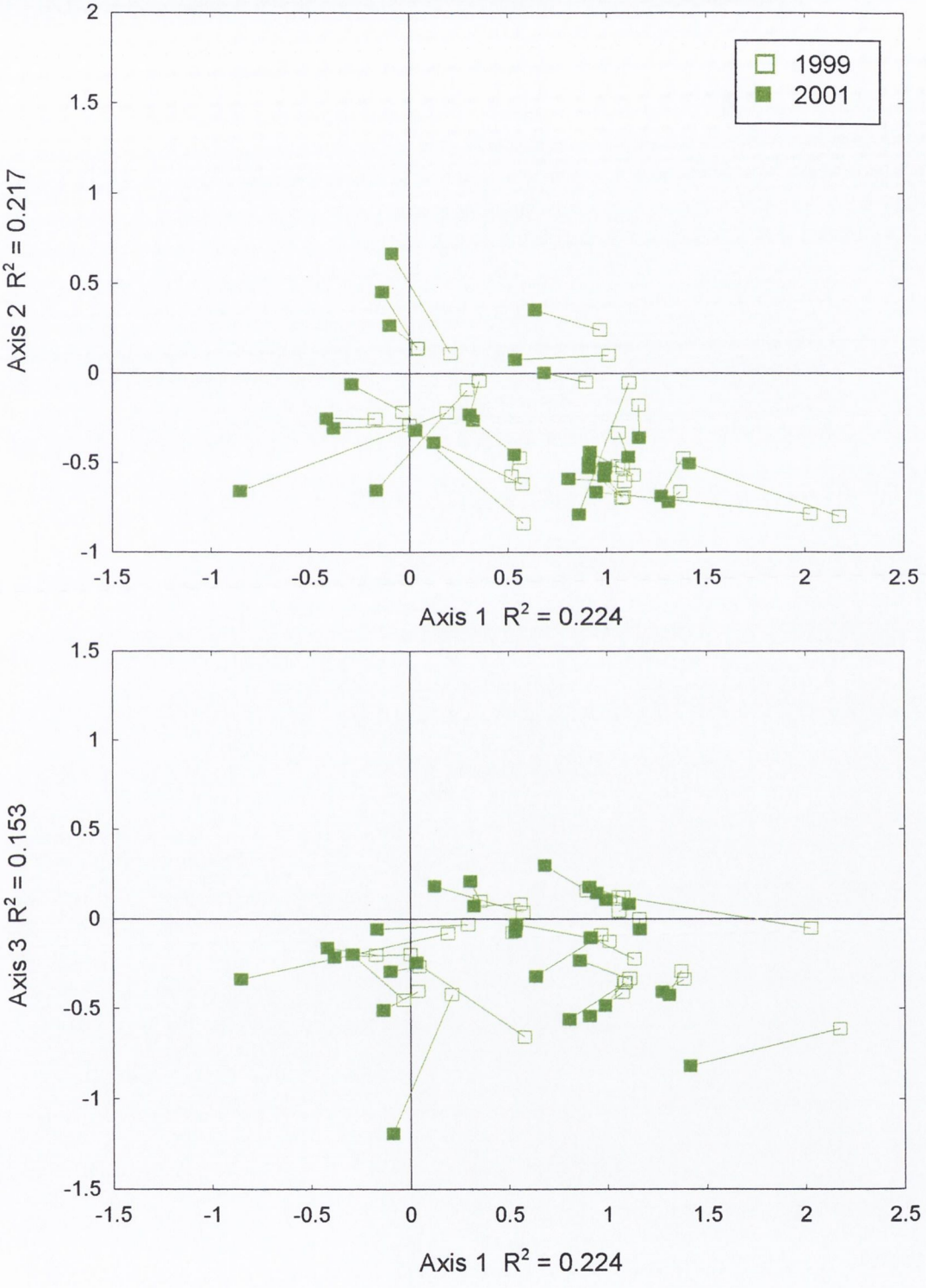


Figure 6.8. NMS ordination of 1999 and 2001 species cover data: subplots in the *Pteridium-Agrostis* vegetation type only are plotted. Samples from the two years from the same subplot are connected by a line.

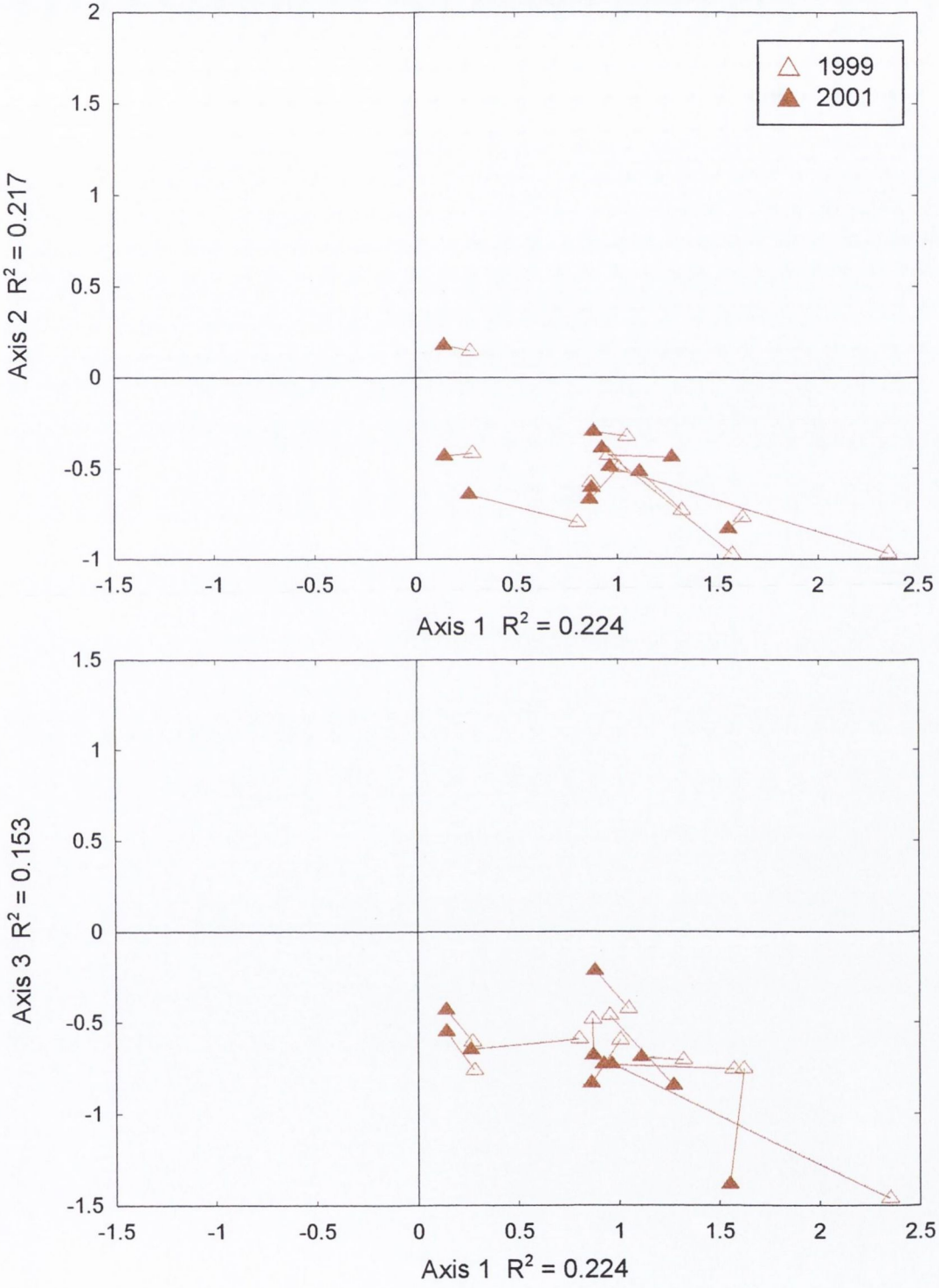


Figure 6.9. NMS ordination of 1999 and 2001 species cover data: subplots in the *Calluna-Galium* vegetation type only are plotted. Samples from the two years from the same subplot are connected by a line.

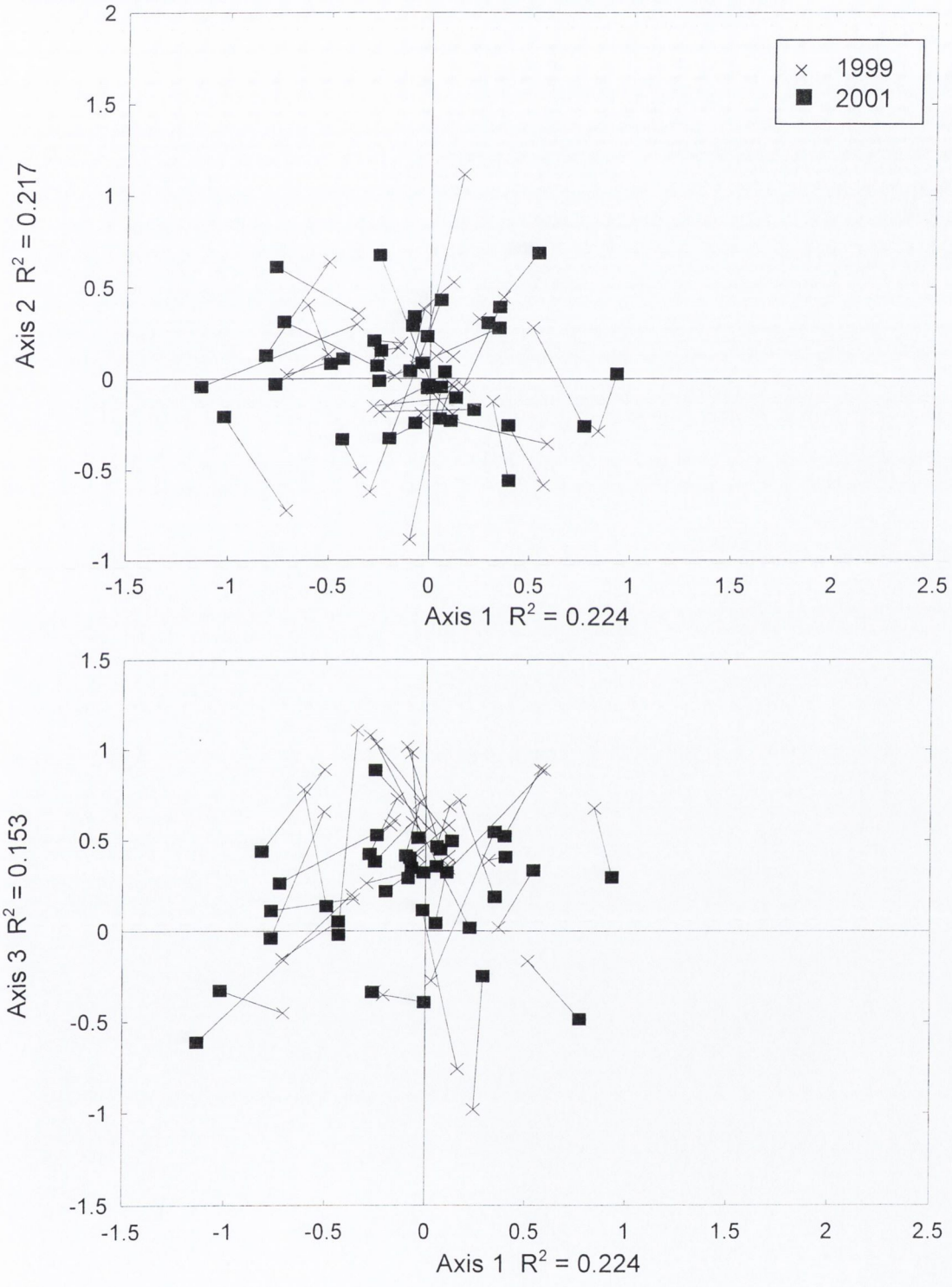


Figure 6.10. NMS ordination of 1999 and 2001 species cover data: subplots in the Low *Calluna-Erica* vegetation type only are plotted. Samples from the two years from the same subplot are connected by a line.

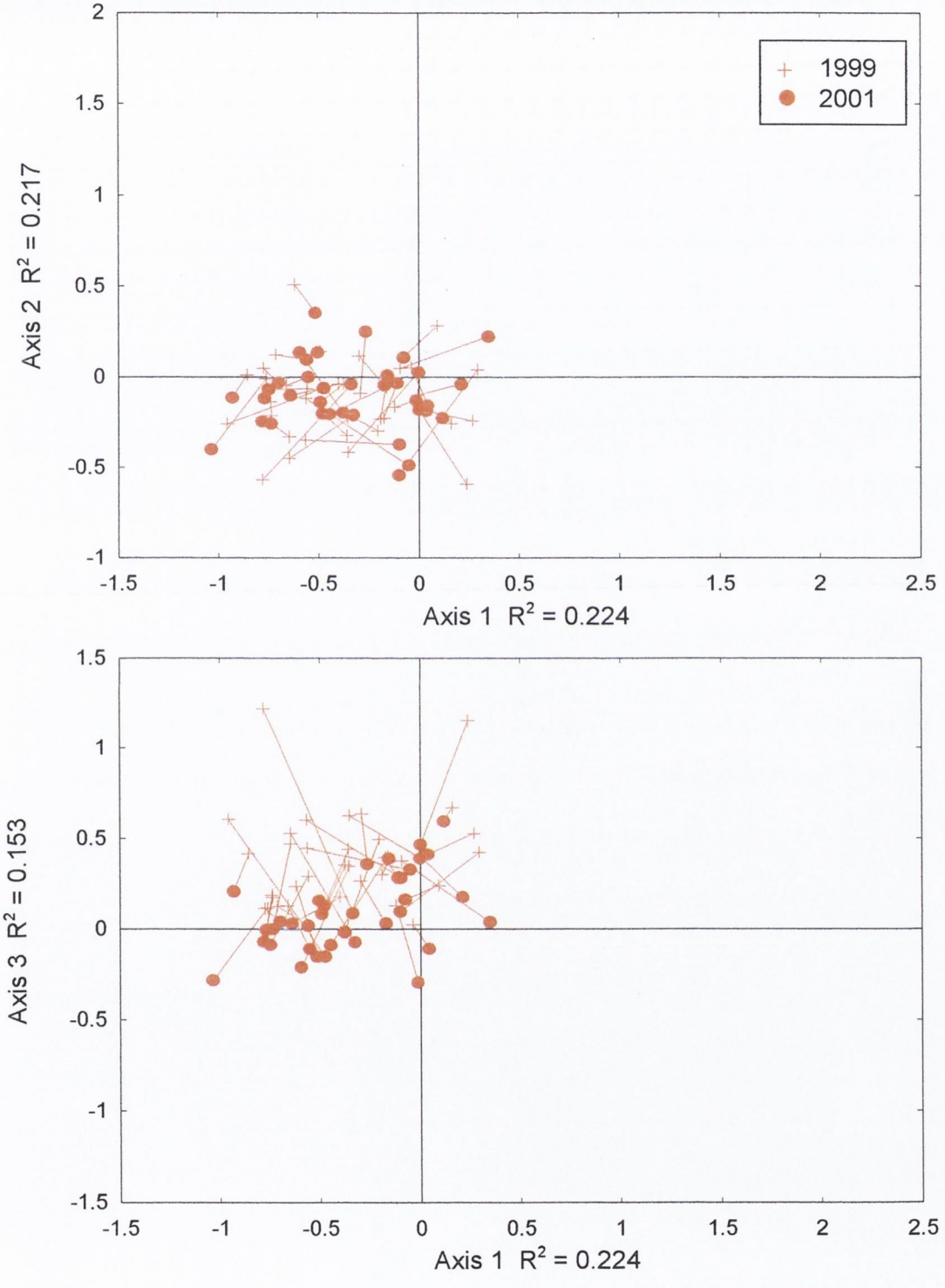


Figure 6.11. NMS ordination of 1999 and 2001 species cover data: subplots in the High *Calluna-Erica* vegetation type only are plotted. Samples from the two years from the same subplot are connected by a line.

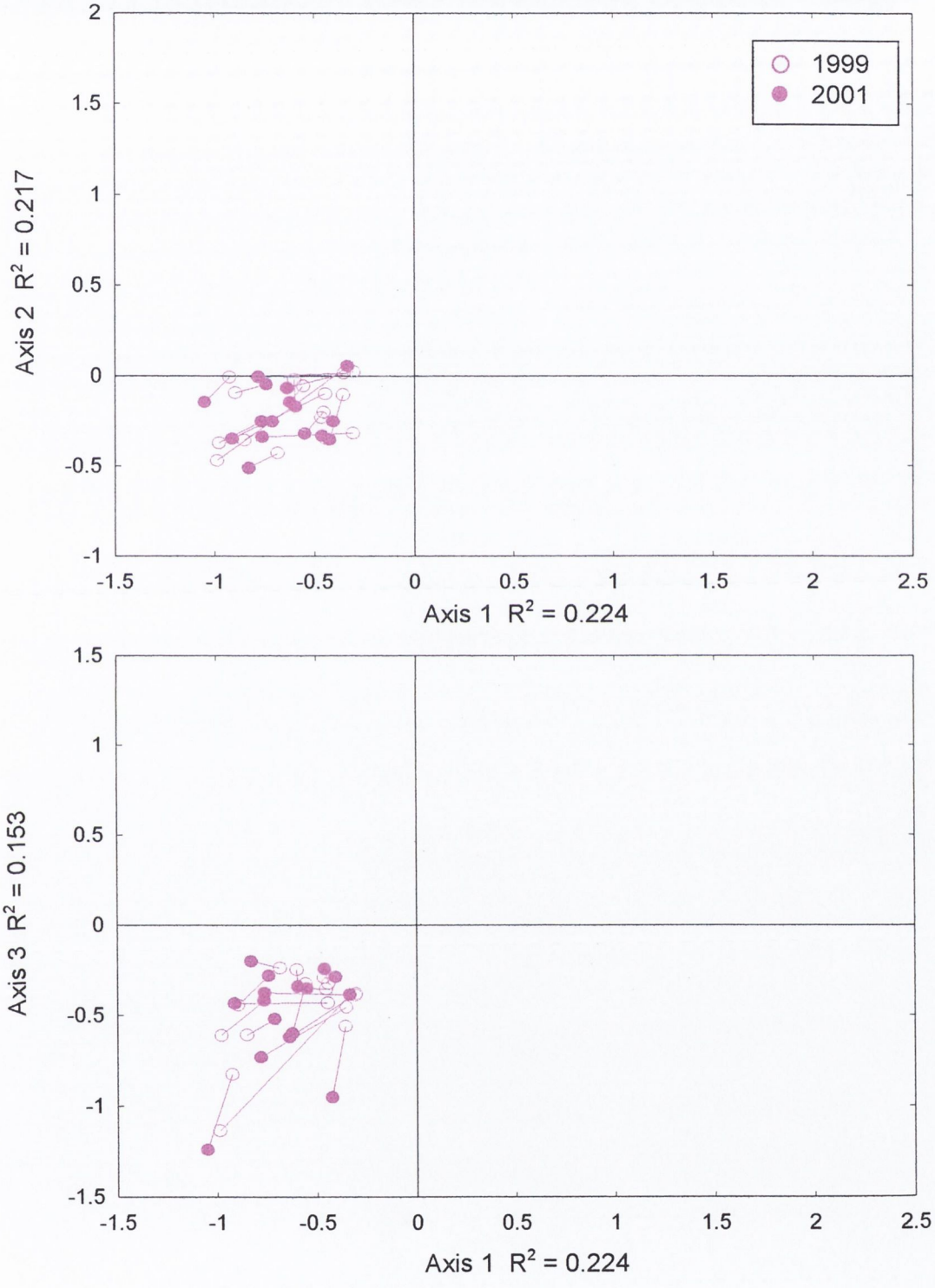
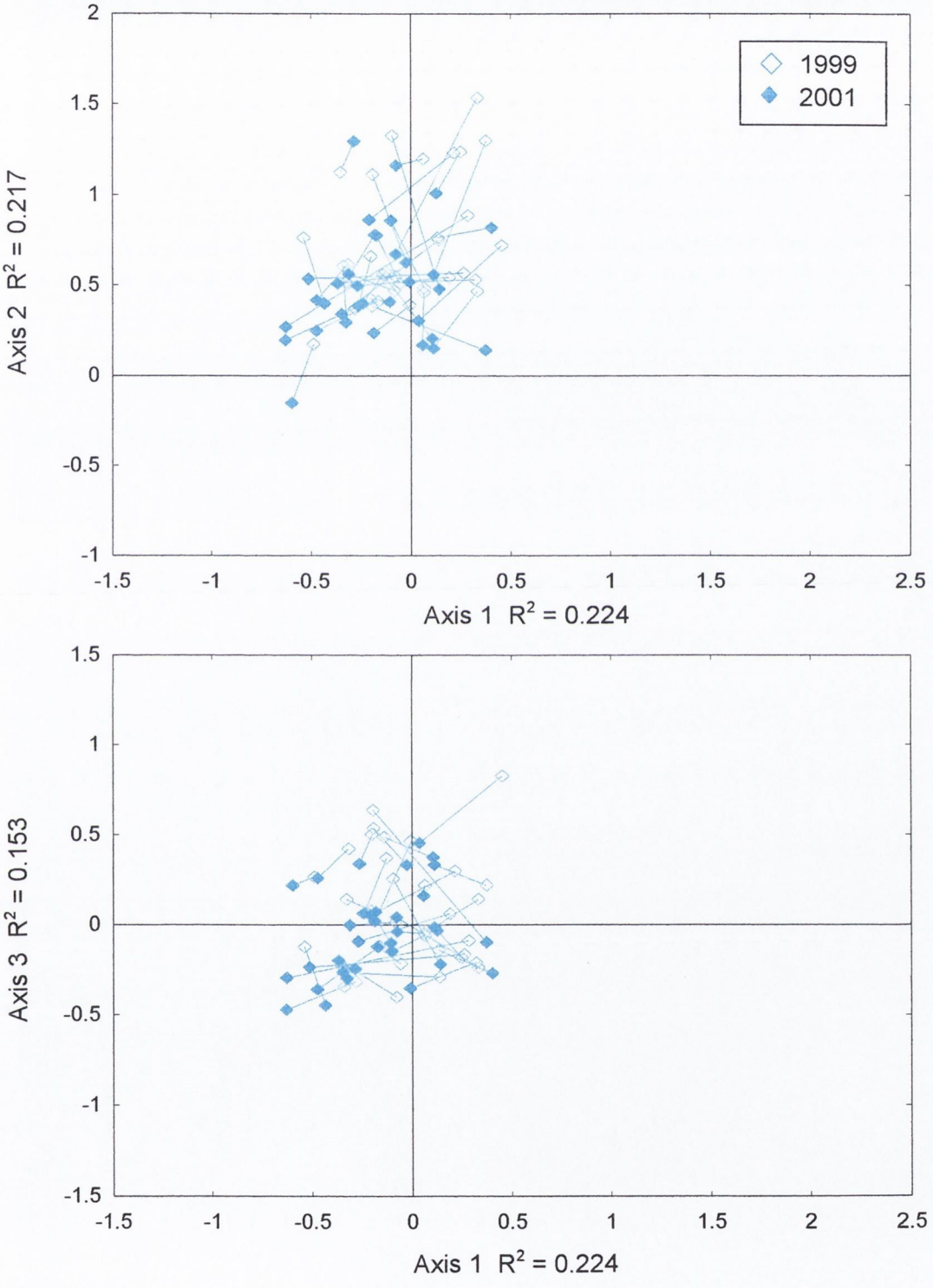


Figure 6.12. NMS ordination of 1999 and 2001 species cover data: subplots in the *Digitalis-Juncus* vegetation type only are plotted. Samples from the two years from the same subplot are connected by a line.



The High *Calluna-Erica* type changed little along any axis (Figs. 6.6, 6.10). Like the *Agrostis-Galium* and *Pteridium-Agrostis* types, High *Calluna-Erica* plots did not move much along the pioneer – developed community axis (Axis 3).

Ordination of the *Digitalis-Juncus* plots suggests a general shift towards High *Calluna-Erica* vegetation (Figs. 6.6, 6.12). *Calluna, Erica cinerea* and *E. tetralix* increased moderately in cover, while *Digitalis* and the *Juncus* species decreased. Like the pioneer vegetation types, the *Digitalis-Juncus* type moved towards the more developed communities on Axis 3.

Euclidean distances in ordination space between the subplots and their centroids were calculated for each combination of sample year and vegetation type. To determine if there was a change in vegetation heterogeneity over the interval, paired t-tests were conducted on (square root transformed) Euclidean distances between sample years within vegetation types. No significant differences between sample years in mean distance to the centroids were found.

To summarise, there was a significant change in the vegetation developing on clearfells over the 1999-2001 sampling interval. Weeding and tree planting mixture had significant effects on vegetation succession, but exclosure did not. In general, vegetation types characteristic of earlier-felled stands changed less than vegetation types typically occurring in more recently felled stands. Similarly, most species increased in cover in the more recently felled stands. The *Agrostis – Galium* and *Pteridium – Agrostis* vegetation types moved towards heath vegetation in ordination space, mostly because of decreases in *Agrostis capillaris* and *Holcus mollis*. These decreases are likely caused in part by weeding treatments, observer error and increases in *Pteridium aquilinum*. The vegetation of the *Calluna – Galium*, Low *Calluna – Erica,* and *Digitalis - Juncus* types moved more along the time axis of the ordination (Axis 3), towards later successional heath vegetation. The ordination and direction of change of subplots in the *Calluna – Galium* vegetation type were more heterogeneous than in the latter two vegetation types.

6.6 Soil Replacement Quadrats

The effectiveness of soil replacement as a strategy for introducing woodland flora to felled conifer plantations gave ambiguous results. Most of the species emerging were typical heath or acid grassland species (Table 6.7), which may have immigrated into the quadrat from the surrounding plot by seed (e.g. *Calluna vulgaris*, especially in plot 7, and *Luzula multiflora*) or by vegetative spread (e.g. *Agrostis capillaris*, *Anthoxanthum odoratum,* and *Galium saxatile*).

Some species like *Calluna* may have been of woodland seed bank origin, becoming incorporated into the seed bank by immigration from outside the woodland or persisting from an earlier, unwooded phase. Interpretation is hindered, however, by the fact that many species are common in both heath and woodland, such as *Digitalis purpurea*, *Vaccinium myrtillus*, and *Luzula sylvatica*. It seems more likely, however, that these species as well as *Hedera helix, Lonicera periclymenum, Oxalis acetosella,* and *Rubus fruticosus* are of woodland seed bank origin. It remains to be seen whether many of these species will persist on site.

Table 6.7. Percent cover of species, not including tree seedlings, emerging in soil replacement quadrats (in exclosed plots) in 2001. Also indicated is the dominant vegetation type of the subplot (or subplots if the soil replacement quadrat was placed between two) in which the soil replacement quadrat was placed.

Plot:	**5**	**7**	**10**	**14**	**15**
Dominant Vegetation Type:	*Luzula sylvatica*[1]	*Agrostis – Galium*	*Agrostis – Galium*	*Calluna – Galium*	Low *Calluna – Erica*
Agrostis canina	10	10	-	-	-
Agrostis capillaris	5	5	35	25	10
Anthoxanthum odoratum	-	-	30	-	-
Calluna vulgaris	5	20	-	-	10
Carex echinata	5	-	-	-	-
Carex pilulifera	-	5	-	5	5
Digitalis purpurea	5	5	-	-	-
Dryopteris affinis	-	5	-	-	-
Erica cinerea	-	5	-	5	5
Festuca ovina	-	-	5	-	-
Galium saxatile	5	5	10	15	-
Hedera helix	5	-	-	-	-
Holcus mollis	-	-	5	-	-
Juncus conglomerata	5	-	-	-	-
Lonicera periclymenum	-	-	5	-	-
Luzula multiflora	-	5	5	-	-
Luzula sylvatica	5	10	-	-	5
Oxalis acetosella	-	-	5	-	-
Potentilla erecta	5	5	5	-	5
Rubus fruticosus agg.	5	5	5	-	5
Ulex europaeus	5	-	-	-	-
Vaccinium myrtillus	5	5	-	5	5
Veronica officinalis	5	-	-	-	-

[1] Most of subplot 5E3 where the soil replacement quadrat was located was dominated by a pure sward of *Luzula sylvatica*. Outside the *Luzula* sward, *Agrostis capillaris*, *Vaccinium myrtillus*, *Juncus squarrosus*, and *Calluna vulgaris* were relatively abundant.

CHAPTER 7

VEGETATION STUDY: DISCUSSION

7.1 Vegetation Development on Conifer Clearfells

7.1.1 Initial Conditions

Like the windthrow of trees in natural forest ecosystems, felling a conifer plantation represents a significant ecological disturbance. Fundamentally, disturbances result in the redistribution of resources among a diminished biotic community (White & Pickett, 1985). It is this change in resource availability that results in vegetation change, or secondary succession (Connell & Slatyer, 1977; White & Pickett, 1985). The initial conditions for succession following clearfelling depend to a great extent on the nature of the former conifer crop. As discussed in section 3.3.1, mature Sitka spruce plantations are well-known for the dense shade they cast, which eliminates nearly all vascular plants by the time the crop is ready for harvesting (Hill & Jones, 1978; Hill, 1979; Wallace & Good, 1995; Fahy & Gormally, 1998; Ferris *et al.*, 2000). *Dryopteris dilatata, Galium saxatile* and *Vaccinium myrtillus* are among the few species that can survive under Sitka spruce (Hill & Jones, 1978). Of course, under canopy gaps or near the plantation edge more plants may persist. Lighter-shading species, such as lodgepole pine and Japanese larch in this study, do not have such a severe effect and can support substantial vascular plant populations (Hill, 1979; Ferris *et al.*, 2000).

Felling a Sitka spruce stand represents a significant disturbance, both in terms severity and size, two factors that are critical to determining the course of plant succession (White & Pickett, 1985; Pickett *et al.*, 1987). Severity of a disturbance is measured by its impact on vegetation and the opportunities created for new colonisation. Because felling represents a virtual elimination of the pre-existing vegetation (i.e. the conifer crop), a clearfelled spruce stand is largely an ecological *tabula rasa*. Therefore, regeneration after clearfelling on former Sitka spruce sites is primarily dependent on the buried seed bank and seed dispersal post-clearance (Hill, 1979; Hill & Stevens, 1981; Granström, 1988). The relative importance of these mechanisms will be influenced by the size of the disturbance. Dispersal into larger clearfells from marginal or remnant habitats will be more difficult, and therefore regeneration from seed banks would be expected to become a more important colonisation mechanism immediately after felling. The correspondence in this study between seedlings emerging from the soil seed bank (sampled in 1999) and the vegetation emerging in the Sitka spruce stands felled in 1998 testifies to the importance of the seed bank in the early stages of vegetation development. Because there were very few mature plants in the plots felled in 1998, very little of the seed

bank could have originated from plants currently present on-site. The most abundant species occurring in the seed bank of recently felled stands were *Calluna vulgaris*, *Juncus effusus*, *Erica cinerea* and *Juncus bulbosus*; *Carex* species were constant seed bank members, while *Digitalis purpurea* was numerous in two plots. In plots where *Digitalis purpurea* and *Erica cinerea* were abundant in the seed bank, the plots had a high probability of being assigned by cluster analysis to the *Digitalis – Juncus* and Low *Calluna – Erica* vegetation types, respectively. Similarly, the presence of *Galium saxatile* in the seed bank makes assignment to the *Calluna – Galium* vegetation type likely.

Previous authors who have investigated seed banks of upland conifer stands have also found high abundances of many of the same species observed in the present study (Hill, 1979; Hill & Stevens, 1981; Granström, 1988). The majority of the seeds of these species were most likely stored for the duration of the plantation: *Calluna, J. effusus, E. cinerea, Carex pilulifera* and *Digitalis* are known to form persistent buried seed banks (Thompson & Grime, 1979; Hill & Stevens, 1981; Granström, 1988; Grime *et al.*, 1988). Grime (1988) considered that *Galium saxatile* can form persistent seed banks, but that "regeneration by seed is probably infrequent". The older seeds present in the soil will of course be buried deeper. In several plots where deep layers of needle litter and humus have developed under Sitka spruce, seeds originating from pre-afforestation vegetation would be several centimetres under the soil surface. Soil disturbance would be necessary to expose the buried seed bank and permit germination; conifer felling operations almost certainly fulfill this requirement.

Other species, particularly trees such as birch, Sitka spruce, and lodgepole pine, have short-lived seeds and cannot form persistent seed banks (Hill & Stevens, 1981; Lotan & Critchfield, 1990; Atkinson, 1992; Clarke, 1992). These must rely on dispersal shortly prior to felling or afterward to establish in clearfells Birch emerged from the seed bank (which included the litter layer) of only two plots, including the plot experiencing highest regeneration of small seedlings. In fact, the paucity of tree seedlings emerging from the seed bank is one of the more notable results in this section of the study (Table 6.3). The detection of species with short-lived seeds such as birch, however, may be hampered by the relatively small area sampled in each plot pair (106 cm^2 total). Nevertheless, the volume sampled (1058 cm^3) is comparable to volumes recommended for determination of the species composition of the buried soil seed bank: 0.8 L for early successional vegetation and 1–1.2 L for grasslands (Bakker *et al.*, 1996). Note that because of much lower seed densities, 8–12 L of soil may be required for adequate sampling of mature woodland (Bakker *et al.*, 1996).

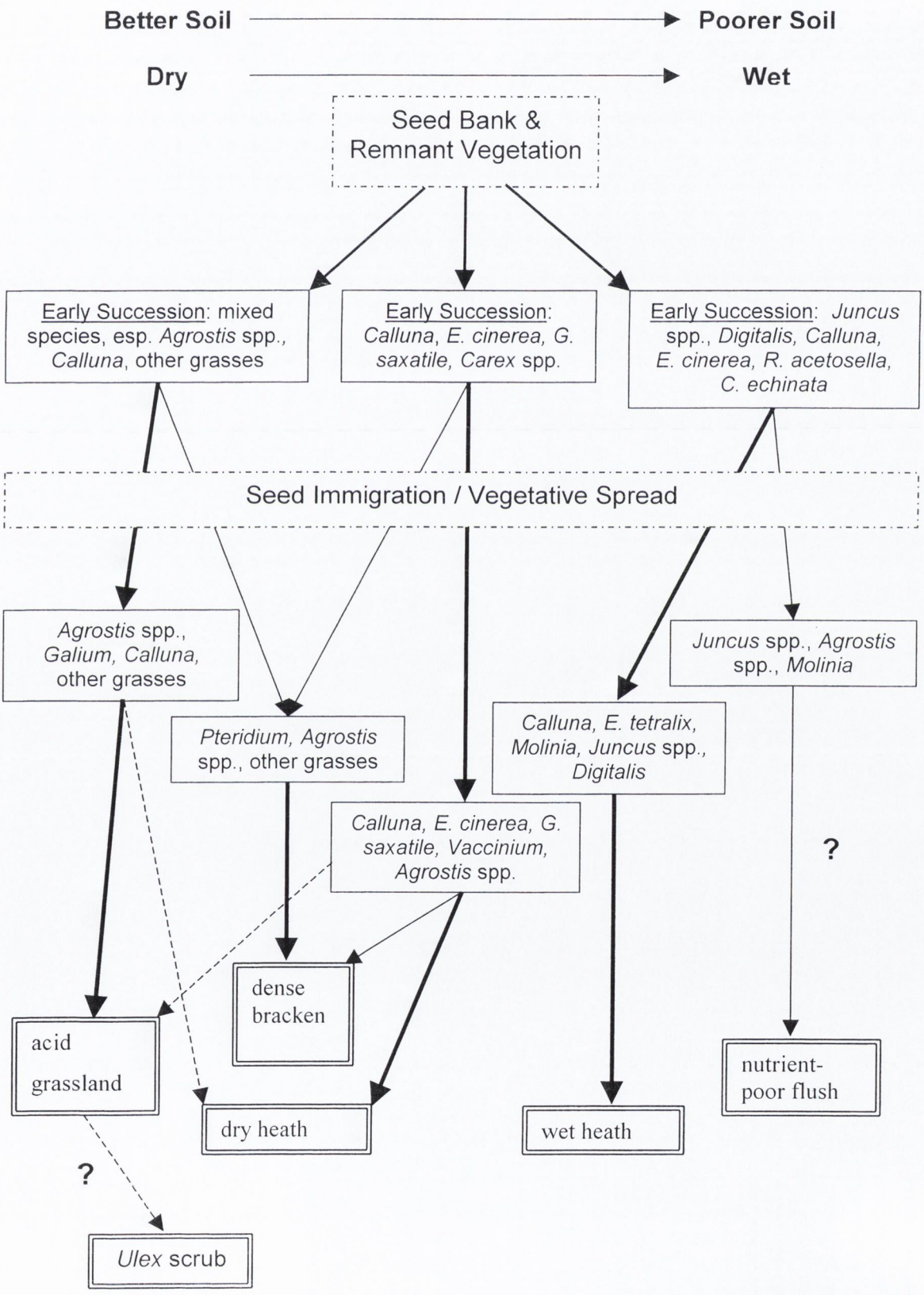
In stands felled longer ago, the more mature vegetation present is more likely to be the cause of observed species abundances in the seed bank rather than the result. The high numbers of *Calluna* seedlings emerging in the seed trays of plots 6 and 7 in the High *Calluna* – *Erica* vegetation type are probably the progeny of mature *Calluna* bushes present on site. A similar argument may be made for the origin of *Agrostis capillaris* seedlings emerging in less-recently felled *Agrostis* – *Galium* plots.

In sites formerly occupied by light-shading species such as lodgepole pine and larch, removal of the canopy does not represent such a severe disturbance as in Sitka spruce stands. Accordingly, there are fewer opportunities for colonisation by new species, and the surviving understory vegetation will play a larger role in subsequent community development. In pine clearfells in Britain, vegetative spread and seed dispersal by plants persisting below the forest canopy have been suggested as more important mechanisms than immigration or seed bank germination (Hill, 1979). The understoreys of larch stands near the Glendalough plots are presently occupied by *Agrostis* and *Pteridium* vegetation similar to that found in the clearfell plots. In such situations, the light environment will not have changed as much between pre- and post-clearance as in felled Sitka spruce stands, so vegetation change will have been correspondingly smaller. Former lodgepole pine stands in Fraughan Rock Glen have greater cover of *Vaccinium myrtillus*, for example, than neighbouring former Sitka spruce plots. *Vaccinium* does not appear to form a persistent seed bank (Hill & Stevens, 1981; Grime *et al.*, 1988), so it is likely that significant populations existed under the pine canopy and have subsequently spread vegetatively.

7.1.2 Successional Trajectories

Although a balance among study sites of felling years, soil types, and other environmental variables was not possible in this study, at least part of the general outlines of how succession proceeds on clearfelled conifer plantations can be sketched. The results suggest that variety of heathland and grassland communities characteristic of acidic, upland situations are likely to develop. A summary of possible successional pathways is presented in Fig. 7.1. These will be mediated by a number of factors including a broad range of environmental conditions, the ecological and physiological characteristics of colonising species, and additional disturbances or stresses such as grazing and drought (Pickett et al., 1987). The classical view of succession holds that vegetation progresses in a number of distinct seral stages deterministically to a climatic climax vegetation type (Putman, 1994). This view, of course, has long been rejected in favour of a sere as a "kind of variable and irregular continuum" (Whittaker, 1951). Change over

Figure 7.1. Possible successional pathways for clearfelled conifer plantations in the uplands of Ireland. Communities are roughly ordered along a soil gradient from drier, more fertile soils on the left to poorer, more organic, and wetter soils to the right. Transitions probably occurring more often are indicated with heavier arrows. See text for discussion of "final" communities.



two years in the present study reflects this view, as shown by the substantial variation among trajectories in ordination space in all but the later successional High *Calluna – Erica* and *Pteridium – Agrostis* vegetation types (Figs. 6.7-6.12). Accordingly, the kinds of vegetation described in the first two tiers of boxes in Fig. 7.1 are not given community names.

The High *Calluna – Erica* and *Pteridium – Agrostis* types, located in stands mostly felled in 1988-1991, have achieved a greater degree of equilibrium (Figs. 6.8, 6.11). This is not to say that they represent "climax" vegetation in the classical sense, however. As discussed below and in later chapters, several factors combine to maintain equilibrium, perhaps preventing succession to woodland, the likely potential vegetation of the sites (Cross, 1998). The High *Calluna – Erica* and *Pteridium – Agrostis* types and other more stable vegetation communities at the bottom of the figure are discussed in terms of phytosociological units previously defined and identified in Ireland. They are also discussed in the context of the broader habitat classification scheme developed by the Heritage Council (Fossit, 2000), which may be of more use to managers. Affinities with British NVC types are also highlighted. Ultimately, Fig. 7.1 represents a hypothesis that can be supported or refuted by future resampling of the study sites.

The starting point of Fig. 7.1 is a largely bare site such as is encountered where Sitka spruce was formerly planted. Regeneration from the soil and litter seed banks and any remnant plants that persisted under the former canopy make up the vegetation shortly after felling (topmost level of solid boxes in Fig. 7.1). Later, immigration and spread contribute to a moderately high vegetation cover at approximately four to five years after felling (middle level of solid boxes in Fig. 7.1), which eventually develops into relatively stable vegetation. The initial conditions under different conifer crops may lead to different successional trajectories (e.g. Smith et al., 1997), but there is little evidence of this after two years of change. Former lodgepole pine stands felled in 1998 have had little opportunity to develop, but they are not segregated from nearby former Sitka spruce stands by vegetation type (section 6.2). Because of the smaller number of plots in former pine and larch stands and the short duration of this study, however, the successional pathways described here should be applied with caution to clearfells of species other than Sitka spruce. In Fig. 7.1, vegetation development in former pine and larch sites could be tentatively considered as having a "head start" on succession when compared with former spruce sites.

As the CCA of the vegetation data suggests, the primary factor responsible for differences in vegetation development is the soil: the more mineral-rich brown earths and brown podzolics contrast with poorer, more organic-rich soils. The early stages of succession on brown earth soils are represented only by two pairs of plots (#18 and #21) in the Baravore, Glenmalure study

site, which somewhat hinders interpretation. The influence of the seed bank, however, in the early development of these plots is strong: *Digitalis*, *Calluna*, and *Erica cinerea* were all well represented (Table 6.3). Correspondingly, a variety of vegetation types occurred on early successional brown earth sites (and no vegetation in the quadrats of one subplot) (cf. Table 6.2). The abundance of other species typical of later successional brown earths, such as the grasses *Agrostis capillaris, A. canina,* and *Anthoxanthum odoratum,* was generally higher in 2001 in plots #18 and #21 than in other plots felled in the same year.

Although insufficient time has passed for confident predictions to be made, these sites may develop vegetation similar to subplots on brown earths and brown podzolics felled in 1995 or earlier. These subplots, located in Glendalough, were all clustered in the *Agrostis – Galium* and *Pteridium – Agrostis* vegetation types. The *Pteridium* dominated areas in particular have achieved a fairly stable community, referable to the dense bracken (HD1) community of Fossit (2000) (Figure 7.1). Most of the *Agrostis – Galium* communities appear to be well-developed examples of dry-humid acid grassland (GS3), which is characterised by dense, low swards of *Agrostis* spp., *Festuca* spp., *Anthoxanthum odoratum*, and other grasses (Figure 7.1). *Pteridium*, however, appears to be expanding in some of these communities (Table 6.4 and section 6.5.2). Both the *Agrostis – Galium* and the *Pteridium – Agrostis* vegetation types are referable to the Achilleo – Festucetum tenuifoliae phytosociological association in the order Nardetalia, class Nardetea (White & Doyle, 1982). The Achilleo – Festucetum is considered by O'Sullivan (1982) as the typical *Agrostis – Festuca* grassland more loosely identified by previous workers (e.g. Pethybridge & Praeger, 1905; Tansley, 1939; Moore, 1960). The association is widespread in the east of Ireland in hilly areas from 200-400 m elevation (O'Sullivan, 1982), and vegetation referable to it has been recorded from the lower slopes of the Dublin and north Wicklow Mountains by Moore (1960). Moore also noted that *Pteridium* was aggressively invading many areas of acid grassland surveyed earlier by Pethybridge and Praeger (1905). He found few floristic differences between *Agrostis – Festuca* grasslands and *Pteridium*-invaded sites, apart from a decline in *Holcus mollis* under *Pteridium* (Moore, 1960) that was also noted in this study (Table 6.4). In Britain, the type of acid grassland occurring in this study has been classified in the NVC as *Festuca ovina – Agrostis capillaris – Galium saxatile* grassland (U4) (Rodwell, 1992).

As bracken and acid grassland communities frequently co-occur in intimate mosaics with heathlands (Fossit, 2000), grass-rich variants of dry heath (discussed below) may develop in some early successional sites with abundant young *Calluna* (Fig. 7.1). Another eventual vegetation type in the Baravore area may be *Ulex europaeus* scrub (Figure 7.1). Although not captured by the vegetation quadrats, *U. europaeus* is regenerating vigorously in places in and

around the plots and dominates areas outside of the plantations along the Avonbeg River. Such gorse scrub may be referable to the Ulicetalia minoris order of the heath vegetation class Calluno – Ulicetea (White & Doyle, 1982)– *U. europaeus* is a character species at both of these syntaxonomic levels– and the rather broad scrub (WS1) habitat type of the Heritage Council scheme (Fossit, 2000). If *Cytisus scoparius*, which is present in Baravore, becomes a significant component of the vegetation, developing gorse scrub communities may be referable to the alliance Sarothamnion scopariae (White & Doyle, 1982). Moore (1960) recorded heaths dominated by *Ulex* species from the lower elevations of the mountains of Dublin and north Wicklow. He found *U. europaeus* dominating "grassy heath" vegetation on neglected farmland below 300 m elevation; above this, *U. gallii* becomes more important. If *U. europaeus* scrub develops without the presence of *U. gallii* or ericaceous shrubs, then such a community could be referable to the NVC type *Ulex europaeus – Rubus fruticosus* scrub (W23), which develops in lowland Britain on free-draining acid brown earths (Rodwell, 1991a), such as are found in Baravore.

Among the poorer, often more organic-rich, soil types, the second major gradient was a continuum from better-drained, coarser textured podzols to poorly drained, organic soils (Fig. 6.3a). The wetter sites in this study were on blanket peats, peaty gleys, and a subset of peaty podzols associated with seepage areas. Although bryophytes were not studied in detail, in these wetter plots *Polytrichum commune* and *Sphagnum* species were abundant, in contrast to the pleurocarpous mosses characteristic of drier sites. Many early successional subplots (in plots 13, 17 and 19) were members of the *Digitalis – Juncus* vegetation type; where *Erica cinerea* was abundant in the seed bank, the vegetation type was often Low *Calluna - Erica*. *Juncus bulbosus* was a particularly prominent species early in succession which declined in abundance as the vegetation developed over time (Table 6.4). Other characteristic species of the early vegetation on wet sites were *Digitalis purpurea*, *Rumex acetosella, Juncus effusus, J. squarrosus,* and *Carex echinata.*

In plots felled in 1995 or earlier, *Juncus* species, *Rumex acetosella* and *Digitalis* decreased over the sampling interval (Table 6.4). *Calluna vulgaris, Erica tetralix, Molinia caerulea* and *Ulex gallii* increased in some earlier- and later-felled plots, especially at the Looscaunagh site, and will probably become more important over time. This shift towards a more shrub-dominated vegetation is reflected in the shift in ordination space over the 1999-2001 sampling interval of *Digitalis – Juncus* vegetation towards High *Calluna – Erica* vegetation (Fig. 6.12). In some sites, increasing *Calluna* dominance may co-occur with drier soil conditions as the site becomes more fully occupied. Other subplots, particularly those in the Glendalough site peaty gley soils,

developed a wetter variant of the *Agrostis – Galium* vegetation type with abundant *Juncus effusus* (cf. Fig. 7 in Appendix 3).

Many of these sites, particularly plots on peat and those where *Erica tetralix* and/or *Molinia* are present, will probably develop into wet heath dominated by a mixture of *Molinia, Calluna* and *E. tetralix*. Irish wet heath vegetation is classified as such ("wet heath- HH3") under the Heritage Council habitat type system (Fossit, 2000). Phytosociologically, wet heaths are referable to the Narthecio – Ericetum tetralicis association, placed in the bog and wet heath class Oxycocco – Sphagnetea (Moore, 1968; White & Doyle, 1982). Several of the character and differential species of the association and alliance occur in the *Digitalis – Juncus* vegetation type, such as *E. tetralix, Juncus squarrosus,* and *Potentilla erecta* (Table 6.1), and also *Carex panicea*. The Narthecio – Ericetum develops on shallow organic soils on the lower slopes of mountains, and also on cutover blanket bog (Moore, 1968). Parts of the blanket peats of the Looscaunagh site were, in fact, cut over prior to afforestation (pers. obs.). Mhic Daeid (1976) identified wet heaths in the Killarney region as a subassociation of the Narthecio – Ericetum, differentiated by the presence of *Ulex gallii* and *Erica cinerea* in addition to *Calluna* and *E. tetralix*. These wet heaths occurred from 500 m elevation in the mountains, down to the level of the Upper Lake. In Britain, similar wet heath communities (without *Trichophorum caespitosum*) are classified as *Erica tetralix – Sphagnum compactum* wet heath (M16) (Rodwell, 1991b).

Seepage areas where *Juncus effusus* and grasses like *Molinia, Agrostis canina* and *Holus lanatus* are abundant, such wetter *Agrostis – Galium* vegetation types, may develop into one or more nutrient-poor flush communities. In the Heritage Council habitat classification, these are aggregated into poor fen and flush (PF2) habitats (Fossit, 2000). One likely community that would develop is the Sphagneto – Juncetum effusi association in the Parvocaricetea class of small-sedge vegetation, an association of drainage channels in bog vegetation (White & Doyle, 1982). Moore (1960) recorded a *Juncus effusus – Agrostis* nodum on sloping, waterlogged ground in the mountains of Dublin and north Wicklow that is referable to the Sphagneto – Juncetum (White & Doyle, 1982). Mhic Daeid (1976) also records the association from the mountains around Killarney. The Sphagneto – Juncetum is synonymous with the British NVC type *Carex echinata – Sphagnum recurvum/auriculatum* mire, *Juncus effusus* sub-community (M6c) (Rodwell, 1991b). Vegetation similar to other sub-communities of this NVC type will probably also develop in the study sites.

The drier types of poor soils included podzols and some better-drained peaty podzols. In the early succession sites, the Low *Calluna – Erica* and *Calluna – Galium* vegetation types

developed most frequently. *Calluna*, *Erica cinerea*, *Galium saxatile*, and *Vaccinium myrtillus* were among the most frequent and vigorous species in the early stages of succession. *Galium* abundance declines over time in stands felled in 1995 or later as the shrubs overtop it. In the Muckross Forest site in Killarney felled in 1988, the High *Calluna – Erica* vegetation type is characteristic of podzol soils. This vegetation type is a relatively well-developed dry heath, and it is likely that more-recently felled sites will develop similarly. Because of the absence of *Ulex* species in the High *Calluna – Erica* type (Table 6.1), the vegetation is best referred to the Calluno – Ericetum cinereae association, which White and Doyle (1982) incidentally note is frequently afforested. Where *Ulex gallii* occurs, such as in the Low *Calluna – Erica* type on former pine stands in Fraughan Rock Glen, Ulici gallii – Ericetum cinereae heath (White & Doyle, 1982) may develop. These associations are aggregated into the Irish habitat type dry siliceous heath (HH1) (Fossit, 2000). *Calluna – Erica cinerea* heath occurs in the Dublin and Wicklow mountains on well-drained slopes, and typically merges with decreasing elevation into heaths characterised by *Ulex gallii* (Moore, 1960). In Killarney, five dry heath subassociations have been recorded from 30 – 720 m elevation (Mhic Daeid, 1976). One of these is an *Ilex aquifolium* subassociation to which the Muckross Forest plots may perhaps be referable. This subassociation has a strong woodland influence and includes such species as *Oxalis acetosella, Quercus petraea, Sorbus aucuparia, Pteridium aquilinum* and *Ilex aquifolium* that also occur in Muckross Forest. The Calluno – Ericetum and the Ulici – Ericetum associations correspond with the NVC types *Calluna vulgaris – Erica cinerea* heath (H10) and *Calluna vulgaris – Ulex gallii* heath (H8), respectively (Rodwell, 1991b).

Subplots on podzols supporting *Pteridium – Agrostis* or *Agrostis – Galium* vegetation will probably develop mature bracken and acid grassland communities discussed above, which are often intimately associated with dry heathlands (Mhic Daeid, 1976; Rodwell, 1991b; Fossit, 2000).

Because of the grazing pressure present at all study sites, woodlands are unlikely to develop without more aggressive herbivore management than exists at present (see section 12.2). It is worth noting, however, that all of the sites in this study are probably capable of supporting at least birch woodland, which can develop on sites as inhospitable as cutover bog (Cross, 1987).

7.1.3 Brash

The most conspicuous feature of clearfelled sites is brash: the dead branches, conifer needles, and broken boles left behind from the harvesting operation. The amount of brash remaining on the sites in this study varied considerably (cf. Appendix 3). As a general rule, brash height and

cover were higher in the more recently felled sites. Brash cover also varied by crop species. Lodgepole pine is more heavily branched and therefore left more brash on site than did Sitka spruce. While both woody debris cover and vegetation type are related to time since felling, the heavier brash present in the earlier successional vegetation types may be inhibiting vegetation development. The subplots felled longer ago that supported poorly developed *Calluna – Galium* vegetation had relatively high covers of brash and wood. In these places, succession may be slowed, relative to more open areas.

The shade cast by dense brash may restrict the development of grassland species such as *Deschampsia flexuosa* and *Festuca ovina*. Studies on Norway spruce clearfells in Sweden have found suppressive effects of brash on *D. flexuosa* and *Luzula pilosa* (Olsson & Staaf, 1995) and, more generally, on grass/sedge and dwarf shrub vegetation, particularly *Calluna* (Bergquist *et al.*, 1999). On the other hand, brash may provide refugia for more shade-tolerant species (Bergquist *et al.*, 1999; Humphrey & Nixon, 1999). In this study, *Luzula sylvatica, Ilex aquifolium* and *Vaccinium myrtillus* are among the species that may be favoured by brash cover (Fig. 6.3b). Increases in the latter two species may also be enhanced by dispersal by birds sheltering in the brash, a behaviour I observed frequently. In the more exposed upland clearfells, such as Fraughan Rock Glen, brash piles provided the only available perches and shelter from wind and perhaps from the local peregrine falcons.

Sites with heavier brash may also receive higher nutrient inputs as the leaf litter and later the twigs and branches decompose (Hornung, 1985; Goulding & Stevens, 1988; Fahey *et al.*, 1991; Titus & Malcolm, 1999; Hyvönen *et al.*, 2000). The fertilizer effect of brash decay can vary considerably over short distances (Hendrick, 1979). *Chamerion angustifolium* and *Molinia caerulea* were well correlated with brash cover in this study, and may be responding to nutrient inputs from brash. Olsson and Staaf (1995) and Bergquist *et al.* (1999) found that *C. angustifolium*, as well as *Rubus idaeus* and *Senecio sylvatica,* were favoured by brash, which Olsson and Staaf attributed to a fertilizer effect. However, as was discussed in section 3.3.1, as large amounts of carbon-rich woody debris decay, there is the possibility of nutrient immobilisation by decomposers.

7.1.4 Grazing

Vegetation change over the two year interval between vegetation sampling was not significantly affected by grazing pressure. This result is somewhat surprising given that large herbivores were abundant in all study sites (see section 10.1 for details on herbivore densities). Bergquist *et al.* (1999) found that deer browsing slowed the rate of succession and reduced abundances of

dwarf shrubs, herbs and ferns, relative to fenced plots, on sites felled three or more years previously. More fundamentally, grazing may deflect succession towards a different end community (Gibson & Brown, 1992). It may be that insufficient time has elapsed for the effects of exclosure to become significant. In the oldest clearfell, Muckross Forest, I observed that sheep grazing was heaviest in more level places closer to the forest road. In these places, the vegetation was a close-bitten *Agrostis capillaris*-dominated sward. On steeper slopes and in rougher terrain, *Calluna* and *Erica cinerea* dry heath was the primary vegetation. Similarly, Hill *et al.* (1992) found that grazing suppressed *Calluna* and *E. cinerea* in hill pastures in Wales.

7.1.5 Rate of Succession

In 1999, each 800 m^2 plot pair supported an average of 28 species which increased to 30-31 after two years (section 6.1). Although the regressions do not provide additional information on the rate of species richness increases with time, there is other evidence that the rate of change in vegetation abundance is greater in early-successional stands. The later-successional High *Calluna-Erica* vegetation type changed very little over the sampling interval in ordination space (Figs. 6.4, 6.6). In contrast, the more early-successional vegetation types moved relatively long distances. *Pteridium*, however, appears to be spreading in some of the later successional *Agrostis – Galium* and *Pteridium – Agrostis* communities in the 1991 felled stands (Table 6.4 and section 6.5.2). The plot photographs in Appendix 3 also show greater vegetation change in early successional sites. Similarly, old field successional studies in North America have found that the rate of succession decreases over time, due to such mechanisms as reduction in the availability of safe sites for regeneration (Shugart & Hett, 1973; Myster & Pickett, 1994). Kelly (2000) noted that vascular plant species richness in an oakwood in Killarney increased markedly over the first two years after felling and subsequently declined at a much slower rate.

7.1.6 Patterns of Species Richness

In the only published study of conifer clearfell vegetation in Ireland, Fahy and Gormally (1998) recorded 24 species of vascular plants in ten 2 × 2 m quadrats in a two-year-old Sitka spruce clearfell adjacent to Derryclare Wood, Co. Galway. *Molinia caerulea* was the dominant species, and *Calluna vulgaris, Potentilla erecta* and *Rubus fruticosus* were also abundant. In comparison, the Sitka spruce plot pairs in Glenmalure felled in 1998 supported an average of 27 species in 1999 and 28 in 2001 (Fig. 6.1). The number of species appears comparable between the two studies, although the area sampled by Fahy and Gormally (1998) was 20 times smaller than the area of the plot pairs in this study. Accordingly, the clearfell sampled by the previous authors was probably more species-rich than my Glenmalure sites on average. They describe their site as "bog/wet moorland" (Fahy & Gormally, 1998), which is therefore most similar

among my study sites to the Looscaunagh plots felled in 1994 which supported an average of 30 species in 1999 and 40 in 2001. Their study site was "adjacent" to semi-natural oak woodland, which probably explains the presence of such species as *Corylus avellana* and *Athyrium filix-femina*, that were not present in Looscaunagh. The plot pair in this study closest to woodland was #11, which was located 69 m south of oak woodland in Glendalough. This plot pair, felled in 1995, was among the most species-rich (Fig. 6.1). The number of species was boosted by some woodland species that did not commonly appear in other plots, such as *Oxalis acetosella*, *Teucrium scorodonia* and several tree species, including sessile oak. This site was also flushed, and so species characteristic of wet places, for example *Viola palustre*, contributed to higher species richness.

7.2 Restoration of Woodland Flora

The flora of upland oakwoods on acid soils in Ireland is similar to that of other upland communities. Many of the species found in the clearfells, including the dwarf shrubs *Calluna vulgaris* and *Vaccinium myrtillus* and herbs like *Blechnum spicant*, *Luzula sylvatica, Agrostis canina* and *Carex pilulifera,* are character or differential species of the Blechno-Quercetum petraeae phytosociological association (Kelly & Moore, 1975). These species are also characteristic of or commonly occurring in heathlands, probably because heath vegetation has its origins in the understorey of upland oakwoods destroyed by human activities in previous centuries (Gimingham, 1972). The similarities between the vegetation regenerating in clearfells and the target community, acidophilous oak woodland, makes the task of restoration simpler in part.

Because many of these clearfell sites are distant from existing semi-natural woodland, immigration of missing woodland species will probably be slow or even impossible. Although practice in England is to wait for canopy closure to introduce woodland ground flora, it is possible for characteristic woodland species to persist naturally outside the woodland canopy in Ireland, as a result of the wet Irish climate and frequency of overcast days. I have observed *Hyacinthoides non-scripta* and *Anemone nemorosa*, for example, thriving outside the cover of trees, perhaps as relicts from a former woodland. Webb (1952) has also noted such species as *Conopodium majus, Primula vulgaris, Fragaria vesca* and *Ranunculus ficaria* persisting in open conditions, especially in the more oceanic west of the country. It may be possible, therefore, to establish such species early in succession while competition is still low.

It is difficult to interpret the success or otherwise of the soil transplantation trial in this study. Because of the similarities among upland vegetation types discussed above, it is difficult to

determine whether certain species emerging in the transplantation quadrats were brought in with the soil or immigrated from the surrounding area. No typically woodland vernal species, such as *Hyacinthoides* and *Anemone*, were found in the soil replacement quadrats in 2001, although they were present in the Wicklow and Killarney donor sites, respectively. Absences of such species are probably because soil replacement was conducted in March 2000, after they are likely to have broken dormancy. The climbers *Lonicera periclymenum* and *Hedera helix* and the woodland herb *Oxalis acetosella* probably entered with the soil (Table 6.7), and it will be interesting to see if they survive over the short to medium term.

CHAPTER 8

PLANTED TREE STUDY: METHODS

8.1 Tree Planting

In each plot, two 10 × 10 m subplots were planted with 18 bare-rooted sessile oak transplants, and the remainder with 6 oak and 12 downy birch bare-rooted transplants (Fig. 4.6). Although the use of cell-grown planting material may improve establishment rates, such planting stock is more expensive and was not available in sufficient quantities for this study. The trees were planted in an 8 m diameter area in the centre of each subplot, to provide areas for monitoring free from planting disturbance. This also separated the trees in different subplots, facilitating field work. Trees were pit-planted in the most suitable places available. In mixed oak and birch subplots, birch were planted towards the outside and oaks towards the centre of the subplot to increase any possible shelter effects the faster-growing birch may have on oak. Because watering trees was not feasible, prior to planting the roots of each tree were coated in a soil/water slurry ("puddled"). A total of 2016 oaks and 1021 birch were planted in 1999. Because of time constraints, baseline measurements, tagging and mapping of planted trees were not performed at planting, but later in 1999 (section 8.3 below).

The birch seedlings were of Aughrim, Co. Wicklow provenance and were approximately 70 – 90 cm tall when planted. They had spent 1 year in seed beds and an additional year "planted out" (known as 1+1s).

Because of the scarcity of native Irish oak seedlings commercially available in 1999, oaks from three different nurseries and eight different provenances were used. All oak seedlings, except for one provenance, were 1+1s ranging from 30 – 120 cm tall. Provenances from the southwest of Ireland were used in Killarney, as the use of local or regional provenances reflects current practice in woodland restoration (section 3.2). Due to insufficient numbers, however, two oak seedlings planted in each pure oak subplot and one in each mixed subplot were from Coolgreany, Co. Wicklow. The remaining oaks were equal proportions of Killarney, Co. Kerry, Glengarriff, Co. Cork, and Beara, Co. Cork provenances from a different nursery. Provenances were distributed equally among subplots to prevent confounding of provenance with experimental treatments. The Coolgreany oaks had smoother bark and more fibrous roots than the Munster oaks, which were fairly indistinguishable. Note, however, that possible genetic differences are confounded with differences in treatment in the nursery.

In Wicklow plots, Coolgreany oaks were planted with provenances from Galway, Donegal, and Antrim from a third nursery. In pure oak subplots, the numbers of trees planted from each provenance were:

- 10 Bollisce, Co. Galway
- 4 Crolly, Co. Donegal
- 2 Coolgreany, Co. Wicklow
- 1 Drumaheglish, Co. Antrim
- 1 Rea's Wood, Co. Antrim

In mixed oak / birch subplots, the oak provenances used were:

- 3 Bollisce, Co. Galway
- 1 Crolly, Co. Donegal
- 1 Coolgreany, Co. Wicklow
- 1 Drumaheglish, Co. Antrim

Because of insufficient numbers, other provenances were substituted for Rea's Wood oaks in 20 subplots and for Drumaheglish oaks in 3 subplots. Again, provenances were distributed equally among subplots insofar as possible.

Coolgreany oaks had better small-diameter root systems than the other provenances. Bollisce trees were 1+2s of widely mixed sizes and usually possessed a good taproot. Crolly oaks were smaller on average and were more often multi-stemmed than other provenances. Drumaheglish trees were usually very large, relative to the other provenances, and had long, stout taproots, whereas Rea's Wood provenance was similar to average-sized Bollisce. Many of the Galway and Antrim trees had been shaped to remove competing leaders and some had had taproots cut. Provenance of oaks planted in Wicklow was marked with coloured PVC tape and subsequently recorded during sampling; this was not done in Killarney.

Killarney plots were planted on 13-14 March, 1999, but delays in fencing postponed planting in Wicklow to 29 April – 30 May. Because of the delays, some of the birch began to break dormancy and were placed in a dark cold room on 1 April, enclosed in polythene bags and with well-wetted roots to prevent desiccation. Unfortunately, the birch continued to leaf-out in cold storage, and on 7 May they were heeled-in in a shady location in Trooperstown Forest near Laragh, Co. Wicklow. The oaks were similarly placed in cold storage in mid-April, but since they did not begin leafing-out, they were kept refrigerated until planting. All trees were removed from cold storage and allowed to acclimate overnight before planting.

Surplus tree seedlings were heeled-in in Trooperstown Forest and some were used in March 2000 as replacements in plots where first-year mortality was greater than 50%. Replacement trees were measured immediately after planting. Replacements were not used in calculations of mortality between 1999 and 2000 sampling, but were used in computing height and basal diameter growth from 1999-2000.

8.2 Birch Seed Experiment

In the spring of 2001, an experiment was conducted to determine if adequate birch regeneration could be achieved by broadcasting seed. Unfortunately, the outbreak of foot-and-mouth disease in Britain interfered with this aspect of the study. On 28th March, two lots of stratified downy birch seed were delivered from Coillte Seed Centre; one provenance was from Co. Cork, to be used in Killarney, and the other was from Tinahealy, Co. Wicklow. The seeds were placed in a refrigerator until permission to conduct fieldwork and sterilisation equipment could be obtained. Unfortunately, on 2nd April, it was discovered that the refrigerator had either malfunctioned or had been turned down so that the birch seeds were frozen. The seeds were then moved to another refrigerator. Forty seeds of each provenance were tested for viability by placing them in separate petri dishes on moistened filter paper in a growth chamber at 15°C in the Trinity College Botanic Gardens. Within a week, five of the Wicklow provenance and seven of the Cork provenance had germinated.

Permission was later obtained from Coillte to conduct field work in Glenmalure. On 11-12th April, 6 g of Wicklow provenance birch seed were scattered by hand in a 4 m^2 area in each of the 11 exclosed plots in Glenmalure. This weight corresponded to approximately 1800 viable seeds, according to data provided by Mr. Pat Doody, Coillte Seed Manager (pers. comm.). The birch seed subplots were searched for seedlings during 2001 sampling. Virtually no seedlings were found in subplots that did not experience significant amounts of natural regeneration from local seed sources. Because of the freezing episode and the long period spent refrigerated, I have no confidence in these results: they are not presented in chapter 9.

8.3 Field Sampling

Sampling of planted trees took place in late summer through autumn of 1999, 2000, and 2001. During sampling in 1999, each seedling in a plot was individually tagged, its position mapped to the nearest 0.5 m, and, in Wicklow, its provenance recorded. Each year, stem height to the nearest cm, basal stem diameter (at 10 cm above ground level) to the nearest mm, and whether

the seedling was alive or dead was recorded. Presence of symptoms of disturbance, including browsing by large and small herbivores, insect herbivory (except galls), evidence of fungal attack, presence of chlorosis or necrotic patches on leaves, and mechanical damage (usually caused by brash) were also recorded. Damage to leaves was recorded if more than 20% of the leaf area was affected. Unless extremely minor, damage to stems was always recorded. Insect galls were rarely seen but were not recorded.

8.4 Data Analysis

8.4.1 Data Handling

Height and basal diameter growth increments over the intervals 1999-2000 and 2000-2001 were calculated for each tree seedling. Mortality was calculated for each year as the proportion of trees found dead during sampling that were live the previous year.

Many trees could not be found during sampling, especially in 1999 prior to mapping. Some were located in subsequent years, but most were never found. Judging by those that were later found, the vast majority of missing trees had probably died and broken prior to 1999 sampling. It is also likely that a small number of trees marked as "missing" were in fact mistakenly never planted. Missing trees were treated in analyses as dead, thus perhaps causing a very small overestimate in mortality. I estimate that a maximum of 15-20 trees in the whole study may have been misclassified as dead in this fashion.

Except where otherwise noted, statistical analyses of planted tree data were conducted using SPSS (1999) after consulting Sokal and Rohlf (1995). When several variables were simultaneously examined with univariate tests, resulting P-values were corrected to control the experimentwise error rate using Hochberg's (1988) procedure. This procedure is more powerful than the traditional Bonferroni correction (Legendre & Legendre, 1998).

8.4.2 Experimental Treatments

The effects of the experimental treatments of exclosure, weeding, and planting mix on planted oak and birch mortality in 1999, 2000, and 2001 were analysed using contingency tables and odds ratios. An odds ratio (ω) compares the likelihood of an outcome in one treatment relative to a second treatment:

$$\omega = \frac{p_i / q_i}{p_j / q_j}$$

where p and q are proportional responses (e.g. percent live and dead) to treatments i and j (Sokal & Rohlf, 1995). In other words, response p (e.g. survival) is ω times more likely under treatment i (e.g. exclosure) than under treatment j (e.g. control).

Experimental treatment effects on tree growth were analysed using multivariate analysis of variance (MANOVA) (Morrison, 1990). Separate MANOVAs were conducted for oak and birch. Mean height and basal diameter growth increments over the intervals 1999-2000 and 2000-2001 were calculated for each 10 × 10 m subplot, thus yielding four variables to be tested in each of the two MANOVAs. Prior to analysis, subplot means were identified as outliers and removed if they were 2.5 standard deviations or more from the grand mean and were calculated using 3 or fewer live trees. In the birch MANOVA, the treatments used to test the four growth variables were exclosure, weeding, and exclosure × weeding interaction. Oak variables were tested with exclosure, weeding, planting mix, and all second- and third-order interaction terms as factors. To partition the variation caused by environmental differences between study sites, the MANOVA was conducted as a randomized complete blocks design with each fenced/unfenced plot pair as a block.

The growth variables were inspected prior to testing, and all but the birch height growth variables showed significant departures from normality. The following data transformations were applied to improve normality: oak height growth 2000-2001 was square root transformed, birch basal diameter growth 1999-2000 was reciprocal transformed, and oak and birch basal diameter growth 2000-2001 were reciprocal square root transformed. The normality of the oak growth 1999-2000 variables could not be improved by transformation. Despite these violations of the assumption of analysis-of-variance, the technique was employed, primarily because it allows an overall multivariate test of significance and the testing of treatment interaction terms. Also, non-parametric tests (Kruskal-Wallis H and Mann-Whitney U) were used to double-check MANOVA main effect results.

8.4.3 Environmental Factors

The effects of the environment on planted tree growth and survival were assessed at the subplot scale using canonical correspondence analysis (CCA) (ter Braak, 1986). Because of the overwhelming effect of browsing outside the fences, only data from exclosed subplots were used. Planted tree variables included in the first matrix were height and basal diameter growth in 1999-2000 and 2000-2001, mortality in 1999, and mortality in 2000 and 2001. Mortality in the last two years was combined because there was little difference between the two variables in preliminary ordinations. To place the tree variables on the same scale (values from 0 to 1),

growth variables were transformed by ranging (Sneath & Sokal, 1973) and mortality variables were relativised by dividing by maximum mortality. Separate CCAs were conducted for planted oak and birch.

The environmental variables included in the second matrix of the CCAs are shown in Table 8.1. As with the vegetation CCA, I attempted to be parsimonious in selection of environmental variables to reduce multicollinearity. Spearman's rank correlation coefficients among the site variables were inspected prior to analysis. Depth of the soil organic layer, C/N ratio, and percent cover of brash (in the 1 × 1 m vegetation quadrats) were considered, but not included in the CCAs because they were highly correlated with several other variables. Available Mg^{2+} was also omitted because of a very high correlation with Ca^{2+}. Former conifer crop and felling year were omitted because these factors would affect tree performance indirectly by influencing many of the variables in Table 8.1. Soil type was not included because much of the information is duplicated by soil chemical and physical variables included in the CCAs.

Table 8.1. Environmental variables used in planted tree CCAs and their degrees of precision. For further explanations, see text.

Variables	Type	Variables	Type
Soil Variables:		***Site Variables:***	
Gleying	presence/absence	Slope (%)	quantitative
Soil Depth (cm)	quantitative	Aspect	quantitative
K^+ (mg/L)	quantitative	Precipitation (mm)	quantitative
Ca^{2+} (mg/L)	quantitative	Temperature (°C)	quantitative
Mn^{2+} (mg/L)	quantitative	Topex	quantitative
Organic Content (%)	quantitative	SW Topex	quantitative
pH	quantitative	Brash Height	quantitative
Upper Soil Index	ranks (1-6)		
Lower Soil Index	ranks (1-7)	***Vegetation Types:***	
		Agrostis - Galium	presence/absence
Ground Cover (%):		Digitalis – Juncus	presence/absence
Field Layer	quantitative	High Calluna – Erica	presence/absence
Litter	quantitative	Low Calluna – Erica	presence/absence
Wood	quantitative	Pteridium - Agrostis	presence/absence
Bryophyte	quantitative		
Soil	quantitative	***Others:***	
Rock	quantitative	Hare Damage (%)	quantitative
		Date of Planting	quantitative

Of the variables included, soil water-holding capacity index, aspect, precipitation, temperature, and topex were handled as in the 1999 vegetation CCA (section 5.3.4). The vegetation types were coded as 0/1 dummy variables, with the *Calluna – Galium* vegetation type treated as the default (i.e. 0 values for all the vegetation types). Also included were the percentage of trees in each subplot damaged by small mammals ("hare damage") and the date when the tree seedlings were planted, expressed as the number of days since planting began.

The CCAs for oak and birch performance were each conducted twice. The first CCA used all the environmental variables in Table 8.1. The final CCA was conducted after removing variables that had correlations between –0.2 and 0.2 with the first three canonical axes. PC-ORD (McCune & Mefford, 1997) was used to perform CCAs. Since PC-ORD only provides results for the first three canonical axes, further canonical axes could not be interpreted.

8.4.4 Other Statistical Testing

Mortality of oaks planted in Wicklow among the five provenances was examined using likelihood ratio contingency tests. Height and basal diameter growth were tested with Kruskal-Wallis H non-parametric tests. Provenance of oaks in Killarney could not be investigated because provenance was not recorded there. The effects of agents of disease and damage, including small mammal herbivory, were tested using likelihood ratio tests and Mann-Whitney U non-parametric tests as appropriate.

CHAPTER 9

PLANTED TREE STUDY: RESULTS

9.1 Experimental Treatments

9.1.1 Mortality

Oak mortality over the three years of the study was 16.9% in exclosed plots and 73.7% outside exclosures. Total birch mortality was 39.1% in exclosed plots and 79.8% in unexclosed plots. Mortality of oak and birch between planting and sampling in 1999 was higher in exclosed plots than mortality in 2000 and 2001 (Table 9.1), most likely because of transplantation shock. In unexclosed plots, highest birch mortality was also in the first year, but oak experienced highest mortality rates in 2000 (Table 9.1).

Exclusion of large herbivores significantly increased survival of planted trees in all years in both weeded and unweeded plots (Tables 9.1, 9.2). In 1999, oaks planted inside exclosures were two to three times more likely to survive than those outside (i.e. odds ratios of 1.8 and 2.9 in Table 9.2). In later years, however, odds of survival for exclosed oaks were approximately 18-26 times better than for unexclosed oaks. The odds ratios for birch survival show a similar, but less pronounced pattern (Table 9.2).

Weeding was much less important for tree mortality than exclosure (Table 9.1). Tree survival odds ratios in exclosed plots were not significantly different from 1 (Table 9.3). Oak survival in unfenced plots in 2000, however, was slightly reduced by weeding. The effect of weeding on

Table 9.1. Mean percent mortality of planted oak and birch in 1999, 2000, and 2001 in exclosed / unexclosed and weeded / non-weeded treatments.

		Exclosed		Unexclosed	
	Year	**Weeded**	**Non-Weeded**	**Weeded**	**Non-Weeded**
Oak	*1999*[1]	10.5	11.7	17.5	28.0
	2000	4.6	4.5	54.1	45.3
	2001	1.8	2.6	32.5	32.3
Birch	*1999*[1]	33.9	35.0	50.6	58.0
	2000	5.0	3.4	37.8	28.8
	2001	4.1	6.5	42.2	39.4

[1] Note that weeding treatments in 1999 took place at the same time as sampling and therefore cannot influence 1999 mortality rates.

Table 9.2. Odds ratios (and 95% confidence intervals) for planted tree survival in exclosed / unexclosed plots, controlled for weeding treatments. The odds ratios express the likelihood of survival in *exclosed* plots relative to *unexclosed* plots. The odds of survival are significantly ($\alpha = 0.05$) different in exclosed and unexclosed plots if the 95% confidence interval does not include 1.

		Weeded		Non-Weeded	
		Odds Ratio	**95% CI**	**Odds Ratio**	**95% CI**
Oak	*1999* [1]	1.8	(1.3 – 2.6)	2.9	(2.1 – 4.1)
	2000	24.4	(15.1 – 39.4)	17.7	(10.8 – 29.0)
	2001	25.7	(12.0 – 55.1)	18.1	(9.3 – 35.2)
Birch	*1999* [1]	2.0	(1.4 – 2.9)	2.6	(1.8 – 3.7)
	2000	11.6	(5.5 – 24.6)	11.5	(4.7 – 28.3)
	2001	17.2	(7.3 – 40.9)	9.3	(4.5 – 19.5)

[1] Note that weeding treatments in 1999 took place at the same time as sampling and therefore cannot influence 1999 mortality rates.

Table 9.3. Odds ratios (and 95% confidence intervals) for planted tree survival in weeded / non-weeded plots, controlled for exclosure treatments. The odds ratios express the likelihood of survival in *weeded* plots relative to *non-weeded* plots. The odds of survival are significantly ($\alpha = 0.05$) different in exclosed and unexclosed plots if the 95% confidence interval does not include 1.

		Exclosed		Unexclosed	
		Odds Ratio	**95% CI**	**Odds Ratio**	**95% CI**
Oak	*2000*	1.0	(0.5 – 1.8)	0.7	(0.5 – 0.9)
	2001	1.4	(0.6 – 3.6)	1.0	(0.7 – 1.5)
Birch	*2000*	0.7	(0.2 – 1.9)	0.7	(0.4 – 1.1)
	2001	1.6	(0.6 – 4.3)	0.9	(0.5 – 1.6)

survival of unexclosed birch showed a similar, but non-significant trend. Analysis of the weeding treatments in each of the six vegetation types defined in section 6.2, similarly revealed little influence on mortality of planted trees. Likelihood ratio tests (the test statistic is distributed as χ^2 (Sokal & Rohlf, 1995)) showed that weeding significantly improved oak survival in 2000 ($P = 0.012$) and birch survival in 2001 ($P = 0.044$) in the *Pteridium-Agrostis* vegetation type. In the *Agrostis-Galium* vegetation type, weeding actually increased oak mortality in 2000 ($P = 0.024$). It may be that efforts to uproot grasses damaged the surface roots of the tree seedlings.

9.1.2 Growth

Where no variables are specified, "tree growth" refers to all four growth variables: height and basal diameter growth over the two intervals 1999-2000 and 2000-2001. Tree "performance" will be used as an umbrella term referring to both tree growth and mortality.

Height and basal diameter growth over both intervals were greater in exclosed plots than in unexclosed plots (Table 9.4). Wilk's Λ multivariate tests of significance (Morrison, 1990) showed that exclosure and plot number (the blocking factor, see section 8.4.2) had significant effects on mean growth of planted birch (Table 9.5a) and planted oak (Table 9.5b). Following the multivariate test (which ensures that the experimentwise error rate is $\alpha = 0.05$ for each of the two MANOVAs), an ANOVA was conducted for each of the growth variables individually, using the same two-way factorial design for birch and three-way factorial design for oak used for the MANOVAs. In Table 9.6, abbreviated results of the ANOVAs are presented; for the sake of brevity, the intercepts, blocking terms and factors not found significant earlier by Wilk's Λ multivariate tests are not shown, although they were included in the model. All growth variables for both species were significantly greater in exclosed plots (Table 9.6). Herbivory in unexclosed plots actually resulted in a mean decrease in oak and birch height (Table 9.4). Oak

Table 9.4. Planted oak and birch height and basal diameter growth means (± se) in fenced and unfenced plots. N (in parentheses) is the number of subplots.

	Exclosed	**Unexclosed**
Oak Height Growth 1999-2000 (cm)	-6.5 ± 1.0 (84)	-16.2 ± 1.0 (71)
Oak Height Growth 2000-2001 (cm)	5.9 ± 0.9 (84)	-4.8 ± 1.0 (57)
Oak Basal Diameter Growth 1999-2000 (mm)	0.9 ± 0.1 (84)	0.09 ± 0.1 (71)
Oak Basal Diameter Growth 2000-2001 (mm)	2.0 ± 0.2 (84)	0.1 ± 0.1 (48)
Birch Height Growth 1999-2000 (cm)	4.2 ± 2.2 (42)	-20.7 ± 2.1 (41)
Birch Height Growth 2000-2001 (cm)	15.1 ± 2.1 (42)	-13.9 ± 2.4 (29)
Birch Basal Diameter Growth 1999-2000 (mm)	2.3 ± 0.3 (42)	0.1 ± 0.1 (40)
Birch Basal Diameter Growth 1999-2000 (mm)	3.6 ± 0.4 (42)	0.0 ± 0.2 (27)

Table 9.5. MANOVA tables for overall significance tests of treatments on: **a.** planted birch and **b.** planted oak height and basal diameter growth over the two intervals 1999-2000 and 2000-2001. The birch and the oak MANOVAs were conducted separately.

a. MANOVA of birch growth variables.

Treatment	Wilk's Λ	P
Intercept	0.005	≤ 0.0001
Plot (Blocks)	0.109	0.01
Exclosure	0.224	≤ 0.0001
Weeding	0.917	0.457
Exclosure × Weeding	0.980	0.931

b. MANOVA of oak growth variables.

Treatment	Wilk's Λ	P
Intercept	0.002	≤ 0.0001
Plot (Blocks)	0.127	≤ 0.0001
Exclosure	0.333	≤ 0.0001
Weeding	0.937	0.174
Plant Mix	0.968	0.522
Exclosure × Weeding	0.917	0.075
Exclosure × Plant Mix	0.962	0.439
Weeding × Plant Mix	0.981	0.750
Exclosure × Weeding × Plant Mix	0.931	0.136

height growth from 1999-2000 was also negative in exclosed plots, most likely the result of dieback following transplantation shock (Table 9.4).

Weeding and planting mix had no significant effects on oak or birch growth (Table 9.5). The interaction between the exclosure and weeding treatments was nearly statistically significant for planted oak ($P = 0.075$). When the oak growth variables were inspected individually, it was found that the near-significance of the multivariate test was primarily due to basal diameter growth from 1999-2000 (univariate ANOVA $P = 0.021$). In exclosed plots, weeding increased first-year diameter growth, whereas in unexclosed plots weeding was associated with a decrease in first-year diameter growth. Mann-Whitney U non-parametric tests also found that exclosure, but not planting mix or weeding, significantly improved height growth. Further investigation of the effects of weeding in each of the vegetation types also demonstrated the weakness of weeding effects on birch and oak growth. A Mann-Whitney U test found that oak basal

Table 9.6. ANOVA tables for **a.** planted birch and **b.** planted oak height and basal diameter growth in 1999-2000 and 2000-2001. Intercept, plot (blocking term), and factors found non-significant by Wilk's Λ tests were omitted from the table but included in the models.

a. Abbreviated ANOVA tables for birch growth variables. Total df = 68.

Variable	Source	df	Mean Square	F	P
Birch Height Growth 1999-2000	Exclosure	1	8508	55.72	≤ 0.0001
	Error	44	152.7		
Birch Height Growth 2000-2001	Exclosure	1	12885	66.63	≤ 0.0001
	Error	44	193.4		
Birch Basal Diam. Growth 1999-2000	Exclosure	1	3.80	59.83	≤ 0.0001
	Error	44	0.063		
Birch Basal Diam. Growth 2000-2001	Exclosure	1	1.32	74.37	≤ 0.0001
	Error	44	0.018		

b. Abbreviated ANOVA tables for oak growth variables. Total df = 128.

Variable	Source	df	Mean Square	F	P
Oak Height Growth 1999-2000	Exclosure	1	2217	40.28	≤ 0.0001
	Error	100	55.03		
Oak Height Growth 2000-2001	Exclosure	1	13.39	73.43	≤ 0.0001
	Error	100	0.18		
Oak Basal Diam. Growth 1999-2000	Exclosure	1	0.20	51.28	≤ 0.0001
	Error	100	0.0039		
Oak Basal Diam. Growth 2000-2001	Exclosure	1	1.10	115.56	≤ 0.0001
	Error	100	0.0095		

diameter growth from 1999-2000 was significantly (P = 0.030) improved by weeding in the *Agrostis-Galium* vegetation type. Weeding treatments had no influence on planted tree growth in any other vegetation type.

9.2 Provenance

The five oak provenances marked and planted in Wicklow experienced different rates of mortality over the three years of the study (Table 9.7). Likelihood ratio tests revealed significant differences between provenances for mortality in 1999 and also for total mortality. Oak from Bollisce, Co. Galway had the highest total mortality and mortality in 1999, while

Table 9.7. Percent mortality by provenance of oak seedlings planted in Wicklow. The number of trees dying follows in italics. Provenance sample size is given in parentheses. P-values are from likelihood ratio tests.

	Galway (792)	Donegal (311)	Antrim-Drum. (118)	Antrim-Rea's (37)	Wicklow (187)
Mortality 1999 (%)	25.3	15.6	16.9	16.2	9.2
$P \leq 0.0001$	*198*	*48*	*20*	*6*	*17*
Mortality 2000 (%)	27.5	27.6	28.6	29	18.3
$P = 0.137$	*163*	*72*	*28*	*9*	*31*
Mortality 2001 (%)	11.6	6.8	12.9	9.1	18.0
$P = 0.080$	*50*	*13*	*9*	*2*	*29*
Total Mortality (%)	51.9	42.8	48.3	45.9	39.0
$P = 0.019$	*411*	*133*	*57*	*17*	*73*

Coolgreany, Co. Wicklow oak experienced the lowest. It is notable that Wicklow oak survived the best in the Wicklow plots. These seedlings, however, were obtained from a different nursery than the other provenances. Wicklow oaks had noticeably better fine root systems, which may be responsible for markedly lower first year mortality (Table 9.7). Differences in nursery treatment, perhaps in soil, instead of genetic factors may therefore be responsible for better growth rates.

Significant differences in height and basal diameter growth among oak provenances were also found (Figs. 9.1-9.4). Galway and Wicklow oaks had lower height growth increments over both intervals than the other three provenances, while the Drumaheglish, Co. Antrim, provenance consistently had the highest height and basal diameter growth rates over both intervals. Again, differences between provenances may simply be due to nursery origin. The consistently poor relative growth and survival of Galway oak, however, suggests that this provenance may not be well suited to Wicklow conditions or that the genetic stock is inferior.

When mortality and growth were divided into exclosed and unexclosed plots, few differences among provenances were found in unexclosed plots. Results from exclosed plots were similar to results from the combined analyses in Table 9.7 and Figs. 9.1-9.4.

Figure 9.1. Oak height growth 1999-2000 histogram. Height growth differs significantly among provenances according to a Kruskal-Wallis H ranks test ($P \leq 0.0001$). Mean ranks (descending) shown in parentheses after legend.

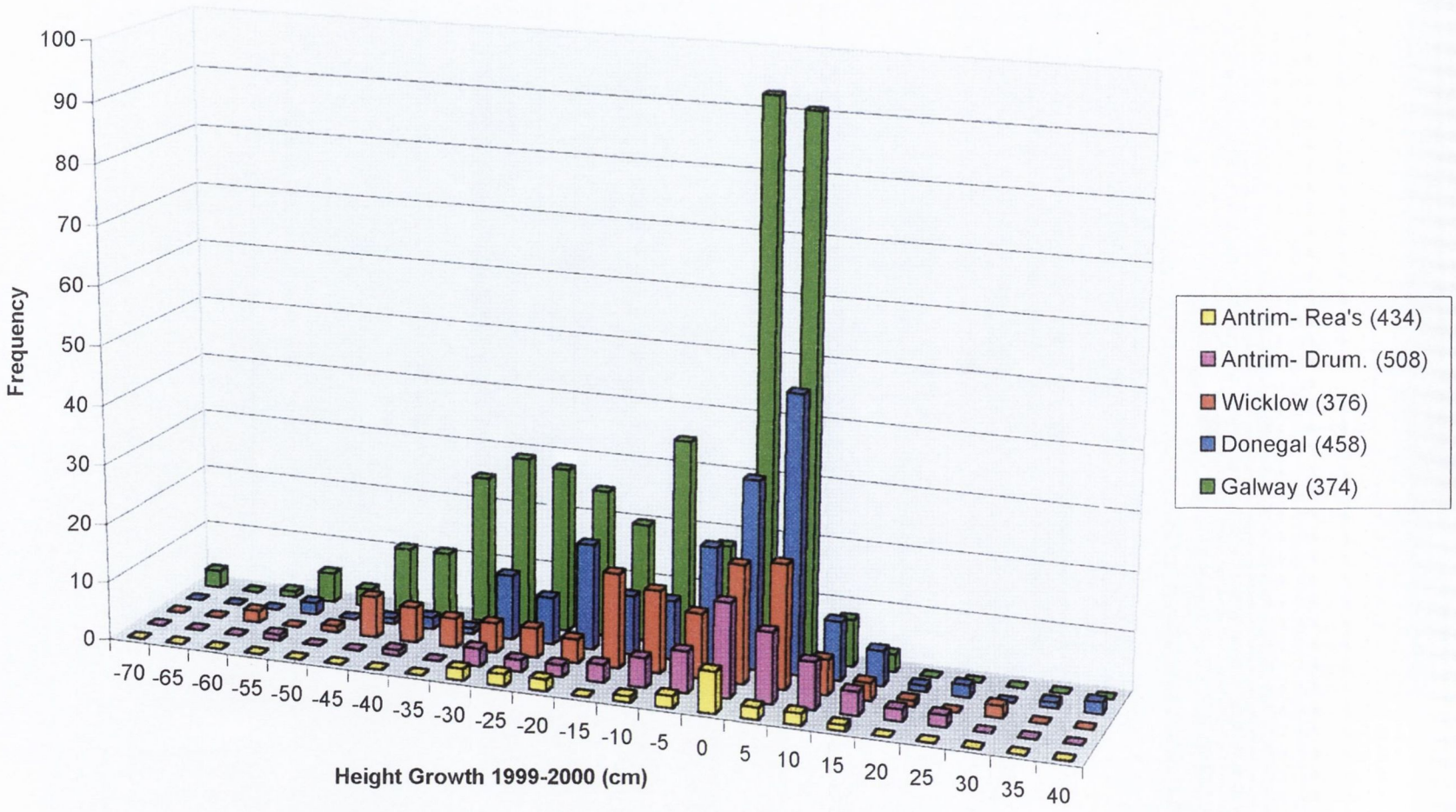


Figure 9.2. Oak height growth 2000-2001 histogram. Height growth differs significantly among provenances according to a Kruskal-Wallis H ranks test (P = 0.001). Mean ranks (descending) shown in parentheses after legend.

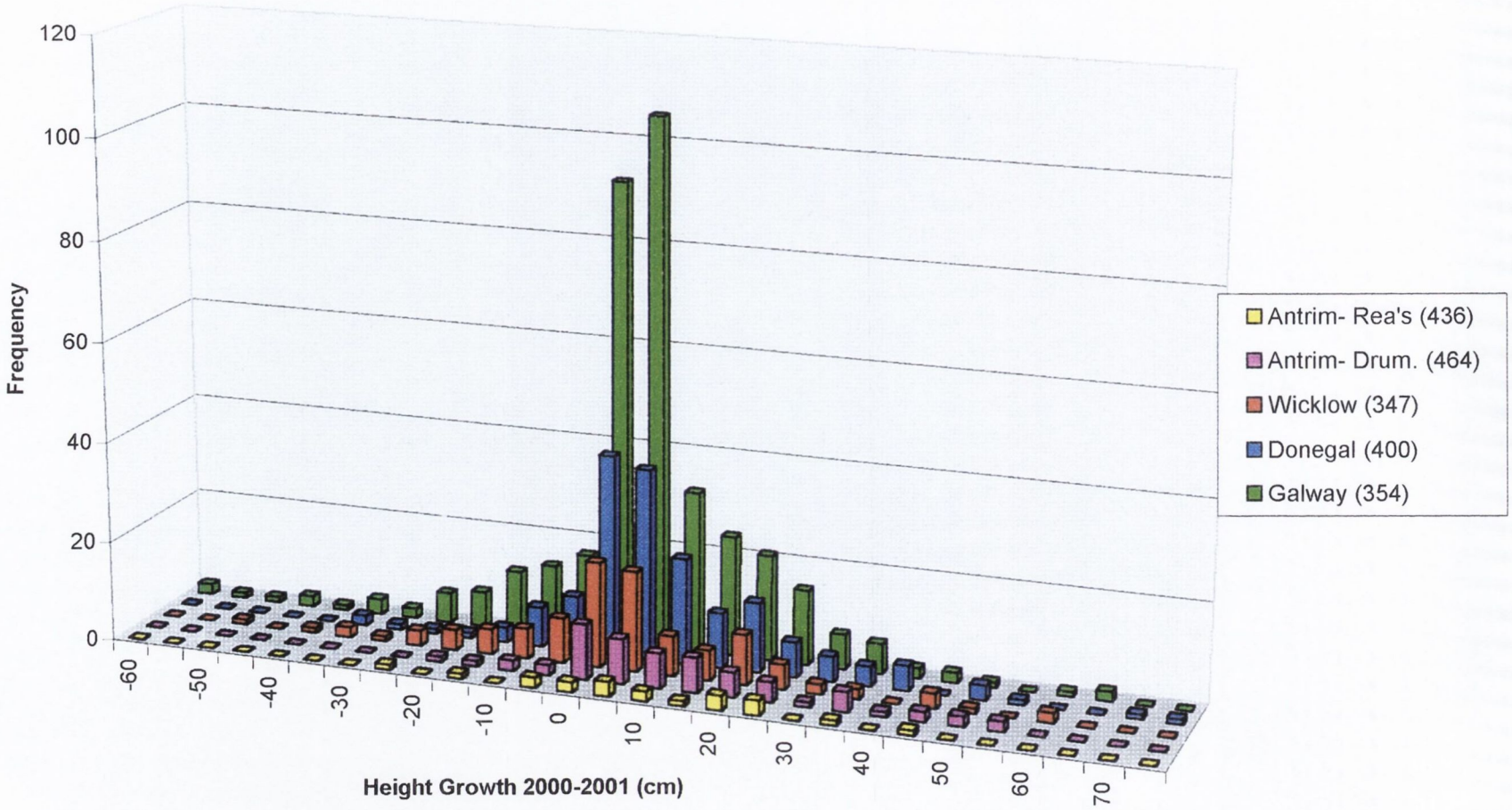


Figure 9.3. Oak basal diameter growth 1999-2000 histogram. Basal diameter growth differs significantly among provenances according to a Kruskal-Wallis H ranks test ($P \leq 0.0001$). Mean ranks (descending) shown in parentheses after legend.

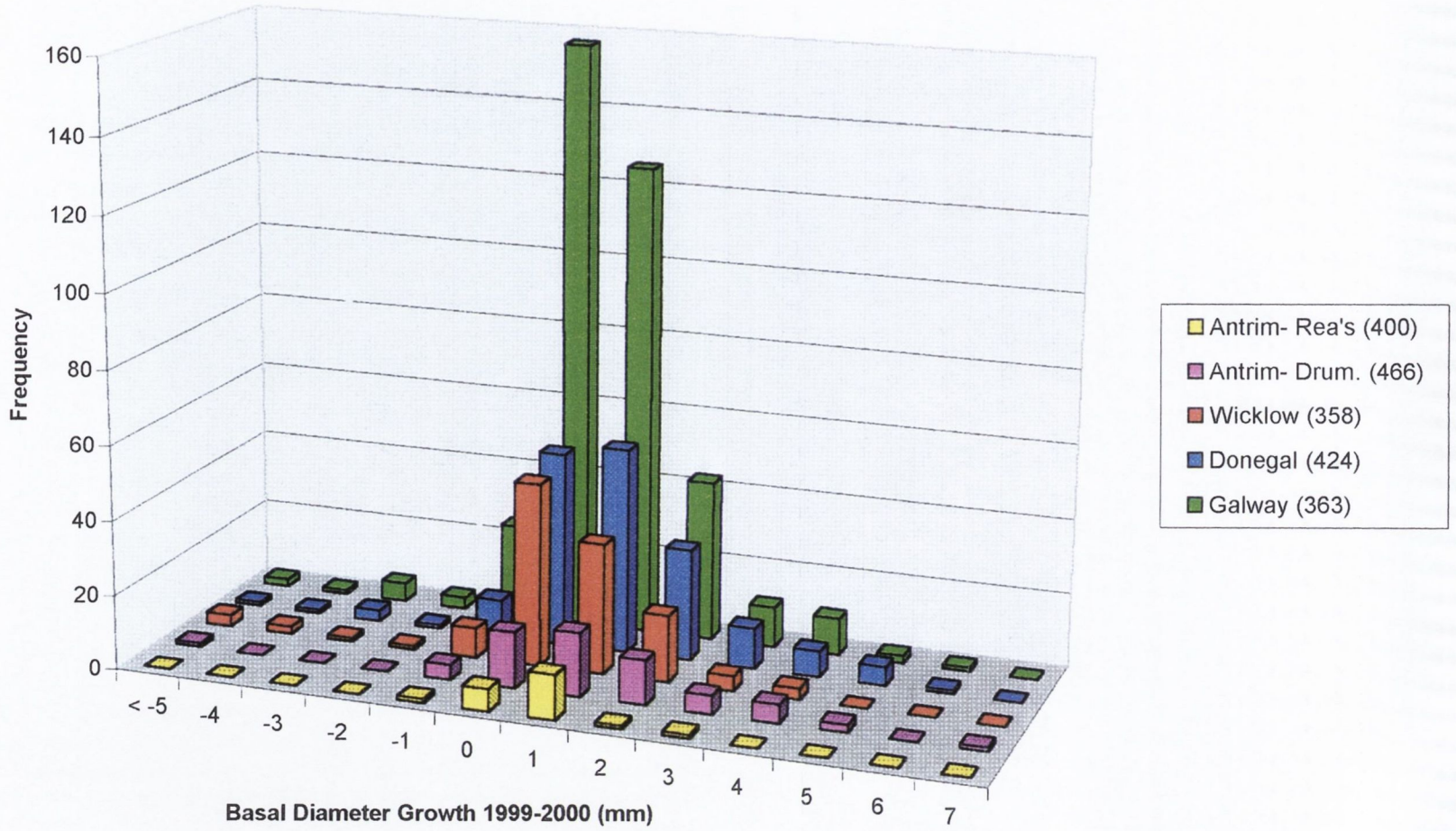
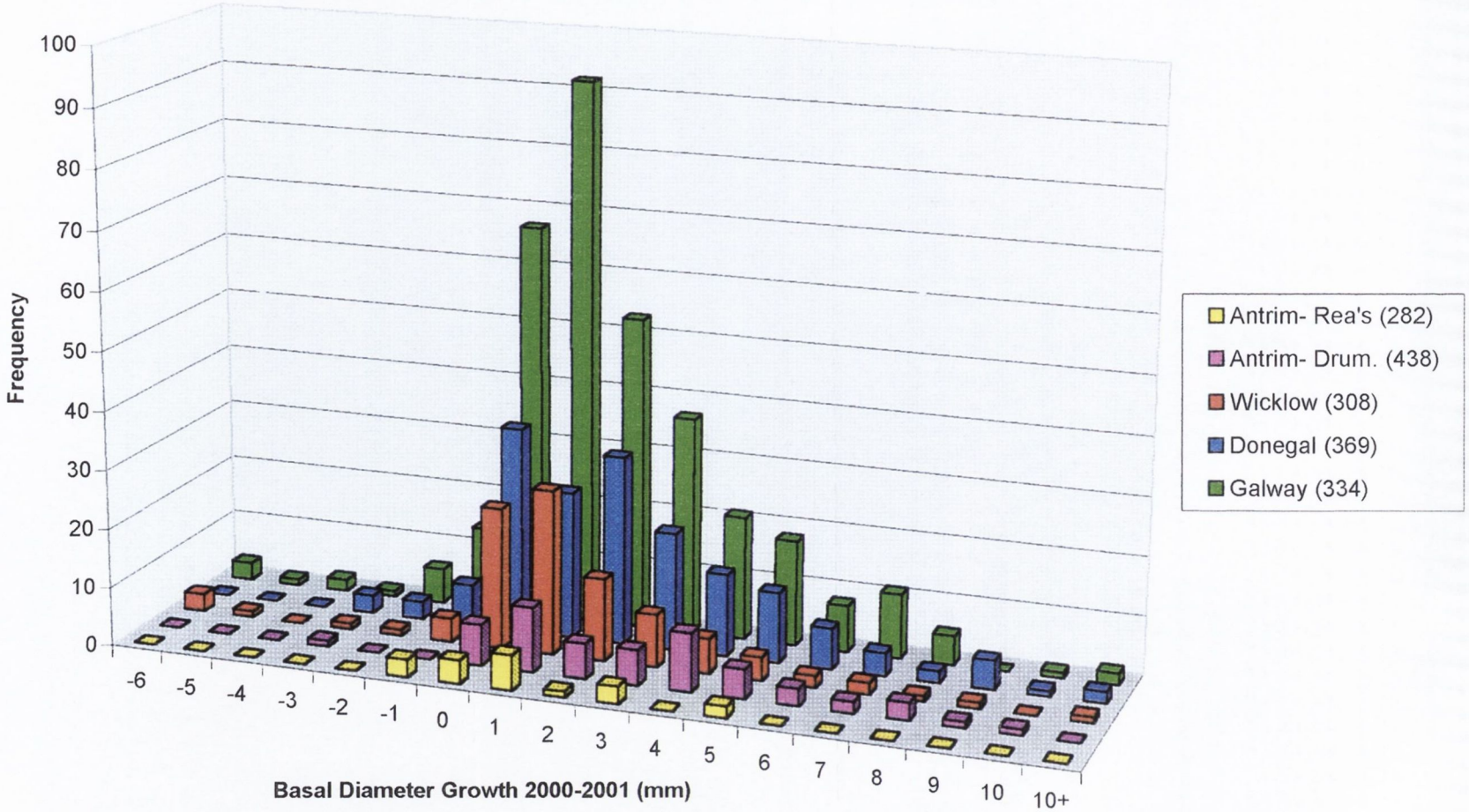


Figure 9.4. Oak basal diameter growth 2000-2001 histogram. Basal diameter growth differs significantly among provenances according to a Kruskal-Wallis H ranks test ($P \leq 0.0001$). Mean ranks (descending) shown in parentheses after legend.



9.3 Small Mammal Browsing

Many planted trees were damaged by small mammalian herbivores able to pass through the fences. Over all three sample years, 41.0% of planted oaks and 39.3% of planted birch were damaged by small mammals. Judging by several signs, hares (*Lepus timidus hibernicus*) were the main culprits: hare droppings were common in most of the plots, damage on trees occurred higher than other small herbivores could reach, and the types of damage were characteristic of hares (Bouchner, 1990). Damage caused by hares was generally of two types: bark-stripping, which in some cases obviously girdled and killed the trees, and severing of the stem or branches which left a clean, slanted cut. Stem severing was most apparent on oaks in *Agrostis-Galium* and *Pteridium-Agrostis* vegetation, which occur mostly in the Glendalough plots. This type of herbivory did not appear to be as lethal as bark-stripping. Fine tooth-marks of mice or similar small rodents were also found on stem bases, but usually caused little harm to the tree.

Herbivory by small mammals in 1999 significantly increased planted oak and birch mortality in 2000, but herbivory in 2000 did not cause a similar mortality increase in 2001, according to likelihood ratio tests (Table 9.8). The relationship between small mammal herbivory and tree growth was not so straightforward. Oaks browsed in 1999 had significantly lower height growth over the 1999-2000 interval (Table 9.9). Oaks browsed in 2000, however, exhibited significantly *higher* height and basal diameter growth during 2000-2001. Birch browsed in 2000 also had higher 2000-2001 growth rates (Table 9.9).

Occurrence of small mammal herbivory varied significantly by vegetation type (Table 9.10). For both oak and birch, the proportion of browsed trees was lowest in the High *Calluna-Erica* vegetation type and *Digitalis-Juncus* vegetation types. Oak herbivory was by far most common in the *Pteridium-Agrostis* type, where stem severing was the main mode of damage.

Table 9.8. Percent mortality of planted oak and birch in exclosures in 2000 and 2001 browsed by small mammals the previous year. P-values are the results of likelihood ratio tests.

		Browsed	Not Browsed	P
Oak	*2000 Mortality*	33.8	23.2	0.0010
	2001 Mortality	10.5	12.3	0.3300
Birch	*2000 Mortality*	31.8	14.6	0.0003
	2001 Mortality	20.7	16.3	0.3300

Table 9.9. Mean (± se) height and basal diameter growth of planted oak and birch in exclosures browsed by small mammals the previous year. P-values are the results of Mann-Whitney U tests.

		Browsed	Not Browsed	P
Oak	*1999-2000 Height Growth (cm)*	-12.3 ± 1.1	-8.4 ± 0.5	0.003
	2000-2001 Height Growth (cm)	5.1 ± 0.9	1.6 ± 0.5	0.001
	1999-2000 Basal Diameter Growth (mm)	0.6 ± 0.1	0.8 ± 0.05	0.379
	2000-2001 Basal Diameter Growth (mm)	1.8 ± 0.1	1.4 ± 0.09	0.013
Birch	*1999-2000 Height Growth (cm)*	-2.7 ± 3.1	0.1 ± 1.1	0.604
	2000-2001 Height Growth (cm)	12.9 ± 2.2	5.7 ± 1.4	0.014
	1999-2000 Basal Diameter Growth (mm)	2.5 ± 0.3	1.7 ± 0.1	0.078
	2000-2001 Basal Diameter Growth (mm)	3.8 ± 0.4	2.4 ± 0.2	0.003

Table 9.10. Percent occurrence of small mammal herbivory in any year by vegetation type in exclosed plots. P-values are results of a likelihood ratio test.

	Agrostis-Galium	*Calluna-Galium*	Low *Calluna-Erica*	High *Calluna-Erica*	*Digitalis-Juncus*	*Pteridium-Agrostis*	P
Oak	54.3	57.6	35.9	5.4	21.3	71.4	≤0.0001
Birch	36.9	58.4	46.2	5.7	18.2	50.0	≤0.0001

9.4 Other Seedling Damage and Disease Symptoms

Numbers of planted oak and birch affected by insect damage, mechanical damage, leaf fungi, and chlorotic and necrotic patches on leaves are presented in Table 9.11. Unidentified leaf herbivores were responsible for most of the observed insect damage. In two Glenmalure plots, large pine weevils (*Hylobius abietis*) severely attacked the stems of planted trees, particularly birches. Mechanical damage was mostly caused by the young trees knocking or abrading against brash. A small number of trees were stepped on by large herbivores, such as deer or sheep, or omnivores with metre sticks. Oak leaves were often affected by the mildew *Microsphaera alphitoides* which can be seriously damaging in some circumstances

Table 9.11. Numbers of live planted trees in exclosed and unexclosed plots affected by insect damage, mechanical damage, leaf mildew or rust, chlorosis, and necrosis. Sample size follows in parentheses. Trees without leaves (because of browsing or other factors) are included only in the mechanical damage summaries. Chlorosis and necrosis were not consistently recorded in 2000 and have been omitted.

		Insect Damage	Mechanical Damage	Leaf Fungi	Chlorosis	Necrosis
Oak	*1999*	70 *(1525)*	45 *(1660)*	135 *(1525)*	58 *(1525)*	58 *(1525)*
	2000	30 *(1183)*	22 *(1246)*	54 *(1183)*	-	-
	2001	51 *(1100)*	63 *(1111)*	92 *(1100)*	182 *(1100)*	147 *(1100)*
Birch	*1999*	14 *(528)*	20 *(565)*	1 *(528)*	98 *(528)*	98 *(528)*
	2000	1 *(467)*	21 *(527)*	7 *(467)*	-	-
	2001	4 *(415)*	30 *(432)*	47 *(415)*	25 *(415)*	20 *(415)*

(Jones, 1959; Shaw, 1974; Kelly, 2002). Birch leaves were commonly infected by the yellow-orange rust *Melampsoridium betulinum*, the major leaf pathogen of birches (Atkinson, 1992). Chlorosis, a yellow mottling of leaves, is the most common symptom of mineral deficiency in trees (Manion, 1981). Dead patches on leaves, necrosis, are generally symptoms of biotic disease agents, especially fungi, but can also be caused by frost damage (Manion, 1981).

In one plot in 2001, sporocarps of the ectomycorrhizal fungus *Laccaria laccata* were found in close proximity to six oaks and three birch. If these trees were infected, the fungus had no significant effect on height and basal diameter growth in 2000-2001 (according to a non-significant Mann-Whitney U test). Infection by parasitic fungi such as *Armillaria mellea* and *Heterobasidion annosum* may cause difficulties in reforestation (Murray, 1974). Although *Armillaria* fruiting bodies were frequently observed on dead conifer roots in and around the plots, the fungus was not found on any live tree seedlings and only on one dead oak. Unidentified stem fungi infected two birch and one oak.

Because most of these agents damage leaves, and trees planted outside exclosures were often browsed heavily, sometimes to bareness, the effects of disturbance agents on seedling growth

and mortality were tested (likelihood ratio and Mann-Whitney U tests) using only trees in exclosures.

Birch height and basal diameter growth in 2000-2001 were significantly ($P = 0.0002$) and positively associated with mechanical damage in 2000. Similarly, mechanical damage in 2000 was positively associated with oak basal diameter growth in 2000-2001 ($P = 0.004$). Given that the majority of mechanical damage was caused by brash, the explanation may be that a greater abundance of brash favours tree growth by sheltering trees from small herbivores or wind, or by some other mechanism. It is also possible that these results simply indicate that taller trees are more likely to be damaged by brash.

Presence of leaf rust on birches had no significant effects on growth or survival. Oak height and basal diameter growth in 1999-2000 was significantly ($P \leq 0.0001$) greater for seedlings infected by oak mildew in 2000. Similarly, greater growth over 2000-2001 was observed in trees infected in 2001 ($P \leq 0.0001$). Infection had no effects on the following year's growth or mortality. The best explanation of these results is that mildew tends to affect the lammas shoots of oaks more than the first flush of growth (Jones, 1959; Murray, 1974; Kelly, 2002). I observed this in the field and also in a young pedunculate oak (*Quercus robur*) plantation in Co. Longford (unpublished data).

Relationships between insect damage and oak and birch growth and survival were not statistically significant. The effects of leaf-eating insects, however, are confounded with damage caused by *Hylobius abietis*. Some of the trees in the two plots badly damaged by weevils died, and more died-back, apparently as a result of girdling primarily around the lower branches. *Hylobius* should therefore be considered a locally important impediment to tree establishment in recent clearfells.

Presence of chlorotic or necrotic patches on leaves were not significantly associated with the growth or survival of planted oak and birch.

9.5 Environmental Factors

9.5.1 Exclosed Oak CCA

The preliminary canonical correspondence analysis (CCA) of exclosed oak performance variables and environmental variables (see section 8.4.3 for details on variables used) resulted in four environmental variables with correlations less than 0.2 or greater than -0.2 with the first three canonical axes: soil depth, topex, Mn^{2+} concentration and percent cover of bare soil.

These variables were then deleted from the environmental data, and a final CCA was performed. The first three canonical axes of the final CCA explained 54.7% of the variance in the planted oak data. Axis 1 accounted for 38.8%, Axis 2 accounted for 9.6%, and Axis 3 explained 6.2% of total variance in the oak data (Table 9.12). Monte Carlo tests on the eigenvalues and species-environment correlations of each axis confirmed significant relationships between the canonical axes and the oak data matrix ($P \leq 0.015$), using 199 randomised runs).

Axis 1 separates the subplots that suffer high mortality on the right from those that experience lower mortality and better first year growth on the left of the ordination biplot (Table 9.12, Figs. 9.5a,b). Axis 2 contrasts sites that experience a large first-year height decrease and good second year growth, towards the bottom of the biplot, with those with better first-year but poor second-year height growth, towards the top of the biplot (Table 9.12, Fig. 9.5a). Axis 3 separates plots with good second-year diameter and height growth from those with poor second-year growth (Table 9.12, Fig. 9.5b).

Mortality in 1999 is most strongly associated with sites with low cover of field layer vegetation and low concentrations of available K^+ (Fig. 9.5a). Damage by small herbivores, steeper slopes, lower soil organic and Ca^{2+} content, and lower annual precipitation are also associated with first-year mortality (Fig. 9.5b). These results suggest that low soil moisture and low cation availability may reduce the survival of recently planted oaks. Mortality for 2000-2001 was more strongly correlated with herbivory by small mammals than was first-year mortality (Fig. 9.5a,b). Second and third-year mortality was also associated with steeper slopes, lower precipitation, lower organic content, lower Ca^{2+} availability, and higher mean annual temperatures.

Since Axis 1 seems to reflect primarily patterns in mortality (Table 9.12), further support for the importance of soil moisture for oak survival can be found in the correlations of the less important environmental variables with Axis 1. Water-retention capability of the upper soil layer, the *Digitalis – Juncus* vegetation type, bryophyte cover and occurrence of gleying are negatively associated with Axis 1, and thus positively associated with survival (Table 9.12). Sites with northeastern aspects, however, are positively associated with Axis 1.

Height growth from 1999-2000 was strongly correlated with organic content, Ca^{2+} availability, precipitation, and shallower slopes (Fig. 9.5a). Like survival, height growth (or failure to die back) in the first year after planting was improved by wetter soil conditions. Small mammal damage appears to have had a stronger influence on height growth over the first interval (Figs.

Table 9.12. CCA of exclosed oak growth variables: correlations between environmental variables and fitted site scores (subplots). Statistical significance (df = 82) is indicated by asterisks: *, $P \leq 0.05$; **, $P \leq 0.01$. Total variance in the oak data was 0.353. Also presented are post-hoc correlations of the oak performance variables with the canonical axes and eigenvalues, the percent variance represented by the eigenvalues, and the species – environment correlations for the first three canonical axes.

	Axis 1	Axis 2	Axis 3
Eigenvalue [1]	0.137	0.034	0.022
Percent Variance Explained	38.8	9.6	6.2
Species-Environment Correlation [2]	0.840	0.744	0.611
			Pearson Correlations
Height Growth 1999-2000	-0.424	0.496	-0.019
Diameter Growth 1999-2000	-0.282	-0.030	0.009
Height Growth 2000-2001	0.252	-0.288	0.362
Diameter Growth 2000-2001	0.116	-0.187	0.441
Mortality 1999	0.780	0.231	0.172
Mortality 2000 and 2001	0.654	-0.109	-0.205
Hare Damage	0.676**	-0.382**	0.193
Precipitation	-0.663**	0.383**	-0.350**
Organic Content	-0.573**	0.205	-0.219*
Slope	0.453**	-0.089	0.273*
Ca^{2+}	-0.418**	0.446**	-0.445**
Field layer Cover	-0.400**	-0.274*	-0.284**
SW Topex	0.377**	-0.099	0.144
Upper Soil Index	-0.355**	-0.218*	0.017
Litter Cover	0.348**	-0.037	-0.191
Digitalis – Juncus type	-0.321**	0.035	0.042
K^{+}	-0.315**	-0.357**	-0.128
Gleying	-0.313**	0.010	-0.234*
Bryophyte Cover	-0.303**	0.148	0.047
Temperature	0.295**	0.144	-0.372**
Aspect (NE)	0.300**	-0.101	-0.070
Date of Planting	0.229*	-0.472**	0.432**
Wood Cover	0.228*	0.272*	0.221*
Low *Calluna – Erica* type	-0.208	0.029	0.053
High *Calluna-Erica* type	-0.202	0.319**	-0.063
Agrostis – Galium type	-0.122	-0.404**	-0.111
Lower Soil Index	-0.107	0.351**	-0.123
Pteridium – Agrostis type	-0.092	-0.301**	-0.041
pH	0.089	-0.312**	0.098
Rock Cover	-0.036	0.260*	0.092
Brash Height	0.004	0.064	0.343**

[1] Statistics are significant ($P = 0.005$) based on Monte Carlo permutation tests using 199 randomised runs.

[2] Statistics are significant ($P \leq 0.015$) based on Monte Carlo permutation tests using 199 randomised runs.

Figure 9.5a. Correlation biplot of axes 1 and 2 of a CCA oak performance and environmental variables. Environmental variables with $R^2 < 0.15$ for any axis are not shown. Correlations between environmental and tree variables are reflected by the angles between their vectors. The percent variance explained ($\lambda_i / \lambda_{sum}$) by each axis is shown. Triangles indicate the ordination of the subplots.

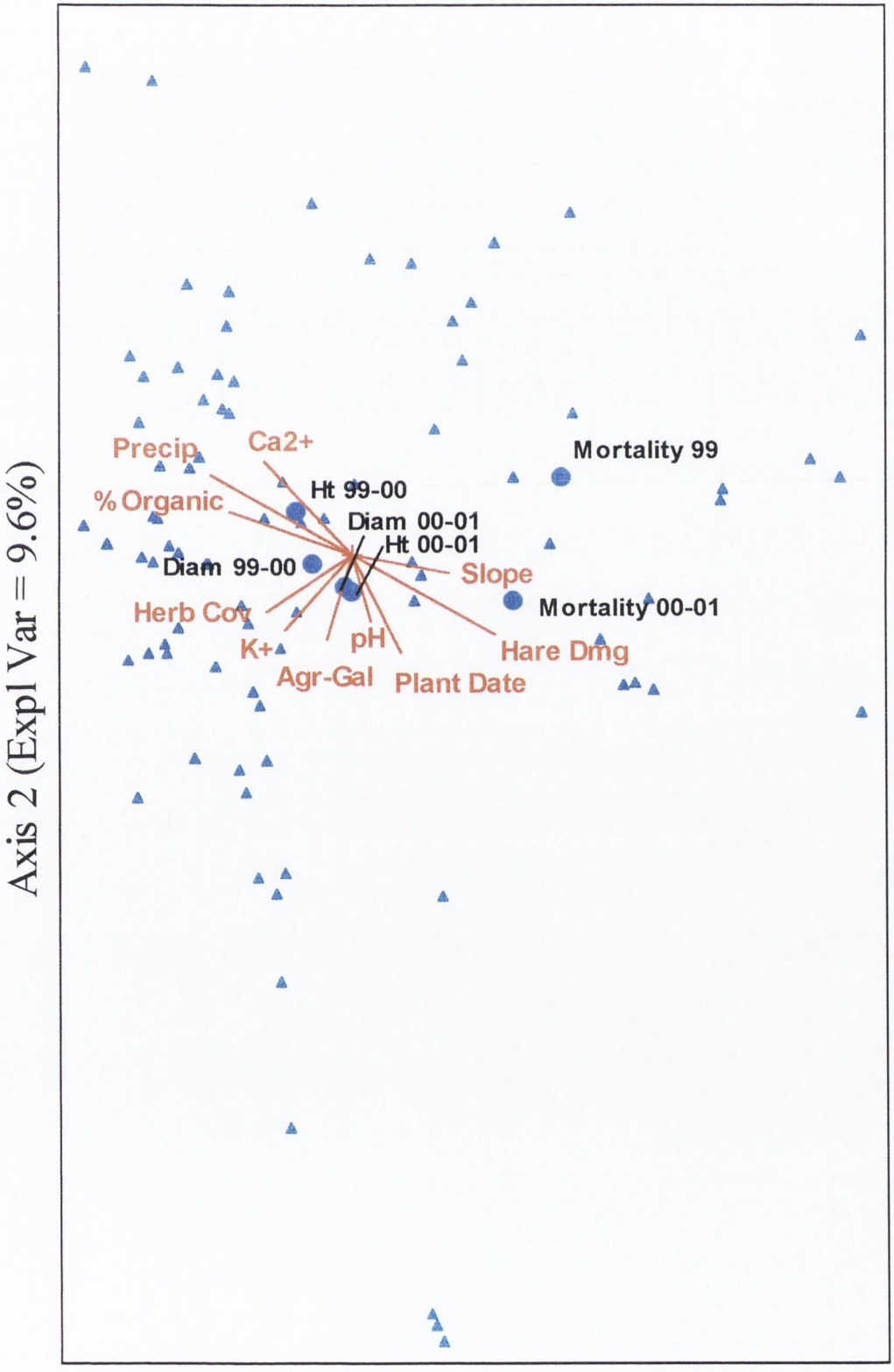
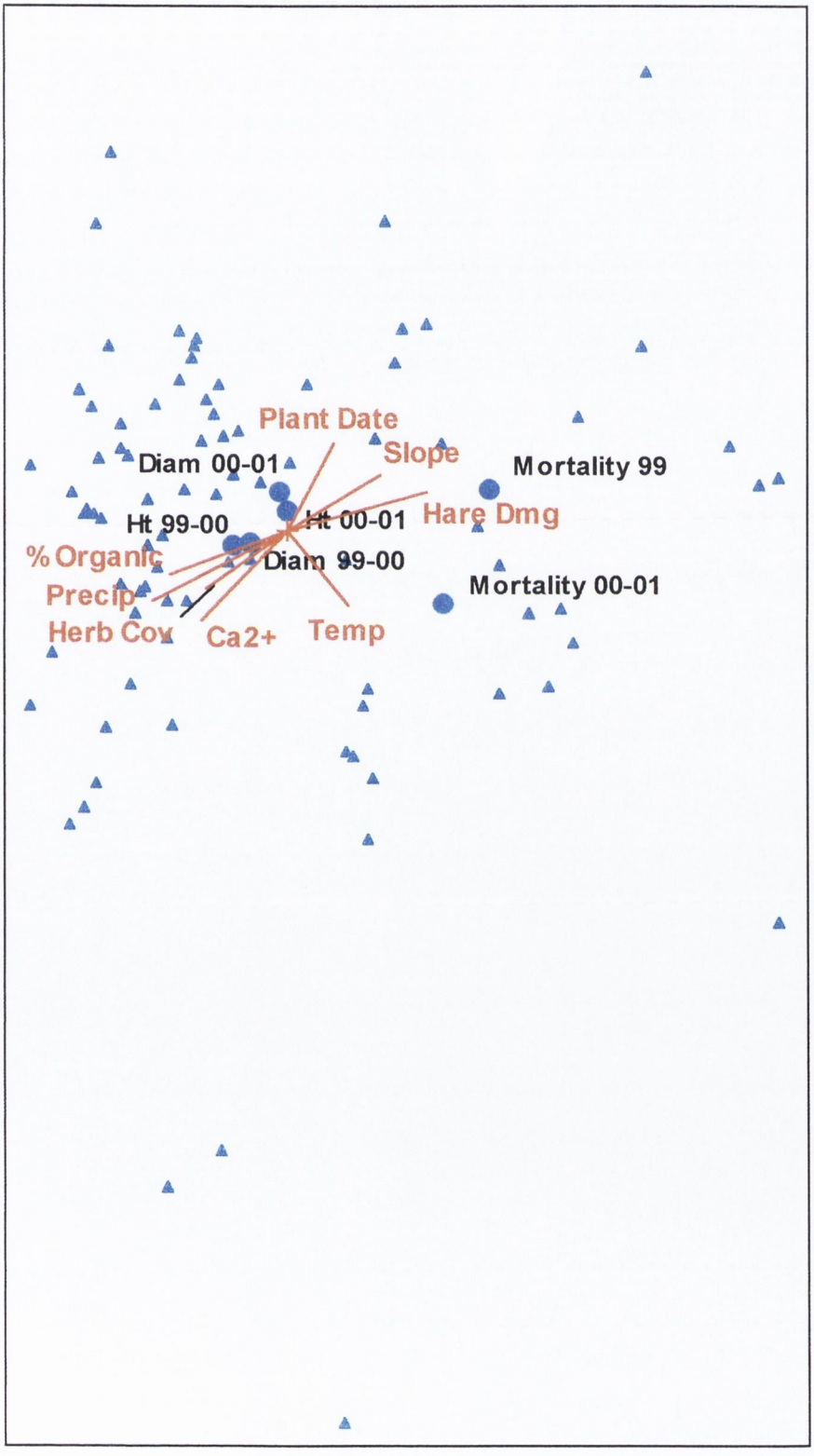


Figure 9.5b. Correlation biplot of axes 1 and 3 of a CCA oak performance and environmental variables. Environmental variables with $R^2 < 0.15$ for any axis are not shown. Correlations between environmental and tree variables are reflected by the angles between their vectors. The percent variance explained ($\lambda_i / \lambda_{sum}$) by each axis is shown. Triangles indicate the ordination of the subplots.



9.5a,b); it was associated with decreases in height in 1999-2000, as confirmed by the Mann-Whitney U test above (Table 9.9). Planting later in the season also exacerbated the problem of dieback in the first year. Diameter growth from 1999-2000 was associated to a lesser extent with most of these factors and to a greater extent with field layer vegetation cover (Figs. 9.5a,b).

Oak height and basal diameter growth in 2000-2001 behaved differently with respect to site and soil variables than in 1999-2000 (Figs. 9.5a,b). Sites with less acid and somewhat drier soils and lower annual temperatures were associated with better growth in 2000-2001 (Figs. 9.5a,b and Table 9.12). Greater brash height also encouraged better second-year growth, as indicated by a positive correlation with Axis 3 (Table 9.12). K^+ availability is well correlated with second-year growth, but Ca^{2+} is not (Fig. 9.5a). In this study, available Ca^{2+} and Mg^{2+} concentrations are higher in more organic soils (Spearman r = 0.69 and 0.62 respectively with organic content) whereas available K^+ had a small negative correlation with organic content (r = -0.12). The negative correlation of organic content with Axis 3 and association with the *Agrostis – Galium* vegetation type also suggests improved second-year growth in sites with more mineral-rich soils (Fig. 9.5a,b).

9.5.2 Exclosed Birch CCA

Three environmental variables with correlations less than 0.2 or greater than –0.2 with the first three canonical axes were removed following the preliminary CCA of birch performance variables: bryophyte cover, rock cover, and brash height. The first three axes of the final CCA explained 68.9% of the variance in the planted birch data. Axis 1 accounted for 42.4%, Axis 2 accounted for 18.5%, and Axis 3 explained 7.9% of total variance in the birch data (Table 9.13). Monte Carlo tests on the eigenvalues and species-environment correlations of each axis confirmed a significant relationship only between the first canonical axis and the birch data matrix (Table 9.13). These results, and an inspection of the ordination of subplots (Fig. 9.6), suggest that the responses of birch growth and mortality to the environment are less complex than those of planted oak seedlings.

Axes 1 and 2 adequately summarise the birch performance data (Fig. 9.6). Mortality in 1999 increases to the lower right, mortality in the subsequent two years increases to the upper right, and growth increases to the left of the ordination plot. The CCA biplot and Table 9.13 show that 1999-2000 birch growth variables and mortality in 1999 were associated with the same set of environmental variables. Many of these were the same soil variables important for oak performance, contrasting wetter, more acidic and more organic sites with drier, better drained

Table 9.13. CCA of exclosed birch growth variables: correlations between environmental variables, and fitted site scores (subplots). Statistical significance (df = 40) is indicated by asterisks: *, $P \leq 0.05$; **, $P \leq 0.01$. Total variance in the birch data was 0.408. Also presented are post-hoc correlations of the birch performance variables with the canonical axes and eigenvalues, the percent variance represented by the eigenvalues, and the species – environment correlations for the first three canonical axes. P-values are the results of Monte Carlo permutation tests using 199 randomised runs.

	Axis 1	**Axis 2**
Eigenvalue	0.173 *(P = 0.020)*	0.076 *(P = 0.395)*
Percent Variance Explained	42.4	18.5
Species-Environment Correlation	0.922 *(P = 0.020)*	0.810 *(P = 0.415)*
	Pearson Correlations	
Height Growth 1999-2000	-0.572	0.310
Diameter Growth 1999-2000	-0.341	0.473
Height Growth 2000-2001	-0.123	0.124
Diameter Growth 2000-2001	-0.006	0.350
Mortality 1999	0.753	-0.332
Mortality 2000 and 2001	0.594	0.496
Ca^{2+}	-0.569**	-0.056
Organic Content	-0.567**	0.229
Hare Damage	0.537**	-0.063
pH	0.513**	-0.244
Date of Planting	0.504**	-0.110
Precipitation	-0.504**	0.250
Digitalis – Juncus type	-0.421**	0.358*
Soil Depth	-0.409**	0.250
Slope	0.383*	-0.309*
Topex	0.370*	-0.054
Mn^{2+}	0.365*	-0.318*
Pteridium – Agrostis type	0.293	0.042
Temperature	-0.278	-0.159
Upper Soil Index	-0.239	0.267
SW Topex	0.236	-0.155
Low *Calluna – Erica* type	-0.204	-0.073
High *Calluna – Erica* type	-0.185	-0.092
Field layer Cover	-0.178	-0.302
Aspect (NE)	0.142	-0.252
Gleying	-0.137	-0.029
Soil Cover	0.116	0.327*
Wood Cover	0.088	0.399**
Lower Soil Index	-0.063	0.058
Litter Cover	0.049	0.240
K^{+}	-0.045	-0.248
Agrostis – Galium type	-0.035	-0.280

Figure 9.6. Correlation biplot of axes 1 and 2 of a CCA of birch performance and environmental variables. Environmental variables with $R^2 < 0.15$ for any axis are not shown. Correlations between environmental and tree variables are reflected by the angles between their vectors. The percent variance explained ($\lambda_i / \lambda_{sum}$) by each axis is shown. Triangles indicate the ordination of the subplots. Note that the eigenvalue for Axis 2 is not significant (P = 0.395).



sites. The *Digitalis – Juncus* vegetation type emerged as a potential indicator community for good first-year birch growth and survival. Also like oaks, later planting dates increased mortality and decreased growth in the first year. Hare damage and, strangely, topex (a measure of the shelteredness of a site) are associated with higher mortality in 1999 and lower growth. Height and basal diameter growth from 2000-2001 are less well predicted by the environmental variables measured. Height growth from 2000-2001 is positively associated with higher temperature and available Ca^{2+} and more exposed sites. Diameter growth over the same interval, however, is uncorrelated with Axis 1, the main axis of variation in the data. Mortality in 2000 and 2001 is not well explained by most of the site variables used in the CCA. Topex, hare damage, lower temperature, and lower Ca^{2+} availability are the best predictors of higher mortality in the last two years.

CHAPTER 10

PLANTED TREE STUDY: DISCUSSION

10.1 Herbivory

10.1.1 Exclosure of Large Herbivores

As the results comparing tree growth and mortality inside and outside exclosures demonstrate (section 9.1), browsing by large herbivores was the most important factor inhibiting tree growth and survival in this study. Although Irish woodland communities may have developed since the last glaciation in the presence of large herbivores, it is widely accepted that the grazing pressure present in many, if not most, woodlands and other habitats prevents tree regeneration (Hester *et al.*, 1998; Kelly, 2002). For example, Kelly (1975; 1981), using experimental deer exclosures, observed that heavy grazing prevented adequate regeneration of the majority of tree species in the Killarney woodlands. Similar experiments in England (Pigott, 1983) and Wales (Linhart & Whelan, 1980) found that excluding sheep and cattle grazing in oak-dominated woodland was sufficient to achieve adequate survival of tree seedlings, especially oak (*Quercus* species), where regeneration was previously prevented.

Although large herbivore densities appear to be too high for good tree growth and survival in all of the study sites, some estimates of their numbers may place the results of this study in context. In Killarney, the large herbivores were sika deer (*Cervus nippon*), red deer (*Cervus elaphus)* and sheep. The Muckross Forest site is used by 30-40 red deer, mostly during the winter months, and approximately 10 sika deer (P. O'Sullivan, pers. comm.). The (illegal) presence of 10-15 sheep during the summer and 50-60 sheep in the winter probably exerted stronger grazing pressure than the deer. In Looscaunagh, about 6 red deer and 10-15 sika deer were resident, although more sika deer in nearby Coillte forests probably also used the area (P. O'Sullivan, pers. comm.). The Looscaunagh clearfell areas are surrounded by a low fence that served to exclude most sheep, although from two to eight were observed inside this fence during each site visit.

In Wicklow, deer populations are red – sika hybrids originating from the Powerscourt Estate north of Glendalough (Cabot, 1999). Deer in woodlands and plantations resemble sika deer more closely, while deer of the open hill exhibit stronger red deer characteristics (W. Atkinson, pers. comm.). In the Glendalough site, deer counts in 1999 estimated a density of 20 animals / km^2 (D. Clarke, pers. comm.). Trespass by sheep also occurs in Glendalough. Although estimates of numbers are not available from the rangers, sheep were observed near plot pairs 8-

10 during most visits. Perhaps the strongest grazing pressure is exerted by the approximately 200 feral goats that range throughout Glendalough (D. Clarke, pers. comm.). Goats are primarily browsers, but switch to grazing if the quality of the forage is high (Mitchell & Kirby, 1990; Hester *et al.*, 1998). Estimates of deer numbers in Glenmalure are less accurate, and are hampered by much movement of the deer among land owners and high levels of poaching. A rough estimate of 10-15 deer / km^2 live in the upper part of the glen, where the plots are located, but further down the glen, surveys have estimated about 35 deer / km^2 (B. Coad, pers. comm.). Sheep are pastured on the south side of Fraughan Rock Glen during the summer, and occasionally enter the unexclosed plots, particularly plot pair 17. Sheep incursions appeared to be more frequent in the Baravore plots, but no signs of sheep were found in either of the Benleagh plots. Feral goats are not known to be present in Glenmalure, but cattle allowed to roam near the Baravore Ford in the summer infrequently entered the unexclosed plots in the Baravore site in 2000 and 2001.

In comparison, Staines *et al.* (1995) suggested a crude estimate of maximum red deer densities of 7 animals / km^2 to allow regeneration of Scots pine or birch (*Betula* spp.) on open ground in the uplands. These densities would need to be lower to permit regeneration of more favoured species, such as oak (*Quercus* species) or rowan. Reduction of trees and shrubs has been found to occur at red deer densities as low as 3 animals / km^2, and severe reduction of trees, shrubs and forbs and increased grass dominance has been observed at densities of 8.3 animals / km^2 (Kraus 1987 in Gill, 1992a). Hester *et al.* (1996) controlled the numbers of sheep grazing in woodland enclosures and concluded that very few seedlings would be able to grow to canopy height with sheep densities greater than 1.2 animals / ha.

10.1.2 Hare Browsing

Hares (*Lepus timidus hibernicus*) had a significant effect on the mortality and growth of planted trees (Fig. 9.5a; Tables 9.8, 9.9), but smaller herbivores such as mice appeared to be unimportant (section 9.3). The latter finding is similar to that of Kelly (2002), who found that while wood mice (*Apodemus sylvaticus*) were a significant cause of mortality to one year old oak seedlings, they had no perceptible impact on older seedlings. (Bank voles were introduced to Ireland around 1950 and are present in the Killarney area, but do not appear to have spread to Wicklow yet (Carruthers, 1998)). The observation that browsing by hares in 1999 but not in 2000 significantly increased mortality the following year (Table 9.8) may be the result of some combination of: (i) interaction with transplantation shock, (ii) a short-term fertiliser effect, (iii) production of chemical defenses by the trees, and (iv) greater availability of food in later years.

Trees particularly weakened by transplantation shock, especially birch, almost certainly suffered higher mortality when browsed. After the first year, the survivors will have become better established, and thus better able to survive additional stress.

There is anecdotal evidence to suggest that herbivores prefer planted trees to naturally regenerating trees (Gill, 1992b), probably because trees raised in nurseries have grown in more nutrient-rich soils. The higher nutrient concentrations in the foliage and bark of nursery-grown trees may make them more palatable to herbivores. An alternative mechanism linking fertilisation of trees with increased herbivory is known as the carbon : nutrient balance hypothesis. According to this theory, when scarcity of nutrients limits growth, excess carbon fixed during photosynthesis is allocated to secondary defensive compounds that render the tree less palatable (Rousi *et al.*, 1993; Hartley *et al.*, 1997). With increasing nutrient availability, carbon is allocated preferentially to growth, and chemical defenses against browsing are reduced. Planted oak and birch growing in nutrient-poor conditions in the second and third years and could have lost the greater palatability resulting from nursery care in the first year through either of these mechanisms.

Production of chemical defenses may also have been stimulated by browsing. Studies have found that defoliation of birch can increase the production of resinous compounds that reduce digestibility (Bryant & Kuropat, 1980; Atkinson, 1992; Gill, 1992b; Hjältén & Palo, 1992). Trees browsed in 1999 could have responded in such a fashion, thereby reducing the severity of browsing in 2000.

Lastly, the majority of the sites in this study are in early stages of succession and several were very poorly vegetated when trees were planted. As vegetation became more abundant in the second and third years, hares may have switched to alternative food sources. Irish hares have been found to prefer eating grasses and sedges to browsing woody species (Tangney *et al.*, 1995; Dingerkus & Montgomery, 2001; Strevens, 2002). They are able to retain this preference throughout the mild Irish winter, because of the absence of prolonged snow cover. Where *Calluna* is burned on the grouse moors of eastern Scotland, the young regrowth has been found to be very palatable to hares (Moss & Hewson, 1985; Hewson, 1989). Sites with high populations of hares, however, will still probably experience some degree of tree browsing. Strevens (2002) found that Irish hares persisted in browsing planted trees as late as June, despite the availability of alternative food.

Of these potential mechanisms, interaction with transplantation shock is probably one of the more important in this study. The preference of hares for trees with higher growth rates in the

second and third years (Table 9.9) suggests that food quality, in the form of higher nutrient concentrations or lower concentrations of defensive compounds as suggested by the carbon : nutrient balance hypothesis, is also a significant factor influencing hare browsing behaviour. Quality of browse is likely to be especially important in recently felled conifer stands, given the overall scarcity of food sources. Browsing behaviour in clearfells may be similar to that in places experiencing deep and prolonged winter snow cover where woody species are usually browsed when little other food is available (Bryant & Kuropat, 1980; Hjältén & Palo, 1992). The low probability of hare damage in the High *Calluna – Erica* vegetation type (Table 9.10) may reflect food-switching away from the planted trees, but it may also simply reflect fewer hares in the Muckross Forest site. Food-switching may also explain the lower probability of birch browsing in *Agrostis – Galium* vegetation. Although the higher likelihood of oak browsing does not support this argument, it is not clear if hare damage to planted oak was actual feeding. In acid grasslands and dense bracken stands in Glendalough, the primary form of damage to oaks was stem-severing rather than bark stripping (section 9.3). Almost always, the severed part of the tree was simply left on the ground with little evidence that much had been eaten. Hares prefer open spaces so they can better detect and evade predators (Hewson, 1977), and it may be that stem-severing behaviour is an effort to maintain such open conditions (Hewson, 1962).

10.1.3 Comparison of Oak and Birch

The differences in growth and mortality between oak and birch (Tables 9.1, 9.6), reflect the differences in ecology between the species. Birch, a pioneer species, is less tolerant of stressful conditions. High first-year mortality of birch was a consequence of both grazing in unfenced plots and transplantation shock in all plots. Oak is a slower-growing species more tolerant of stress, including browsing (Gill, 1992b), in part because of its much greater root : shoot ratio (Jones, 1959; Atkinson, 1992). With the densities of grazers present in the study sites, however, the oaks' hardiness only serves to delay mortality for a year. When protected from grazing, the growth of surviving birch was superior to that of oak, as would be expected.

10.1.4 Insect Herbivory

Unlike some studies conducted in woodlands (Watt, 1919; Shaw, 1974; Humphrey & Swaine, 1997b), insect herbivory of oak and birch was not a major factor in the majority of the study sites (Table 9.11). In woodlands in Britain, most of the insect damage to oak seedlings is usually caused by caterpillars dropping from the canopy (Shaw, 1974; Humphrey & Swaine, 1997b). In at least two plots, however, the large pine weevil, *Hylobius abietis*, was observed to be a significant cause of damage and mortality. *Hylobius* breeds under the bark of stumps and

roots of felled conifer plantations; in Britain, small-diameter lodgepole pine stands are most at risk of developing high populations (Heritage & Moore, 2001). The two worst-affected plots in this study, however, were in former Sitka spruce stands. Although prophylactic use of insecticides provides the greatest protection to trees planted in or near conifer clearfells, a number of other measures can be taken to reduce damage, such as felling between June and December and maximizing the area of bare mineral soil prior to planting (Löf, 2000; Heritage & Moore, 2001).

10.2 Vegetation Effects on Planted Trees

The weak effects of weeding in this study indicate that the effects of vegetation competition are not strong (section 9.1). In the low cover vegetation types, *Calluna – Galium* and Low *Calluna – Erica*, there was very little vegetation to weed, mostly very young *Calluna, Erica cinerea*, and low-growing *Galium saxatile*. In more competitive vegetation, weeding did have a beneficial effect on tree growth and / or survival. In the *Pteridium – Agrostis* type, improved survival with weeding of oak and birch in some years agrees with previous studies that have found that shading by *Pteridium* and smothering by dead fronds in the winter reduce growth of young oaks (Watt, 1919; Humphrey & Swaine, 1997a). The effects of weeding were more equivocal for oaks in *Agrostis – Galium* vegetation, resulting in both increased 2000 mortality and increased first-year basal diameter growth (sections 9.1.1 and 9.1.2). The increase in mortality was perhaps caused by damaging roots near the surface of the soil during weeding. In agreement with the increase in basal diameter growth after weeding, *Agrostis capillaris* swards have been found to reduce oak seedling growth in Killarney (Kelly, 2002). Weeding (over all vegetation types) may also have exposed planted trees to herbivores (Table 9.3). Kelly (2002) observed that, during a short-term incursion of sika deer into an exclosure, 49% of weeded oak seedlings were browsed compared with only 11% of unweeded seedlings.

For oaks, vegetation cover may benefit survival in clearfelled conifer plantations (Figs. 9.5a, b). Although dense growth increases competition for water, vegetation cover can reduce evaporation from the soil. This effect may be relatively more important in recently-felled stands where the dark colours of conifer leaf litter and humus serve to increase absorption of solar radiation. Dark-coloured soils experience higher temperatures and greater diurnal fluctuations in temperature relative to lighter coloured soils, and this has been found to affect plant growth (Ludwig & Harper, 1958). Of course where needle litter is thick, it would more likely have a mulch effect, reducing soil evaporation.

10.3 Environmental Factors

10.3.1 Oak

Like the vegetation and ground cover data, the environmental data also suggest that water availability is of significant importance to planted trees. Oak survival and first-year growth were favoured by several variables indicating higher moisture status. The potential for water stress in oaks planted in Wicklow was exacerbated by late planting. If the Wicklow sites had been planted close to the same time as the Killarney sites, moisture would most likely have been a less important factor in this study. In any case, the importance of water availability for oak growth and mortality is supported by variables such as slope and organic content that are not confounded with planting date. It may seem strange that water could be one of the more crucial factors in early oak survival in Ireland. The period from February to June is "distinctly drier" than July to January in Ireland (Rohan, 1986). June was the driest month on average from 1951-1980 in weather stations in south Leinster and most of Munster, including Killarney (Rohan, 1986). The use of cell-grown, rather than bare-rooted planting stock would probably reduce the potential for water stress, particularly in situations where trees are planted late.

Water availability was less important for second-year oak growth, which was favoured by more mineral-rich, somewhat less acid soils. The planted trees appear to be changing their abiotic requirements, after a period of stress, back to the reported preferences of sessile oak for well-drained mineral soils (Jones, 1959; Joyce *et al.*, 1998). In comparison, Kelly (2002) reported growth reductions of sessile oak seedlings on wet peaty gley soil (O layer mean depth of 13 cm) in a clearing in Tomies Wood, Killarney after one year and increases in mortality after three years. Sessile oak seedlings, however, have been found to be tolerant of wet soils in experimental studies. Tansley (1939) states that "recent (unpublished) experiments have shown that first year seedlings of the sessile oak tolerate wet soil better than those of the pedunculate oak," although he gives no further details. Another study found that optimum growth of sessile oak seedlings occurred at 80% hygroscopic soil water, whereas 75% was the optimum for pedunculate oak (Feher (1942) cited in Jones (1959)). In the present study, there is as yet no indication of higher mortality in more organic soils (Fig. 9.5a, b).

Oak is widely regarded as being tolerant of a wide range of soil nutrient conditions (Jones, 1959; Ovington & MacRae, 1960; Shaw, 1974; Joyce *et al.*, 1998). Nevertheless, in woodland environments, fertilization has been found to enhance growth of young trees. Shaw (1974) found a short-term growth response to addition of 10:10:10 N:P:K fertiliser, followed by a peak of mortality. Kelly (2002) found a longer-term (23-year) response to P fertilisation, but no response to Ca and a negative response to N addition. Newnham and Carlisle (1969) considered

soils in the Lake District to be P deficient but to have sufficient available N for oak seedling needs. Shaw (1974) concluded that loss of P and K through herbivory exceeded uptake by seedlings on brown podzolic soils in Wales.

In this study, Ca and Mg availability are associated with greater survival and first-year growth (Fig. 9.5). Because Ca and Mg availability are strongly correlated with soil organic content (section 9.5.1), however, these cations may simply be further indicators of moisture status. Second-year height growth is more closely associated with K availability. In this case, growth responses to nutrient levels are more convincing, especially considering that K is rapidly leached from litter and soils with poor cation exchange capacities following clearfelling of conifer plantations (Goulding & Stevens, 1988; Titus & Malcolm, 1999). Although the P data from the present study are unsatisfactory, it appears likely that second-year growth was greater in sites with higher total P. Total P data were negatively correlated with percent organic matter (Pearson's r = -0.67) and positively correlated with pH (Pearson's r = 0.37).

Although brash abundance did not emerge as a major factor affecting planted oak performance, its positive correlation with Axis 3 of the CCA (Table 9.12) suggests that greater heights of brash favour second-year oak growth. If so, there are several possible mechanisms. Brash may have a fertiliser effect on oak like that discussed in section 7.1.3, or enhance soil moisture through shading. Taller brash mounds could have a protective effect by sheltering trees from wind. Felling brash has been found to protect young trees from browsing by large herbivores (Grisez, 1960; Gill, 1992b; Palmer *et al.*, 2001). Although dense brash can increase damage caused to planted trees by small rodents (Palmer *et al.*, 2001), it may serve as a deterrent to hares, which are much larger animals that prefer open spaces with good fields of view (Hewson, 1977; Hayden & Harrington, 2000). Inspection of data on frequency of browsing did not show that trees in plots with more brash were browsed less often. The *intensity* of browsing of individual seedlings, however, was not recorded, and so it is possible that browsing was less severe in plots with more brash. Trees in former lodgepole pine stands in Fraughan Rock Glen, in fact, did appear to be less severely browsed by deer and hares than trees in nearby former Sitka spruce stands with lighter brash cover. I also observed less browsing damage on trees planted in parts of plots with heavier brash cover than average (Figure 10.1). The relative importance of each of these mechanisms is unclear, but it seems that any protection provided by brash against herbivory is small relative to the densities of herbivores present on site and the influence of other environmental variables.

Figure 10.1. Oak in unexclosed plot (#17U) protected by dense brash.



10.3.2 Birch

Survival and good growth of birch in the first year are perhaps more strongly dependent on wet soil and climate conditions than for oak (Fig. 9.6; Table 9.13). Birch is relatively intolerant of drought (Perala, 1990; Atkinson, 1992); seedlings are especially sensitive, suffering up to 90% mortality during dry periods (Miles & Kinnaird, 1979). Again, transplantation shock exacerbated by late planting dates served to amplify water stress in the first year. Mortality in the second and third years was not as closely associated with moisture indicators.

Like sessile oak, downy birch is tolerant of a wide range of soil types and soil nutrient conditions (Evans, 1984; Atkinson, 1992). Only Ca and Mg availability appeared to be particularly important for planted birch performance (Fig. 9.6), and it is likely that here cation concentrations are functioning as indicators of organic soils. N and P fertilisation may improve

establishment and growth of birch, but is likely to impede the development of mycorrhizae (Miles & Kinnaird, 1979; Perala, 1990). Inoculation with mycorrhizae is crucial to early survival and growth with birch (Miles & Kinnaird, 1979), and may be important for growth and survival after the first year, which are not well-explained by the CCA of birch variables (Fig. 9.6).

10.4 Provenance of Oak

Although local provenances are preferred when restoring native woodlands (Soutar & Peterken, 1989; Rodwell & Patterson, 1994; Gilbert & Anderson, 1998; Sackville Hamilton, 2001), this was not possible because of the scarcity of Irish sessile oak planting stock available at the beginning of this study. Local provenances are favoured not only because they conserve local genotypes, but also because they may be better "adapted" to local conditions (Gilbert & Anderson, 1998; but see Wilkinson, 2001 for an opposing viewpoint). The question of the suitability of different provenances under local conditions could not be satisfactorily addressed because of the confounding of provenances with nurseries. There is evidence, however, that the Bollisce, Co. Galway provenance performed less well overall in the Wicklow sites than the other provenances (section 9.2), which may reflect a preference for a more oceanic climate. (Note that provenances were not recorded in Killarney and so could not be compared - see section 8.1). Regardless of whether local provenances are better suited to the site, Sackville Hamilton (2001) emphasizes that their use is important for conservation of genetic biodiversity.

CHAPTER 11

NATURAL TREE REGENERATION STUDY: METHODS

11.1 Field Sampling

11.1.1 Regenerating Trees

Sampling of naturally regenerating trees (including *Rhododendron*) took place in late summer through autumn of 1999, 2000, and 2001, along with sampling of planted trees. (Although *Rhododendron* is not generally considered a "tree", it will be included in this category in the following chapters for the sake of brevity.) Trees were sampled in two height classes: greater than 30 cm tall ("saplings") and less than or equal to 30 cm tall ("seedlings"). Data collected for saplings > 30 cm tall were the same as for planted trees (see section 8.3), with two exceptions: 1) basal diameter was not recorded for *Rhododendron*, and 2) diameter at breast height (at 1.37 m) was recorded for saplings greater than 2 m tall instead of basal diameter. Saplings were also tagged and mapped to facilitate resampling. Seedlings ≤ 30 cm height were counted by species in two further height classes: 1 – 20 cm and 21 – 30 cm. After sampling in each year, all exotic species (i.e. conifers, including Scots pine but not yew (*Taxus baccata*), *Rhododendron*, and beech) in subplots assigned weeding treatments were uprooted or cut down. In most plots it was feasible to sample all naturally regenerating trees, but in 2000 and 2001, or only in 2001, in plots with especially high densities, trees were subsampled in two 2 × 10 m strips per subplot (thus representing 40% of the plot area). In weeded subplots, however, all exotic woody species were sampled and removed. Oak seedlings were treated as a special case in this study. Each oak seedling found was measured, tagged and mapped as if it were > 30 cm height, and efforts were made to locate and sample every seedling in each plot (i.e. no subsampling).

Trees regenerating in the five soil replacement quadrats (see section 4.3) were counted by species in 1-20 cm, 21-30 cm and 31-40 cm size classes.

Pines could not be identified to species level. Because felled and remnant mature Scots pine and lodgepole pine did not co-occur in any sites, pines were assigned to the species present or formerly present in the area. Sitka spruce and Norway spruce could be distinguished with some difficulty. Oaks were assumed to be *Quercus petraea* as no *Quercus robur* trees occurred near the study sites. Most young *Salix* could be identified with confidence as *Salix cinerea* ssp. *oleifolia*. In 2001, however, *Salix* regeneration was observed that appeared to belong to a different taxon. These were identified with some reservation as *Salix* ×*multinervis*, hybrids of *S.*

cinerea and *S. aurita* (Meikle, 1984). It is likely that *Salix ×multinervis* was overlooked in 1999 and 2000, but since they were not numerous, this did not introduce serious error into the data.

In the Muckross Forest site in Killarney, Dúchas staff had killed several of the larger *Rhododendron* bushes, using herbicide, two or three years prior to plot establishment. When sampling began in 1999, I observed that numerous *Rhododendron* seedlings had emerged in areas where herbicide had killed the vegetation (herbicide-use thereby preparing an ideal seed bed). Additional *Rhododendron* spraying took place in the unexclosed plots between 1999 and 2000 sampling, killing most of the previously tagged *Rhododendron*. Because of these manipulations, reported abundances of *Rhododendron* seedlings ≤ 30 cm size class are probably overestimates and abundances of saplings > 30 cm size classes are underestimates of abundances in the untreated situation.

In the winter of 1996/7, Dúchas staff in Glendalough removed natural regeneration of Sitka spruce and hemlock, but not of Japanese larch, from the area in which plot pairs 8 and 9 were located (Fig. 4.2) (D. Clarke, pers. comm.). The total number of trees removed was not large, however.

11.1.2 Seed Sources

To determine the importance of dispersal for natural regeneration, the abundances, direction, distance, and species of seed sources were estimated. Distance to mature trees from the centre of exclosures was measured with tapes where feasible, but was usually measured using a Bushnell Yardage Pro 400 laser rangefinder with a maximum range of approximately 400 m. Where obstructions such as hills and intervening trees prevented direct distance measurements, they were made from a nearby (within 30 m) vantage point and subsequently corrected. In some cases, distances had to be calculated from measurements from neighbouring plots. Abundances of seed trees were estimated on an approximate log scale: single trees or small groups were coded 1; copses, remnant conifer pockets and riparian corridors of trees were coded 10; and plantations and native woodlands were coded 100. Distances and abundances of seed sources were estimated in eight direction classes corresponding with the eight sub-ordinal compass directions (N, NE, E, etc.). If a large plantation or linear tree feature extended into more than one direction category, each part of the seed source in a different direction was measured independently. Species identifications were assisted by the use of binoculars and forestry compartment maps.

11.1.3 Sitka Spruce Regeneration Transects

To gain a clearer understanding of Sitka spruce regeneration in clearfells, the plot data were supplemented by belt transects run perpendicularly from a Sitka spruce plantation edge into an adjoining clearfell. Spruce seedlings were counted at 1 m intervals in a $2m^2$ area extending 1 m behind the tape mark and 1 m to either side of the tape marking the transect. Where the site permitted, the transects were 100 m long. The transects were located in former Sitka spruce stands in Glenmalure and Blessington Forests, Co. Wicklow (Table 11.1). Prior to sampling in the summer and early autumn of 2001, the Blessington Forest sites had been prepared for replanting by drain excavation and mounding, and the brash had been piled into windrows. Where the transects crossed brash piles and drains, no data were entered (i.e. left blank instead of entering 0). Similarly, no data were entered where the transects in Blessington Forest and Glenmalure crossed former canopy gaps occupied by dense, older spruce regeneration.

Table 11.1. Sitka spruce regeneration transect locations, direction (in degrees), and year in which the former spruce crop was felled. Letters following some subcompartment numbers indicate replicate transects in the same felled subcompartment.

Forest	Location	Subcompartment	Direction (degrees)	Fell Year
Glenmalure	Baravore	13589W1a	70	1998
	Baravore	13589W1b	32	1998
	Baravore	13589W1c	131	1998
	Benleagh	13596I6	298	1998
	Benleagh	13597D1	221	1998
	Fraughan Rock Glen	13591K3a	244	1998
	Fraughan Rock Glen	13591K3b	244	1998
Blessington	Ballinascorney	12015M1	212	2000
	Ballinascorney	12016H4a	2	2000
	Ballinascorney	12016H4b	2	2000
	Ballinascorney	12015M3	156	2000
	Commons	12001P4	90	2000
	Commons	12002K3	38	2000

11.2 Data Analysis

11.2.1 Data Handling

For saplings (and oak seedlings), height and basal diameter growth increments over the intervals 1999-2000 and 2000-2001 were calculated. Recruitment to the > 30 cm height class in 2000

and 2001 was calculated as the number of seedlings sampled in that height class for the first time. Missing trees were treated in analyses as dead, as was done for planted trees (section 8.4.1).

Except where otherwise noted, statistical analyses of naturally regenerating tree data were conducted using SPSS (1999) after consulting Sokal and Rohlf (1995). When several variables were simultaneously examined with univariate tests, resulting P-values were corrected to control the experimentwise error rate using Hochberg's (1988) procedure. This procedure is more powerful than the traditional Bonferroni correction (Legendre & Legendre, 1998). Note that equality between some of the P-values presented in the following chapter is an artefact of the Hochberg corrections for experimentwise error rates.

11.2.2 Exclosure

The effects of exclosure on naturally regenerating trees were analysed for the six most abundant species only: birch, holly, sally, rowan, Sitka spruce and *Rhododendron.* Distributions of regeneration abundances and growth rates were highly skewed and parametric statistics could thus not be employed. Mann-Whitney U tests were therefore used to test the effects of exclosure. Densities of native tree seedlings ≤ 30 cm tall in exclosed and unexclosed plots were analysed. Exotic species densities in weeded and non-weeded subplots were tested separately. Because *Rhododendron* regeneration in Wicklow was virtually nil, only data from the Killarney plots were used for *Rhododendron*. Because Sitka spruce and *Rhododendron* were removed each year from weeded subplots, densities in 2000 and 2001 provide estimates of annual rates of immigration into the plots.

Differences in densities of saplings > 30 cm tall in 1999 between exclosed and unexclosed plots were tested by species using Mann-Whitney U tests. The effect of exclosure on annual recruitment to the > 30 cm size class in 2000 and 2001 was also examined. Recruitment of exotics was investigated using non-weeded subplot data, and again only Killarney data were used for *Rhododendron*. Differences in mean height and basal diameter growth of birch, rowan, holly and Sitka spruce (the last in non-weeded subplots) in exclosed and unexclosed subplots were examined with Mann-Whitney U tests. Sally and *Rhododendron* growth were not investigated because of insufficient sample sizes. The effect of exclosure on mortality of birch, rowan, holly and Sitka spruce saplings was examined using Fisher's exact tests.

11.2.3 Small Mammal Damage

Mann-Whitney U tests were used to identify differences in mean height and basal diameter growth between birch and rowan >30 cm tall browsed and unbrowsed by small herbivores in exclosed subplots. Sally, holly, and Sitka spruce were not tested because of very low numbers of browsed trees of these species inside exclosures.

11.2.4 Environmental Factors

The effects of several environmental factors on density and recruitment of naturally regenerating birch, holly, sally, rowan, and Sitka spruce were investigated using canonical correspondence analysis (CCA) (ter Braak, 1986). Because of the overwhelming effect of browsing outside the fences, only data from exclosed subplots were used. Natural regeneration variables used separately for each of the five species were: densities of seedlings ≤ 30 cm tall in 1999, 2000, and 2001, densities of saplings > 30 cm tall in 1999, and recruitment to the > 30 cm size class in 2000 and 2001. Sitka spruce recruitment in 2000 and 2001 was omitted because no recruitment occurred in weeded subplots. Data were expressed as the number of individuals / 100 m^2.

The environmental variables included in the second matrix of the CCAs are shown in Table 11.2. As with the CCAs in the previous chapters, I attempted to be parsimonious in selection of environmental variables to reduce multicollinearity. Correlations among the site variables were inspected prior to analysis, using Spearman's rank correlation coefficients. Depth of the soil organic layer and C/N ratio were not included in the CCAs because they were highly correlated with several other variables. Available Mg^{2+} was also omitted because of a very high correlation with Ca^{2+}. Initial analyses using the variables in Table 5.1, field layer cover, vegetation types, and seed source indices (see below), produced unstable solutions, most likely because of the inclusion of noisy or irrelevant environmental variables. Soil type was removed because much of the information is duplicated by soil chemical and physical parameters included in the CCAs.

The environmental variables in Table 11.2 are explained fully in sections 5.3.4 and 8.4.3, except for the seed source indices for the five species. To calculate the seed source indices, the density of each seed source (1, 10 or 100) was divided by the distance to the seed source, and these values were summed for each species – plot combination. For a given number of mature trees, therefore, the seed source index decreases geometrically with distance from the trees. A

Table 11.2. Environmental variables used in CCA of naturally regenerating tree data and their degrees of precision. For further explanations, see text.

Variables	Type	Variables	Type
Soil Variables:		***Ground Cover (%):***	
Gleying	presence/absence	Field Layer	quantitative
Soil Depth (cm)	quantitative	Brash	quantitative
K^+ (mg/L)	quantitative	Litter	quantitative
Ca^{2+} (mg/L)	quantitative	Bryophyte	quantitative
Mn^{2+} (mg/L)	quantitative	Soil	quantitative
Organic Content (%)	quantitative		
pH	quantitative	***Vegetation Types:***	
Upper Soil Index	ranks (1-6)	*Agrostis - Galium*	presence/absence
		Digitalis – Juncus	presence/absence
Site Variables:		High *Calluna – Erica*	presence/absence
Slope (%)	quantitative	Low *Calluna – Erica*	presence/absence
Aspect	quantitative	*Pteridium - Agrostis*	presence/absence
Precipitation (mm)	quantitative		
Temperature (°C)	quantitative	***Seed Source Indices:***	
Brash Height	quantitative	Birch	quantitative
Felling Year	quantitative	Sally	quantitative
Sitka Spruce Site	presence/absence	Rowan	quantitative
		Holly	quantitative
		Sitka spruce	quantitative

reciprocal function of distance was chosen rather than a linear function, because seed fall for wind disseminated species like birch does not decrease linearly with distance (Miles & Kinnaird, 1979; Perala, 1990). A geometric function may have an approximately linear relationship with dispersal, and thus be a more sensitive estimator for CCA.

Prior to CCA, chi-square distances among the subplots were computed to identify outliers which may distort the ordination. Four subplots were more than 2.3 standard deviations from the mean and were removed. Two additional subplots were 2.08 standard deviations from the mean, but since they were not widely separated from the main body of the data, these subplots were retained. Subplot 12E1 was also omitted from the analysis because no naturally regenerating trees were found there in any year. As in the CCAs in the previous chapters, the CCA was performed twice. The first CCA used all the environmental variables in Table 11.2, and then the final CCA was conducted after removing variables that had correlations between -0.2 and 0.2 with the first three canonical axes. This procedure did not radically change the ordination, but had the benefit of removing the least relevant variables which may otherwise interfere with interpretation.

11.2.5 Sitka Spruce Regeneration

To better characterise sites where Sitka spruce regeneration is occurring, a logistic regression model was fitted. The presence or absence of Sitka spruce regeneration in weeded subplots in 2000 or 2001 was used as the dependent variable, and the environmental variables in Table 11.2, with the exception of non-spruce seed source indices, were used as the independent variables. A backward elimination solution was employed where all variables were initially included in the regression equation. Variables with a likelihood ratio of $P > 0.05$ were then removed individually progressing from highest P-values to lowest. The suitability of soil types for Sitka spruce invasion was investigated using a contingency table.

The development of Sitka spruce populations was investigated by constructing size class distributions for groups of plot pairs with similar felling years, former crop species, and study site locations. Composite Sitka spruce size class distributions were constructed for:

- former Sitka spruce plots in the Muckross Forest site in Killarney felled in 1988,
- former larch and spruce/lodgepole mixture plots in Glendalough felled in 1991 and 1993,
- a plot pair in the Benleagh site in Glenmalure formerly planted with Sitka spruce and felled in 1993,
- former Sitka spruce plots on cutover blanket peats in Looscaunagh, Killarney felled in 1994,
- a plot pair in Glendalough formerly planted with Sitka spruce and felled in 1995,
- former lodgepole pine stands in Fraughan Rock Glen, Glenmalure felled in 1997, and
- former Sitka spruce stands in Glenmalure (Fraughan Rock Glen, Baravore, and Benleagh sites combined) felled in 1998.

Further details of site conditions and vegetation are given in sections 4.2 and 6.2 and Tables 4.1 and 4.2. Numbers of Sitka spruce trees in non-weeded subplots were divided into 20 cm height classes, summed over all subplots in the group, and converted to density scale (stems/ha).

The importance of the direction in which Sitka spruce seed sources lay was examined visually by constructing radar diagrams and comparing these to densities of Sitka spruce seedlings invading weeded plots in 2000 and 2001. In addition, the transect data (section 11.1.3 above) were summarised and plotted in two groups, determined by compass direction of the transect relative to the prevailing wind. The prevailing wind in Ireland blows from the southwest (Rohan, 1986), but mountainous topography can have complex effects on wind direction. The glens in the Glenmalure transect sites, however, were oriented generally west-to-east.

Topography in the Blessington Forest area is more complex, but the sites were located in the northern part of the Dublin Mountains and are not shielded by massifs to the west.

CHAPTER 12

NATURAL TREE REGENERATION STUDY: RESULTS

12.1 Study Sites

The most abundantly regenerating tree species were downy birch, rowan, Sitka spruce, holly, sally and *Rhododendron* (Tables 12.1, 12.2). Six other species of exotic conifers and four other deciduous species, including the exotic beech also regenerated naturally in the plots (Table 12.3). There were marked differences between study sites in natural regeneration abundances, some of which are paralleled by differences in seed tree abundances among sites (Table 12.4). Birch regeneration was most abundant in the lower elevation Baravore site and least abundant in the other Glenmalure sites. In Fraughan Rock Glen, only two trees occurred within 400 m of some of the plots (Table 12.4e), and no birch were seen in the area of the Benleagh site (Table 12.4f). The vast majority of birch regeneration in Glendalough was found in one pair of plots, which were more recently felled than the rest and adjacent to native woodland (plot pair 11, see Table 12.4c and Fig. 7 in Appendix 3). Rowan regeneration was far more abundant in Muckross Forest than elsewhere (Tables 12.1, 12.2), although more mature rowan occurred in Fraughan Rock Glen (Tables 12.4a, 12.4e). Sitka spruce regeneration was highest in the Benleagh site (Tables 12.1, 12.2), with most found in the earlier felled pair of plots (#22). Young holly was most abundant in Looscaunagh and Baravore (Tables 12.1, 12.2); the former site had many scattered individuals and small groups of holly trees within about 350 m (Table 12.4b). Sally seedlings and saplings occurred most abundantly in Baravore (Tables 12.1, 12.2), where riparian scrub lines the nearby Avonbeg River (Table 12.4d). Natural regeneration of the invasive exotic *Rhododendron* occurred in the Killarney plots, and was particularly high in the Muckross Forest site (Tables 12.1, 12.2), where mature *Rhododendron* was abundant (Table 12.4a). Only one *Rhododendron* seedling was found in Wicklow, in a plot in the Baravore site in Glenmalure; because it was found in a weeded subplot (and was therefore removed), it is not shown in Table 12.1.

Natural regeneration of the less commonly occurring tree species also varied by location (Table 12.3). Conifer regeneration was closely associated with the presence of conifer crop species in the area. Remnants of mature silver fir (*Abies procera*) plantations, for example, were present in Looscaunagh, but nowhere else (Table 12.4). Note, however, that identification of *Pinus* seedlings to species was determined by what mature *Pinus* species were planted nearby. Similarly, some Norway spruce seedlings may have been misidentified as Sitka spruce.

Table 12.1. Mean density (individuals/ha) ± se of commonly occurring natural tree regeneration ≤ 30 cm height averaged over three field seasons. Sitka spruce and *Rhododendron* means are from non-weeded subplots only.

Location	Site	No. of Plots	Birch	Holly	*Rhododendron*	Rowan	Sitka spruce	Sally
Killarney	***Muckross Forest***	6	256 ± 53	238 ± 60	12 395 ± 7213	2590 ± 620	40 ± 20	23 ± 9
	Looscaunagh	6	992 ± 156	407 ± 93	40 ± 20	115 ± 32	13 ± 8	117 ± 33
Wicklow	***Glendalough***	8	1579 ± 555	8 ± 4	-	83 ± 21	126 ± 70	13 ± 6
	Glenmalure - *Baravore*	6	5077 ± 948	509 ± 150	-	105 ± 22	194 ± 42	369 ± 127
	Glenmalure - *Fraughan Rock Glen*	12	5 ± 2	37 ± 9	-	19 ± 6	89 ± 19	3 ± 2
	Glenmalure - *Benleagh*	4	28 ± 15	51 ± 23	-	109 ± 36	3700 ± 976	25 ± 13

Table 12.3. Total numbers of less commonly occurring natural tree regeneration counted in 1999 – 2001. Seedling counts for all taxa except *Quercus* are likely inflated by counting the same seedling in different years. All oak seedlings were individually tagged and are thus not duplicated.

Location	Site	No. of Plots	*Abies procera*	*Fagus sylvatica*	*Larix kaempferi*	*Picea abies*	*Pinus contorta*	*Pinus sylvestris*	*Prunus* species	*Quercus petraea*	*Salix* ×*multinervis*	*Tsuga heterophylla*
Killarney	*Muckross Forest*	6	0	0	0	0	0	42	0	0	0	3
	Looscaunagh	6	5	0	0	0	15	0	0	0	3	0
Wicklow	***Glendalough***	8	0	6	12	0	0	5	1	13	0	4
	Glenmalure - *Baravore*	6	0	17	1	2	3	0	0	5	2	0
	Glenmalure - *Fraughan Rock Glen*	12	0	0	0	0	24	0	0	0	4	0
	Glenmalure - *Benleagh*	4	0	0	0	2	13	0	0	0	0	0

Table 12.4. Mean number of seed sources per exclosed plot in three density classes in the six study sites. Density classes increase in a logarithmic progression: class 1- 1s, class 2- 10s and class 3- 100s of trees (section 11.1.2). Also shown are the range of distances (min-max) from the plots to seed sources in density classes 1 and 2 and the distance range from the plots to density class 3 seed sources (i.e. woodland or plantation edges). Note that only seed sources within 400 m were estimated.

a. Muckross Forest. N = 3 plots.

	Density Class 1	Density Class 2	Class 1 & 2 Distance Range (m)	Density Class 3	Class 3 Distance Range (m)
Downy birch	1.7	1.0	31-173	-	-
Holly	3.7	1.0	28-131	-	-
Japanese larch	-	0.3	82	0.3	78
Rhododendron[1]	*	*	*	*	*
Rowan	3.7	2.0	29-321	-	-
Sally	2.0	-	62-335	-	-
Scots pine	0.3	1.0	31-261	1.0	37-269
Sitka spruce	0.3	1.7	34-131	0.3	86

[1] *Rhododendron* was abundant throughout the site in densities not amenable to measurement in the same manner as other woody species.

b. Looscaunagh. N = 3 plots.

	Density Class 1	Density Class 2	Class 1 & 2 Distance Range (m)	Density Class 3	Class 3 Distance Range (m)
Downy birch	0.3	-	332	1.0	225-302
Noble fir	-	3.3	23-174	-	-
Holly	4.0	6.7	26-273	-	-
Japanese larch	0.3	2.3	102-321	2.0	104-253
Lodgepole pine	0.3	2.0	41-309	4.7	44-310
Sessile oak	0.7	1.0	49-203	-	-
Rhododendron	2.7	-	67-190	-	-
Rowan	0.7	3.7	50-302	-	-
Sally	0.3	-	257	-	-
Sitka spruce	0.3	3.7	105-309	5.0	44-310

Table 12.4. cont'd

c. Glendalough

	Density Class 1	Density Class 2	Class 1 & 2 Distance Range (m)	Density Class 3	Class 3 Distance Range (m)
Beech	0.5	-	61-173	0.3	69
Downy birch	3.5	2.8	15-184	0.8	81-132
Douglas-fir	0.5	-	106-217	0.8	108-210
Hemlock	0.5	-	101-103	-	-
Holly	1.0	1.0	61-216	-	-
Japanese larch	4.0	1.8	19-197	0.8	121-155
Lodgepole pine	0.3	0.3	120-190	-	-
Sessile oak	0.8	1.8	50-216	1.0	69-221
Rhododendron	0.3	-	69	-	-
Rowan	0.3	-	117	-	-
Scots pine	0.5	1.0	45-182	3.0	26-309
Sitka spruce	0.3	1.0	55-207	2.3	19-183

d. Glenmalure- Baravore. N = 3 plots.

	Density Class 1	Density Class 2	Class 1 & 2 Distance Range (m)	Density Class 3	Class 3 Distance Range (m)
Beech	-	3.7	48-246	-	-
Downy birch	1.3	2.7	48-267	-	-
Eared Willow	-	1.7	145-267	-	-
Hawthorn	0.7	1.0	123-353	-	-
Holly	0.7	1.3	88-353	-	-
Lodgepole pine	-	0.7	62-316	-	-
Norway spruce	0.7	0.3	110-220	2.3	50-305
Sessile oak	-	0.7	145-199	-	-
Rhododendron	1.0	1.7	40-320	-	-
Rowan	2.7	1.7	36-267	-	-
Sally	1.0	1.7	101-267	-	-
Sitka spruce	0.7	2.7	63-188	2.0	54-380
Sycamore	0.7	-	330-408	-	-

Table 12.4. cont'd

e. Glenmalure- Fraughan Rock Glen. N = 6 plots.

	Density Class 1	Density Class 2	Class 1 & 2 Distance Range (m)	Density Class 3	Class 3 Distance Range (m)
Alder	-	0.7	184-291	-	-
Downy birch	1.3	-	124-300	-	-
Holly	0.7	-	152-320	-	-
Japanese larch	0.2	-	65	1.2	60-287
Lodgepole pine	1.2	2.3	28-350	2.2	71-289
Norway spruce	0.2	0.3	182-285	0.2	206
Rhododendron	0.5	-	50-272	-	-
Rowan	5.0	4.2	82-378	-	-
Sitka spruce	0.8	1.5	64-358	1.3	41-362

f. Glenmalure- Benleagh. N = 2 plots.

	Density Class 1	Density Class 2	Class 1 & 2 Distance Range (m)	Density Class 3	Class 3 Distance Range (m)
Japanese larch	1.0	0.5	207-328	-	-
Lodgepole pine	1.0	1.0	14-247	1.5	108-190
Rowan	1.0	-	40-50	-	-
Sitka spruce	1.5	0.5	35-159	6.0	43-251

Nevertheless, I can state with confidence that the amount of Norway spruce regeneration is much lower than Sitka spruce regeneration, even where mature Norway spruce trees were more abundant than Sitka spruce, such as in Baravore (Table 12.4d). Most *Fagus* regeneration was observed in 2001, following what was apparently a mast seed year. Natural regeneration of oak was uncommon and restricted to Glendalough, where the plots are relatively near the extensive oakwoods there (Table 12.4c), and Glenmalure/Baravore, where two plots were within 200 m of riparian areas containing mature oak (Table 12.4d). Although oak is also present near the Looscaunagh plots, no regeneration was found, and perhaps should not be expected on blanket peat (Table 4.1). Some species occurring in the landscape did not regenerate at all in the plots, including Douglas-fir (*Pseudotsuga menziesii*), hawthorn (*Crataegus monogyna*), sycamore (*Acer pseudoplatanus*), and alder (*Alnus glutinosa*) (Tables 12.3, 12.4). Eared willow (*Salix aurita*) occurred along the Avonbeg River in Glenmalure, near the Baravore plots (Table 12.4d).

Salix ×*multinervis*, which regenerated there and also in the more distant Fraughan Rock Glen site, is a commonly occurring hybrid between *S. aurita* and *S. cinerea* (Meikle, 1984).

12.2 Exclosure

12.2.1 Seedling Densities

Exclosure had no significant effects on the abundances of seedlings ≤ 30 cm tall of the four most common native species (Table 12.5). In 2001, birch and rowan densities were higher outside exclosures whereas holly and sally densities were higher inside exclosures. Exclosure had no significant effects on the abundances in non-weeded subplots of the two most commonly regenerating exotic woody species, Sitka spruce and *Rhododendron* (Table 12.6). The *Rhododendron* data also demonstrate strong spatial heterogeneity in density of seedlings ≤ 30 cm tall.

Regeneration of exotic woody species in weeded subplots that have been cleared of exotics the previous year allows an estimation of the annual rate of invasion. Although no significant differences were discovered between exclosed and unexclosed plots, Sitka spruce and *Rhododendron* invasion tended to be higher outside exclosures (Table 12.7).

Table 12.5. Mean density (seedlings/ha) ± se of naturally regenerating native tree seedlings ≤ 30 cm height in exclosed and unexclosed plots. P-values are the results of Mann-Whitney U tests.

		Exclosed	Unexclosed	P
Birch	*1999*	1005 ± 326	401 ± 129	0.940
	2000	868 ± 181	918 ± 266	0.940
	2001	1554 ± 426	2504 ± 738	0.940
Holly	*1999*	205 ± 46	158 ± 39	0.940
	2000	198 ± 45	151 ± 52	0.940
	2001	224 ± 59	155 ± 39	0.940
Rowan	*1999*	301 ± 71	380 ± 144	0.829
	2000	445 ± 122	437 ± 171	0.322
	2001	409 ± 129	628 ± 286	0.940
Sally	*1999*	54 ± 16	21 ± 7	0.940
	2000	93 ± 34	46 ± 17	0.940
	2001	158 ± 86	99 ± 33	0.940

Table 12.6. Mean density (seedlings/ha) ± se of naturally regenerating Sitka spruce and *Rhododendron* ≤ 30 cm height in exclosed and unexclosed plots in non-weeded subplots. *Rhododendron* means are for Killarney plots only. P-values are the results of Mann-Whitney U tests.

		Exclosed	Unexclosed	P
Sitka spruce	*1999*	507 ± 256	576 ± 269	0.810
	2000	331 ± 188	455 ± 214	0.810
	2001	290 ± 166	463 ± 166	0.567
Rhododendron	*1999*	508 ± 198	10,208 ± 6162	0.810
	2000	1133 ± 572	10,400 ± 5893	0.810
	2001	1071 ± 558	13,988 ± 11,529	0.810

Table 12.7. Mean density (seedlings/ha) ± se of naturally regenerating Sitka spruce and *Rhododendron* ≤ 30 cm height in exclosed and unexclosed plots in weeded subplots. *Rhododendron* means are for Killarney plots only. P-values are the results of Mann-Whitney U tests.

		Exclosed	Unexclosed	P
Sitka spruce	*2000*	93 ± 35	155 ± 92	0.934
	2001	117 ± 45	245 ± 103	0.934
Rhododendron	*2000*	342 ± 168	658 ± 361	0.934
	2001	208 ± 118	458 ± 205	0.934

Although the Mann-Whitney U test tests ranks, means are shown in Tables 12.4-12.6 rather than medians, because in most cases the median was 0. Equality of the highest P-values is an artefact of the Hochberg corrections for experimentwise error rates (Hochberg, 1988).

12.2.2 Sapling Recruitment and Growth

Mean densities in 1999 of birch, holly, rowan and sally saplings greater than 30 cm tall were higher in exclosed plots than in unexclosed plots (Table 12.8). Although the differences were not statistically significant, these results suggest that fencing in early 1999 facilitated a rapid growth response in pre-established trees. Mean annual recruitment (i.e. the number of trees per year reaching heights greater than 30 cm for the first time) of birch, holly and rowan seedlings was significantly higher in exclosed plots (Table 12.8). In contrast to the native species, densities in 1999 and recruitment in 2000 and 2001 of Sitka spruce and *Rhododendron* saplings in non-weeded plots were not significantly different between exclosed and unexclosed plots

Table 12.8. Mean density (saplings/ha) ± se in 1999 and mean recruitment (saplings/ha) ± se in 2000 and 2001 of native species > 30 cm height in exclosed and unexclosed plots. P-values are the results of Mann-Whitney U tests.

		Exclosed	Unexclosed	P
	1999	215 ± 91	49 ± 22	0.263
Birch	*2000*	282 ± 68	48 ± 19	0.001
	2001	400 ± 87	68 ± 23	0.004
	1999	20 ± 7	14 ± 7	0.757
Holly	*2000*	33 ± 10	4 ± 2	0.030
	2001	76 ± 24	5 ± 4	0.007
	1999	55 ± 27	29 ± 14	0.757
Rowan	*2000*	80 ± 15	13 ± 8	< 0.0001
	2001	122 ± 26	17 ± 8	< 0.0001
	1999	4 ± 3	0	0.624
Sally	*2000*	10 ± 5	2 ± 2	0.757
	2001	35 ± 16	5 ± 3	0.263

(Table 12.9). As with Tables 12.4-12.6, means are shown in Tables 12.7-12.8 because in most cases the median was 0.

Height increments in 1999-2000 and 2000-2001 of birch, holly and rowan were significantly higher inside exclosures (Table 12.10). Basal diameter growth of these species during 2000-2001 was also significantly greater inside exclosures. This latter result confirms that browsing by large herbivores does not simply reduce or prevent height growth, but affects tree growth in a

Table 12.9. Mean density (saplings/ha) ± se in 1999 and mean recruitment (saplings/ha) ± se in 2000 and 2001 of naturally regenerating Sitka spruce and *Rhododendron* > 30 cm height in exclosed and unexclosed plots in non-weeded subplots. *Rhododendron* means are for Killarney plots only. P-values are the results of Mann-Whitney U tests.

		Exclosed	Unexclosed	P
	1999	300 ± 154	381 ± 167	0.947
Sitka spruce	*2000*	148 ± 85	160 ± 84	0.947
	2001	335 ± 211	183 ± 79	0.947
	1999	117 ± 58	67 ± 47	0.947
Rhododendron	*2000*	38 ± 22	25 ± 13	0.947
	2001	21 ± 21	46 ± 26	0.947

more complex fashion. Sitka spruce height and basal diameter growth increments were not significantly different between exclosed and unexclosed plots. Sitka spruce had the highest growth rates, followed by birch and rowan.

Table 12.10. Medians (and range) of mean height and basal diameter growth increments for birch, holly, rowan, and Sitka spruce saplings in exclosed and unexclosed plots. Sample size (N) is the number of subplot means. Growth intervals were 1999-2000 and 2000-2001. P-values are the results of Mann-Whitney U tests.

		Exclosed		Unexclosed		P
		N	Median *(Min – Max)*	N	Median *(Min – Max)*	
Birch Ht Growth (cm)	*99-00*	21	20.2 *(-11.0 – 57.0)*	12	-3.6 *(-13.0 – 6.9)*	0.001
	00-01	39	20.2 *(-11.0 – 75.0)*	17	-1.0 *(-8.0 – 26.0)*	< 0.0001
Birch Diam Growth (mm)	*99-00*	21	2.5 *(-8.2 – 7.0)*	12	0.5 *(-3.0 – 2.0)*	0.079
	00-01	39	3.0 *(-8.0 – 18.0)*	17	0.6 *(-6.0 – 7.0)*	< 0.0001
Holly Ht Growth (cm)	*99-00*	13	13.3 *(2.0 – 41.0)*	10	3.3 *(-28.0 – 7.0)*	0.011
	00-01	21	13.3 *(2.0 – 34.0)*	13	-1.0 *(-35.0 – 5.0)*	< 0.0001
Holly Diam Growth (mm)	*99-00*	12	2.7 *(-1.0 – 8.0)*	9	1.3 *(0 – 0.6)*	0.982
	00-01	20	4.0 *(-1.0 – 7.0)*	12	0.5 *(-2.0 – 3.0)*	0.004
Rowan Ht Growth (cm)	*99-00*	13	17.6 *(1.0 – 80.0)*	11	-1.0 *(-3.5 – 9.9)*	0.002
	00-01	35	23.0 *(-2.0 – 78.0)*	14	-3.0 *(-66.0 – 34.0)*	< 0.0001
Rowan Diam Growth (mm)	*99-00*	13	1.3 *(-1.0 – 13.0)*	11	0.0 *(-1.0 – 1.4)*	0.122
	00-01	35	3.0 *(-4.0 – 8.0)*	14	0.1 *(-3.0 – 3.0)*	0.002
Spruce Ht Growth (cm)	*99-00*	11	23.1 *(6.0 – 70.0)*	13	27.6 *(-3.0 – 132.1)*	0.982
	00-01	16	28.6 *(-2.0 – 62.0)*	16	27.3 *(-3.0 – 66.0)*	0.982
Spruce Diam Growth (mm)	*99-00*	10	3.0 *(-1.5 – 7.7)*	12	5.3 *(-1.0 – 15.0)*	0.645
	00-01	15	5.3 *(0 – 12.0)*	13	5.3 *(-0.5 – 12.0)*	0.982

Mortality of naturally regenerating saplings was quite low, even in unexclosed plots (Table 12.11). Mortality was significantly higher in unexclosed plots only for birch in 2000. It appears that once tree seedlings reach this size, they have effectively become established.

Table 12.11. Percent mortality of naturally regenerating saplings > 30 cm tall in exclosed and unexclosed plots. N is the number of live trees sampled in the previous year.

		2000		2001	
		Exclosed	**Unexclosed**	**Exclosed**	**Unexclosed**
Birch	*% Mortality*	3.2	15.5 [1]	2.6	2.9
	N	252	58	233	70
Holly	*% Mortality*	0	5.3	0	0
	N	23	19	41	21
Rowan	*% Mortality*	3.1	3.3	1.0	0
	N	65	30	98	20
Sitka spruce	*% Mortality*	1.6	0	0	2.4
	N	126	160	103	169

[1] Birch mortality in 2000 was significantly higher in unexclosed plots compared with exclosed plots, according to Fisher's exact test (P = 0.001). No other significant differences were found.

12.3 Small Mammal Damage

Native, naturally regenerating trees were browsed much less often than planted trees by hares and other small herbivores. Percentages of saplings of commonly regenerating species browsed by small herbivores in any year were: 19.4% of rowan, 14.8% of sally, 13.3% of birch, 3.8% of holly, and 1.8% of Sitka spruce. No *Rhododendron* individuals were browsed by small mammals. Of the 18 naturally regenerating oaks (in all size classes), 4 were browsed, i.e. 22.2% of the total.

Rowan saplings in exclosed plots browsed by small herbivores tended to have higher growth rates in the season after browsing (Table 12.12). For rowan diameter growth over the 2000-2001 period, this difference was statistically significant. Height and basal diameter growth in 2000-2001 also tended to be higher for browsed birch saplings. Birch growth in 1999-2000 and growth of holly, sally and Sitka spruce were not tested because of small sample sizes.

Table 12.12. Medians (and range) of height and basal diameter growth increments for birch and rowan saplings browsed and unbrowsed by small herbivores in 1999 (for 1999-2000 growth increments) and in 2000 (for 2000-2001 growth increments). Sample size (N) is the number of trees. P-values are the results of Mann-Whitney U tests. Birch growth variables in 1999-2000 were not tested because of insufficient sample size.

		Browsed		Unbrowsed		P
		N	Median *(Min – Max)*	N	Median *(Min – Max)*	
Birch Ht Growth (cm)	*99-00*	1	-25 -	237	22 *(-21 – 91)*	-
	00-01	25	33 *(-11 – 87)*	196	26 *(-24 – 106)*	0.159
Birch Diam Growth (mm)	*99-00*	1	-1 -	236	2 *(-9 – 12)*	-
	00-01	25	4 *(-2 – 18)*	193	3 *(-8 – 15)*	0.444
Rowan Ht Growth (cm)	*99-00*	4	47 *(16 – 76)*	59	13 *(-10 – 80)*	0.064
	00-01	15	26 *(-9 – 66)*	82	20 *(-5 – 89)*	0.463
Rowan Diam Growth (mm)	*99-00*	4	4 *(3 – 6)*	59	1 *(-6 – 13)*	0.052
	00-01	15	4 *(1 – 6)*	80	1 *(-5 – 9)*	0.016

12.4 Environmental Factors

The preliminary CCA of densities of naturally regenerating tree species resulted in three variables that had correlations with CCA axes 1 - 3 between -0.2 and 0.2: slope, soil organic content, and presence/absence of Sitka spruce in the former conifer crop. These variables were removed prior to the final CCA. The sum of eigenvalues of the first three canonical axes of the final CCA was $\lambda_{sum} = 1.55$, which explained 56.1% of the variance in the tree species data. The first eigenvalue of Axis 1 accounted for 24.5% of the variance in the species data ($\lambda_1 = 0.677$) and the species-environment correlation was 0.981. Axis 2 explained 22.5% of the variance ($\lambda_2 = 0.622$) and had a species-environment correlation of 0.981. Axis 3 explained 9.0% of the variance ($\lambda_3 = 0.250$) and had a species-environment correlation of 0.966. All eigenvalues and species-environment correlations were significant, according to Monte Carlo permutation tests with 99 randomised runs (P = 0.01).

Because of the number of variables involved, the ordination biplots for the first three axes are divided into four figures: ordination on Axes 1 and 2 of the tree variables is shown in Fig. 12.1a, and environmental variables are overlaid in Fig, 12.1b; tree variables plotted on Axes 1 and 3 are shown in Fig. 12.1c and environmental variable ordinations are presented in Fig. 12.1d. Axis 1 primarily separated Sitka spruce from the native tree species variables (Fig. 12.1a, c). Rowan occupied the middle of the ordination, between spruce and holly, birch and sally. Density of holly > 30 cm tall in 1999 was separated from the rest of the holly regeneration variables and was positioned next to large Sitka spruce density in 1999 along Axis 1. Axis 2 separated rowan regeneration from the remainder of the tree regeneration variables (Fig. 12.1a). Axis 3 spreads out the birch variables, and sally variables to a lesser extent, that were clustered together by the first two axes (Fig. 12.1c).

Densities of Sitka spruce seedlings in 1999-2001 and density of spruce saplings in 1999 were associated with lower temperatures, higher brash, higher cover of bryophytes, northeastern aspect, and the Sitka spruce seed source index (Fig. 12.1b). The associations with seed source and northeast aspect are stronger for density of spruce saplings in 1999 than for spruce seedlings (Fig. 12.1d). Abundances of spruce saplings in 1999 are also greater in stands felled longer ago with higher field layer covers, greater K^+ availability, and soil gleying. Spruce seedling densities are favoured more by increased brash height, available Ca^{2+}, and bryophyte cover (Fig. 12.1d).

Because rowan was particularly abundant in the Muckross Forest site in Killarney (Tables 12.1, 12.2), the environmental variables highly associated with it largely reflect conditions at that site. Rowan densities were higher in High *Calluna – Erica* vegetation on shallow soils with relatively high base status, low water-holding capacity in the upper layer ("upper soil index"), but impeded drainage lower in the profile (i.e. gleying) (Fig. 12.1b). Availability of rowan seed sources was not well correlated with rowan regeneration (Fig. 12.1b, d).

Density of holly saplings > 30 cm tall in 1999 had a strong positive association with brash height and bryophyte cover and a negative association with mean annual temperature (Fig. 12.1b, d). Density of seedlings in 1999-2001 and annual recruitment to the sapling size class responded differently to the environment. Holly seedling densities and sapling recruitment were greater in more recently felled sites with higher covers of soil and litter and deeper soils (Fig. 12.1b). *Digitalis – Juncus* and Low *Calluna – Erica* were favourable vegetation types for holly seedling abundances and recruitment (Fig. 12.1b, d). Holly seed source abundances seemed to be more important for maintaining seedling densities than did rowan seed sources. Holly

Figure 12.1a. Correlation biplot of axes 1 and 2 of a CCA of naturally regenerating tree species variables and environmental variables in exclosed plots: ordination of tree species variables. Black symbols indicate birch, orange symbols indicate sally, blue symbols indicate holly, red symbols indicate rowan, and green symbols indicate Sitka spruce. Densities of seedlings ≤ 30 cm tall are shown using filled symbols: ■: 1999, ●: 2000, and ▲: 2001. Hollow squares, □, represent densities of saplings > 30 cm tall in 1999 ("Lg"). Annual recruitment of trees > 30 cm tall ("New Lg") are also shown using hollow symbols: ○: 2000 and △: 2001. Ordinations of the subplots are not presented for readability. The percent variance explained (λ_i / λ_{sum}) by each axis is shown.

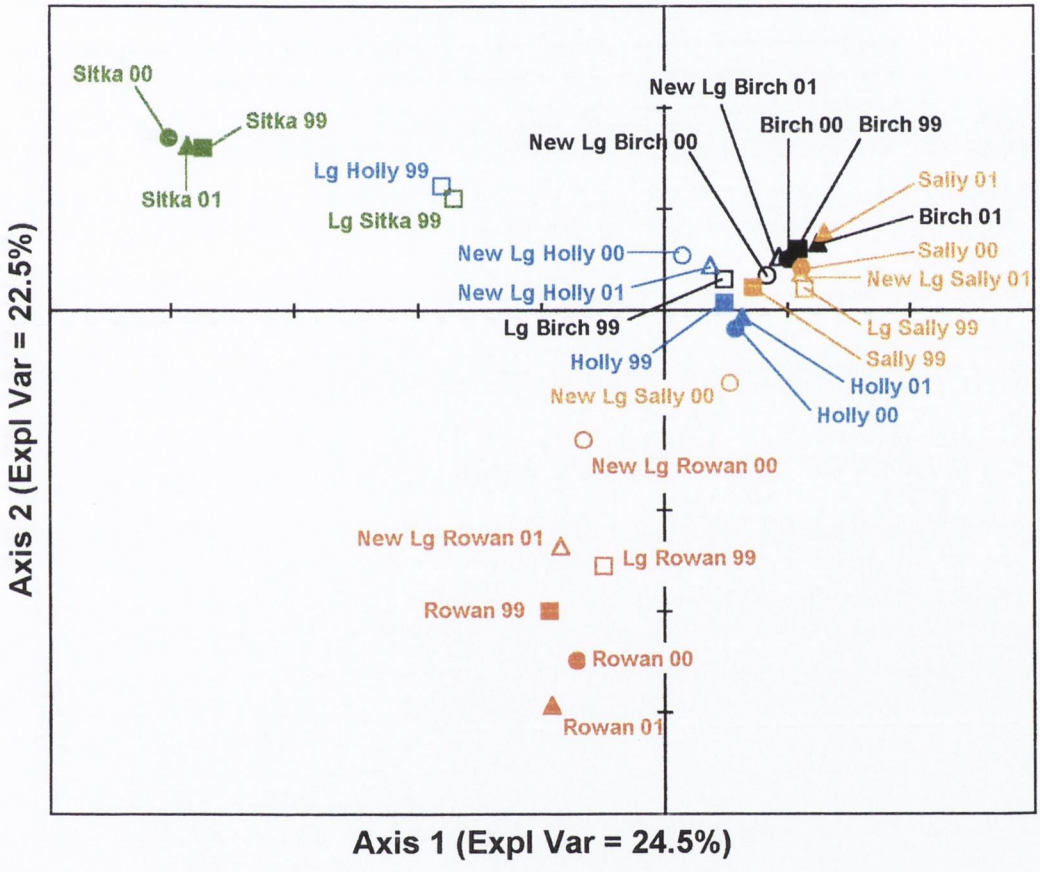


Figure 12.1b. Correlation biplot of axes 1 and 2 of a CCA of naturally regenerating tree species variables and environmental variables in exclosed plots: ordination of environmental variables. Continuous variables are indicated by vectors, and the ordinations of presence/absence variables are shown by filled boxes with yellow crosses. Tree species are indicated by symbols (as per Fig. x.1a) but are not labelled. Correlations between environmental and tree variables are reflected by the angles between their vectors. Ordinations of the subplots are not presented for readability. The percent variance explained (λ_i / λ_{sum}) by each axis is shown.

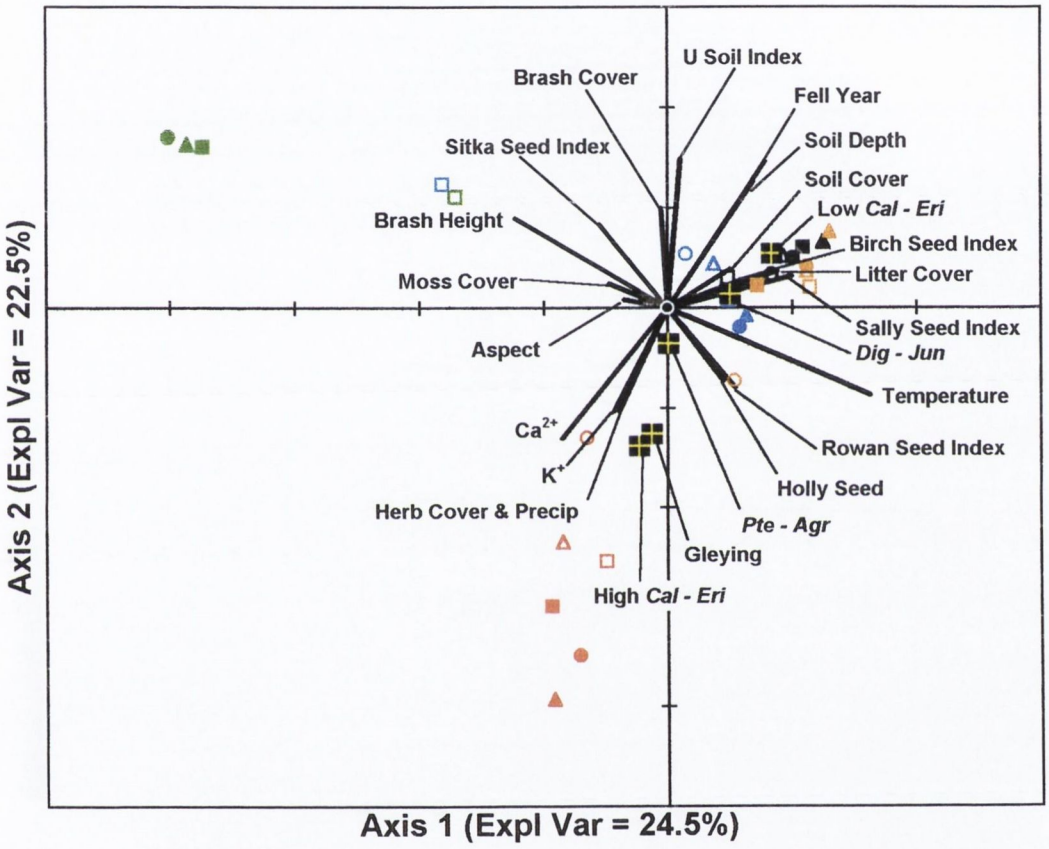


Figure 12.1c. Correlation biplot of axes 1 and 3 of a CCA of naturally regenerating tree species variables and environmental variables in exclosed plots: ordination of tree species variables. Black symbols indicate birch, orange symbols indicate sally, blue symbols indicate holly, red symbols indicate rowan, and green symbols indicate Sitka spruce. Densities of seedlings ≤ 30 cm tall are shown using filled symbols: ■: 1999, ●: 2000, and ▲: 2001. Hollow squares, □, represent densities of saplings > 30 cm tall in 1999 ("Lg"). Annual recruitment of trees > 30 cm tall ("New Lg") are also shown using hollow symbols: ○: 2000 and △: 2001. Ordinations of the subplots are not presented for readability. The percent variance explained (λ_i / λ_{sum}) by each axis is shown.

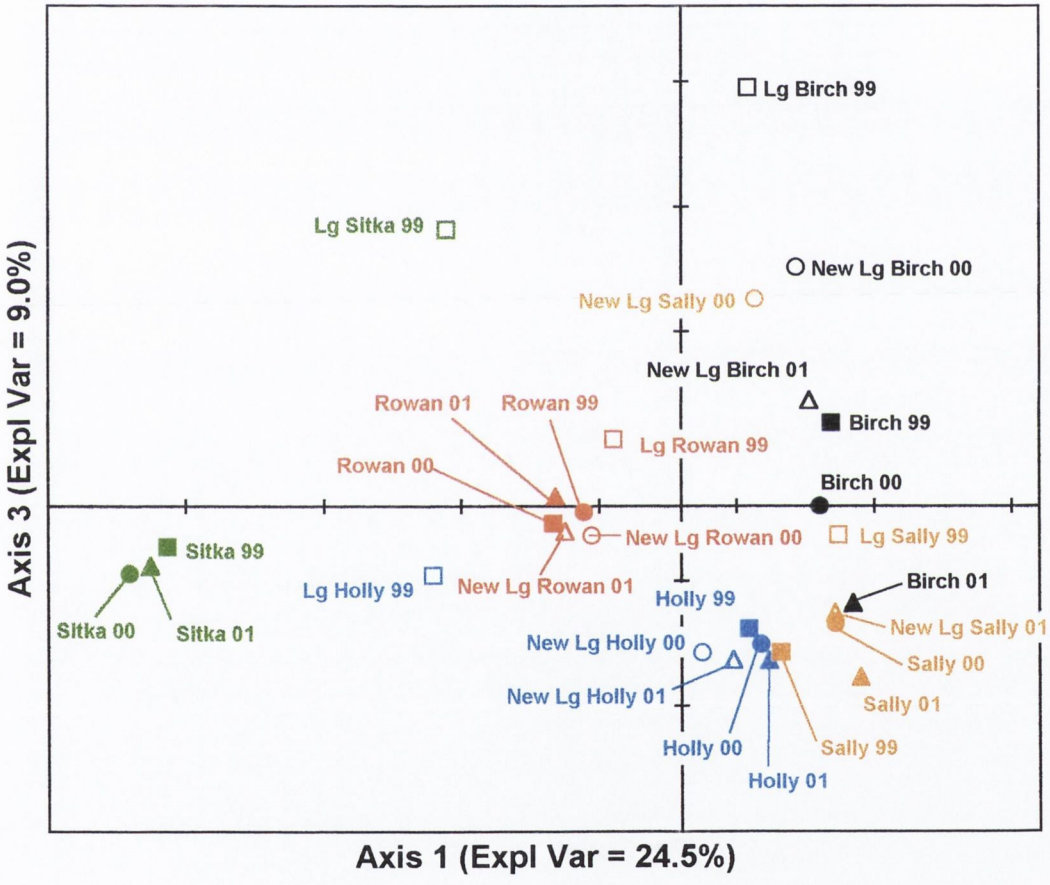
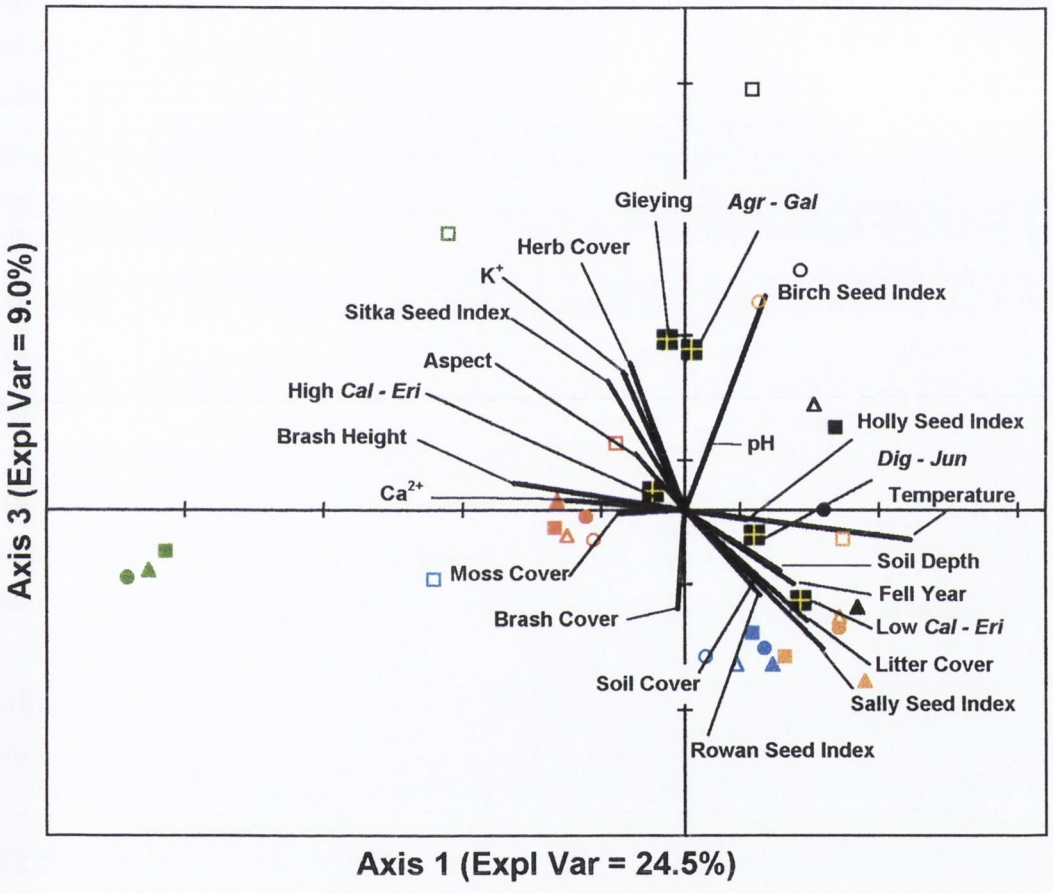


Figure 12.1d. Correlation biplot of axes 1 and 3 of a CCA of naturally regenerating tree species variables and environmental variables in exclosed plots: ordination of environmental variables. Continuous variables are indicated by vectors, and the ordinations of presence/absence variables are shown by filled boxes with yellow crosses. Tree species are indicated by symbols (as per Fig. x.1c) but are not labelled. Correlations between environmental and tree variables are reflected by the angles between their vectors. Ordinations of the subplots are not presented for readability. The percent variance explained (λ_i / λ_{sum}) by each axis is shown.



recruitment was favoured by higher soil water-holding capacity of the upper layer and higher brash cover.

Birch natural regeneration was positively associated with the birch seed source index, warmer temperatures, litter cover, soil cover, and the *Digitalis – Juncus* and Low *Calluna – Erica* vegetation types (Fig. 12.1b). Negatively correlated with birch were base cation availability and field layer cover. The birch variables were ranked along Axis 3 on an approximate age scale, with the earliest established saplings scoring high on Axis 3 and the most recently appearing seedlings scoring lowest (Fig. 12.1c). The birch seed source index was most strongly correlated with sapling recruitment in 2000 (Fig. 12.1d). Correlated to a lesser degree were 2001 recruitment and 1999 densities of both size classes, but recent regeneration in 2000 and 2001 had weaker associations with birch seed source availability (Figs. 12.1c,d). Recent regeneration was correlated with recent felling year, deeper soils, higher covers of litter and bare soil, lower covers of vegetation, and lower base cation availability. Longer established birch regeneration (i.e. 1999 density and 2000 and 2001 recruitment) was more associated with gleying, the *Agrostis – Galium* vegetation type, and lower brash cover.

All sally variables, except recruitment to the sapling size class in 2000, were highly correlated with the sally seed source index (Fig. 12.1b, d). These variables were also correlated with environmental variables characteristic of more recently felled sites, similar to small birch seedlings (Fig. 12.1b, d). Recruitment in 2000, however, behaved differently from the other sally variables. It was not well characterised by the CCA, but appears most related to warmer sites with little cover of brash (Fig. 12.1b, d).

12.5 Sitka Spruce Regeneration

12.5.1 Effects of Site and Environment on Invasion

To gain a clearer understanding of what factors allow Sitka spruce to regenerate after clearfelling, the presence or absence of Sitka spruce in weeded subplots in either 2000 or 2001 was investigated using logistic regression. Of the twenty-six environmental variables included in the model (section 11.2.5), nine were significant at the $\alpha = 0.05$ level after backward elimination. This model, however, had an overall significance of $P = 0.899$ (Hosmer-Lemeshow $\chi^2 = 3.50$ (Hosmer & Lemeshow, 1989)). Because the ten-variable solution reached one step earlier was significant (Hosmer-Lemeshow $\chi^2 = 18.16$, $P = 0.020$), this model was selected, and is presented in Table 12.13. The variable removed from this solution to reach the non-significant nine-variable model was the presence/absence of Sitka spruce in the former conifer crop.

Table 12.13. Logistic regression of environmental variables on the presence/absence of Sitka spruce invasion in weeded subplots in 2000 or 2001. Shown for each environmental variable are the slope in the regression equation (b), slope exponentiated (e^b), and its significance in the model. The value e^b can be interpreted as an odds ratio, i.e. the likelihood, relative to 1, of spruce invasion for each unit increase of the environmental variable. Overall model significance was P = 0.020, according to Hosmer-Lemeshow χ^2.

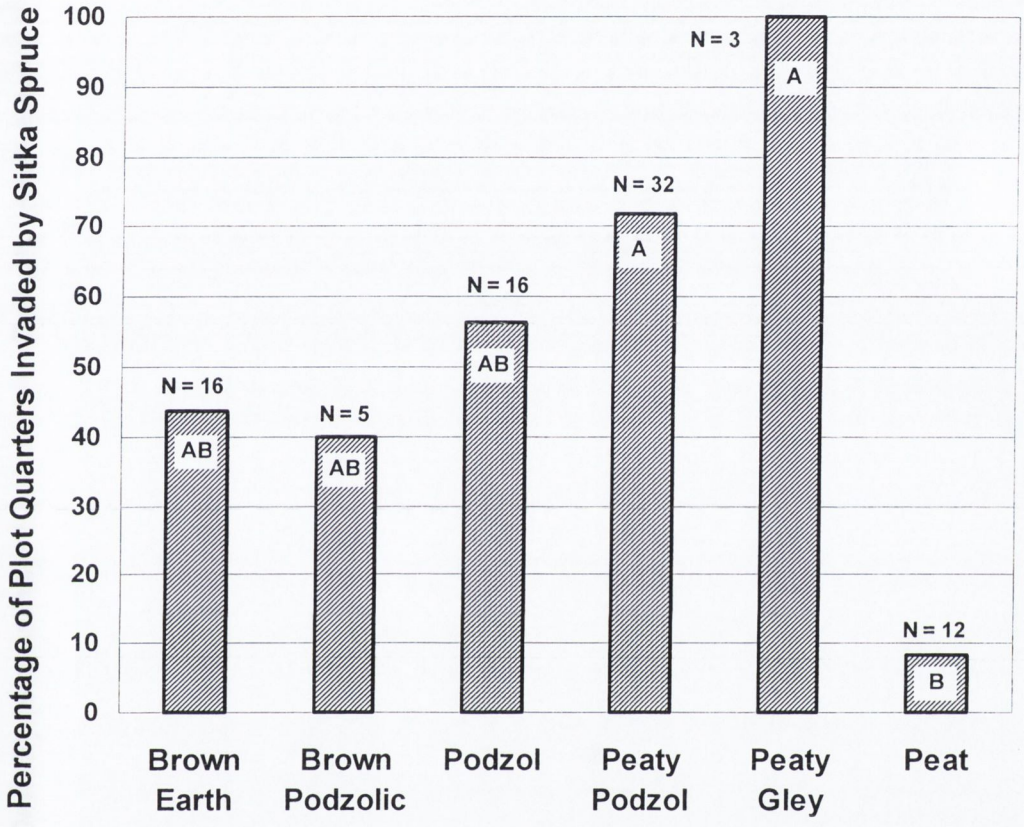
	b	e^b (Odds Ratio)	P
Gleying[1]	-4.011	0.018	0.028
Soil Depth (cm)	-0.332	0.718	0.015
Slope (deg)	0.264	1.302	0.006
Former Sitka spruce crop[1]	2.066	7.890	0.104
Aspect[2]	2.656	14.243	0.005
Agrostis – Galium Type[1]	4.342	76.856	0.023
pH	-8.073	0.001	0.006
Soil Cover (%)	0.113	1.120	0.107
Litter Cover (%)	0.036	1.036	0.039
Upper Soil Index[3]	1.195	3.305	0.002
Constant	29.955	-	0.020

[1] Bivariate (0/1) variable.
[2] Aspect (A) in degrees transformed to linear scale, A' = cos(45-A) + 1.
[3] Ranked (1-6) index of soil water holding capacity of upper 15 cm (see section 5.3.4).

The likelihood of Sitka spruce invasion in 2000 or 2001 was reduced by the presence of gleying in the soil, greater soil depth, and higher pH (Table 12.13). Sitka spruce invasion was favoured by steeper slopes, northeast aspect, increased cover of litter and bare soil, and higher soil water holding capacity in the topmost layer ("upper soil index"). The former conifer crop may be useful as an indicator of active spruce regeneration (Table 12.13). The encouragement of Sitka invasion in *Agrostis – Galium* vegetation relative to the *Calluna – Galium* type is surprising, especially considering that higher soil and litter cover increase the likelihood of spruce invasion.

The likelihood ratio contingency test of the presence/absence of Sitka spruce invasion found significant differences among the six soil types in the proportion of subplots invaded by spruce in 2000 or 2001 (P = 0.001). Homogeneous subsets of soil types were constructed (Sokal & Rohlf, 1995) to determine which soil types were more hospitable to Sitka spruce immigration. Sites on peaty gleys and peaty podzols were significantly more likely than blanket peat sites to experience Sitka spruce immigration (Fig. 12.2). Spruce also tended to invade a greater percentage of subplots on the poorer soil types than those on brown earths or brown podzolics.

Figure 12.2. Percentage of weeded plot quarters invaded by Sitka spruce in 2000 or 2001. Sample size (n) is the number of weeded subplots in each soil type. Percent invasion was significantly different (P = 0.001) among soil types according to a likelihood ratio contingency test. Soil types indicated with the same letter are not significantly different (α=0.05), according to unplanned contingency tests of independence (Sokal and Rohlf, 1995).



12.5.2 Size Class Distributions

The Sitka spruce size class distributions presented in Figs. 12.3-12.9 can be used to some extent to draw inferences about past patterns of natural regeneration. In addition, the changes in the size distributions over repeated sampling intervals illustrate changes in recruitment and growth of the spruce population in different sets of plots. For example, a unimodal or hump-shaped distribution visible in several of the size class distributions below, suggests a slowdown in the rates of site invasion. Another common feature of the Sitka spruce size distributions is the co-occurrence of peak seedling densities of 1-20 cm tall seedlings in 2001, which indicates that 2000 may have been a good seed year for Sitka spruce, a known mast seeding species (Brown & Neustein, 1972; Harris, 1990; Clarke, 1992).

The site felled longest ago, Muckross Forest in Killarney, had the largest Sitka spruce regeneration, with some individuals ranging from 5-6 m tall (Fig. 12.3). Overall Sitka spruce

Figure 12.3. Size class distributions in 1999-2001 of Sitka spruce natural regeneration in non-weeded subplots in former Sitka spruce plots felled in 1988 (plot pairs 5-7) in Muckross Forest, Killarney. Size classes are in 20 cm height increments; the final size class represents Sitka spruce 5-6 m tall.

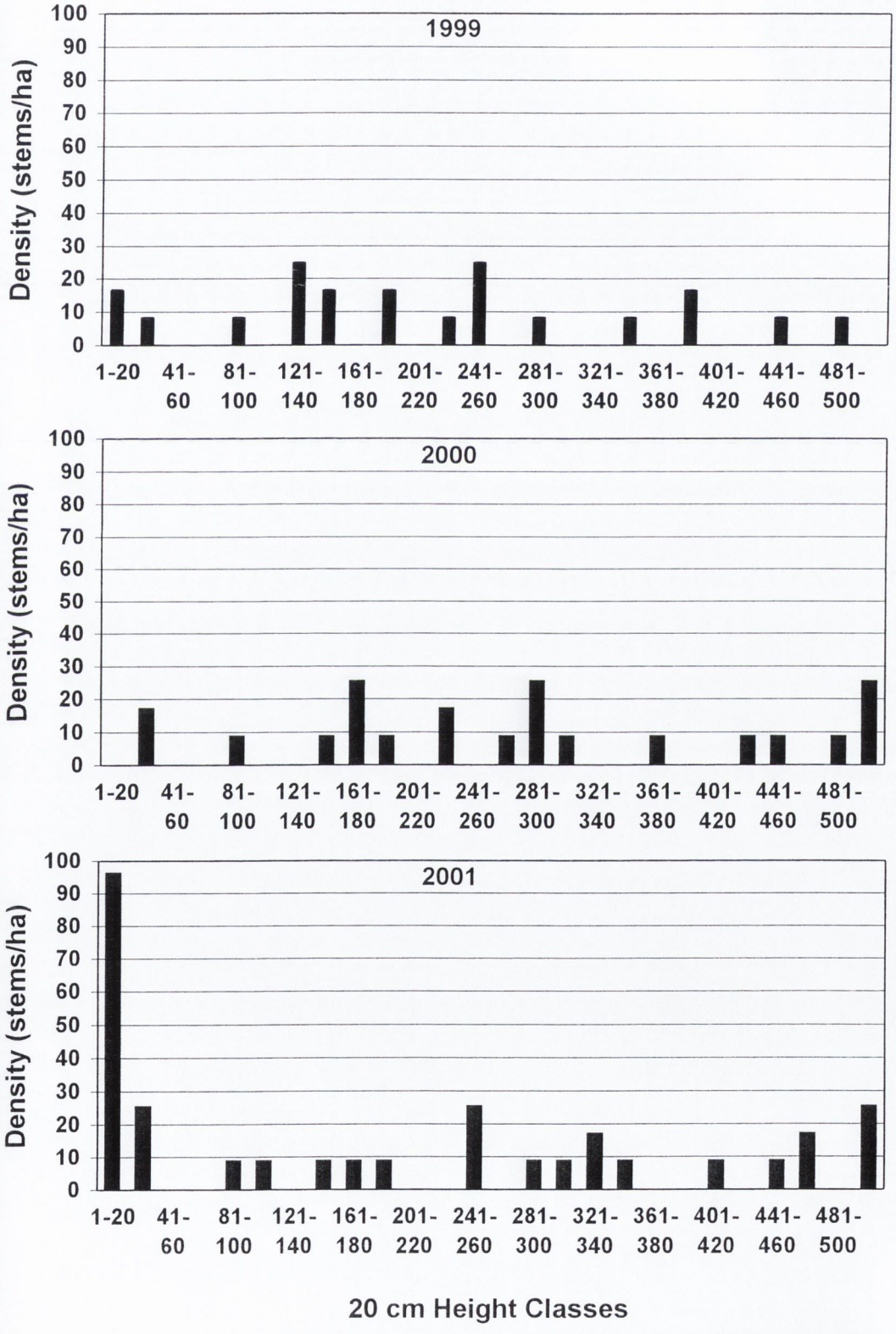


Figure 12.4. Size class distributions in 1999-2001 of Sitka spruce natural regeneration in non-weeded subplots in three Glendalough plots: two former larch plot pairs (#8 and #9) felled in 1991 and one former Sitka spruce/lodgepole pine mixture (#10) felled in 1993. Size classes are in 20 cm height increments.

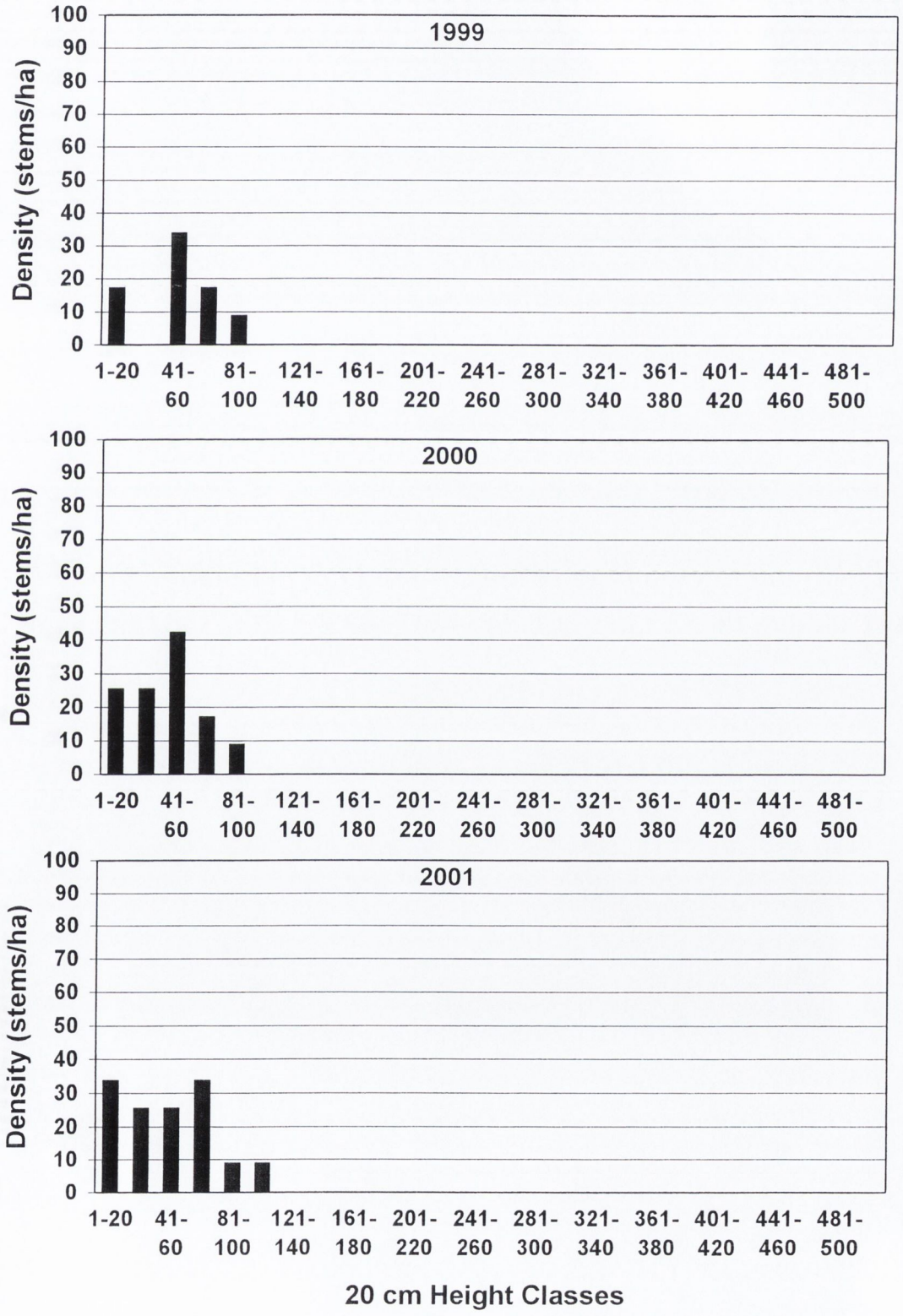


Figure 12.5. Size class distributions in 1999-2001 of Sitka spruce natural regeneration in non-weeded subplots in a former Sitka spruce stand felled in 1993 (plot pair 22) in Benleagh, Glenmalure. Size classes are in 20 cm height increments. Note that the entire plot area was sampled in 1999 and 2000, whereas Sitka spruce was subsampled in 2001 (section 11.1.1).

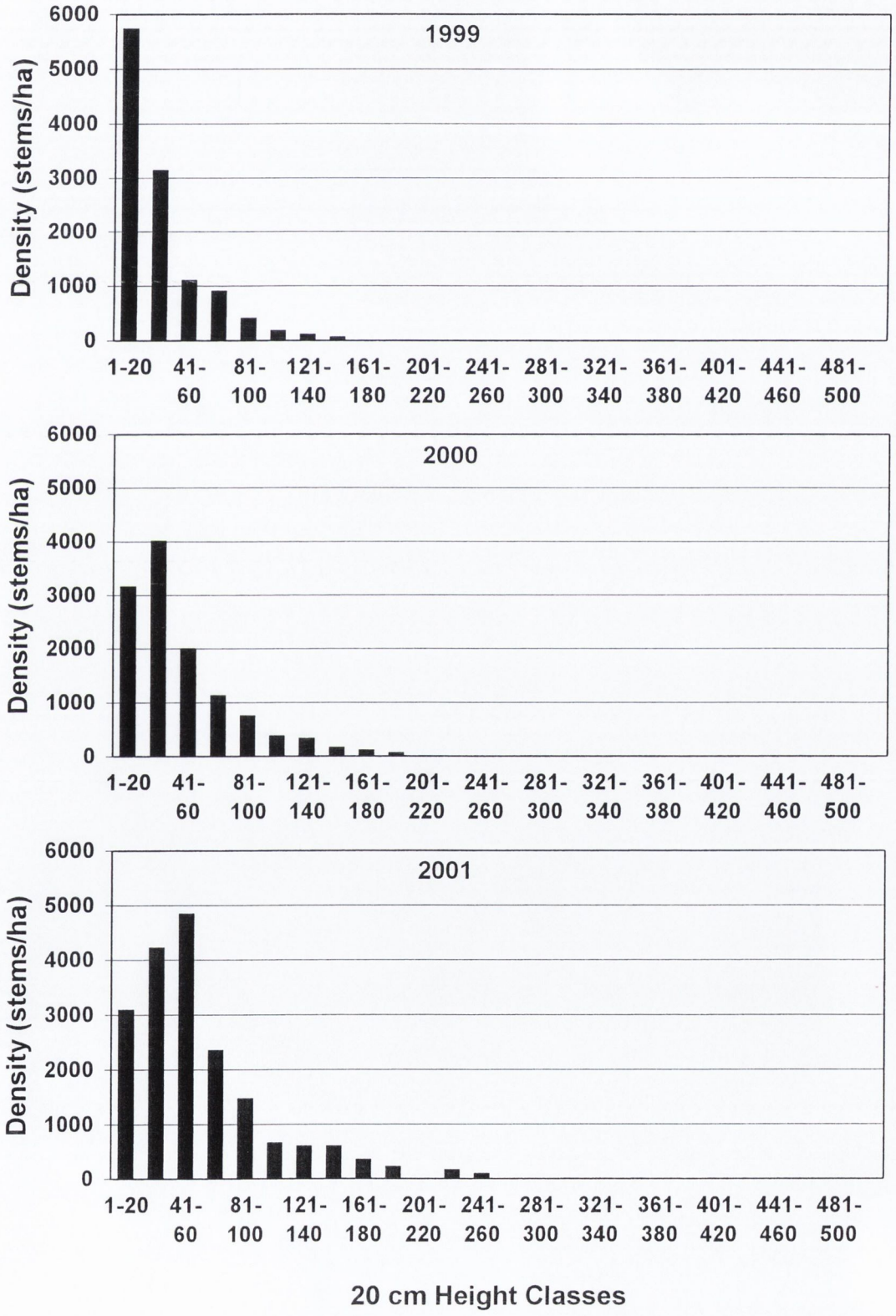


Figure 12.6. Size class distributions in 1999-2001 of Sitka spruce natural regeneration in non-weeded subplots in former Sitka spruce plots felled in 1994 (plot pairs 1, 3, 4) in Looscaunagh, Killarney. Size classes are in 20 cm height increments.

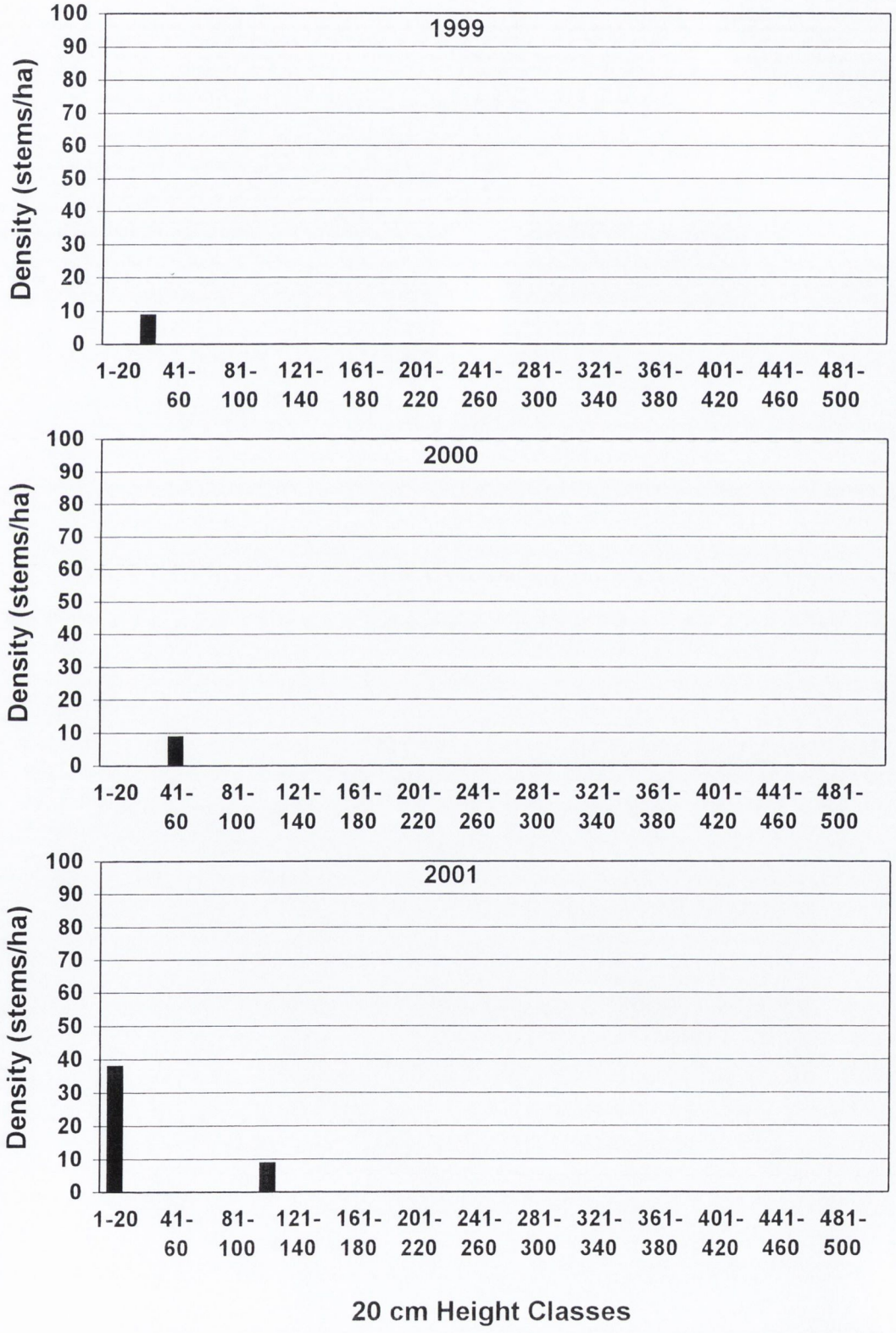


Figure 12.7. Size class distributions in 1999-2001 of Sitka spruce natural regeneration in non-weeded subplots in a former Sitka spruce plot pair felled in 1995 (plot pair 11) in Glendalough. Size classes are in 20 cm height increments. Note that the entire plot area was sampled in 1999 and 2000, whereas Sitka spruce was subsampled in 2001 (section 11.1.1).

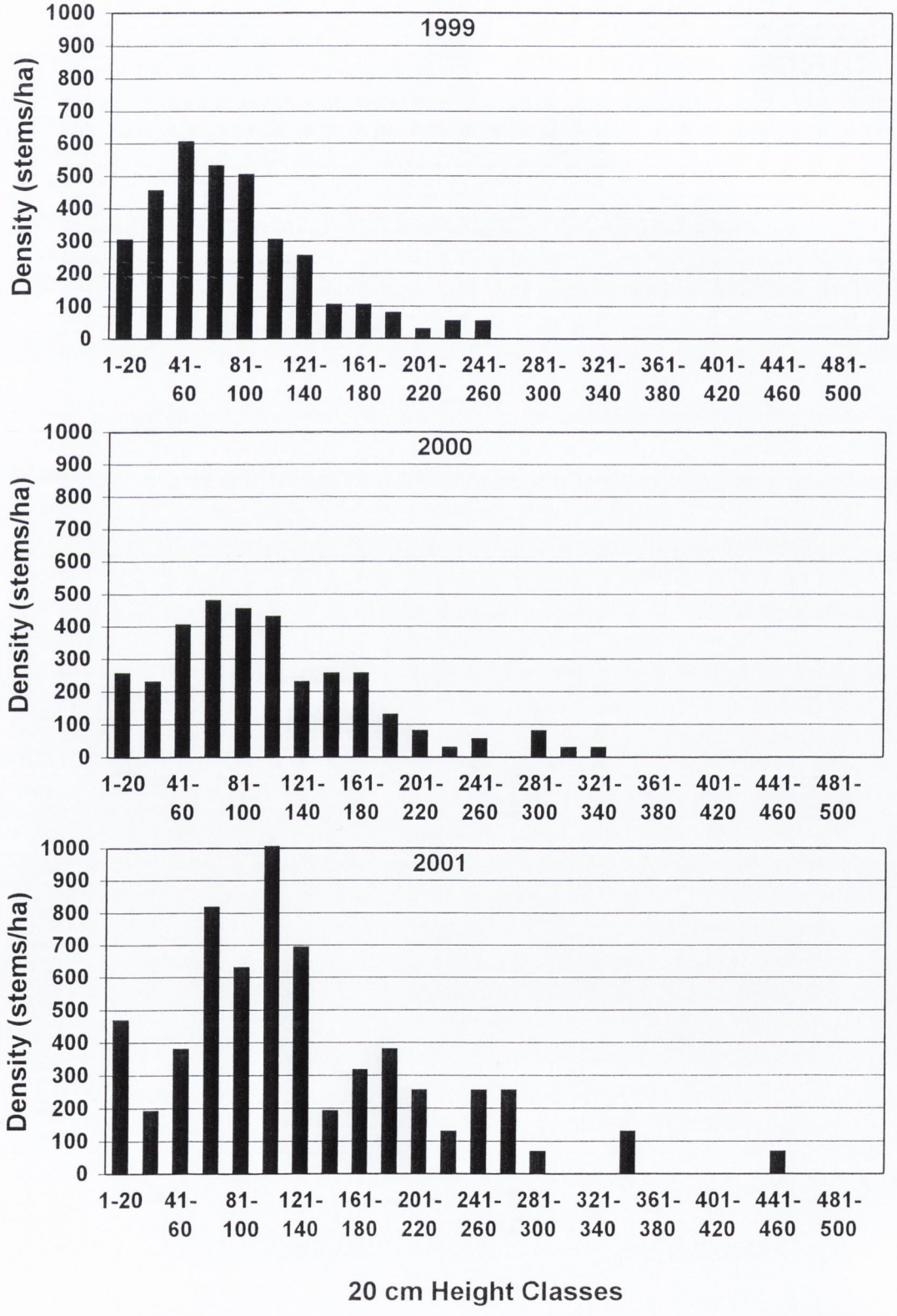


Figure 12.8. Size class distributions in 1999-2001 of Sitka spruce natural regeneration in non-weeded subplots in former lodgepole pine plots felled in 1997 (plot pairs 15, 16, 20) in Fraughan Rock Glen, Glenmalure. Size classes are in 20 cm height increments.

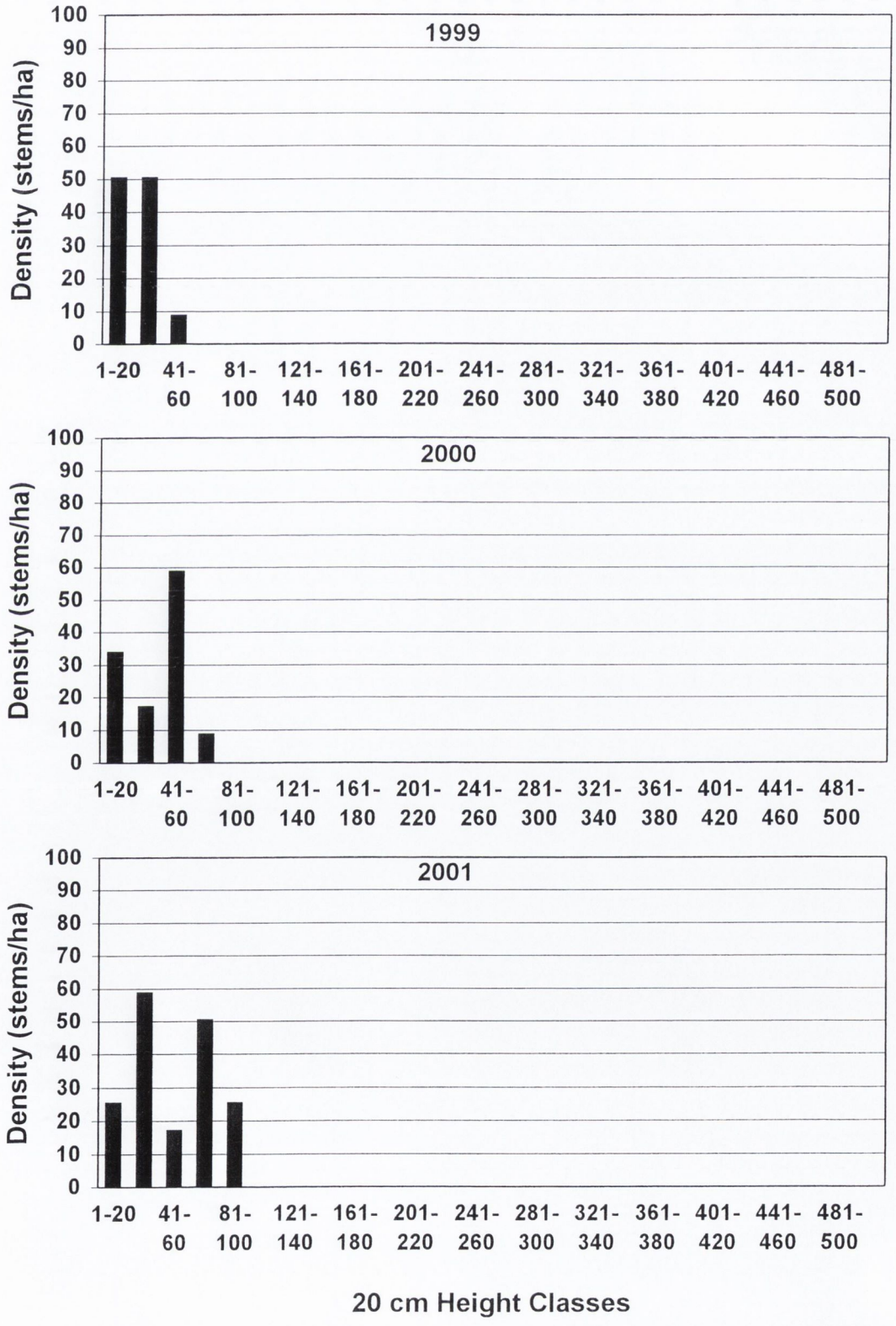
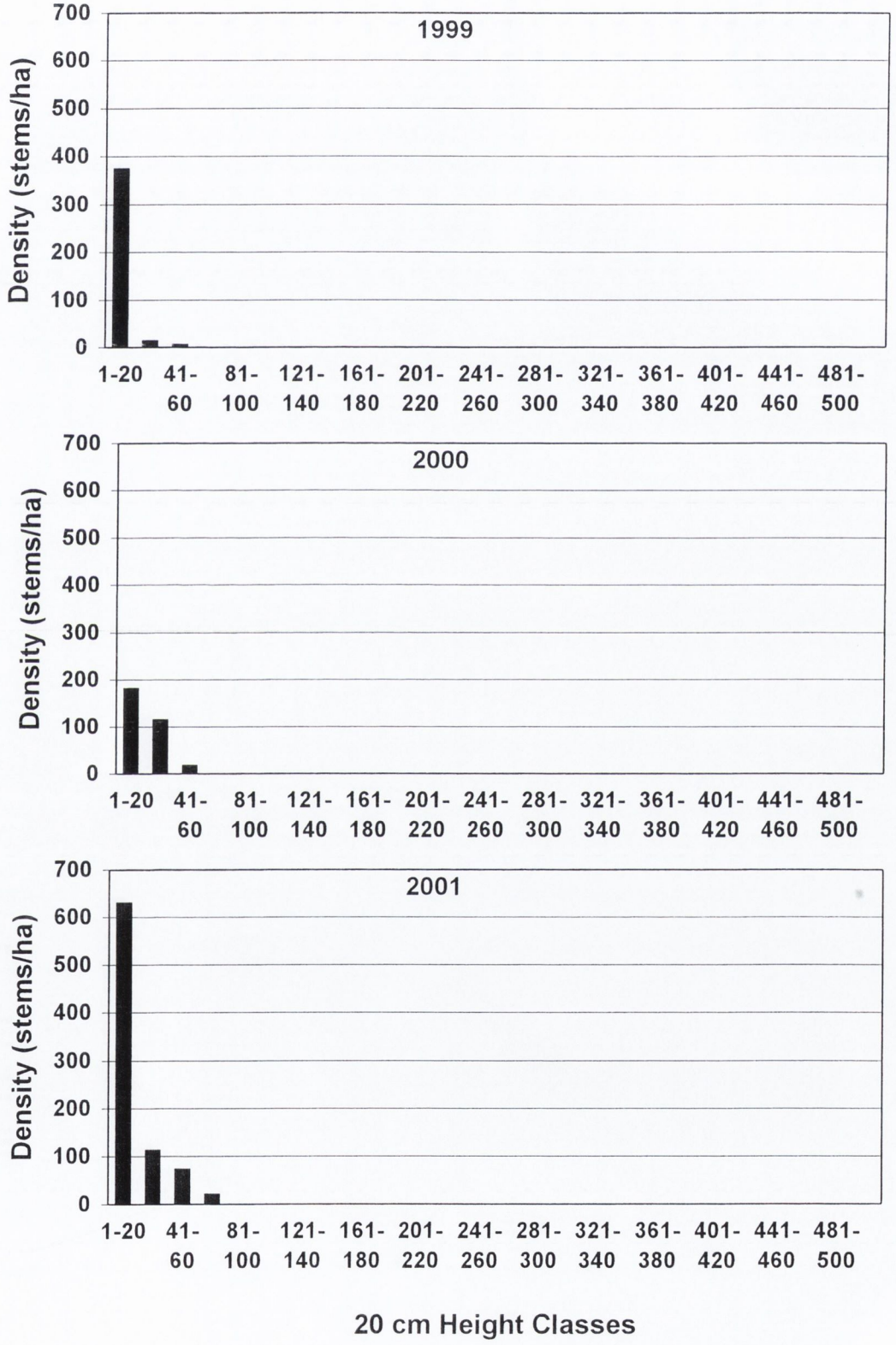


Figure 12.9. Size class distributions in 1999-2001 of Sitka spruce natural regeneration in non-weeded subplots in former Sitka spruce plots felled in 1998 (plot pairs 12-14, 17-19, 21) in Glenmalure. Size classes are in 20 cm height increments.



densities were low, and the low densities in the smaller size classes demonstrate that there was little recent regeneration until 2001.

Three of the Glendalough plot pairs, two felled in 1991 and one in 1993, had no spruce trees larger than 1.5 m tall, in contrast to the Muckross Forest site (Fig. 12.4). This is due in large part to removal of Sitka spruce regeneration by Wicklow Mountains National Park staff prior to the commencement of this study. The low densities of smaller spruce trees suggests that establishment opportunities were limited over the study period.

One plot pair at the Benleagh site in Glenmalure (#22) felled in 1993 experienced regeneration densities many times higher than in the other study sites (Fig. 12.5). For comparison, the stocking rate required for grant-aid of Sitka spruce plantations is 2500 stems/ha. Note, however, that apparent increases in abundance in nearly all size classes between 2000 and 2001 were likely to be an artefact of changing from whole-plot sampling to subsampling (section 11.1.1). The inverse-J shape to the size class distribution in 1999 is indicative of active site invasion. The change to unimodal distributions in 2000 and 2001 suggests a slowdown in the rates of invasion. The most likely mechanism is increasing occupation of the site by vegetation, including the spruce seedlings and saplings themselves.

The Looscaunagh plot pairs, felled in 1994, had the poorest spruce regeneration of any of the sites (Fig. 12.6). There was no recent immigration until 2001, similar to the other Killarney site where there was a sizeable increase in 2001 (Fig. 12.3).

A plot pair in Glendalough (#11) felled in 1995 had much higher densities of young Sitka spruce than the earlier felled Glendalough plots (Fig. 12.7). The larger sizes of spruce at this site compared with the Benleagh plot pair (#22) felled two years earlier (Fig. 12.5), suggest that growing conditions are better in plot pair 11. This site is sheltered and at a low elevation with brown podzolic and peaty gley soils, whereas plot pair 22 is an exposed, high elevation site on a wet peaty podzol. The unimodal shapes to the size class distributions in 1999 and 2000 suggest that the rate of Sitka spruce invasion has slowed recently (Fig. 12.7). In 2001, however, there was an increase in the relative amount of very small, probably germinal, seedlings. Note, however, that the switch between whole-plot sampling and subsampling is responsible for some of the changes in relative and absolute densities in size classes between 2000 and 2001.

The former lodgepole pine stands in Fraughan Rock Glen, Glenmalure felled in 1997 experienced little spruce regeneration (Fig. 12.8).

The Sitka spruce stands in Glenmalure felled in 1998 provide estimates of regeneration immediately after felling (Fig. 12.9). In addition to seed immigration from standing trees in the vicinity, the former crop can contribute to the seed rain if it is felled when mature cones are present. Most, if not all, of the stands were felled in autumn and winter when cones are ripe. Therefore, the contribution of the former crop to spruce regeneration can be estimated by comparing densities in the 1-20 cm height class between 1999 and 2000. Comparison between recently felled Sitka spruce stands and lodgepole pine stands (Fig. 12.8) also indicates the effect of former crop species on Sitka spruce regeneration. The highest densities of 1-20 cm tall seedlings in the most recently felled sites, however, occurred in 2001 (Fig. 12.9).

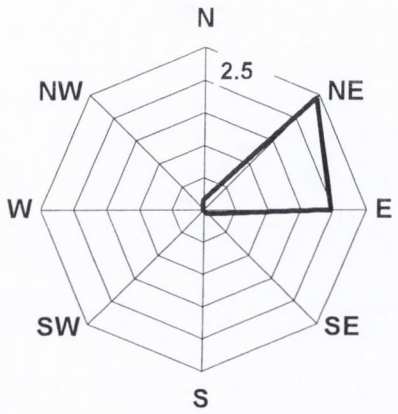
12.5.3 Direction of Seed Sources

The importance of the direction in which Sitka spruce seed sources lay was examined visually by constructing radar diagrams and comparing these to densities of Sitka spruce seedlings invading weeded plots in 2000 and 2001 (i.e. where woody exotics had been removed the previous year). In plot pairs felled longer ago, high overall seed source availability was not well correlated with spruce seedling abundance.

For plots felled in 1997 or 1998, values of the Sitka spruce seed source index (density/distance), summarized by compass direction, are presented in Fig. 12.10. The value of the index at the outermost line is indicated near the top of each diagram. Seed source index equals 0 at diagram centre and increases along the axes in 5 equal increments. For example, to the east (E) of plot 12, the index approximately equals 2.0; to the southwest (SW) of plot 16, the index approximately equals 0.1 (Fig. 12.10). To put the seed source indices in context, an index value of 2.5 is equivalent to a plantation edge (density=100) 40 m distant, whereas and index value of 0.5 corresponds to a plantation edge 200 m distant. A seed source index value of 0.5 is also equivalent to a remnant cluster of spruce (density=10) 20 m distant, and a value of 0.1 corresponds to a cluster 100 m away.

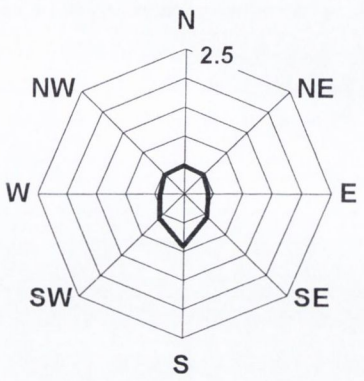
Spruce regeneration in plot pairs felled in 1997 and 1998 appeared to be more strongly influenced by seed source availability towards the west, northwest, and southwest, in the general direction of the prevailing winds (Fig. 12.10). For example, the edge of a standing spruce plantation was close to the east and northeast of plot pair 12, which experienced moderate densities of spruce regeneration in 2001 only. A similar plantation edge was positioned to the northwest of plot pair 18, which had much higher densities of spruce regeneration in 2000 and 2001.

Fig. 12.10. Radar diagrams showing values of the seed source index (density/distance) for Sitka spruce for 10 selected plot pairs. Letters indicate compass bearings from plot centre. Numbers near north (N) indicate the value of the seed source index at the outermost line of the radial axes. Seed source index equals 0 at diagram centre and increases along the axes in 5 equal increments. Also indicated are the former crop (spruce = Sitka spruce, pine = lodgepole pine), felling year, and the densities (numbers /ha) of Sitka spruce seedlings in weeded plots in 2000 and 2001.



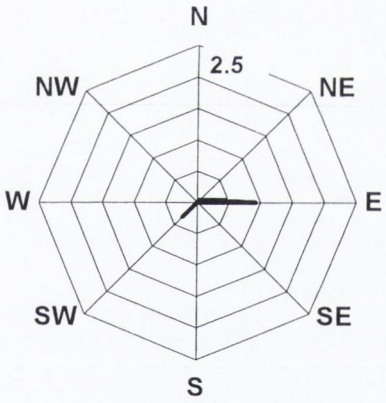
Plot 12: spruce felled 1998

2000: 0/ha 2001: 275/ha



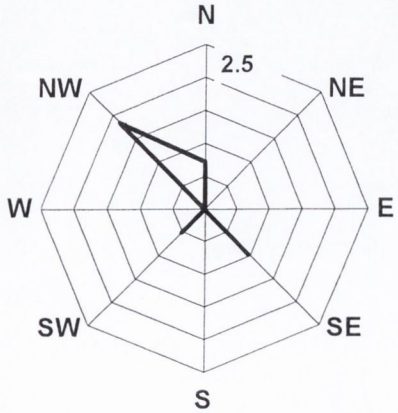
Plot 13: spruce felled 1998

2000: 325/ha 2001: 575/ha



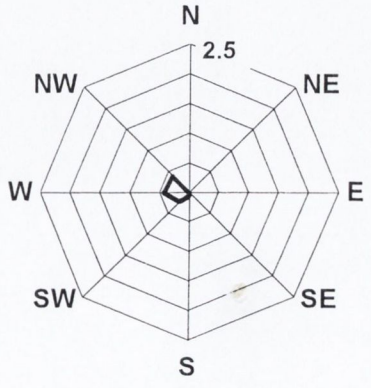
Plot 14: spruce felled 1998

2000: 0/ha 2001: 75/ha



Plot 18: spruce felled 1998

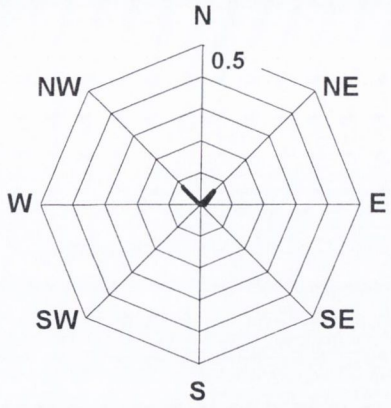
2000: 300/ha 2001: 1400/ha



Plot 21: spruce felled 1998

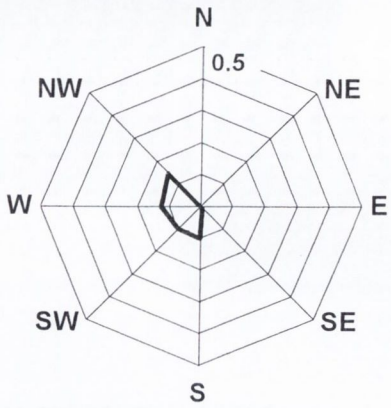
2000: 0/ha 2001: 150/ha

Fig. 12.10. cont'd



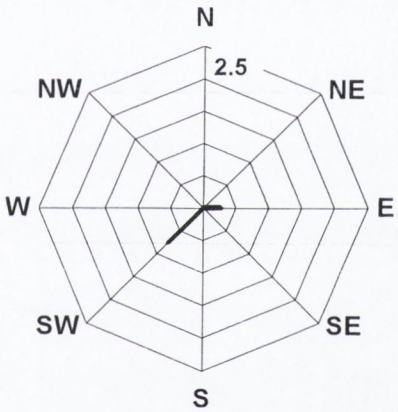
Plot 17: spruce felled 1998

2000: 50/ha 2001: 75/ha



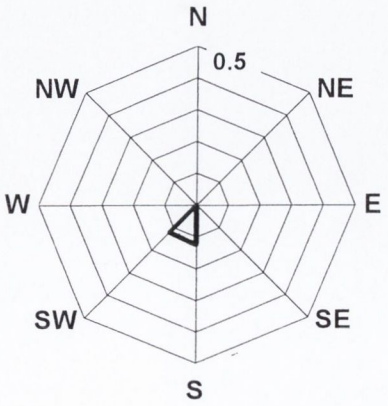
Plot 19: spruce felled 1998

2000: 75/ha 2001: 175/ha



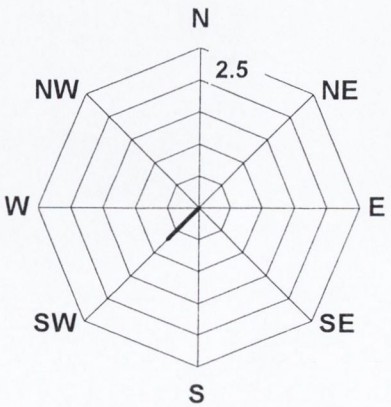
Plot 15: pine felled 1997

2000: 0/ha 2001: 25/ha



Plot 16: pine felled 1997

2000: 25/ha 2001: 50/ha



Plot 20: pine felled 1997

2000: 75/ha 2001: 25/ha

12.5.4 Sitka Spruce Regeneration Transects

To further investigate the importance of seed source direction on spruce regeneration, Sitka spruce counts along the regeneration transects were averaged by direction relative to southwesterly prevailing winds (Rohan, 1986). Eight transects running in the general direction of the wind were averaged to form an "east transects" group. The transects were oriented from north to southeast (compass bearings from 2° to 156°, Table 11.1). Five transects oriented to the south, southwest, west and northwest (compass bearings from 212° to 298°, Table 11.1) were averaged to form a "west transects" group. Spruce densities were higher in the east transects within 6 m of the edge of the adjacent plantation (Fig. 12.11). Further along the transect, strong heterogeneity in the abundance of spruce regeneration was visible in both groups. Many of these peaks and troughs in regeneration are likely to be the result of differences in microsite environments, particularly those caused by site preparation disturbances in the Blessington Forest sites.

The spruce regeneration transects were also averaged by felling year and site. When plotted, the data show that the increase in Sitka spruce regeneration near the plantation edge seen in Fig. 12.11 occurs only in the Blessington Forest sites felled in 2000 (Fig. 12.12). The majority of the peaks in spruce regeneration also occur in these transects. If most of the regeneration observed in both sites are seedlings of the former crop, mortality may account for part of the difference in seedling abundances between felling years. Differences in quality between the Glenmalure and Blessington Forest sites may also be partly responsible. The size class distributions (Figs. 12.3-12.9), however, suggest that 2000/2001 may have been a mast seed year for Sitka spruce. It is likely that this phenomenon is primarily responsible for higher Sitka spruce regeneration abundances in 2000.

12.6 Soil Replacement Quadrats

Naturally regenerating tree seedlings appeared in only two soil replacement quadrats, both in Muckross Forest, Killarney (Table 12.14). None were found in the three Wicklow soil replacement quadrats. Although the trees present in 2000 may have been present in the litter or seed bank, some may have arrived by normal dispersal mechanisms and become established on the bare soil. Mature rowan, birch, holly and sally trees were all found within 350 m. Many occurred along a stream about 100 m from plot 7 and 300 m from plot 5, but others were scattered throughout the area. No ash (*Fraxinus excelsior*) or yew trees were in the vicinity, however. Because ash seeds generally require two winters to break dormancy and may persist for six years in the soil (Wardle, 1961), the ash seedling may have entered with the soil despite first appearing in 2001 (Table 12.14). Yew also requires two winters before dormancy is

Figure 12.11. Mean Sitka spruce counts (individuals/2m^2) and 95% CIs at 1 m intervals along thirteen 100 m transects. "West Transects" run from Sitka spruce plantation edges into clearfells against the assumed direction of the prevailing wind. "East Transects" run from plantation edges in the direction the prevailing winds blow. "West Transects" spruce counts are the means of five transects oriented from 212° to 298°. "East Transects" spruce counts are the means of eight transects oriented from 2° to 156°.

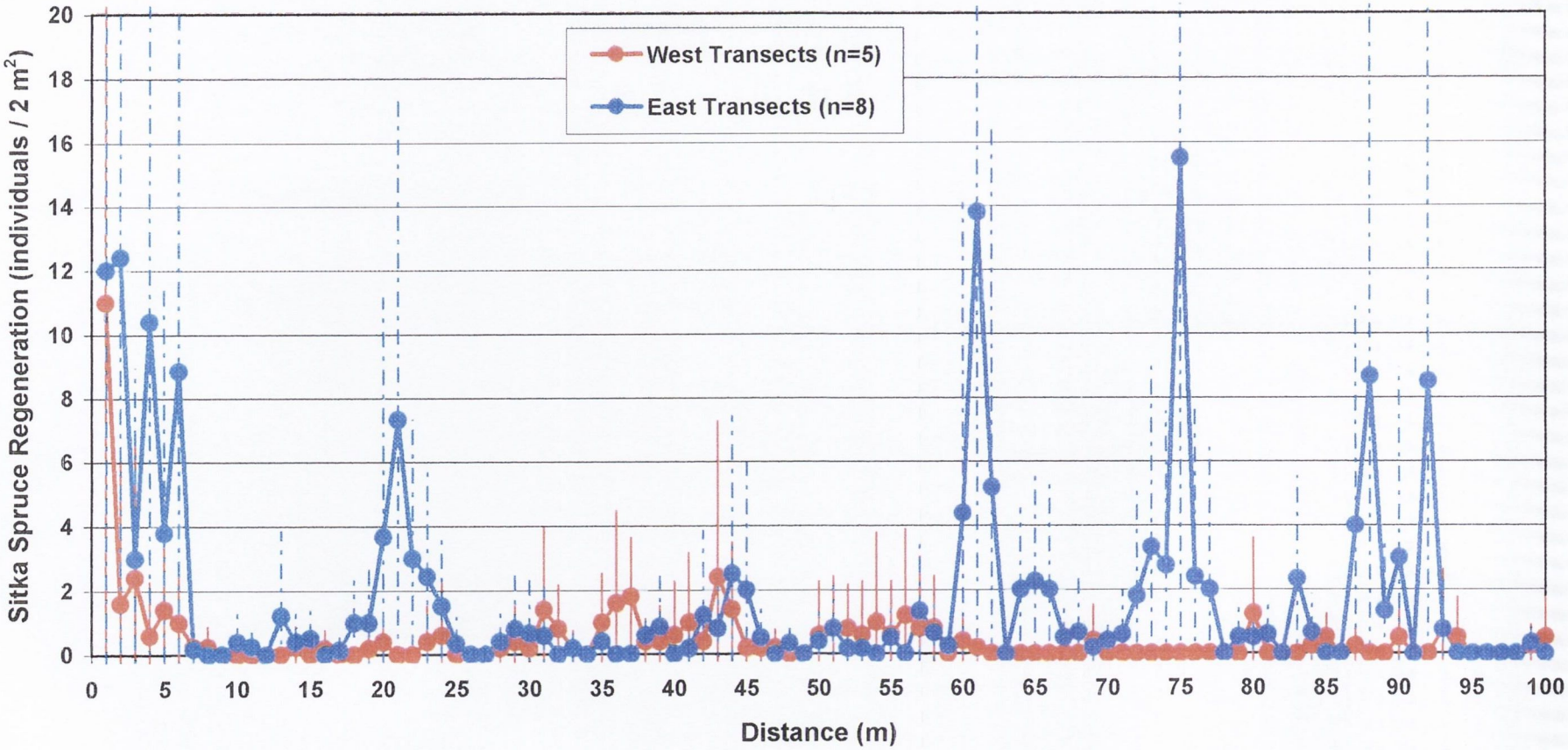
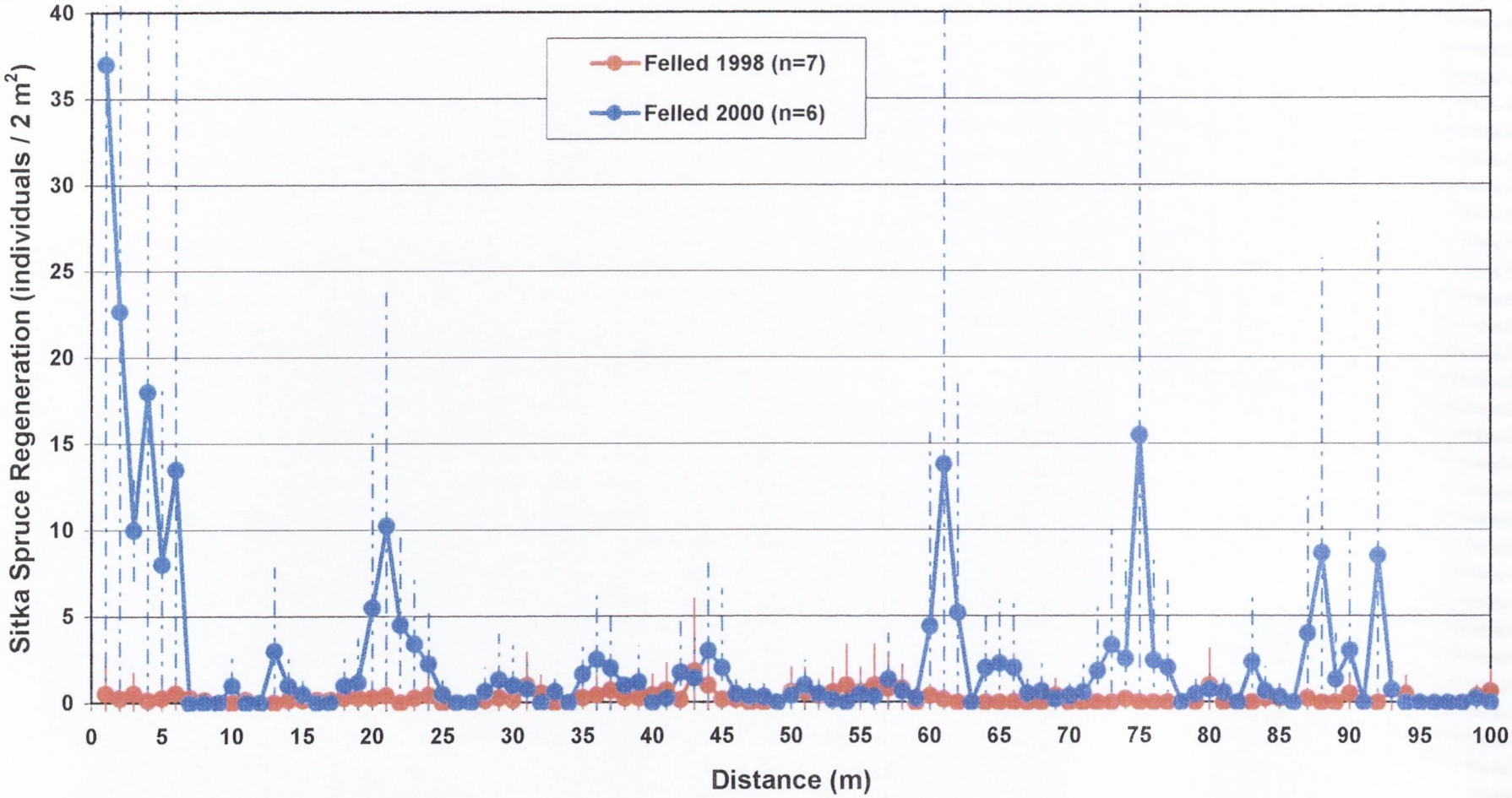


Figure 12.12. Mean Sitka spruce counts (individuals/2m^2) and 95% CIs at 1 m intervals along thirteen 100 m transects. Transects run from Sitka spruce plantation edges into plantations felled in 1998 (red) or 2000 (blue).



broken (P. Perrin, pers. comm.). Similarly, holly normally germinates after two or three winters (Peterken & Lloyd, 1967). Since the soil donor site was under a dense holly canopy, it is likely that the seeds were stored in the soil. However, this does not explain the absence of holly from plot 5 (Table 12.14).

Table 12.14. Numbers of tree seedlings regenerating in two soil replacement quadrats in exclosed plots 5 and 7 in Muckross Forest, Killarney in 2000 and 2001.

		2000	2001		
		1-20 cm	*1-20 cm*	*21-30 cm*	*31-40 cm*
Plot 5	*ash*	-	1	-	-
	birch	9	13	1	-
	rowan	1	1	-	-
	sally	2	2	-	-
Plot 7	*birch*	28	13	1	-
	holly	-	17	-	-
	rowan	2	-	-	1
	yew	1	1	-	-

CHAPTER 13

NATURAL TREE REGENERATION STUDY: DISCUSSION

13.1 Herbivory

13.1.1 Large Herbivores and Exclosure

Perhaps the most striking, albeit not unexpected, result of the natural regeneration study is the reduction in annual recruitment to the rowan, birch, and holly sapling size classes caused by large mammal herbivory (Table 12.8). Browsing had no effect on recruitment of the invasive exotic species Sitka spruce and *Rhododendron* (Table 12.9). The growth data also clearly indicate the severe effect of browsing on native trees, but not Sitka spruce (Table 12.10). Rowan, birch and holly are well-known to be susceptible to high levels of grazing by deer, sheep, and other large herbivores (Kelly, 1975; Linhart & Whelan, 1980; Mitchell & Kirby, 1990; Gill, 1992a; Hester *et al.*, 1996; Higgins, 2001). Sitka spruce (Gill, 1992a) and *Rhododendron* (Cross, 1981) are less palatable, which accounts in part for their invasiveness in Irish habitats.

Exclosure, however, had no significant effects on the densities of seedlings, native or exotic (Tables 12.5, 12.6). New tree seedling germination each year compensates for losses to herbivory and growth to the larger size class. Although not statistically significant, the trend for birch, rowan, Sitka spruce, and *Rhododendron* seedlings to be more abundant outside the exclosures in later years is intriguing (Tables 12.5, 12.7). This suggests that plots inside the exclosures are becoming more fully occupied by older tree regeneration and other vegetation, resulting in a reduction of suitable sites for germination and establishment. Reductions in tree seedling establishment in exclosures following an initial pulse of regeneration have been documented in Ireland (Kelly, 2002) and Britain (Pigott, 1983; Hester *et al.*, 1996). On the other hand, Cross (1981) concluded that overgrazing facilitates *Rhododendron* invasion in the Killarney woodlands by suppressing the field layer and exposing bare soil through poaching. In the Benleagh site in Glenmalure felled in 1993 (#22), high abundances of small Sitka spruce seedlings (Fig. 12.5) appeared to be maintained by high levels of deer activity which created numerous trails, exposing the peaty soil.

Curiously, mortality of saplings of even of the more palatable species was not strongly influenced by herbivory (Table 12.11). The likelihood of mortality due to herbivory is greatest for younger and smaller tree regeneration (Gill, 1992b) most likely because other agents of stress or disturbance, such as shading by the field layer and root competition, further weaken the

plants. Studies have found that browsing-induced mortality declines after a certain age, dependent on species and site conditions (Gill, 1992b). Sessile oak, holly and rowan saplings can survive repeated browsing damage better than many other species (Peterken & Lloyd, 1967; Shaw, 1974; Gill, 1992b; Raspé *et al.*, 2000), and even birch can survive browsing for over 15 years in a stunted form (Kinnaird, 1974). In addition, tree regeneration that has survived to grow above 30 cm height may also have some particular advantage over those that have succumbed. The survivors may occupy a microsite with higher fertility which allows adequate growth and survival even in the face of heavy browsing. Alternatively, the sites occupied by surviving unexclosed saplings may be sheltered from browsing by brash (Grisez, 1960; Palmer *et al.*, 2001), boulders or other rough terrain (Morgan, 1991), or unpalatable or thorny vegetation such as *Juncus effusus* or *Rubus fruticosus* (Linhart & Whelan, 1980; Morgan, 1991; Howell, 1996). The low mortality rates experienced by naturally regenerating saplings demonstrates that once they have reached 30 cm height, they have passed the most difficult period of their lives and have effectively become established.

13.1.2 Hares

Studies investigating tree species preferences of hares in Ireland have not had consistent results. In this study, the species preferences of hares were ranked oak > rowan > sally > birch >> holly > Sitka spruce; no *Rhododendron* were browsed by hares (section 12.3). Higgins (2001) found that birch and pedunculate oak were preferred to rowan in a study of planted saplings in Tomies Wood, Killarney. In her Charleville Wood, Co. Offaly site, however, rowan was favoured over pedunculate oak and birch. Similarly, in a forestry plantation in Co. Westmeath, hares preferred oak over birch, and Norway spruce was unbrowsed (Strevens, 2002). In general, in open, upland habitats in Ireland, grasses and sedges are the preferred food species (Tangney *et al.*, 1995; Dingerkus & Montgomery, 2001). Trees and shrubs are browsed less often than in Finland or Scotland, where longer periods of snow cover increase hares' reliance on browse as a winter food (Hewson, 1962; Pulliainen & Tunkkari, 1987).

Comparison of the results between planted and naturally regenerating trees provides further insights into the mechanisms influencing likelihood of hare browsing (sections 9.3, 12.3). The observation that planted trees are more likely to be browsed by hares than naturally regenerating trees lends support to the argument that browsing in this study is strongly motivated by the quality of the browse. Further support is provided by the tendency for hares to browse the more vigorously growing trees (Table 12.12), just as was found for planted trees.

13.2 Dispersal

As would be expected for bird-disseminated species, rowan and holly regeneration was not strongly dependent on the availability of mature trees in the vicinity of the plots (Fig. 12.1). Patterns of dispersal are probably more strongly influenced by abundances and behaviour of frugivorous birds, especially blackbirds and thrushes which are some of the most common consumers of rowan and holly berries (Peterken & Lloyd, 1967; Raspé *et al.*, 2000). It may be that the very high abundances of rowan seedlings and saplings in the Muckross Forest site reflect higher frugivorous bird populations in the area, but the absence of high holly abundances does not support this speculation.

Regeneration of the native wind-disseminated species, birch and sally, are strongly influenced by seed source availability (Fig. 12.1). Although they are light-seeded species, most birch seed, for example, falls within 50 m of the parent tree (Atkinson, 1992). The strongest example of the limited dispersal abilities of birch is provided by the low abundances in the Fraughan Rock Glen and Benleagh sites, where only a few solitary birch trees were present (Tables 12.4e, 12.4f). Birch seed availability appears to be a more important factor in the earliest years of succession. Birch seedling abundance in 2001, for example, is the birch variable least well correlated with the seed source index (Fig. 12.1d). Again, this indicates that regeneration sites become less available over time as the site becomes more fully occupied by vegetation.

If sufficient seed trees are available near a site, then natural regeneration may be able to establish woodland cover without the need for planting. An assessment of what seed sources are necessary to achieve natural regeneration adequate for woodland restoration should be based on densities of established saplings rather than seedlings. But what sapling densities are required to achieve woodland cover? Minimum stocking levels for woodland restoration or creation under the Native Woodland Scheme (NWS), to be achieved by planting or natural regeneration after four years, are 6,600 stems/ha for oak and 3,300 stems/ha for all other native species (Forest Service, 2001b). Part of the reason behind these stocking levels, especially that of oak, is to improve stem quality for timber production. The NWS guidelines, however, implicitly recognize that these levels may be too high where timber production is a secondary concern, and advise that "where required for ecological reasons, respacing can be applied to reduce stocking levels once establishment has taken place" (Forest Service, 2001b). In Britain, the minimum stocking level for new native woodlands under their Woodland Grant Scheme is 1,100 stems/ha (Forestry Commission, 1998). In the Mississippi River alluvial valley, where bottomland hardwood forests are being extensively restored, stocking levels employed under a US Dept. of Agriculture scheme are only 247 stems/ha after three years; reviewers of the

success of the scheme, however, recommended 750 stems/ha as a more appropriate target (Stanturf *et al.*, 2001). It appears that, for Irish restoration projects unconcerned with timber production, stocking levels of approximately 1,000 stems/ha would be appropriate, and densities as low as 500 stems/ha may be adequate, if the species are potentially canopy dominants and mortality is relatively low.

Applying these criteria to natural regeneration of birch saplings (Table 12.2), it appears that the Looscaunagh, Glendalough and Baravore sites have enough mature birch trees nearby to provide for adequate woodland cover. In the Looscaunagh and Glendalough sites, woodland with numerous birch occurred within 225-302 m and 81-132 m respectively of most plots (Table 12.4b, 12.4c). In Baravore, the plots were located within 48-267 m of two or three moderate-sized clusters of birch (some in areas of riparian scrub). The Muckross Forest site may also experience adequate birch regeneration (Table 12.2); there, the plots were 31-173 m distant from a riparian strip of birch (Table 12.4a). Using these distances and densities as guidelines, and assuming site conditions are favourable, adequate birch regeneration should be likely on clearfell sites within 250 m of woodlands containing a significant birch component. Smaller numbers of birch – on the order of 20-30 trees – within approximately 150 m of the site may also provide sufficient seed for regeneration.

Oak did not regenerate well over the study as a whole. The best regeneration occurred in a pair of plots in Glendalough (#11) where 10 oak seedlings were found, equalling a density of 125 stems/ha. The plot pair was 69 m away from oak-dominated woodland (Table 12.4c). The same density of oak regeneration was observed in an exclosed plot in Baravore, Glenmalure (#19E), where 5 oaks were found. This plot was 145 m from a small group of oaks growing near a stream (Table 12.4d). Single oak seedlings were found in three other Glendalough plots that were 113-231 m distant from oakwoods and 50-216 m away from smaller groups of trees (Table 12.4c). Because these plots were dominated by *Agrostis – Galium* and *Pteridium – Agrostis* vegetation types, it is likely that more oak regeneration would have occurred had the vegetation been less competitive. From these few data, it appears that some oak regeneration is likely in clearfells within 150-200 m of oak woodland or a few smaller groups of trees, but that densities are likely to be low. This estimate is more conservative than Jones's (1959) observation that "seedlings are often frequent in the turf of fields up to 200 or 300 yards from woods." The main medium to long distance dispersers of acorns are jays (*Garrulus glandarius*) and other corvids, squirrels and mice, especially *Apodemus sylvaticus* (Jones, 1959; Corbet, 1974; Shaw, 1974). Populations and behaviour of these species may be important variables affecting oak regeneration away from woodlands.

13.3 Site Factors

13.3.1 Rowan

As discussed above, the high abundances of rowan in the Muckross Forest site ensure that the CCA of environmental variables (Fig. 12.1) emphasizes the importance of variables that characterise that site. Rowan is similar to birch in preferring acidic, well-drained soils, and can regenerate well in heathland and on skeletal soils (Raspé *et al.*, 2000). Rowan is also fairly shade-tolerant, and may therefore be able to persist in dense brash and benefit from the shelter provided (Fig. 12.1d).

13.3.2 Holly

Holly is likewise a shade-tolerant species that benefited to some extent from tall brash in this study. Saplings in 1999 (which had established prior to fencing) were strongly associated with brash height. Because holly is a favoured browse species (Peterken & Lloyd, 1967), it is likely that, in this case, brash protected young trees from browsing. In several plots, I observed that holly (and rowan) saplings were confined to areas of heavy brash, and that parts of the trees emerging from the brash pile were heavily browsed.

Of the remaining site variables recorded, those indicating availability of germination sites, such as soil and litter cover and early successional vegetation, were important for holly seedling densities and recruitment. Soil moisture also appears to be an important factor for holly regeneration. Drought has been found to be an important cause of mortality for holly seedlings (Peterken & Lloyd, 1967). Although base cations are negatively associated with holly regeneration in this study, holly is tolerant of a wide range of substrates, including limestone pavement (Peterken & Lloyd, 1967; Kelly, 1981).

13.3.3 Birch and Sally

Birch and sally responded to the environment in much the same manner (Fig. 12.1). Like holly, birch and sally seedling densities were favoured by the availability of microsites with little vegetation cover and high soil and litter cover. As for Sitka spruce (section 13.4.2 below), the moisture regime of a site probably determines the suitability of litter as a substrate for birch and sally (Harris, 1990; Clarke, 1992). Apparently the sites in the present study receive sufficient rainfall during birch and sally germination to maintain adequate litter moisture. As discussed above, availability of suitable germination sites appears to be more important than dispersal for birch regeneration in older clearfells. Birch is well known for its inability to establish well in dense vegetation and its preference for bare mineral soil (Perala, 1990; Atkinson, 1992). Once established, however, given adequate moisture, birch appears able to tolerate levels of

competition present in this study. The association of birch recruitment with *Agrostis – Galium* vegetation and gley soils (Fig. 12.1d), however, is largely the result of very high birch sapling densities in one plot in Glendalough on peaty gley soils (#11E; Fig. 7 in Appendix 3).

13.4 Sitka Spruce Regeneration

13.4.1 Dispersal

Like the native wind-disseminated species, Sitka spruce abundances were positively correlated with the seed source index in the natural regeneration CCA (Fig. 12.1), indicating that dispersal is an important factor in spruce regeneration. Several biotic and abiotic factors affect dispersal, including: (i) quantity of seed produced, (ii) distance between seed source and site, and (iii) wind direction relative to the seed source and site.

The amount of seed produced by Sitka spruce varies considerably between years. It is a mast-seeding species that produces large seed crops every four to five years on average (Brown & Neustein, 1972; Mair, 1973) beginning when the tree is 25-35 years old (Nixon & Worrell, 1999). Recent mast years in Ireland include the autumn/winter of 1984/85, 1993/94 and 1996/97 (Dagg, 1998). The size class distributions of spruce show that 2000/01 was also a mast year (as it was for beech – see section 12.1). Similarly, Dagg (1998) found that natural regeneration of Sitka spruce in two large sites in Co. Wicklow, Ballygobban and Lugduff, was "directly related" to felling after seed fall in a mast year. The Lugduff site in Glendalough (located to the west of plot pairs #8 and #9– Fig. 4.4) was felled between 1984 and 1985. In this site he recorded spruce regeneration densities ranging from 60,000 to 264,000 per hectare in 1997. A smaller site of Dagg's was the subcompartment in which plot #11 is located (Fig. 4.4), felled in 1995 (J. Mulkern, pers. comm.)[1]. Here, Dagg estimated Sitka spruce regeneration densities in excess of 3,000 trees/ha in 1997. In comparison, I recorded a mean density of 3,813 trees/ha in 1999 in plot #11 (cf. Fig. 12.7) – a figure higher than in most of my study sites. Most of the saplings in this plot are probably the seedlings of the 1996/97 mast year, but some of the larger may have survived under the canopy from 1993/94.

Although Sitka spruce seed is light, seed-trapping experiments in Scotland have found that 80% of seed falls within 30 m of a clearfell edge (Mair, 1973). In the present study, seedling

[1] Dagg (1998) gives 1993 as the fell year for the site in question, compartment 13322P, subcompartment 1. The sources of information used in his study were Coillte's forest inventory records and timber sales records, but he does not specify which were used in this case. Sales records may not provide accurate felling years, as timber is sold standing and might not be felled the same year.

abundances were markedly higher within about 6 m of the clearfell edge (Figs. 12.11, 12.12). Longer dispersal distances have been recorded in North America (Harris, 1990), in part because of the greater height of Sitka spruce in natural forests there. Secondary dispersal over snow-covered surfaces can also increase the distances seed travels (Brown & Neustein, 1972), but this factor is not likely to be very important in Irish conditions. Current silvicultural advice for encouraging natural regeneration considers that dense regeneration from a stand of 20 m tall Sitka spruce "is unlikely to occur beyond 100 m from the forest edge" (Nixon & Worrell, 1999). The vast majority of spruce seed falls directly beneath a stand (Clarke, 1992), effectively a dispersal distance of zero. For this reason, forestry strategies to encourage regeneration of Sitka spruce focus on felling a stand with heavy cone crops immediately after the main period of seed release, from October to April, but before significant germination (Nixon & Worrell, 1999). Although I could not ascertain the month or season of felling for my study sites, apart from Glenmalure plots felled in the winter of 1999, plot #22 was felled in 1993, possibly after some dispersal in the 1993/94 mast year. This plot experienced the highest densities of Sitka spruce regeneration, and it may be that the larger saplings are the progeny of the 1993/94 mast year (cf. Fig. 12.5). The much higher seedling densities observed in the transects in stands felled in 2000 relative to those felled in 1998 shows more clearly the importance of felling stands after dispersal in a good seed year (Figs. 12.11, 12.12).

The orientation of the edge between a clearfell and a neighbouring Sitka spruce stand relative to wind direction may influence dispersal. In Ireland, southwesterly and westerly winds are the most frequent (Rohan, 1986), and therefore clearfells to the east of plantations might be expected to experience greater seed input. Sitka spruce cones, however, remain closed during wet weather and open to release seed during dry periods (Harris, 1990). In Scotland, a seed-trapping experiment found that more seed was dispersed by drier easterly winds into clearfells to the west of a plantation (Mair, 1973). Similarly, Dagg (1998) found that proximity to an eastward plantation edge favoured Sitka spruce regeneration in a site in Wicklow. In the present study, however, clearfell sites with greater seed availability to the west tended to have higher regeneration abundances (Figs. 12.10, 12.11). The influence of wind and seed source direction in this study, however, was small relative to other factors, most notably felling year and site conditions.

13.4.2 Site Conditions

Once seeds have dispersed to the site, successful germination and establishment of Sitka spruce is strongly influenced by soil conditions, site climate, and the presence and growth of vegetation (Brown & Neustein, 1972; McNeill & Thompson, 1982; Clarke, 1992; von Ow *et al.*, 1996;

Nixon & Worrell, 1999). Post-dispersal seed losses to fungi and predators such as insects, birds and rodents may also be significant, but these factors have received little or no research attention (Nixon & Worrell, 1999). In the present study, former Sitka spruce stands provided more suitable sites for germination and establishment than former lodgepole pine and larch stands, according to logistic regression analysis (Table 12.13). (Former Sitka stands may also indicate a greater availability of spruce seed sources, but the seed source index was not a significant part of the model.) For this analysis, new seedling immigration in 2000 and 2001 was used, which could not have resulted from the former crop. Seeds very rarely remain viable on the ground for more than one year (Clarke, 1992; Nixon & Worrell, 1999), but von Ow *et al.*(1996) suggest that seeds remaining in cones in the felling brash may retain viability for an additional year. Germination normally occurs in late spring and early summer following seed release.

Soil moisture is regarded as the most critical site factor determining the abundance of natural Sitka spruce regeneration (Brown & Neustein, 1972; Clarke, 1992; Nixon & Worrell, 1999). Drought is most important in the first year, when the developing roots of young seedlings are concentrated solely in the top few centimetres of the soil or other substrate (Brown & Neustein, 1972). The substrates on which germinal seedlings can become established differ in their abilities to conserve water during dry periods. In a study of natural regeneration in Cos. Wicklow and Dublin, von Ow *et al.* (1996) found that pleurocarpous mosses, litter, decaying wood, and bare mineral or peat soil (no distinction was made between soil types) were the most favourable seed beds for Sitka spruce. In North America, similar work has ranked preferred regeneration sites as wood, humus, mineral soil and mixed mineral/organic soil (Day, 1964, cited in Clarke (1992)). Other studies, however, have concluded that conifer needle litter is a hostile environment for young seedlings because it desiccates rapidly (Clarke, 1992) and experiences greater temperatures because of its dark colour (Nixon & Worrell, 1999). Mineral soils have been found to be better substrates than organic soils by some researchers for similar reasons (McNeill & Thompson, 1982; Clarke, 1992). The moisture regime of a site probably determines whether litter or peaty soils will encourage or discourage natural regeneration (Harris, 1990; Clarke, 1992).

Litter and bare soil cover in this study were found to increase the likelihood of invasion by Sitka spruce seedlings (Table 12.13), as was found by von Ow *et al.* (1996). The latter authors considered that "wet conditions encountered on the sites examined" counteracted the poor water holding abilities of litter (von Ow *et al.*, 1996), which also appears to be the case in this study. Finer textured and organic soils (i.e. higher values of the soil water holding index) also favour seedling germination and first year survival, according to the logistic regression analysis.

Because steeper slopes are more likely to be invaded and sites with soils experiencing some degree of gleying less likely, waterlogged sites also appear to be unsuitable for Sitka spruce invasion. This may explain why the blanket peats in the Looscaunagh site were the least likely soil type to be invaded (Fig. 12.2): most of the Looscaunagh site was quite wet, even in summer, and had standing water in many places in the winter. In contrast, von Ow *et al.* (1996) found a (non-significant) tendency for deep peats to have the highest percent cover of Sitka spruce, followed by peaty podzols, shallow peats, peaty gleys and mineral soils, in descending order. The deep peats in von Ow *et al.*'s (1996) study may not have been as wet as in the present study, but they provide no information to ascertain this possibility. It is likely that the abundances of spruce regeneration on deep peat were overestimated relative to other soil types by von Ow *et al.* Sitka spruce regeneration in their single deep peat site was the product of the 1990/91 mast year, whereas, for other soil types, three sites were averaged, two of which were felled after the poorer seed years of 1988/89 and 1989/90.

Investigation of Sitka spruce invasion in weeded subplots provides a clear picture of factors important for spruce germination and survival over the first few months. Sites favourable for germination, however, may not necessarily favour growth and survival over the longer term. Although litter and bare soil substrates make spruce invasion more likely, these factors are not closely associated with densities of spruce seedlings and saplings in the CCA analysis (Fig. 12.1), which are mostly over one year old. Higher mortality over time on litter and bare soil may compensate to some extent for greater receptivity to invasion. The apparent lack of association between litter and bare soil cover and spruce densities may also be an artefact of vegetation spread over time. Saplings in particular could have become established on soil or litter which has subsequently become occupied by herbs and dwarf shrubs. Soil moisture, however, remains an important factor for growth and survival of Sitka spruce beyond the first year, as is indicated by the associations between seedling and sapling densities and bryophyte cover and soil gleying, among other variables.

Site climate is another important factor for Sitka spruce regeneration. Northeast aspect and lower temperatures have been identified as favouring spruce in this study (Fig. 12.1; Table 12.13) and by previous workers in North America (Clarke, 1992). Previous studies in Britain, however, have not found significant relationships between aspect and regeneration densities (Nixon & Worrell, 1999). Northeast aspect and lower temperatures serve to enhance soil moisture, reduce transpiration and reduce the risk of heat girdling (Clarke, 1992; Nixon & Worrell, 1999). Shelter can have the same effect by providing shade, and can also provide protection from desiccating winds and frost (Clarke, 1992; von Ow *et al.*, 1996; Dagg, 1998). In Ireland, spruce regeneration has been found by other workers to be favoured by the shelter

provided by boulders and logs, stump bases and light brash cover favoured spruce regeneration; however, heavy brash, defined as being dense enough to prevent light transmission, prevented regeneration (von Ow *et al.* (1996), see also Dannatt and Davies (1970)). Similarly, in this study brash height (and brash cover to a lesser extent) were positively associated with Sitka spruce densities, especially seedlings (Fig. 12.1). The brash cover in most places was not sufficient to exclude light, except in the former lodgepole pine stands. These plots experienced little regeneration of Sitka spruce (Fig. 12.8) or lodgepole pine (100 trees/ha, cf. Table 12.3); heavy brash cover may be partially responsible.

It is well known that the presence of dense vegetation, particularly grasses, *Pteridium*, *Calluna*, *Vaccinium*, *Sphagnum* spp. and tall acrocarpous mosses such as *Polytrichum commune*, can inhibit or prevent natural regeneration of Sitka spruce (Robertson, 1976; McNeill & Thompson, 1982; Clarke, 1992; von Ow *et al.*, 1996; Nixon & Worrell, 1999). If spruce invasion occurs concurrently with vegetation colonisation, however, established seedlings can usually survive when competition becomes stronger in later years (McNeill & Thompson, 1982; Nixon & Worrell, 1999). This finding probably accounts for the positive association between sapling densities and field layer cover and the absence of an inhibiting effect of the denser vegetation types in this study. The *Agrostis – Galium* vegetation type in fact increased the likelihood of spruce invasion relative to the more open *Calluna – Galium* type. The favourability of *Agrostis – Galium* vegetation for spruce, however, was not apparent in the drier acid grassland sites in Glendalough, and was most evident in flushed sites (cf. Figs. 7, 8 in Appendix 3). Nevertheless, there is evidence for the inhibitory role dense vegetation can play for Sitka spruce in this study. Although field layer cover did not significantly reduce the likelihood of spruce invasion, litter and bare soil cover, which imply little vegetation cover, increased the probability (Table 12.12). Increased vegetation competition is also most likely responsible for reductions in abundances of smaller spruce over time in some of the earlier-felled stands (Figs. 12.3, 12.5, 12.7).

CHAPTER 14

CONCLUSIONS AND RECOMMENDATIONS

14.1 Conclusions

The results of my research considered in the context of previous studies lead to several conclusions about vegetation development on felled conifer plantations in the uplands of Ireland and the feasibility of restoring native woodlands to such sites.

1. *Conifer clearfells develop a range of semi-natural grassland and heath communities characteristic of upland, acidic conditions.* In the first few years after felling, vegetation composition was strongly influenced by the seed bank and vegetative spread of pre-felling vegetation, if any. Within ten years after felling, relatively stable communities have developed. Acid grassland and bracken vegetation were the most likely to occur on better soils. On poorer soils, dry heath will be the main type of vegetation, with wet heath and rush-dominated communities in wetter sites.

2. *Planting can be a successful method for establishment of oak and birch on former conifer plantations.* Mortality of oaks planted in exclosures was acceptably low (16.9%) over the first three years. Oak survival was encouraged by higher soil moisture, greater K^+ availability and higher vegetation cover. Birch mortality was higher than that of oak (39.1%) and exceeded one-third in the first year. Late planting in Wicklow was responsible for much of the initial mortality, which was higher in sites with drier soils.

3. *Control of large herbivores is a prerequisite for tree establishment.* Browsing by deer, sheep and goats in the unexclosed plots unequivocally reduced planted tree growth and survival and the recruitment and growth of naturally regenerating saplings. Only a very few planted or naturally regenerating trees will survive in the unexclosed plots in the long term.

4. *Browsing by small herbivores, particularly hares, can be a serious impediment to tree establishment in some sites.* Mortality of planted trees browsed by hares was highest in the first year, when trees were weakened by transplantation shock. Results also suggest that hare browsing in felled conifer stands is influenced by palatability of available food sources, and browsing intensity may decline as the vegetation of the site develops.

5. *Vegetation competition is not a major factor affecting planted tree growth and survival in most clearfelled sites.* Vegetation develops slowly on the relatively poor soils on

which upland conifer plantations typically occur and therefore competitive pressures on planted trees are low. The lack of an effect of the weeding treatments shows that, with the notable exception of bracken-dominated vegetation, the vegetation of clearfelled sites has little effect on planted trees. Note, however, that established vegetation was found to reduce opportunities for natural regeneration.

6. *The role of conifer brash in restoring native woodlands to felled plantations is neutral or beneficial.* Although brash cover was not adequate to protect tree seedlings and saplings in general from herbivory in this study, the shelter provided by brash against browsing and climate appears to benefit such shade-tolerant, woodland species as holly, *Luzula sylvatica* and *Vaccinium myrtillus*. Brash may also have a small positive effect on trees through shelter effects, enhancement of soil moisture and fertilisation effects.

7. *Regeneration of wind-disseminated tree species is strongly influenced by seed source availability.* The location of a woodland with a significant birch component, for example, within 250 m of a site, or smaller groups of birch within 150 m, appears sufficient to provide enough seed for adequate birch regeneration. Regeneration of such species as birch and sally is also encouraged by low vegetation and high bare soil and needle litter covers.

8. *Regeneration of bird-disseminated tree species will probably occur at low levels in most sites, where they occur in the landscape.* Such species as rowan and holly in this study were not dependent on densities of trees within the immediate area of the site. Where such trees are not absent in the larger landscape, they will be able to regenerate in suitable sites. There is some evidence from this study and the literature that rowan prefers well-drained, acidic soils and holly establishment is favoured by moist soils, but these species were able to become established in all sites in this study. Oak regenerated poorly in the clearfells, primarily because of a lack of seed sources at most sites. Where oak woodland or a few smaller copses are located within 150-200 m, some oak regeneration is likely, but probably not in densities that would permit the development of an oak-dominated canopy.

9. *Sitka spruce regeneration is strongly limited by dispersal distance.* Results showed an inverse relationship between seedling and sapling densities and distance to spruce seed sources. Previous studies have found that high densities of spruce regeneration are unlikely beyond approximately 100 m from a forest edge, and markedly high spruce densities were found only within 6 m of the canopy edge in this study. Because most seed is dispersed below the canopy, the greatest risk of high spruce regeneration occurs when a stand is felled after significant seed dispersal during a mast seeding year.

10. *Sitka spruce regeneration is favoured on sites with higher soil moisture and greater cover of bare soil and needle litter.* In addition to the physical properties of the soil, the availability of water to regenerating spruce seedlings is affected by site climate, including aspect. Shading by brash may also increase soil moisture. However, sites with excessive soil moisture, such as the frequently waterlogged blanket peats in Looscaunagh, are not hospitable for spruce regeneration. Provided that soil moisture is adequate, Sitka spruce regeneration was higher in sites without competing vegetation. As several of the size class distributions showed, there is in effect a "window of opportunity" of a few years for spruce regeneration, before the site becomes occupied by vegetation. The length of time when a site is receptive to spruce invasion may be reduced on more fertile sites, such as those on brown earth or brown podzolic soils.

In summary, felled and abandoned conifer plantations have the potential to naturally develop semi-natural vegetation communities of some conservation value. Woodlands are unlikely to develop naturally in most clearfell sites because of the high abundances of large herbivores in most upland areas in Ireland. Where herbivore pressure is low, natural woodland development will be most rapid near existing woodlands or copses. If seed sources are insufficient to provide for adequate tree regeneration in the short- to medium-term, tree planting can be a successful means of establishing tree cover. Early survival rates of planted trees in this study demonstrate that most former conifer sites can support native, broadleaved trees. Natural regeneration of Sitka spruce will be an impediment to native woodland restoration in some sites; high regeneration densities are most likely to occur in moist sites where the former spruce crop was felled after significant dispersal during a mast seed year. Regeneration of other exotic conifers is unlikely to occur at densities that pose significant difficulties in woodland restoration.

14.2 Recommendations

Based on the conclusions of this study and a review of the findings of other studies, I can make several recommendations for those attempting to restore native woodlands to conifer clearfells, particularly Dúchas, the Heritage Service. It should be borne in mind that these recommendations are most applicable under conditions similar to those in my research, i.e. conifer stands on acid soils in the upland regions of Ireland. These recommendations may be less applicable under lowland conditions on more fertile soils or in Britain or elsewhere in Europe. In addition, this research was conducted with the establishment of semi-natural oak woodlands for conservation purposes as the goal. If timber production is to be a major component of future woodland management, then an approach closer to normal silvicultural practices should be employed.

1. *All woodland restoration efforts should be treated as experiments.* Because there has been little experience in native woodland restoration in Ireland, all restoration projects, regardless of size or scope, should be considered experimental trials, even when not designed as formal experiments (Michener, 1997). This includes setting clear objectives, particularly the target vegetation community or woodland type to be achieved, and assessing progress towards them. In this way, the relative costs and benefits of different approaches under different conditions can be measured, and the knowledge gained can be applied to future projects.

2. *Control of large herbivores will be necessary in most sites before trees can become established.* Fencing or other arrangements will be necessary to control domestic livestock, but culling should be preferred to fencing as a means of reducing grazing pressure from deer and feral goats. The complete elimination of grazing caused by fencing is as "unnatural" as overgrazing, and can reduce species and structural diversity by overly favouring a small number of highly competitive species, such as *Luzula sylvatica* and holly (Mitchell & Kirby, 1990; Kelly, 2000).

3. *Delay planting or other intensive management for a few years to assess natural vegetation development and to allow improvement in site conditions.* Former Sitka spruce stands in particular have very poor vegetation cover immediately after felling. Delaying more intensive restoration practices (apart from large herbivore control) will allow an assessment of what vegetation community is likely to develop, the adequacy of natural tree regeneration, the threats posed by regenerating conifers or other invasive exotic species and the severity of small mammal and, perhaps, insect herbivory. In addition, this research has found that newly-felled plantations can be harsh environments for planted trees. The establishment of some vegetation cover prior to planting may ameliorate site conditions and also provide alternative food sources for hares and other small herbivores.

4. *Rely on natural regeneration to achieve woodland cover and understorey flora insofar as possible.* Use of natural regeneration can have several benefits, including reduction of establishment costs, conservation of local genotypes and a more natural variation in species composition and structure (Rodwell & Patterson, 1994). Where certain desired species are slow or unable to colonise and it is desirable to "accelerate" natural succession, species such as oak, yew, alder and aspen (*Populus tremula*) can be introduced by supplementary planting, while still relying on natural regeneration to provide the bulk of tree cover. When introducing trees, shrubs or herbs by planting or translocation, local provenances should be used insofar as possible.

5. *Restoration efforts should focus on areas near woodlands or other areas of native tree cover, such as hedgerows or riparian zones.* Focusing on such areas will increase the likelihood of adequate native tree regeneration and spread of woodland understorey vegetation to clearfelled sites. Some typical Irish woodland herbs have poor powers of dispersal and would therefore have to be introduced to clearfells situated far from existing woodlands or refugia such as hedgerows. It may be possible to introduce woodland species before canopy closure, since some can persist outside woodland cover in Ireland; however, the results of soil replacement trials in this study were inconclusive. In clearfells far from existing woodlands or copses, it may be more feasible to allow clearfells to develop into heathland or acid grasslands. Nevertheless, because the floras of upland oakwoods and other upland communities, such as heathlands, are similar, restoration of upland oakwoods on acid soils should be easier than restoration of many other types of native woodland. New woodland establishment adjacent to existing woodlands and copses will have the added benefit of reducing the isolation and fragmentation of the wooded landscape as a whole.

6. *Where planting is used as the primary means of establishing tree cover, care should be taken to mimic native woodland structure and composition.* In sites that experience little natural tree regeneration, the trees that are planted will dominate the woodland canopy for the next century or longer. It is important, therefore, that the species composition and spatial arrangement of the planted trees should mimic those of the target native woodland type. For example, trees should not be planted in rows as in commercial plantations and provision should be made for open spaces within the new woodland (Rodwell & Patterson, 1994). Compositional and structural goals need not be achieved immediately, however, as additional planting or thinning can be employed at later stages of woodland development to rectify some deficiencies. What the "natural" composition and structure of a particular type of native woodland may be is a separate and perhaps more difficult question, considering the long history of human interference in Irish woodlands. However, given that many native woodlands were managed to favour oak (e.g. Mitchell, 2000), the establishment of an oak-dominated canopy should not necessarily be an objective.

7. *In most cases, vegetation control will not be necessary.* Because of the slow development and generally low competitiveness of vegetation on former conifer clearfells, vegetation control should not normally be necessary to ensure the survival of young trees. Dense bracken stands are an obvious exception to this recommendation. Vegetation control may be desirable in some circumstances, however, such as where herbivory has prevented natural regeneration of trees and dense vegetation has developed, thus inhibiting tree establishment once grazing pressure has been reduced.

8. *Brash should be retained on site.* Because of the positive, albeit small, effects of brash on woodland restoration in this study, brash should be retained *in situ* on conifer clearfells. An additional benefit of brash retention may be structural diversity in vegetation and tree regeneration caused by brash piles of different sizes and densities. Windrowing brash on the other hand, would impose a regular, unnatural structure on sites. Dense brash mats used as paths for harvesting machinery, which were not encountered in this study, may be an exception to this recommendation, and may need to be broken up in some fashion. Similarly, extraction of conifers by cables to a central place for processing into logs creates large, extremely dense brash piles that decompose slowly.

9. *Sitka spruce stands should be felled in summer to reduce spruce regeneration.* Sitka spruce was the only conifer in this study that regenerated in densities that would be a serious impediment to native woodland establishment. Felling spruce stands from June through September, before cones mature and seed dispersal occurs, should prevent regeneration originating from the standing crop. Summer felling would be particularly important during Sitka spruce mast years, which appear to be responsible for the extremely high spruce densities observed in some plots in this study and in previous work (Dagg, 1998).

10. *Spread of exotic species should be monitored.* Exotic conifer species other than Sitka spruce did not regenerate in large numbers in this study, and may perhaps be tolerated in native woodland restorations, depending on how "purist" the restoration goals are. Regeneration densities of these species should nevertheless be monitored. The disturbance caused by felling may also provide opportunities for the spread of other exotic species, such as *Rhododendron*, that may not have proved a threat previously. For example, I observed several young seedlings near mature *Rhododendron* bushes occurring in the Baravore site in Glenmalure. Canopy opening and the lack of competition may be encouraging the spread of *Rhododendron* at this site. Removal of potentially invasive exotics should be a priority operation.

11. *Additional research should be conducted to investigate further aspects of woodland restoration on former conifer clearfells.* Because of the lack of experience in restoration of conifer clearfells, many potentially important factors and methods could not be investigated. Potentially fruitful areas for investigation include: 1) an assessment of different ground preparation methods, such as ripping or discing, 2) the costs and benefits of fertilisation of planted trees, including the possibility of increasing competition from herbaceous vegetation and shrubs, 3) an investigation of tree establishment by broadcasting or planting seeds, and 4) a study of the development of bird and insect fauna in clearfells and newly established woodlands.

12. *The plots used in this research should be resurveyed at 5 – 10 year intervals.* The results of this study assess the feasibility of and factors influencing woodland restoration over the first three years only. Resurveying is clearly necessary to learn more of the longer-term woodland development and success of the methods employed. For example, sites that appear suitable for oak establishment in the early years may later prove to be unsuitable. The effects of birch on oak, such as whether birch can act as a nurse crop or as a competitor, remain to be seen. The possibility of birch successfully competing against Sitka spruce likewise requires further study. The study sites used here can also be used for additional experiments, such as a more detailed investigation of methods for introduction of woodland understorey flora.

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APPENDIX 1: SOIL CHEMICAL AND PHYSICAL DATA

Soil chemical and physical data are presented for each plot pair (Plot) and each of two replicate samples (Rep) where these were analysed. See section 4.4.1 for details of sampling and analysis methodology. Shown are percent carbon, percent nitrogen, total P (mg/L soil), Ca^{2+} (mg/L soil), K^{+} (mg/L soil), Mg^{2+} (mg/L soil), Mn^{2+} (mg/L soil), percent loss-on-ignition (LOI), bulk density (g/mL soil) and pH. Samples marked with an asterisk are extra samples collected in areas with distinctly different vegetation communities than the majority of the plot pair, as detailed in section 4.4.1. One replicate sample from plot pair 1 and one from the extra sample from plot pairs 3 and 4 (3/4* in the table) were destroyed by the LECO analyser during carbon and nitrogen analysis.

Site	*Plot*	*Rep*	% C	% N	Total P (mg/L)	Ca^{2+} (mg/L)	K^{+} (mg/L)	Mg^{2+} (mg/L)	Mn^{2+} (mg/L)	LOI (%)	Bulk Density (g/mL)	pH
Looscaunagh	1	A	.	.	70.82	203.84	45.97	88.62	15.51	83.60	0.1776	4.13
	1	B	47.23	2.141	78.20	212.22	48.63	124.35	15.47			
	3	A	49.61	2.278	112.88	139.94	25.07	136.75	4.10	92.77	0.1469	4.35
	3	B	50.52	2.378	45.30	147.93	25.65	139.69	3.66			
	3/4*	A	.	.	41.95	165.28	52.89	142.40	4.58	87.59	0.1638	4.30
	3/4*	B	46.82	2.262	61.44	163.24	48.10	133.05	4.61			
	4	A	34.87	1.713	69.54	144.04	42.89	117.34	10.52	63.18	0.2601	4.21
	4	B	37.42	1.773	58.43	127.33	42.99	158.15	10.54			
Muckross Forest	5	A	24.56	1.088	102.62	207.19	70.53	163.99	125.20	58.42	0.2832	4.38
	5	B	30.67	1.482	144.05	208.07	66.72	186.13	135.20			
	6	A	40.07	1.307	151.43	275.59	73.78	166.37	15.91	69.47	0.2322	4.24
	6	B	37.35	1.162	85.40	288.24	73.15	162.95	15.93			
	7	A	16.78	0.662	150.82	334.51	63.35	150.03	26.67	45.13	0.3593	4.24
	7	B	16.38	0.659	288.25	265.29	57.96	117.04	21.18			
Glenmalure- *Benleagh*	13	A	16.10	0.769	336.59	29.58	39.85	64.37	7.66	28.84	0.4912	4.75
	13	B	10.97	0.548	195.85	29.73	39.85	64.37	7.66			
	22	A	22.02	0.960	122.62	193.69	47.98	96.84	15.10	58.16	0.2845	4.20
	22	B	34.06	1.670	142.11	182.21	44.22	91.99	14.15			

Site	*Plot*	*Rep*	% C	% N	Total P (mg/L)	Ca^{2+} (mg/L)	K^{+} (mg/L)	Mg^{2+} (mg/L)	Mn^{2+} (mg/L)	LOI (%)	Bulk Density (g/mL)	pH
Glenmalure- *Baravore*	18	A	10.89	0.558	279.61	84.88	37.35	56.02	37.35	23.85	0.5472	4.19
	18	B	10.81	0.643	145.03	90.31	42.60	61.34	37.49			
	19	A	27.70	1.293	202.84	56.40	34.91	123.53	5.37	57.57	0.2875	4.2
	19	B	29.88	1.511	136.29	61.07	39.52	123.93	5.39			
	21	A	7.78	0.430	163.24	3.87	20.38	28.54	30.58	16.70	0.6523	4.48
	21	B	8.77	0.436	149.79	3.87	22.39	22.39	28.50			
Glenmalure- *Fraughan Rock Glen*	12	A	11.65	0.698	319.76	40.64	24.88	69.66	56.39	25.20	0.5310	4.83
	12	B	10.62	0.468	65.27	45.36	33.11	69.52	57.94			
	14	A	8.13	0.503	319.68	21.08	29.85	37.31	70.89	19.87	0.6010	4.55
	14	B	10.74	0.570	78.02	20.46	30.03	35.67	71.33			
	15	A	43.76	1.650	173.90	141.26	22.17	63.98	6.97	76.59	0.2034	4.49
	15	B	41.01	1.622	159.41	139.18	21.61	63.55	6.99			
	16	A	44.75	1.848	31.50	105.41	26.75	72.77	4.28	85.41	0.1713	4.29
	16	B	45.55	1.948	67.52	103.06	24.56	68.35	4.27			
	17	A	27.58	1.211	101.17	42.88	28.45	45.14	17.66	52.42	0.3152	4.25
	17	B	23.40	1.268	116.90	34.80	31.45	40.30	14.74			
	20	A	46.74	1.901	90.44	79.33	34.36	58.11	3.54	87.94	0.1627	4.07
	20	B	48.01	2.047	157.91	82.28	33.82	47.96	3.53			
Glendalough	8	A	9.65	0.781	202.94	30.14	99.89	53.39	37.89	23.26	0.5547	4.82
	8	B	9.76	0.635	314.53	16.98	86.63	46.78	39.85			
	9	A	9.38	0.621	98.43	26.20	94.47	48.13	65.95	22.05	0.5704	4.95
	9	B	10.05	0.571	201.22	28.91	111.74	51.43	63.85			
	10	A	17.38	0.990	146.38	4.29	56.81	27.77	58.07	38.18	0.4085	5.12
	10	B	14.59	0.838	173.60	2.15	53.21	25.34	55.74			
	11	A	26.71	1.330	249.36	59.20	52.29	80.91	17.76	52.22	0.3163	4.46
	11	B	25.95	1.194	264.35	47.13	54.00	74.62	16.69			
	11*	A	22.75	1.111	167.12	37.93	66.19	53.46	106.92	38.08	0.4093	4.86
	11*	B	19.92	0.980	194.78	37.68	62.38	52.20	98.03			

APPENDIX 2: SPECIES LIST

Species occurring in vegetation quadrats in a given year are marked with a tick (✓). Species occurring in plots, but not in vegetation quadrats are marked with an asterisk (*). Note that species occurring only in soil replacement quadrats (sections 4.3 and 6.6) are not included. Nomenclature follows Stace (1997).

Species	1999	2001
Abies procera	✓	*
Agrostis canina	✓	✓
Agrostis capillaris	✓	✓
Aira praecox	✓	*
Anthoxanthum odoratum	✓	✓
Betula pubescens	✓	✓
Blechnum spicant	✓	✓
Calluna vulgaris	✓	✓
Carex binervis	✓	✓
Carex echinata [1]		✓
Carex panicea [1]		✓
Carex pilulifera [1]		✓
Carex species [1]	✓	
Chamerion angustifolium [1]		✓
Cirsium palustre	*	✓
Danthonia decumbens		✓
Deschampsia caespitosa	✓	*
Deschampsia flexuosa	✓	✓
Digitalis purpurea	✓	✓
Dryopteris affinis	✓	✓
Dryopteris dilatata	✓	✓
Epilobium obscurum		*
Epilobium species [1]	✓	
Erica cinerea	✓	✓
Erica tetralix	✓	✓
Eriophorum angustifolium		✓
Fagus sylvatica	*	*
Festuca ovina	✓	✓
Festuca species [1]	✓	
Festuca vivipara	✓	✓
Galium saxatile	✓	✓
Hedera helix	✓	✓

Species	1999	2001
Holcus lanatus	✓	✓
Holcus mollis	✓	✓
Hypericum elodes		*
Hypericum pulchrum	✓	✓
Hypochaeris radicata		*
Ilex aquifolium	✓	✓
Jasione montana		*
Juncus bulbosus	✓	✓
Juncus conglomeratus	✓	✓
Juncus effusus	✓	✓
Juncus squarrosus	✓	✓
Larix kaempferi	*	*
Luzula multiflora [1]		✓
Luzula species [1]	✓	
Luzula sylvatica	✓	✓
Molinia caerulea	✓	✓
Nardus stricta	*	✓
Osmunda regalis		*
Oxalis acetosella	✓	✓
Picea abies	*	
Picea sitchensis	✓	✓
Pinguicula lusitanica	*	*
Pinus contorta	*	*
Pinus sylvestris	✓	✓
Polygala serpyllifolia	✓	✓
Polypodium vulgare		✓
Potentilla erecta	✓	✓
Prunus species		*
Pteridium aquilinum	✓	✓
Quercus petraea	✓	✓
Rhododendron ponticum	✓	✓
Rosa species	*	
Rubus fruticosus	✓	✓
Rumex acetosella	✓	✓
Salix cinerea ssp. *oleifolia* [2]		✓
Salix ×*multinervis* [2]		*
Salix species [2]	✓	
Saxifraga spathularis	*	*
Sorbus aucuparia	✓	✓
Teucrium scorodonia	*	*
Tsuga heterophylla	*	*

Species	1999	2001
Ulex europaeus	✓	✓
Ulex gallii	✓	✓
Umbilicus rupestris	*	*
Vaccinium myrtillus	✓	✓
Viola palustris	*	✓
Viola species [3]	✓	✓

[1] See section 5.3.1 for details.

[2] See section 11.1.1 for details.

[3] Probably *V. riviniana*.

In addition, in 1999 unidentified dicotyledonous plants were observed in three plots, and unidentified grasses were observed in four plots.

APPENDIX 3: PLOT PHOTOGRAPHS

A photographic record of the study plots was made to visually display changes in clearfell vegetation. With a few exceptions, photos were taken in late summer / autumn of 1999 and 2001 from the same corner of the plot facing towards the plot centre. Choice of the plot corner from which the photos were taken was dictated by topography and the position of the sun. A subset of these photos, representing all the major study sites, the six vegetation types and a range of felling years, is presented in this Appendix. The plots are identified by plot pair number and whether the plot was exclosed (E) or unexclosed (U). Former conifer crop species, felling year, and the vegetation type of the subplot in the foreground are also indicated.

Figure 1. Plot 3E in 1999 (top) and 2001 (bottom). The plot was a former Sitka spruce stand felled in 1995. The subplot in the foreground was assigned to the *Digitalis – Juncus* vegetation type.



Figure 2. Plot 3U in 1999 (top) and 2001 (bottom). The plot was a former Sitka spruce stand felled in 1995. The subplot in the foreground was assigned to the *Digitalis* – *Juncus* vegetation type.



Figure 3. Plot 6E in 1999 (top) and 2001 (bottom). The plot was a former Sitka spruce stand felled in 1988. The subplot in the foreground was assigned to the High *Calluna – Erica* vegetation type. Note that the Sitka spruce in the foreground in 1999 was removed as part of weeding treatments.



Figure 4. Plot 6U in 1999 (top) and 2001 (bottom). The plot was a former Sitka spruce stand felled in 1988. The subplot in the foreground was assigned to the High *Calluna* – *Erica* vegetation type.



Figure 5. Plot 9E in 1999 (top) and 2001 (bottom). The plot was a former larch stand felled in 1991. The subplot in the foreground was assigned to the *Pteridium - Agrostis* vegetation type.



Figure 6. Plot 9U in 1999 (top) and 2001 (bottom). The plot was a former larch stand felled in 1991. The subplot in the foreground was assigned to the *Pteridium - Agrostis* vegetation type.



Figure 7. Plot 11E in 1999 (top) and 2001 (bottom). The plot was a former Sitka spruce stand felled in 1995. The subplot in the foreground was assigned to the *Agrostis - Galium* vegetation type; it was wetter and more rush-dominated than the typical example of this vegetation type.



Figure 8. Plot 11U in 1999 (top) and 2001 (bottom). The plot was a former Sitka spruce stand felled in 1995. The subplot in the foreground was assigned to the *Agrostis - Galium* vegetation type. As with the exclosed plot, it was wetter and more rush-dominated than the typical example of this vegetation type.



Figure 9. Plot 12E in 1999 (top) and 2001 (bottom). The plot was a former Sitka spruce stand felled in 1998. The subplot in the foreground was assigned to the *Calluna - Galium* vegetation type.



Figure 10. Plot 12U in 1999 (top) and 2001 (bottom). The plot was a former Sitka spruce stand felled in 1998. The subplot in the foreground was assigned to the Low *Calluna - Erica* vegetation type.



Figure 11. Plot 15E in 2000 (top) and 2001 (bottom). The plot was a former lodgepole pine stand felled in 1997. The subplot in the foreground was assigned to the *Calluna* - *Galium* vegetation type.



Figure 12. Plot 15U in 2000 (top) and 2001 (bottom). The plot was a former lodgepole pine stand felled in 1997. The subplot in the foreground was assigned to the High *Calluna* - *Erica* vegetation type.



Figure 13. Plot 19E in 1999 (top) and 2001 (bottom). The plot was a former Sitka spruce stand felled in 1998. The subplot in the foreground was assigned to the Low *Calluna - Erica* vegetation type.



Figure 14. Plot 19U in 1999 (top) and 2001 (bottom). The plot was a former Sitka spruce stand felled in 1998. The subplot in the foreground was assigned to the Low *Calluna - Erica* vegetation type.



Figure 15. Plot 22E in 1999 (top) and 2001 (bottom). The plot was a former Sitka spruce stand felled in 1993. The subplot in the foreground was assigned to the *Calluna* - *Galium* vegetation type.



Figure 16. Plot 22U in 1999 (top) and 2001 (bottom). The plot was a former Sitka spruce stand felled in 1993. The subplot in the foreground was assigned to the *Calluna - Galium* vegetation type.



APPENDIX 4: SPECIES CODES

Below are the six-letter codes used in ordination and other figures. The codes are based on the first three letters of the genus and the first three letters of the specific epithet. Nomenclature follows Stace (1997).

agrcan	*Agrostis canina*
agrcap	*Agrostis capillaris*
antodo	*Anthoxanthum odoratum*
betpub	*Betula pubescens*
blespi	*Blechnum spicant*
calvul	*Calluna vulgaris*
carbin	*Carex binervis*
carech	*Carex echinata*
carpil	*Carex pilulifera*
chaang	*Chamerion angustifolium*
desfle	*Deschampsia flexuosa*
digpur	*Digitalis purpurea*
dryaff	*Dryopteris affinis*
drydil	*Dryopteris dilatata*
ericin	*Erica cinerea*
eritet	*Erica tetralix*
fesovi	*Festuca ovina*
galsax	*Galium saxatile*
hedhel	*Hedera helix*
hollan	*Holcus lanatus*
holmol	*Holcus mollis*
hyppul	*Hypericum pulchrum*
ileaqu	*Ilex aquifolium*
junbul	*Juncus bulbosus*
juneff	*Juncus effusus*
junsqu	*Juncus squarrosus*
luzmul	*Luzula multiflora*
luzsyl	*Luzula sylvatica*
molcae	*Molinia caerulea*
oxaace	*Oxalis acetosella*
picsit	*Picea sitchensis*
potere	*Potentilla erecta*
pteaqu	*Pteridium aquilinum*
quepet	*Quercus petraea*
rhopon	*Rhododendron ponticum*
rubfru	*Rubus fruticosus* agg.
rumace	*Rumex acetosella*
salcin	*Salix cinerea* ssp. *oleifolia*
sorauc	*Sorbus aucuparia*
uleeur	*Ulex europaeus*
ulegal	*Ulex gallii*
vacmyr	*Vaccinium myrtillus*