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The Occurrence of Canopy Gaps in some Semi-natural Irish Woodlands

and the

Natural Regeneration of Tree Species therein

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April 2001

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G. Thérèse Higgins

Dedication:

To those who matter the most - you know who you are

To the memories of

Toby Hodd, a fine botanist and naturalist

&

Mary Joan Rice, a Lady

Requiescat in pace

Summary of Contents

Acknowledgements
List of figures
List of tables
List of plates
Summary
Terms

Chapter 1 General Introduction	1
Chapter 2 Irish Woodlands	5
Chapter 3 Woodland Regeneration	15
Chapter 4 Introduction to Canopy Gaps	26
Chapter 5 Methodology	39
Chapter 6 Details of Woodlands studied	49
Chapter 7 Canopy Gap Regime in Irish semi-natural woodlands	59
Chapter 8 Vegetation in Canopy Gaps in semi-natural Irish woodlands	76
Chapter 9 Browsing of Tree Saplings	99
Chapter 10 Canopy Disturbance in Irish woodland	122
Chapter 11 Vegetation in Canopy Gaps	135
Chapter 12 Browsing of Tree Saplings	151
Chapter 13 General Conclusions	165
Bibliography	170
Appendix I	193
Appendix II	196
Appendix III	199

Table of Contents

Chapter 1	**General Introduction**	**1**
1.1	Background	1
1.2	Aims	3
1.3	Thesis layout	3
Chapter 2	**Irish Woodlands**	**5**
2.1	An outline history of Irish Woodlands	5
2.2	Irish Woodland today	9
2.2.1	*Irish Woodland trees*	*11*
2.2.2	*Irish Woodland types*	*12*
2.3	Irish woodland soils	13
2.4	The climate of Ireland	14
2.5	Conclusion	14
Chapter 3	**Woodland Regeneration**	**15**
3.1	Defining woodland regeneration	15
3.2	Mechanisms of woodland regeneration	15
3.2.1	*Gap-phase regeneration*	*15*
3.2.2	*Timing of regeneration*	*16*
3.2.3	*Modes of regeneration*	*16*
3.2.4	*Species interaction in regeneration*	*16*
3.3	Regeneration of tree species	17
3.3.1	*Oak*	*18*
3.3.2	*Ash*	*19*
3.3.3	*Beech*	*19*
3.3.4	*Birch*	*20*
3.3.5	*Rowan*	*21*
3.4	Other factors affecting regeneration in woodland	21
3.4.1	*Grazing and woodland regeneration*	*21*
3.4.2	*Management practices and regeneration*	*23*
3.5	Factors pertaining to regeneration in Irish woodlands	25
Chapter 4	**Introduction to canopy gaps**	**26**
4.1	Disturbance in the forest ecosystem	26
4.2	Woodland canopy gaps	26
4.2.1	*Defining the gap*	*27*
4.2.2	*Hemispherical canopy photography*	*27*
4.3	Gap formation	28
4.3.1	*Mode of gap formation*	*28*
4.3.2	*Frequency of gap formation*	*29*
4.3.3	*Factors affecting gap formation and gap structure*	*30*
4.4	Gap structure	31
4.5	The gap environment	33
4.6	Response to canopy gaps	35
4.6.1	*Community level*	*35*
4.6.2	*Species level*	*37*
4.7	The role of canopy gaps in the forest ecosystem	37
4.8	Conclusion	38
Chapter 5	**Methodology**	**39**
5.1	Selection of study sites	39
5.2	Belt transects for sampling the woodland disturbance regime	40
5.3	Natural regeneration in woodland gaps	41
5.3.1	*Selection of gaps*	*41*
5.3.2	*Gap structure*	*41*
5.3.3	*Gap age*	*41*
5.3.4	*Gap area*	*42*
5.3.5	*Gap vegetation*	*42*
5.3.6	*Gap soils*	*43*
5.4	Browsing and natural regeneration	46
5.4.1	*Site description*	*46*

5.4.2	*Experimental design*	*47*
5.4.3	Monitoring	47
5.4.4	Data analysis	48
Chapter 6	**Details of woodlands studied**	**49**
Chapter 7	**Canopy gap regime in Irish semi-natural woodlands**	**59**
7.1	Canopy disturbance regime	59
7.2	Characteristics of canopy disturbance	62
7.2.1	*Modes of disturbance*	*62*
7.2.2	*Species involved in disturbance*	*63*
7.2.3	*Woodland response to disturbance*	*64*
7.3	Characteristics of canopy gaps	65
7.3.1	*Gap formation*	*65*
7.3.2	*Gap zonation: structure and soil properties*	*69*
7.3.3	*Gap size*	*73*
Chapter 8	**Vegetation in canopy gaps in semi-natural Irish Woodlands**	**76**
8.1	Vegetation in canopy gaps	76
8.2	Regeneration in canopy gaps	79
8.2.1	*Distribution of regeneration*	*79*
8.2.2	*Composition of regeneration in canopy gaps*	*80*
8.2.3	*Abundance of regeneration*	*83*
8.3	Regeneration on the woodland scale	88
8.4	Regeneration on the gap scale	90
8.5	Regeneration patterns within canopy gaps	94
Chapter 9	**Browsing of tree saplings**	**99**
9.1	Extent and severity of browsing	99
9.1.1	*Differences between species in extent and severity of browsing at Tomies*	*101*
9.1.2	*Differences between species in extent and severity of browsing at Tomies*	*102*
9.2	Species of browser and grazer	103
9.2.1	*Grazing by invertebrates*	*103*
9.2.2	*Browsing by deer and hares*	*103*
9.3	Species preferences displayed by browsers	108
9.4	Browsing and sapling growth	109
9.4.1	*Change in sapling height*	*112*
9.4.2	*Performance of saplings*	*116*
9.4.3	*Survival*	*119*
Chapter 10	**Canopy disturbance in Irish woodland**	**122**
10.1	Methodology	122
10.2	The disturbance regime	123
10.2.1	*Factors affecting canopy disturbance*	*124*
10.2.2	*Modes of disturbance*	*126*
10.2.3	*Canopy species and disturbance*	*127*
10.3	Characteristics of canopy gaps	128
10.3.1	*Gap size*	*128*
10.3.2	*Gap makers*	*130*
10.3.3	*Gap formation*	*130*
10.3.4	*Gap age*	*131*
10.3.5	*Heterogeneity of gap structure*	*131*
10.3.6	*Heterogeneity of soils in gaps*	*132*
10.4	Conclusion	134
Chapter 11	**Vegetation in canopy gaps**	**135**
11.1	Differences between gaps and intact canopy	135
11.1.1	*General vegetation*	*135*
11.1.2	*Regeneration of tree species*	*136*
11.2	Heterogeneity of the general vegetation within canopy gaps	136
11.3	Regeneration in canopy gaps	137
11.3.1	*Factors affecting regeneration composition in gaps*	*137*
11.4	The response of Irish woodland communities to canopy gaps	141

11.4.1	*Vegetative replacement of canopy*	*142*
11.4.2	Replacement of canopy by growth of seedlings and saplings	143
11.4.3	Maintenance of canopy gap conditions	144
11.5	The regeneration status of the principal native species in canopy gaps	145
11.5.1	*Oak*	*146*
11.5.2	*Ash*	*146*
11.5.3	*Birch*	*147*
11.5.4	*Holly*	*147*
11.5.5	*Rowan*	*147*
11.5.6	*Elm*	*148*
11.5.7	Other species	148
11.6	Conclusion	149
Chapter 12	**Browsing of tree saplings**	**151**
12.1	Background	151
12.2	Experimental procedure	151
12.3	Incidence of browsing	152
12.3.1	*Extent and severity of browsing*	*152*
12.3.2	*Species of browser*	*153*
12.3.3	*Seasonality of browsing*	*154*
12.4	Species preferences shown by browsers	155
12.5	Response browsing of saplings to browsing	157
12.5.1	*General trends*	*157*
12.5.2	*Response browsing of oak to browsing*	*158*
12.5.3	*Response browsing of ash to browsing*	*159*
12.5.4	*Response browsing of beech to browsing*	*159*
12.5.5	*Response browsing of birch to browsing*	*160*
12.5.6	*Response browsing of rowan to browsing*	*160*
12.5.7	*Browsing and sapling growth*	*161*
12.6	Other factors affecting the growth of transplanted saplings	161
12.7	Implications for woodland regeneration	163
Chapter 13	**General conclusions**	**165**
13.1	Methodology Appraisal	165
13.2	Disturbance regime in Irish woodlands	165
13.3	Response of woodland to canopy gaps	166
13.4	Regeneration of trees in canopy gaps	167
13.5	Browsing and regeneration	168
13.6	Implication for Irish woodlands	168
13.7	Further studies	169
13.8	Concluding remarks	169
	Bibliography	**170**
	Appendix I	**193**
	Appendix II	**196**
	Appendix III	**199**

Acknowledgements

The author gratefully acknowledges the funding of this research by Enterprise Ireland (formerly Forbairt); the European Union Cost Action for funding to allow a visit to forest reserves at Fontainbleau, Paris; the Graduate Studies Office, TCD for assistance for travel to conferences, and workshops. Bollard Nurseries generously donated the saplings used in the field experiment.

Thanks are due to the many landowners that permitted access to their woodlands: David Hutton-Bury, Marquess of Waterford, Brickendon family, Dúchas, and Coillte.

To all the staff of Dúchas, particularly those at Killarney (Dan Kelleher, Paudie O' Leary, Pascal Dower, Peter O' Toole, John O' Connor, Brendan O' Shea, Kathryn Freeman, Padraig O' Sullivan, Tim Burkitt) and at Glenveagh for their support and assistance.

Many people shared their valuable time and gave me knowledge, experience and information which much assisted this work: Alan Craig, Michael Neff, David Jeffrey, Anthony Prins, Jim Latham, Ruth Cardon and the Irish Deer Society, Glen Iason, Tom at Met Éireann, Keith Kirby, J.F. Ponge, Marc Théry, Jean-Yves Pontailler.

For advice on soil analysis and endless help in the laboratory, I am very grateful to Dearblha Walsh, Siobhan Mac Namee and especially Dawn Carroll.

Many people provided assistance without which this work might not have been completed. Thankyou so much: Naomi Kingston, Karl and Esther Higgins, Kathryn Freeman, Deirdre Lynn, Chris Barron, Andrew Carroll, Simon Barron and Susan Murphy for assistance with field work. Thanks to Gerry, Fran, Siobhan, Jackie and Adrienne, Pamela and Mary for technical and administrative help, and to Edwina, Sumaya, Rebecca, Steve, Orla, Myra, Thecla, Mary and Ann for support and advice.

To my family (Mam, Dad, Martin, Mary Joanna) and Chris and Naomi for listening to the finer details repeatedly and for helping to relieve the stress!

This project was supervised by Dr. Daniel Kelly and co-supervised by Fraser Mitchell to whom I am very, very grateful for their encouragement, advice, direction and friendship.

Figures in the text:

Fig. 2.1	Distribution of Woodland in Ireland	10
Fig. 6.1	Location of woodlands investigated in this survey.	50
Fig. 7.1	Variation in the number of gaps per 100m.	61
Fig. 7.2	Modes of canopy disturbance in surveyed woodlands.	62
Fig. 7.3	Modes and species involved in disturbance events.	63
Fig. 7.4	Modes of gap formation.	67
Fig. 7.5	Species involved in gap formation.	67
Fig. 7.6	The occurrence of different modes of disturbance for the more common gap makers.	68
Fig. 7.7	The frequency of gap zones.	69
Fig. 7.8	Mean pH for soils in gap zones in four woodlands.	71
Fig. 7.9	Mean organic content (% by weight) of soils in gap zones in four woodlands.	71
Fig. 7.10	Mean total nitrogen (ug/ml) in soils sampled from gap zones in four woodlands.	72
Fig. 7.11	Mean total phosphate (ug/ml) in soils sampled from gap zones in four woodlands.	72
Fig. 7.12	Distribution of gap sizes.	75
Fig. 8.1	Mean percentage cover in gaps and under canopy.	77
Fig. 8.2	Mean percentage cover of gap zones by vegetation groups.	78
Fig. 8.3	Taxa regenerating in canopy gaps.	79
Fig. 8.4	Regeneration (all classes) in canopy gaps.	80
Fig. 8.5	Diversity of regeneration in canopy gaps.	82
Fig. 8.6	Mean density of seedlings in canopy gaps.	83
Fig. 8.7	Mean number of saplings per gap.	85
Fig. 8.8	The occurrence of saplings in canopy gaps and their frequencies as leaders (tallest sapling present).	87
Fig. 8.9	Abundance of saplings in woodlands.	89

Fig. 8.10	DCA plot comparing gaps based on regeneration composition.	90
Fig. 8.11	Overlay of environmental variables onto DCA plot.	91
Fig. 8.12	The relationship between seedling densities and gap characteristics.	92
Fig. 8.13	DCA plot for regeneration composition of gaps, comparing the distribution of species and regeneration class.	93
Fig. 8.14	Regeneration classes (canopy and sub-canopy species) in gaps.	94
Fig. 8.15	Regeneration of canopy species in gap zones.	95
Fig. 8.16	Regeneration of sub-canopy species in gap zones.	95
Fig. 8.17	Distribution of regeneration classes of long-lived canopy species within gaps.	97
Fig. 8.18	Distribution of regeneration classes of short-lived and sub-canopy species within gaps.	98
Fig. 9.1	Percentage of saplings browsed at Tomies and Charleville.	100
Fig. 9.2	The occurrence of browsing by hares and deer at Tomies and Charleville over the experimental period.	104
Fig. 9.3	The frequency of deer and hare browsing at Charleville.	105
Fig. 9.4	The frequency of deer and hare browsing at Tomies.	106
Fig. 9.5	Browsing preferences expressed by deer and hares at Tomies and Charleville Woods.	108
Fig. 9.6	Mean height of saplings at Charleville.	110
Fig. 9.7	Mean height of saplings at Tomies.	111
Fig. 9.8	Mean overall change in height for browsed and unbrowsed saplings .	113
Fig. 9.9	Net change in height (cm) for saplings transplanted into Charleville Wood.	114
Fig. 9.10	Net change in height (cm) for saplings transplanted into Tomies Wood.	115
Fig. 9.11	Performance of saplings.	117
Fig. 9.12	Percentage survival of saplings transplanted into Tomies Wood.	120
Fig. 9.13	Percentage survival of saplings transplanted into Charleville Wood.	121

Tables in the text:

Table 2.1	Native Irish trees.	11
Table 6.1	Woodlands Surveyed.	49
Table 6.2	Characteristics of Woodland Sites.	58
Table 7.1	Disturbance regime in selected Irish woodlands.	60
Table 7.2	Disturbance events resulting in canopy gaps.	60
Table 7.3	Wind conditions at woodlands studied.	61
Table 7.4	Relationships between site factors and disturbance values.	61
Table 7.5	Gap formation and structure.	65-66
Table 7.6	Variation in soil properties with location, gap and gap zone.	73
Table 7.7	Variation in soil properties.	73
Table 7.8	Canopy gap size.	74
Table 7.9	Relationships between measures of gap size and related factors.	75
Table 8.1	Species occurring only in gap quadrats.	76
Table 8.2	Variation in cover between site, gap and canopy, and gap zone.	77
Table 8.3	Regeneration composition in canopy gaps.	81
Table 8.4	Mean density of seedlings per gap.	84
Table 8.5	Numbers of saplings in canopy gaps.	86
Table 8.6	Regenerating species in the surveyed woodlands.	88
Table 8.7	Regeneration in gap zones.	96
Table 9.1	Effects of location, period and species on the amount and severity of browsing of saplings.	99
Table 9.2	Occurrence of the uprooting of saplings at Tomies.	107
Table 9.3	Browsing score for saplings at Tomies and Charleville.	108
Table 9.4	Performance of saplings planted into Charleville and Tomies.	116
Table 12.1	Species preferences expressed by browsing animals.	156

List of Plates:

Plate 1 Charleville Wood, Co. Offaly

Plate 2 Tomies Wood, Killarney, Co. Kerry

Plate 3 Birch regenerating in a canopy gap

Plate 4 Young birch tree that has escaped browsing on a root plate

Summary

The reported failure of regeneration in British oakwoods and some observations of a dearth of saplings and young trees in Irish woods has prompted concerns about the ability of Irish semi-natural woodland to self-perpetuate. The native tree species are limited in number and generally light demanding, and their regeneration may be expected to occur in canopy gaps. However, little is known about the distribution of gaps in Irish woodland, and few quantitative data regarding regeneration in canopy gaps have been available. Observations in Irish woodlands suggest that the production of seed and establishment of seedlings is sufficient for many species, but that saplings and young trees are absent. In some cases this has been attributed to the impact of heavy browsing by deer and domestic stock.

The canopy disturbance regime was investigated using belt transects to sample 12 Irish woods. Disturbance events were identified, classified and their impact on the woodland canopy assessed. 45 canopy gaps from 13 woods were investigated in detail. Their formation, size, and other characteristics were described. Gaps were subjectively delineated into zones that differed structurally. The vegetation and specifically the regeneration of tree species were assessed for each gap. Variation in soil properties and vegetation with gap zone was investigated.

The results indicate that the Irish woodland disturbance regime is characterised by frequent small-scale disturbance that results in gap formation, the rate of which varies in time and space. Many factors including wind, stand structure and site factors, affect gap formation, and no one factor appears to be the primary determinant of the disturbance regime. Rare, large-scale events are not discounted for the future. The frequency of disturbance events and gap formation is not associated with species, but the mode of disturbance and subsequent gap characteristics vary with species. Canopy gaps contain a range of structurally diverse zones, and environmental conditions differ between with these zones.

Several vegetation responses to canopy gap formation have been identified, and these are affected by stand characteristics and woodland management. Vegetative growth, release of suppressed seedlings and saplings, and the establishment of new individuals from seed occur at canopy gaps. Replacement of the canopy is sometimes interrupted by competition from understorey and ground vegetation with tree species.

Canopy gaps clearly play a role in the regeneration of tree species and promote species diversity by offering a range of structurally differing zones for colonisation. However, the depauparate Irish tree flora and the range of conditions present owing to management practices means that canopy gaps may not be so central to species diversity in Irish woodland as they are reported to be in other regions.

The natural regeneration of the principal canopy tree species appears to be successful in canopy gaps in general. Regeneration is prohibited, however, by heavy browsing at some sites, and the lack of suitable germination sites at others. Tree species vary in their regeneration requirements and this is reflected in their distribution. The present regeneration composition in canopy gaps suggests that the future canopy will be composed of the same range of species that is currently found, but that the proportions of these will differ. The existence of almost pure stands of oak is unlikely to persist in the long term.

Browsing deer and hares were found to exhibit preferences between different tree species under field conditions. Rowan, ash and oak were generally the preferred species, while beech and birch were less preferred. These species also differed in their tolerance of and response to browsing and this may have significant implications for the competitive interactions between saplings of tree species. The avoidance of beech by browsers may assist the invasion of suitable woodland sites by this species.

The results of this research demonstrate the impact of past and present management on natural regeneration in woodland, and have implications for the future management of this resource.

Glossary (including abbreviations):

BP: Before present (present is 1950 AD by convention).

Disturbance event (DE): any event in the woodland that gives rise to an opening in the canopy. It involves damage to a tree or part of a tree, and thus the removal of that vegetation from the woodland canopy. Three modes of natural disturbance event were recognised here - uprooting, snapping and crown damage (see below). Cutting of trees may also be considered as disturbance events.

Uprooting (U): the falling of a tree involving the tearing of the roots or some of the roots from the soil in which the tree was previously anchored.

Crown damage (CD): the loss of part or all of the crown of a tree.

Snapping (S): the breaking of a tree at any point along its trunk up to the point of branching.

Hemiphots: hemispherical canopy photographs derived from photographs of the woodland canopy by using a fish-eye (180 degrees) lens. The image is thus a 2-dimensional representation of the 3-dimensional canopy. Images may be digitised for analysis in appropriate computer programs.

Gap zones: areas within canopy gaps which have been identified as differing structurally from other areas within the same gap. They are subjectively delineated, and the zones applied may vary from author to author. The types of zone present within a particular gap is dependent on the mode of formation of that gap.

Root zone: This is the area surrounding and including the rootplate and exposed soil to the base of an uprooted tree. In this study, the root zone was further divided into pit (the depression left where the gap makers roots were previously anchored) and mound (the elevated and upturned root-plate and associated soil and vegetation).

Trunk zone: This is the area within the canopy gap on either size of the fallen trunk. It is bound, at one end, by the rootplate (if the gap maker was uprooted) and at the other end, by fallen crown. In this study the trunk zone was further divided into bole (the area directly adjacent to the fallen bole and thus subject to shelter and runoff from it) and periphery (areas within the gap not affected by the presence of fallen debris, exposed soil or decaying trunk etc.).

Crown zone: This is the area within the gap on which branches from the gap maker have fallen. Where the gap was formed by uprooting or snapping of a tree, the crown zone tends to be located at one end of the gap. Where crown damage is involved, the crown zone may dominate the centre of the gap. In this study the crown zone is referred to as 'fallen canopy'.

CHAPTER 1 GENERAL INTRODUCTION

1.1 Background

The potential natural vegetation of Ireland is woodland (Cross 1998) and most of the Irish landscape was covered by woodland following the last Glacial c. 10,000 BP. Millennia of human activity have dramatically reduced the woodland cover, and that which remains is limited in extent, scattered in distribution and much modified from the primeval forest. The Republic of Ireland is one of the least wooded countries in Europe with only 9.02% of the state under woodland (Forest Service 1999). However, less than one fifth of this is broadleaved and less than 1% of the state is semi-natural woodland, derived from the original wildwood (Forest Service 1999). Despite their paucity, woodlands are an important ecological resource in Ireland. They support a wide range of native species. Twenty percent of native plant species (excluding algae), 50% of invertebrates, and 28% of breeding birds are woodland species (Cross 1987) and many of our mammals depend on woodland.

Ireland's semi-natural woodlands can be broadly divided into two categories. In upland regions, where acidic bedrock, such as granite and Old Red Sandstone prevail, semi-natural woodlands are dominated by sessile oak (*Quercus petraea*), with abundant birch (*Betula pubescens),* rowan (*Sorbus aucuparia*) and holly (*Ilex aquifolium*) in the canopy and sub-canopy. Over limestone, where deep glacial till typically exists, pedunculate oak, (*Quercus robur*) and ash (*Fraxinus excelsior*) are the principal canopy species with hazel (*Corylus avellana*) commonly in the sub-canopy.

The failure of semi-natural woodland to regenerate has been widely reported in Britain and Europe (Vera 2000, Humphrey & Swaine 1997, Tansley 1953, Watt 1919). A lack of young trees and saplings has also been observed in many woods throughout Ireland (*e.g.* Kelly 1981, Neff 1974, Hester *et al.* 1998) and this is a cause of concern for the future of these vital habitats. However, no quantitative survey to assess the extent of the failure of Irish woodland to regenerate has been undertaken. Thus, the status of the principal tree species and the general status of Irish woodlands with respect to natural regeneration are not clear.

The factors that affect the regeneration of tree species are many. However, seed production and seedling establishment, for many tree species, appear to be more frequently successful than the transition from seedling to sapling status and beyond. Herbivory is clearly a primary limiting factor to regeneration in some Irish woods (Hayes *et al.* 1991) and has been recognised as one of the two major conservation issues facing the managers of Ireland's semi-natural woodlands (Neff, 1974). However,

while it is widely accepted that many Irish woodlands are over-grazed, the exact management régime which will allow woodland regeneration, and simultaneously sustain a population of grazers, remains to be clearly defined. Total exclusion of grazers will not necessarily result in optimum regeneration or maximum biodiversity (Kelly 2000, Kirby *et al.* 1994). In addition, species preferences displayed by browsers may affect the regeneration success of the various tree species present within woodland. The factors affecting these preferences include local circumstances (*e.g.* the availability of alternative forage, population density of browsers) as well as the actual inherent preferences of the browser. The response of a sapling to browsing will also vary with species, extent of damage and other site factors, and this will affect the relative success of different tree species in regenerating under browsed conditions.

Seedlings and saplings of the native canopy species are more or less light demanding (Wardle 1959, Rackham 1980). It is suggested that the most common dominant species in Irish woodlands (*Quercus* spp.) are largely incapable of regenerating in their own shade (Shaw, 1974). It is to be expected, then, that their regeneration is more likely to be successful in canopy gaps and at woodland edges than under closed canopy.

One hypothesis to explain the paucity of natural regeneration within woodlands is a lack of woodland gaps (Rackham 1980). This situation has arisen in many English woodlands because active woodland management in recent centuries has not allowed mature trees to degenerate into old age (Streeter 1974). Irish broadleaved woodlands have, in general, been less intensively managed than their English counter-parts. However, the structure of Irish semi-natural woodland has been little investigated (Iremonger (1986) is an exception) and no data regarding the frequency and distribution of gaps in Irish woodland and natural regeneration therein are available. The present study has sought to redress this.

The occurrence of treefall gaps and their contribution to forest dynamics has been the focus of much study over the past few decades. However, the majority of this research has been undertaken in the tropics (Brokaw 1982, Spies & Franklin 1989, Van der Meer & Bongers 1996), North America (Runkle 1981, Canham 1988), and Japan (Nakashizuka & Numata 1982). These phenomena are relatively under-studied in European terms. While there are a number of reports on post-storm woodland dynamics from Britain (Lamb 1989, Whitbread 1991, Kirby & Buckley 1994), the role of canopy dynamics in woodland regeneration has not been the subject of any detailed investigation in Irish woods.

1.2 Aims

In order, then, to understand the situation in Irish woodland with regard to natural regeneration of tree species, several processes require investigation. Given the light requirements of the dominant species, this study investigates the extent of canopy gaps in Irish woodland and the factors that affect the canopy disturbance regime. The distribution of regeneration of the principal tree species in canopy gaps is explored, and the role of browsing animals investigated.

The objectives of this research are:

(i) to survey the occurrence and characteristics of canopy gaps in some Irish broadleaved woodlands;

(ii) to survey and monitor the response of the woodland plant community to canopy gaps in Irish broad-leaved woodlands;

(iii) to survey the regeneration process in canopy gaps in some Irish broad-leaved woodlands;

(iv) to study the effects of grazing animals on regeneration of native tree species within canopy gaps;

(v) to investigate species preferences displayed by browsers;

(vi) to investigate the growth responses of different tree species to browsing.

1.3 Thesis layout

This thesis is presented in four parts. The first comprises three chapters, which introduce the main themes of this research and review some of the literature in each area. Chapter 2 outlines the history of Irish woodland, and describes that which exists today. Chapter 3 investigates the components of woodland regeneration, the autecologies of the relevant canopy tree species and the factors affecting their regeneration. Chapter 4 reviews the area of canopy gap dynamics and considers the role of disturbance in natural regeneration in woodland.

The second part of this thesis comprises Chapter 5, in which the methods employed in the research are described.

The results of this study are presented in Chapters 6 - 9. Chapter 6 includes site-by-site descriptions of the woodlands studied. Chapter 7 presents 2 datasets pertaining to the occurrence of gaps in Irish woodland. The first dataset was obtained from random sampling (by transect) in a number of woodlands, and describes the occurrence of disturbance events in the woodland canopy. The second

dataset is derived from the sampling of subjectively chosen canopy gaps in a range of woodlands and includes information about gap structure and zonation. [Note: some of the woodlands sampled for disturbance regimes (7.1-7.2) and canopy gap structure (7.3) overlap, but the datasets are independent of each other.] Chapter 8 contains data about the vegetation, and specifically, regeneration of tree species, in canopy gaps. These data were gathered from the subjectively chosen gaps referred to in Section 7.3. Chapter 9 contains data derived from the experimental investigation into the browsing, by hares and deer, of tree saplings in canopy gaps in two Irish woodlands.

The final part of this thesis comprises interpretation and discussion of the results presented in Chapters 6-9, in the light of relevant information from the available literature. Each dataset is discussed separately (Chapters 10-12), and in Chapter 13, a broad overview of the tree regeneration in canopy gaps and the role of browsing animals in woodland regeneration in Ireland is presented.

CHAPTER 2 IRISH WOODLANDS

2.1 An outline history of Irish woodlands

The following account of the development of woodland vegetation is summarised from Mitchell & Ryan (1997) unless otherwise stated.

The maximum of the last glacial cold stage was reached about 20,000 years ago. This was followed by ice melt and the available evidence suggests that Ireland was ice free by 14,000 years ago. A brief warm stage, the Woodgrange Interstadial, persisted for *c.* 2,400 years and grasses and later juniper scrub invaded Ireland. However, the return of cold conditions during the Nahanagan Stadial interrupted this succession with ice-masses present in the uplands and permafrost halting soil processes in the lowlands. Thus at the beginning of the present (Littletonian) Interglacial, *c.* 10,000 years ago, much of the Irish landscape was covered by a treeless tundra landscape.

The release of the ground from permafrost allowed the development of vegetation, and land bridges existed between Ireland and Britain, and Britain and Continental Europe although details of their location, extent and date of submergence are still under investigation (Mitchell *in press*). In any case, after the submergence of these routes, any new species must have arrived by air or water, or have been carried with birds/human settlers.

The initial response to warming conditions was the development of grasslands. However, within 250 years juniper scrub had replaced large areas of meadow. This was later invaded by willows (*Salix* spp.) and birches (*Betula* spp.), so that Ireland's first woodlands of the present warm phase were dominated by birch. By about 9,000 years ago, hazel (*Corylus*) and pine (*Pinus*) had become dominants, probably on different soil types. From this time oak (*Quercus*), elm (*Ulmus*), alder (*Alnus*), ash (*Fraxinus*) and Yew (*Taxus*) were also present. By *c.* 8,500 before present (BP) oak and elm had overshadowed hazel on heavier soils; pine was expanding on exposed acid soils, and alder dominated wet areas along lakeshores and riverbanks. It is of note that several of the tree species that are native to British woods didn't reach Irish shores until their introduction, centuries later, by human settlers. These include beech (*Fagus sylvatica*), small-leaved lime (*Tilia cordata*), hornbeam (*Carpinus betulus*) and field maple (*Acer campestre*).

At around 7,000 BP rainfall increased and alder expanded, and the exposed soils on which pine had dominated were reduced in extent. Woodlands dominated by oak and elm, with alder and hazel in the lowlands, and birch-pine woods on higher ground, dominated the landscape for the next 2,000 years.

Mesolithic peoples, present from *c.* 8,000 BP, led a hunter-gatherer existence apparently making little impact on the wooded landscape. At *c* .6,000 years BP, Neolithic communities began to settle in Ireland. The Neolithic people were farmers, and brought with them tools to clear areas of woodland, so that they could grow their cereal crops and graze their animals. A sharp decline in elm from around this time may be due to the species' preference for highly fertile soils, which presumably would have been the primary targets of these farming people, and the use of elm foliage for fodder (Richens 1983). However, the wide extent of this decline also suggests a pathogen outbreak similar to the Dutch Elm Disease which has decimated European elm populations in recent times. In any case, woodland decline began at this time. Expansion of peatlands (*c.*7,000 BP) restricted pine woods in the uplands, and the increasing population of farmers resulted in active woodland clearance on an increasing scale. Initially this clearance was undertaken in a shifting cultivation practice. Evidence of the increase in population and cultural organisation include the many earthworks and stone monuments that have survived in the landscape from this time (*e.g.* passage graves of the Boyne Valley *c.* 5,200 BP). Over time, larger numbers of grazing animals (sheep, pigs, goats and cattle) were herded, requiring larger areas of pasture. As population increased, competition for resources became an issue and the active organisation of land became a feature of the landscape. Field boundaries from this time, such as those of the Cèide Fields of Co. Mayo, are still visible today.

The Bronze Age (4,000-2,600 BP) peoples mined copper (for example at Killarney) and used wood to heat the rock and smelt the ore from the veins. This and the use of wood for domestic implements and weaponry and fuel ensured that the woodland exploitation continued. The arrival of Iron-age technologies (*c.*2,300 BP), such as early forms of the plough must have allowed for more efficient clearance and cultivation. Large scale clearance for agriculture seems to have stalled about this time however, and secondary woodland colonised many of the previously cleared areas.

A dramatic increase in arable farming and the development of cattle farming from *c.*300-840 AD resulted in the large-scale clearance of woodland, both secondary and primary (de Paor & de Paor 1961). Animals were grazed on hills and mountains over the summer months, so that land previously left fallow was prevented from reverting to scrub and woodland. Field enclosure systems were developed so that the level of grazing could be controlled and crops could be protected from grazers when necessary.

Over the next few centuries, the arrival of the Vikings (840 AD), development of organised agricultural commerce by the Cistercians (1157 AD), and Norman Invasion (1169 AD) ensured that exploitation of the woodlands continued, as cities were built (primarily of wood), and extensive areas of agriculture became permanent fixtures in the landscape (O' Corráin 1972). Giraldus Cambrensis, travelling around

Ireland in 1185, reported that there were 'many woods and marshes', and noted the 'fine plains' and 'flocks on the mountains'.

By the time of the Tudor Plantations, much of the landscape had been cleared of its woodlands. The absence of any major survey of the country means that we only have a vague picture of the extent of woodland at this time. It is known that the Pale (a large area on the east coast stretching from Dundalk, westwards to Kells and Trim, and as far south as the foothills of the Wicklow Mountains) was largely devoid of woodland, while the mountains of Wicklow and Munster, and the valleys of the rivers Blackwater and Lee were at least partly wooded. McCracken (1971) estimated that at least one eighth of the country was wooded in 1600 AD. However, this figure is disputed by Forbes (1932) and Rackham (1995) who argue that the figure is much less but admit that 'scanty' evidence prevents arrival at an accurate estimate. Rackham (1995) observes that during the next two centuries, woodland clearance advanced at a rapid pace and that by 1830, pre-1600 woodland covered only about 0.2% of the country.

The plantations of Laois and Offaly (1550), Munster (1585), Ulster (1603) and other areas had a significant impact on the Irish woodlands. When large tracts of land were allotted to the new settlers, many natives were displaced onto poorer land, often in the uplands. The concentration of these populations together with their herds of grazing cattle and sheep, exerted considerable pressure in these marginal areas. At the same time commercial exploitation of the woodlands burgeoned. McCracken (1971) says that over 160 iron works were opened during the seventeenth and eighteenth centuries, ship and house building abounded and Ireland became a major exporter, most of the goods being transported in wooden barrels. Tanning and cooperage were significant industries. Reports also exist of woodland clearance for military reasons. Any extensive area of woodland was a barrier to troop movement and provided sanctuary for rebellious natives. Woodland clearance could therefore reduce the activity of insurgents.

By 1700 AD, the political situation had settled considerably, and landlords, now comfortable in their estates, built new homes and planted native and exotic species into their demesne woodlands. Landlords were encouraged in their endeavours by a series of Acts of Parliament (1698 onwards) and the Royal Dublin Society (RDS), who offered grants (from 1735) for the planting of trees (Neeson 1990). Species planted included beech, sycamore, elm, ash, mountain ash, chestnut, maple, Scots fir (Scots pine), larch and silver fir. The RDS also encouraged the laying of hedgerows and planting of hedgerow trees for the better management of livestock.

From 1785 onwards the population of Ireland grew dramatically, and the dearth of trees in the countryside is illustrated by reports of timber poaching, with hedging and even fencing being stolen for

firewood. After the potato famine (1845-49) the population declined and the economy floundered. Land abandoned owing to the decline in rural population was allowed to return to scrub. However, the economic strain was felt by landowners so that, while planting continued, it was often financed by the sale of timber harvested from other woodland. The situation was compounded with the Land Acts (1881, 1903, and 1909), which resulted in the compulsory transfer of lands from landlords to the State. Dispossessed landowners rushed to cut their woods and sell the timber before submitting their property to the State for redistribution among former tenants. Likewise, new tenants saw agriculture as the way to a steady income and future prosperity and cleared scrub and woodland for this purpose. So, despite the fact that the newly established Irish Forestry Society (1900) and the Department of Agriculture and Technical Instruction (DATI) were actively promoting afforestation, woodlands throughout the country were being felled at a dramatic rate (Neeson 1990).

In 1909 legislation was introduced to prohibit tree felling on estates to be compulsorily purchased by the State, and such woodland was placed under the trusteeship of the DATI. However, despite the acquisition of land for afforestation, the setting up of tree nurseries and the funding of planting schemes, woodland cover continued to decline. Of the 380,000 acres (153,900 ha) of estate woodland which had existed in 1880, only 90,000 acres (36,450 ha) remained in 1958 (Neeson, 1990).

The state embarked on an active policy for afforestation. A minimum cover of 1 million acres (405,000 ha) of forest was the target set and planting proceeded over the decades of the 20th century with varying success, depending on the political and economic climate of the day. By 1951, forest cover in the Republic of Ireland was 1.8%. Sitka spruce (*Picea sitchensis*), lodgepole pine (*Pinus contorta*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) were the most abundantly planted species. In 1985, a review of Irish woodlands concluded that 6% of the state (382,000 ha) was wooded (Review Group on Forestry, 1985). 21% of this was privately owned, and 79% was held in public hands. The composition of the state forest was 49% sitka spruce, 47% other conifer species and 4% broadleaved. Given that most of the state plantations originated from the 1950s and 1960s, most plantations are today a maximum of 50 years old.

During the 1970s many state forests were opened to the public (Forest and Wildlife Service, (FWS) 1985) and their amenity and wildlife value became an issue. By 1985, a single species, sitka spruce, accounted for almost half (49%) of state planting and broadleaved species only 5%. Since the 1980s, increasing public concern over the environmental effects of coniferous block planting, and lobbying by various groups (*e.g.* The Tree Council of Ireland, Crann) has prompted Coillte (the state forestry body) to increase the proportion of broadleaved species planted.

In 1999, it was estimated that 13,182 ha of the Coillte forest are under broadleaved species. Of this beech accounts for almost 30%, oak for 22.6%, ash for 17% (Coillte, 1999). Sycamore, birch and alder are among the other species planted.

The most recent census of woodland cover in the Republic of Ireland is that carried out as part of the Forest Inventory and Planning System (FIPS). This project, a Coillte-led venture, involved the use of satellite imagery and orthophotography to locate and classify Irish woodland. The project aims were forestry orientated and this is reflected in the categories assigned to woodland types (*e.g.* Conifer Mature Spruce, Broadleaf Mature Oak). Nonetheless, the data generated are also useful in assessing the current extent of woodland in Ireland.

Total woodland cover in the State, as of 1999, stands at 621,450 ha which amounts to 9.02% of the land area. However, most of this is recent (20th century) plantation forestry, and only 7.8% of the state total are classified as 'mature oak and other broadleaves'. While this figure undoubtedly contains some plantations, it also includes the semi-natural woodland that remains in Ireland. This semi-natural resource includes old plantations from the 17th and 18th centuries and stands that were managed as coppice in the past, as well as more recent secondary woodland. Less than 0.7% of Ireland is covered with mature semi-natural woodland.

2.2 Irish woodland today

Native woodland in the Republic of Ireland is limited in extent, occupying only 0.7% of the land (Forest Service 1999). Most woodlands are fragmented and widely scattered, with the largest concentration occurring in the south-west, notably in the Killarney Valley (Aalen 1997, Fig. 2.1). Wet woodlands are diverse and species rich and are found along rivers, on fen and bog margins and on the fringes of better-drained woodland (Kelly and Iremonger 1997). Semi-natural woodlands on free-draining soils are found in upland areas, on rocky or steep hill slopes, and in the lowlands most often persist on esker ridges and as Estate woodlands. Many woodlands contain introduced species which have naturalised to a greater or lesser extent. *Prunus laurocerasus, Rhododendron ponticum, Acer pseudoplatanus* and *Fagus sylvatica* are among the more widespread introductions, and have achieved local dominance in some places. Many woodlands are browsed by deer, sheep, cattle, hares and rabbits. Few broadleaved stands are managed for timber. Many sites are designated as Natural Heritage Areas (*c.*27,000ha of semi-natural woodland, (Higgins 1999)) and the profile of woodland conservation is increasing in Ireland. Nonetheless, poaching of timber, overgrazing, infestation with introduced species and infrastructural development all pose significant threats to the Irish native woodland resource.

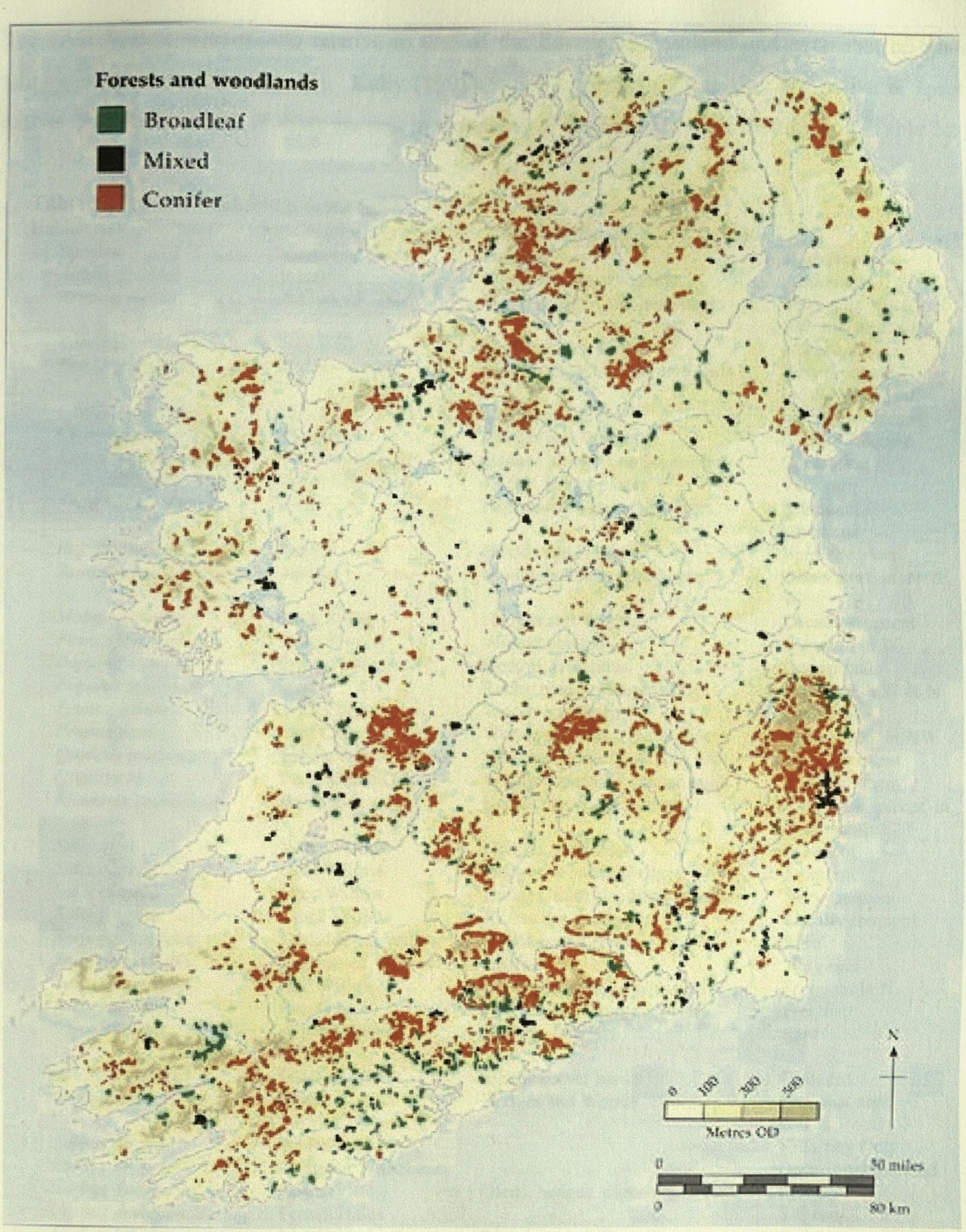

Fig. 2.1 Distribution of woodland in Ireland. (From Aalen 1997) Compiled from visual analysis of Landsat data from May 1990. Minimum unit size shown is 25 ha.

2.2.1 *Irish woodland trees*

The Irish flora is depauparate relative to that of the European mainland and even that of our close neighbour, Britain (Webb 1982). Kelly (1991) lists 33 species of tree that are native or 'probably native' in Ireland. Many of these are rare in woodland or restricted in their distribution (Table 2.1).

Table 2.1 Native Irish Trees (after Kelly, 1991).
Habitat and Distribution are from Webb *et al.*(1996). W: West; S: South; N: North; E: East.

Species	Common Name	Habitat	Distribution
Alnus glutinosa	Alder	Damp Woods, riversides	Abundant
Arbutus unedo	Strawberry Tree	Wood margins and lakeshores	Very rare except in SW and local sites
Betula pendula	Silver Birch	Bog-margins, woods	Occasional
Betula pubescens	Downy Birch	Woods, especially on acid soils	Very frequent, locally abundant.
Corylus avellana	Hazel	Woods and Scrub	Locally abundant
Crataegus monogyna	Hawthorn	Hedges and Woods	Locally frequent
Euonymus europaeus	Spindle-tree	Hedges, thickets on limestone	Occasional
Frangula alnus	Alder buckthorn	Rocky, boggy places	Very rare
Fraxinus excelsior	Ash	Hedges, woods, rocky places	Abundant on limestone
Ilex aquifolium	Holly	Woods and Hedges	Very Frequent
Juniperus communis	Juniper	Mountain heath, lakeshores	Occasional in N & W
Malus sylvestris	Crab Apple	Hedges and Woods	Locally frequent
Pinus sylvestris	Scots Pine	Widely planted	Frequent in W
Populus nigra	Black Poplar	Hedges, roadsides	Occasional
Populus tremula	Aspen	Rocky places, hedgerows	Frequent in W & N
Prunus avium	Wild Cherry	Woods and hedges	Occasional
Prunus padus	Bird Cherry	Woods and damp rocky places	Rare except in NW
Quercus petraea	Sessile Oak	Woods especially on acid soils	Very Frequent
Quercus robur	Pedunculate Oak	Woods especially on rich soils	Very Frequent
Rhamnus catharticus	Buckthorn	Rocky places, lakeshores	Very rare except in W & centre
Salix alba	White Willow	Hedges, riversides	Frequent
Salix caprea	Goat Willow	Hedges, woodland edges	Frequent
Salix cinerea	Grey Willow	Hedges, thickets, damp woods	Very frequent
Salix fragilis	Crack Willow	Riversides, hedges	Locally frequent
Salix myrsinifolia	Dark-leaved Willow	By lakes and rivers	Rare
Salix phylicifolia	Tea-leaved Willow	Cliffs	Very rare
Salix pentrandra	Bay Willow	Riversides, thickets, hedges	Frequent in N
Salix purpurea	Purple Osier	Hedges, bog-margins, rivers	Frequent
Salix triandra	Almond-leaved Willow	Hedges, thickets	Rare
Salix viminalis	Osier	Ditches, river banks	Frequent
Sambucus nigra	Elder	Hedges and Woods	Frequent near houses
Sorbus anglica	Whitebeam		Killarney Only
Sorbus aria	Common Whitebeam		Occasional: planted
Sorbus aucuparia	Rowan	Glens, hedges, mountain streams	Frequent
Sorbus devoniensis	French Hales		S-E only
Sorbus hibernica	Irish Whitebeam	Woods and cliffs on limestone	Centre: occasional
Sorbus ripicola	Rock Whitebeam		W & N: occasional
Taxus baccata	Yew	Woods, cliffs, rocky areas	Rather rare
Ulmus glabra	Wych Elm	Upland glens in North	Frequently planted

Thus the number of trees that are frequent in woodland in Ireland is restricted to less than 10 species.

2.2.2 *Irish woodland types*

The phytosociology of Irish woodland is treated in detail in Kelly and Iremonger (1997) (wet woodlands), Kelly and Kirby (1982) (woodland over limestone) and Kelly and Moore (1975). White and Doyle (1982) have reviewed previous phytosociological studies on Irish vegetation and present three main classes of native woodland association in Ireland. These are as follow.

Alnetae glutinosae

This encompasses fen woodland vegetation dominated by *Alnus glutinosa,* where the substrate is usually waterlogged neutral-acid peat.

Quercetea robori-petraeae

This is species poor, deciduous woodland with a well-developed bryophyte flora and is considered to be the vegetation which would exist on base-poor, podzolised soils with raw humus, were it not for anthropogenic factors. It includes the association Blechno-Quercetum petraeae (Braun-Blanquet et Tuxen, 1952) with three sub-associations described in Kelly and Moore (1975). Many Irish oakwoods over infertile soils can be ascribed to this association.

(i) scapanietosum - woodland with a large number of bryophytes, occurring in areas of high rainfall such as the south west.
(ii) typicum - woodland lacking an extensive bryophyte layer, occurring in the drier eastern areas of the island.
(iii) coryletosum - woodland with several species more typical of the Corylo-Fraxinetum to which it is transitional.

Querco-Fagetea

This is deciduous woodland with a species-rich herb layer occurring over mineral-rich, well-drained soils. It includes the association Corylo-Fraxinetum, which has three sub-associations (Kelly and Kirby 1982). Many Irish woodlands over fertile soil can be included here.
(i) nekeretosum - this describes *Corylus* scrub on shallow and stony limestone bedrock.
(ii) veronicetosum - woodland on deep soils with mull humus and with *Hyacinthoides non-scriptus* in the field layer.
(iii) typicum - woodland similar to that in (ii), but lacking the presence of moisture demanding species (*e.g. Chrysosplenium oppositifolium*) in the field layer.

2.3 Irish woodland soils

Apart from the effects of anthropogenic factors it is predominantly the local variation in soil that determines the assemblage of plants present at a given site. Soils are heavily influenced by climate. The combination of high precipitation and low evapotranspiration in many parts of Ireland results in a tendency towards podzolisation of free-draining soils, and gleying and peat formation where drainage is impeded. O' Carroll (1984) lists seven groups of (forest) soil in Ireland:

Peats These are organic soils which are generally wet, acidic and have low nutrient availability. There is a wide variation in peat depth ranging from 30cm – 3m in upland blanket bog to 12m in midland raised bogs. Peatlands which have been drained or which are naturally drying have become colonised by birch and willows (Kelly and Iremonger, 1997). Cutaway bogs have frequently been the sites for afforestation with coniferous species (especially sitka spruce) during state forestry programmes.

Gleys These are poorly drained mineral soils which have a heavy texture and poor structure. They may be podzolised (*i.e.* leached of minerals) and peaty gleys have a shallow layer of peat at the surface. Gleys occur extensively over carboniferous strata (such as the limestone of the midlands) and Cross (1998) describes the woodland communities found here as '*Alnus-Quercus-Corylus* forest with *Salix cinerea subsp. oleifolia'* equivalent to Corylo-Fraxinetum deschampsietosum caespitosae (Braun-Blanquet et Tuxen 1952). While these soils are relatively fertile in the context of coniferous forestry, the poor drainage restricts rooting and stands may be susceptible to windthrow.

Podzols These are intensely leached mineral soils derived from light textured parent material. They often have a shallow layer of raw humus at the surface with a pale upper layer beneath this, and brown/red lower layer. If an iron pan (where leached iron oxides have precipitated out of solution to form an impermeable layer) is present, drainage may be impeded thus restricting the depth of rooting. These soils generally have a low pH, occurring over acid bedrock such as Old Red Sandstone (in the south-west), Mica-Schist (in the Wicklow Mountains) and Quartzite (in the north-west). Many Irish oakwoods exist over podzols (Little *et al.* 1997), and these are usually dominated by *Quercus petraea* and have low nutrient availability.

Brown Podzolics These are deep free-draining soils showing some evidence of podzolisation. They are most common under old forests of the south-east. Cross (1998) describes such woodland as '*Species-poor Quercus petraea forests'* and equates them to the Blechno-Quercetum typicum (Braun Blanquet & Tuxen 1952). *Quercus petraea* is the principal species, and *Fagus sylvatica,* when introduced, grows strongly on such sites (Cross 1998).

Grey-Brown Podzolics Such soils in Ireland are productive and usually found under agricultural grassland (O' Carroll 1984). However, Cross (1998) predicts that the potential woodland vegetation of such sites would be dominated by a mixture of oak and ash, and would be classified as Blechno-Quercteum coryletosum (Braun-Blanquet et Tuxen 1952).

Brown Earths These deep free-draining soils are slightly acidic with a good structure and texture and show little development of horizons. As they are very productive, they are usually under agriculture (O' Carroll 1985). Cross (1998) predicts that woodland on such soils would be species-rich and dominated by *Quercus robur* and *Fraxinus excelsior,* and equivalent to Corylo-Fraxinetum veronicetosum and typicum (Kelly and Kirby 1982).

2.4 The climate of Ireland

Ireland is situated off the northwest coast of the European continent and its position on the Atlantic seaboard means that the prevailing winds are warm south-westerlies, and the climate is mild, moist and strongly oceanic (Mitchell & Ryan 1997). Oceanicity decreases as one moves from west to east. Winters are relatively warm and summers rather cool, with average January and July daily temperatures of 4 and 15 ° C respectively. The weather is dominated by frontal depressions and rainfall is generally high. The average annual number of rain days varies from 225 per annum in upland areas on the west coast, to less than 150 days per annum in the south east. Ireland has a windy climate, and mean monthly wind speed varies from less than 6 knots, in the midlands, to 16 knots on the exposed north west coast (Anon. 1979). Nonetheless, most places experience less than 4 days per annum with gale force winds (>33 knots), with gales occurring more frequently (up to about 60 days per year) only on the exposed north west coast. The effects of wind on vegetation in Ireland are most visible in the stunted and leeward growth of trees on the west coast, and in the limiting of the tree line (Goodwillie 1984).

2.5 Conclusion

Semi-natural woodland in Ireland is limited in extent and the native tree flora is relatively poor. Semi-natural broadleaved high forest is restricted to inaccessible sites (mostly over acid bedrock) and old estate woodlands. Past management practices are probably partially responsible for the dominance of *Quercus* spp. in the canopy at many sites.

CHAPTER 3 WOODLAND REGENERATION

3.1 Defining woodland regeneration

Forest succession or regeneration is described by Runkle (1981) as 'the sum of the processes by which one canopy individual is replaced by another'. He says that in a succession the new individuals tend to be of a different species to the replaced individuals, whereas in the regeneration of a 'climax' forest, the same species, at least on average, are represented in roughly the same proportions after each regeneration cycle. However, while successional ecology is moderately well understood for many ecosystems (*e.g.* Olson 1958), decades of ecologists have debated and researched the mechanisms by which so-called 'climax' or 'steady-state' ecosystems persist in a particular space. Indeed, various contributors to the argument question the validity of such terms as 'climax' and 'steady state', given the variation and dynamism of all natural systems (Pickett & White 1985).

Ultimately, the regeneration of woodland depends on the successful regeneration of individuals either already present in the existing community or arrived from outside of the system. In practice, then, woodland regeneration does not always result in replacement of the woodland community by an exact or even similar community. In the absence of substantial disturbance over a prolonged period, a forest stand may exhibit a shift towards shade-tolerant species, as light demanding species fail to regenerate (Ward and Parker 1989). Barden (1980) predicted the future canopy composition of mixed forests in the Appalachian mountains, USA, based upon the leader species in canopy gaps. He concluded that the future canopy would be almost the same in composition as that of the present. Paleoecological research has demonstrated that woodland composition can remain relatively stable over hundreds of years at least on the landscape scale (Mitchell and Ryan 1997), but fluctuations are likely to occur at the stand level (Peterken 1996).

3.2 Mechanisms of woodland regeneration

3.2.1 Gap-phase regeneration

Watt's 'gap-phase' model (or variations of this) is probably the most widely accepted mechanism of regeneration in semi-natural woodland (Tansley 1953, Peterken & Tubbs 1965, Runkle 1981, 1982, 1985, Putman 1994, Peterken 1996, Pontailer *et al.* 1997). This model (Watt 1924) proposes that woodland passes through a number of stages in its development, and that regeneration of canopy species is largely confined to the gap-phase, because it is inhibited under shade conditions. It is established that the ability to regenerate in the shade is restricted to tolerant species such as beech, and that even these species require access to gaps in order to achieve maturity and canopy status (Ellenberg 1988).

3.2.2 *Timing of regeneration*

Disturbance is widely accepted as an essential component in regeneration, facilitating the vacation of space for the growth of new individuals in the community (Pickett & White 1985, Attiwill 1994). Runkle and Yetter (1987) describe the two extremes of disturbance/regeneration regime. The first involves areas that experience periodic, severe, large-scale disturbances, and results in waves or pulses of fairly even-aged regeneration. At the opposite end of the scale are areas that experience frequent, mild, small-scale disturbances, which result in asynchronous regeneration in canopy gaps. However, factors other than the availability of gaps also affect the frequency of regeneration, and Peterken (1996) postulates that regeneration is rarely, if ever, continuous. A period of high seedling mortality owing to drought, plague by pathogens, or temporary increase in browsing pressure may eliminate the accumulation of several years' regeneration. This has been observed in the New Forest, England (Peterken and Tubbs 1965) where periods of more relaxed grazing pressure allowed pulses of regeneration to succeed.

3.2.3 *Modes of regeneration*

Bazaaz (1983) lists five types of response to canopy gaps: crown expansion; sprouting from mature individuals; advance regeneration; seedling regeneration (from seeds on site); and regeneration from immigrant seed. The prevalent regeneration type following a particular disturbance will depend on the nature of the disturbance and the regenerative capacities of the species present (Peterken 1996). In cases of mild disturbance, regeneration is often dominated by the release of advance regeneration, while more severe disturbance is frequently followed by seed germination and establishment of 'new' individuals (Kozlowski *et al.* 1991). Species are adapted to react to gaps in different ways (cf. 4.6.2 and 3.3) and this will influence the regeneration patterns observed.

3.2.4 *Species interactions in regeneration*

The phenomenon of alternation of regeneration has been shown to exist for some species *e.g.* ash and sycamore in some English woodlands (Waters and Savill 1992). This involves the predominance of regeneration of one species under the canopy of the alternate species and vice versa. The result is a cycle of woodland regeneration (Watt 1947). The processes that drive such a pattern are thought to be related to the environmental conditions required by the seedlings of the species involved (Waters & Savill 1992). Such alternation of dominance has been proposed for oak-birch (Peterken 1996) and the tendency for ash to replace oak has been noted (Rackham 1980). The existence of such regeneration patterns will be especially significant in woodlands dominated by only two or three species, and may not be so clearly displayed or recognised in more complex stands.

Patterns involving a seral succession of tree species in canopy gaps have been proposed (Watt 1924, Kozlowski *et al.* 1991). This involves the early colonisation of gaps by pioneer species such as birch, which are subsequently replaced by late-colonising and slow-growing species such as beech. Watt (1925) described the colonisation of gaps in English beechwoods: ash and sycamore are the first saplings to establish themselves and do so in quite high densities. Beech and some oak may arrive later, and the beech gradually out-competes the other species, with the exception of an occasional ash, which survives and joins the canopy. Kozlowski *et al.* (1991) propose that when both pioneer and tolerant species arrive at a gap together, the pioneer species will initially dominate, but will gradually be replaced by the tolerant species.

Understorey vegetation can also play a role in woodland regeneration. Natives such as holly and introduced species such as *Rhododendron ponticum* may form dense thickets, preventing the regeneration of tree species beneath (Peterken 1996, Cross 1981). Peterken (1996) describes the development of almost pure holly woods after the alleviation of high browsing pressure in the New Forest in 1851. The holly canopy continues to prevent the regeneration of the original (*c.*1850) canopy species, and Peterken suggests the possibility that holly may continue to dominate the site for yet another century. Dense stands of bracken in woodland clearings and gaps may inhibit tree regeneration by the physical smothering of seedlings and saplings (Humphrey & Swaine 1997) and by allelopathic interaction (Gleissman 1977). The development of dense swards of herbaceous vegetation as a response to grazing may eliminate germination sites for seeds of certain species. Such phenomena may result in an 'arrested succession' as the natural regeneration of tree species is suspended, at least for a time.

3.3 The regeneration of tree species

Whatever the community-scale processes involved in woodland development, the perpetuation of woodland vegetation at a particular site is ultimately dependent on the successful regeneration of individuals of woodland tree species. The composition of regeneration at a particular place and time is the result of the interaction of species-level processes and other factors relating to conditions of the stand in question. Some species successfully replace old growth by the vegetative production of suckers, (*e.g. Populus tremula*) and the ability of cut stems of many species to regrow is successfully exploited in coppice systems (Evans & Barkham 1992). However, in unmanaged woodland, regeneration from seed is generally prevalent, and in order for an individual of any species to regenerate, a number of distinct steps must be successfully completed. These include seed production, seed dispersal, seed germination, seedling establishment, sapling growth and development of the sapling to a mature individual, itself capable of producing seed. The timing and exact details of each of these steps varies with species and circumstance.

3.3.1 Oak (*Quercus petraea* & *Q. robur*)

Oak is the commonest tree of British woodland (Steele & Peterken 1982) and its ecology, and particularly its regeneration, have been the subject of extensive research (Watt 1919, Turner & Watt 1939, Jones 1959, Morris & Perring 1974, Newbold & Goldsmith 1981, le Duc & Havill 1998, Kelly in press). Oak is a long-lived tree that may survive for more than 500 years, and for longer if coppiced or pollarded (Rackham 1980). It exhibits characteristics of non-pioneer species in its slow growth rate, late maturity (peak seed production is at 60-120 years (Newbold & Goldsmith 1981)), irregular production of large seeds and its being frequently found as the canopy dominant. However, oak is not a typical tolerant species in that it is relatively light demanding (Shaw 1974, Kelly in press). *Quercus petraea* is the more common species in ancient woodland in England (Rackham 1980) and, both in Britain and Ireland, is the more common of the two native oaks on more acid substrates. *Quercus robur* is associated with higher pH and more fertile sites (Grime *et al.* 1988).

Acorn production varies significantly from year to year, and is reduced as a consequence of knopper gall infection (in *Q. robur*), and defoliation by tortrix moths in previous years (Gurnell 1993). Acorns are eaten by jays, squirrels and other small mammals, but while this undoubtedly affects the rate of seedling recruitment (Watt 1919, Shaw 1968), it is unlikely to be the cause of the perceived failure of oak to regenerate at some sites (Mellanby 1968, Shaw 1974). *Q. robur* is successful in colonising calcareous grassland (Rackham 1980) and is the more pioneer-like of the two oak species (Jones 1959).

Acorn density is generally highest under the canopy from which the crop has fallen, however birds and mammals may disperse the fruits some distances (Kollmann & Schill 1996). Acorns are prone to desiccation, frost and rot, and normally germinate soon after falling from the tree (Jones 1959). They rarely remain viable beyond the first summer after production (Watt 1919) and no seed bank is formed. Germination is best achieved in moist sites, often among leaf litter, which may also afford the germinule some protection from predators (Jones 1959). Seedlings of oak are tolerant of shade initially, but become more sensitive to shade with age (Welander & Ottosson 1998). The allocation of resources to the development of a sizeable taproot, and the relatively plentiful seed reserves allow for good competitive ability with ground vegetation, compared with that in seedlings of other tree species (Ovington & MacRae 1960, Newbold & Goldsmith 1981). Establishment in closed vegetation, including bramble, is reported to be greater than that achieved by beech, ash or birch (Jones 1959). Despite the high tannin content of its foliage, oak is reported to be preferred over beech by browsing deer (Jones 1959). Damage to the bark by squirrels and other rodents is less frequent than that experienced by beech and sycamore (Gill 1992a). Oak shows some resistance to browsing damage, and many small seedlings are found to have well developed woody roots, evidence of their long-term survival of repeated biting off (Crawley 1986).

The apparent failure of oak regeneration has been a subject of much debate over the last century (Watt 1919, Turner & Watt 1939, Morris & Perring 1974). More recently, authors have questioned the previously accepted concept of 'climax' oakwoods in these islands, and the consequent expectation that regeneration of the species *should* be occurring to replace the current, oak-dominated canopy (Rackham 1980, Peterken 1996, Grime *et al.* 1988). Indeed, it has been recognised that the current abundance of oak in many woodland canopies is probably the result of centuries of human activity, which favoured this species over others (Rackham 1980).

3.3.2 Ash (Fraxinus excelsior)

Ash is a relatively short-lived tree, usually attaining 180 years, but coppiced individuals may survive for more than 300 years (Rackham 1980). Optimal sites are moist, well-drained, sheltered and fertile, and ash is usually absent from acid soils (Grime *et al.* 1988). Ash is common on base-rich soils and often dominant on calcareous substrates (Wardle 1961) and is described as a competitor by Grime *et al.* (1988). Despite the fact that ash is a common dominant in the woodland canopy (Steele & Peterken 1982) it is a pioneer species, adapted to the colonisation of disturbed ground, fast-growing and casting only light shade as a mature tree (Wardle 1961). Natural regeneration is entirely from seed, although the tree is suitable for coppice management. Fruiting begins at 30-40 years and heavy crops are usual every other year (Wardle 1961). The fruit (ash keys) are relatively small and the presence of 'wings' promotes dispersal by wind. Germination takes place in the second spring and is confined to gaps in the ground vegetation; a seed bank may persist for up to 6 years (Wardle 1961). This shortly-persistent seed bank may accommodate the swift colonisation of disturbed ground after canopy gap formation (Grime *et al.* 1988). The seedlings are very sensitive to shade, even from herbaceous vegetation, in which damping off may play a role in high mortality (Wardle 1959). In addition, seedlings are highly susceptible to competition from grasses and other ground vegetation including bramble and ferns (Wardle 1961). Where suitable conditions exist, seedlings usually arise in groups (Grime *et al.* 1988) and can achieve large growth increments if sufficient light is available. However, once the herb-layer has been overtaken, shade can be tolerated for periods of up to 28 years (Gardner 1976) and a seedling bank, ready to exploit canopy gaps, may form (Wardle 1961). Popert (1950) says that, once saplings have achieved a height of *c.* 4m, light requirements increase. Ash is preferred by many browsers (Gill 1992a), but is quite resilient to browsing (Wardle 1961, Hester *et al.* 1996).

3.3.3 Beech (Fagus sylvatica)

Beech is a relatively long-lived tree but rarely exceeds 300 years (Rackham 1980). It is frequently the canopy dominant on acid soils within its range, and apparently has the potential to replace oak in some woodland where it has naturalised (Peterken 1996) including suitable sites in Ireland (Dierschke 1982, Quinn 1994). Seed (beech mast) is produced irregularly from *c.*60 years and heavy crops tend to occur only once every 5-10 years (Newbold & Goldsmith 1981). Seed

production may continue over 200 years (Brown 1953). Despite some scattering by birds and squirrels, seed dispersal is poor and Grime *et al.* (1988) found that seedling distribution was closely related to that of parent trees in the Sheffield region. While seeds are toxic to some domestic stock (Cooper & Johnson 1984 cited in Grime *et al.* 1988), they are heavily predated by birds and small mammals (Harmer 1994). However, seed production in mast years is usually sufficient to allow some germination, and the simultaneous fall of seed and leaves may afford the seeds some protection from predators (Newbold & Goldsmith 1981).

The seeds are somewhat vulnerable to desiccation (though less so than acorns) and require moist but not waterlogged conditions for seedling establishment. Seeds are not persistent in the soil (Cooper & Johnson 1984). Light is not required for germination and seedlings are tolerant of shade (even that of a beech canopy) at least for a few years. Beech is representative of the 'tolerant' regeneration strategy (Ellenberg 1988), with saplings developing readily below the canopy of other deciduous tree species (Vera 2000). Seedling banks were found to form in Polish beechwoods at relative light intensities above 4%, although these were unstable at light levels lower than 9% of full daylight (Szwagrzyk *et al.* 2001). The apparent unpalatability of its foliage (Gill 1992a, Peterken 1996) renders seedlings and saplings of beech less susceptible to browsing than those of other tree species.

3.3.4 Birch (Betula pubescens)

Birch is commonly cited as a typical example of a pioneer (shade-intolerant) species (Ellenberg 1988, Grime *et al.* 1988, Peterken 1996) and has many of the characteristics of this group. Birch is short-lived, achieving only 60-80 years, and is light demanding, fast growing and casts only a light shade as an adult. While juveniles of the species are found over a wide range of pH, birch is most frequent and abundant on acidic soils (Grime *et al.* 1988). The tree is quick to mature and sets seed from 5-10 years (Harding 1981). Copious amounts of small, winged seeds are produced regularly, though several years of lower production tend to follow a particularly good year (Atkinson 1992). The seeds are widely dispersed, and require open ground and light for germination and successful seedling establishment. Seedlings often occur in groups and if successful may form pure stands (Atkinson 1992). Bare soil is required for germination, as the relatively short radicle cannot penetrate vegetation or litter (Pigott 1983). The seeds do not appear to persist in the soil (Grime*et al.* 1988). Seedling mortality is high (up to 80%) in the early years (Miles & Kinnaird 1979). The seedlings are small and lack seed reserves and the taproot aborts soon after germination, rendering the seedling susceptible to drought. In later years, shade causes mortality in saplings (Harding 1981). While birch is a common invader of heathland, the sapling must overcome root competition from *Calluna* and *Deschampsia flexuosa,* and there may be allelopathic relationships here. Although birch is apparently less favoured by browsers than some other broadleaved species (Gill 1992a), it is browsed, especially in May-June when its foliage is most nutritious (Harding 1981).

There is some evidence that browsing can induce higher levels of secondary metabolites in birch tissue, which act as a deterrent to further browsing (Tuomi *et al.* 1990).

Rackham (1980) observes that a succession from oak to birch often occurs. Birch is common in canopy gaps (Kinnaird 1974) and clear-fells where there is disturbance of the ground, and is considered a 'weed' of forestry (Grime *et al.* 1988). The occurrence of forest fire may encourage birch regeneration, as exposed soil with increased nutrient status is rapidly colonised (Harding 1981). Birch is generally considered an improver and de-acidifier of soils (Atkinson 1992). It has been found to increase litter decomposition, nitrogen mineralisation and the incorporation of organic matter into the bleached horizons of podsolised heathland soils in Scotland and England (Miles & Young 1980).

3.3.5 Rowan (Sorbus aucuparia)

Rowan is a relatively short-lived tree with a maximum lifespan of 150 years (Grime *et al.* 1988). It is favoured by well-drained acid conditions and in Britain is generally restricted to soils of pH < 5.5 (Grime *et al.* 1988). Seed production begins at about 15 years and, though fruit production varies from year to year, it is high almost every year. Seed set is better in individuals exposed to more light than in those under closed canopy (Raspé *et al.* 2000). Rowan reproduces almost entirely by seed, but epicormic shoot growth can be stimulated by cutting or browsing. It is generally considered to be shade-tolerant (McVean & Radcliffe 1962, Pigott 1983), and investigations in Finland and Norway suggest that regeneration is greater close to other trees or within forest than in clearfells. Whether this is related to light conditions or the fact that birds use trees as roosts resulting in maximum seed rain below their crown, is unresolved (Raspé *et al.* 2000). Grime *et al.* (1988) found no persistent seed in the soil but Hill (1979) suggests that there may be some seed longevity. Light is not necessary for germination but seems to increase it (Devillez 1979, cited in Raspé *et al.* 2000) and seed dormancy is broken by cold moist stratification. Germination occurs in the first or second spring (Grime *et al.* 1988). Seedlings and saplings of rowan are frequently preferred by browsers (Gill 1992a) but this species shows high tolerance to damage (Miller *et al.* 1982).

3.4 Other factors affecting regeneration in woodland

3.4.1 Grazing and woodland regeneration

The impact of grazing animals (rodents, rabbits, hares, deer, domestic stock) on woodland has been assessed by various researchers in various locations (Cummins & Miller 1982, Hester *et al.* 1996, Linhart & Whelan 1980, Mitchell *et al.* 1995) and several reviews of the subject have been presented (Adams 1975, Gill 1992a,b,c, Mitchell & Kirby 1990).

Browsing animals are undoubtedly a natural part of the woodland ecosystem (Putman 1994) and their activities (browsing, trampling, wallowing, bark stripping, seed predation and dispersal) affect the woodland vegetation and in particular the regeneration of tree species. These effects are especially visible in woodlands where the populations of browsers are maintained at artificially high levels (Gill 1992a), but interactions between natural regeneration and animal activity are by no means confined to such situations.

Effects of grazing on vegetation structure:

Grazing results in an increased abundance of plants that are tolerant of or resistant to grazing. Putman *et al.* (1994) found that vegetation such as bracken, woodrush, and grasses increased in abundance in grazed areas, while ivy, brambles, hawthorn and willows were absent from grazed plots. Grazing animals tend to avoid mosses and so heavily grazed woodlands provide good habitats for moss species that may otherwise be outcompeted by shade-casting vegetation (Mitchell & Kirby 1990). Grazing can promote the co-existence of competitors, by checking the vigour of the more aggressive species, and at certain levels can promote biodiversity (Kelly 2000). Promotion of more open conditions by grazers can facilitate the success of light demanding ground flora (Putman *et al.*1994).

Effects of grazing on soil processes:

The removal of nutrients (by grazing) from one location and transfer to another (by defecation) affect the availability of soil nutrients to plants. This diversifies growth conditions and can increase diversity in woodland (Putman *et al.* 1994). Trampling by grazers can increase the amount of bare soil on the woodland floor, and some areas are continually disturbed as grazers use them as wallow holes (Kelly & Iremonger 1997). The poaching of the woodland floor by animals has been adopted as a management tool, as it provides germination sites for seeds and can thus promote woodland regeneration (Morison & Stoneman 1998, Miles & Kinnaird 1979).

Effects of grazing on seedlings and saplings:

If grazing levels are sufficiently high, regeneration of tree species can be severely impeded, and the repeated biting back of seedlings may result in saplings being totally lacking from such woodlands (Mitchell & Kirby 1990). Such woodland often lacks a developed shrub layer, and a 'browse line' may be evident. Where the density of grazers is lower, the expression of preferences, in terms of species and of seasonality of browsing may be observed (Gill 1992a). Many studies have shown that deer can be quite selective in their grazing behaviour, with marked preferences for certain species, and consistent avoidance of others (Gill 1992a). However, the expressed preferences of grazing deer are also affected by site factors such as forage availability, and Gill (1992a) points out that the preferences expressed at one site cannot automatically be applied elsewhere. For example, Eiberle & Bucher (1989 cited in Gill 1992a) found that silver birch was the preferred food of roe

deer when beech was the alternative. However, when rowan and ash were available, birch was shunned by the deer. Such preferential browsing of one species over another can confer a significant disadvantage on preferred species, and thus influence the composition of saplings present in woodland. Deer grazing in Lady Park Wood has allowed the regeneration of birch, but inhibited that of beech (Peterken and Jones 1989).

Grazing behaviour may also affect the spatial pattern of regeneration, as deer are less secure in areas of low cover, and so avoid path edges and tracks through woodlands. Saplings may then be confined to these areas (Rackham 1980, Gill 1992a). Iason & Palo (1991) found that browsing by hares was more frequent in canopy gaps and openings than under closed canopy.

The response of saplings to browsing varies with species and with severity of browsing. Mitchell *et al.* (1995) found that ash saplings were very tolerant even of repeated grazing and removal of shoot tissue, and could replace lost leaf material up to four times in one season. Saplings of oak, on the other hand, were vulnerable to the removal of shoot material and showed less resilience to repeated grazing than ash. While various authors have reported that oak is tolerant of grazing (Shaw 1974, Crawley 1986), it is likely that this applies only to the removal of leaf material (Mitchell *et al.* 1995).

The release of woodland from heavy grazing pressure can have a dramatic effect on tree regeneration, and may result in an initial burst of seedling and sapling growth (Peterken 1996). Species whose seedlings survived the previous level of grazing have an advantage over others, and can immediately achieve height increments. However, the vigorous growth of ground vegetation that also follows cessation of grazing may compete with seedlings, and some tree species can cope more effectively with this than others. Establishment of birch in woodland in Sheffield was restricted to immediately after the erection of a sheep exclosure (Pigott 1983), while recruitment of oak and rowan was continuous over a number of years.

3.4.2 *Management practices and regeneration*

The effects of management on stand structure can have implications for the ability of woodland to regenerate. Canopy composition, ground vegetation, status of the understorey, and structural diversity are all affected by various forms of woodland management (both current and past) and, in turn, such characteristics influence seed rain, germination, seedling establishment and growth of tree species.

Management of woodland for timber crops frequently involves manipulation of the canopy composition. The removal of 'weed' species and active encouragement of crop species reduces the diversity in the canopy and promotes dominance by one or two favoured species. The current

dominance of oak in many woodlands is probably an inheritance of such intervention, and such woodlands probably have much lower proportions of other species than before (Peterken 1993). Thus the availability of 'parent' trees for seed production is limited. In addition, the introduction of non-natives, such as beech and sycamore, adds new components to the seed rain and may affect the canopy density. Depending on the competitive ability of such a species in its new environment, the success of the tree species previously present may be affected. This has been demonstrated in some Irish woodlands where beech has been introduced and is successfully out-competing oak (Dierschke 1982, Quinn 1994). Similar situations have been described for introduced sycamore in some English woods (Rodwell 1991, Peterken 1993).

The abandonment of active management practices also affects the woodland community. For example, the cessation of annual 'swyping' of the ground vegetation can allow the development of an even-aged stand of regeneration (D. Hutton-Bury *pers.comm.*).

Past use of woodland by coppice management was widespread in England (Rackham 1980, Peterken 1993) and was certainly practised in at least some parts of Ireland (Jones 1986, Rackham 1986). Such a system ensured that increased light availability occurred regularly (increasing the chances of success of regeneration from seed) and in addition, facilitated regeneration by vegetative means. It has been suggested that the abandonment of this system has disfavoured oak regeneration (Rackham 1980). In addition, the intensive management of high forest for timber production in recent centuries did not permit the development of old-growth stands in which gap formation is relatively common. Thus canopy gaps were eliminated from many woodlands (Streeter 1974).

The management of some woodlands for game and amenity involved the planting of certain shrubby species (notably *Rhododendron ponticum, Cornus sericea* and *Prunus laurocerasus*) for ground cover and/or showy flowers (Cross 1981). In some cases these species have become invasive and now cover large areas, seriously impinging upon the natural woodland vegetation and regeneration of the tree species (Cross 1981).

Development of extensive stands of bracken in woodland clearings is especially associated with drainage, ploughing and burning in the past (Andrews & Rebane 1994). This reduces the suitability of canopy gaps for tree regeneration, as bracken competes with seedlings and saplings for nutrients, and tall stands cast shade and may physically smother regeneration (Watt 1919, Humphrey & Swaine 1997).

3.5 Factors pertaining to regeneration in Irish woodland

Irish woodlands are described in Chapter 2 and the characteristics of the particular woods surveyed in this study are contained in Chapter 6. Some general observations can be made in reference to issues that may affect regeneration in Irish woodland. As is the case for woodlands in Britain, a paucity of natural regeneration has been noted in some Irish woodlands, particularly those in the Killarney Valley (Turner & Watt 1939, Tansley 1953, Kelly & Moore 1975, Hayes *et al.* 1991). However, whether or not this reflects a problem particular to Killarney, or simply the fact that these have woods been the site of a large proportion of the ecological investigations in Irish woodland, is unclear.

It is of note that Irish woodlands are less diverse in species of both canopy and field layer than their European and even British counterparts (Webb 1982, Kelly 1991; cf. Table 2.1). The common canopy species in Irish woodland are often confined to two or three species. Upland oakwoods over acid substrates are composed mostly of sessile oak, with birch and rowan and an understorey of holly (Kelly & Moore 1975). Woodland in more fertile sites is usually dominated by pedunculate oak and ash, with hazel and hawthorn in the understorey (Kelly & Kirby 1982). Elm is relatively rare in woodland, and beech, sycamore and sweet chestnut are absent from the native flora (Webb *et al.* 1996). The diversity of regeneration in woodland may be expected to be correspondingly low.

The production of viable seed and successful seedling establishment does not appear to be limiting, and the cause of the failure of regeneration has been widely attributed to overgrazing by deer and in some cases sheep (Neff 1974, Hayes *et al.* 1991). Irish woods are grazed by red (*Cervus elaphus*), sika (*Cervus nippon*) and fallow deer (*Dama dama*) (cf. Appendix I) and numbers of all species are increasing (R. Cardon *pers. comm.*). The expansion of red, sika and sika-red hybrids is more localised than that of fallow deer, and is associated with: the success of populations in and around National Parks; an increase in the area of coniferous plantations; and escapes from the increasing numbers of deer farms. While rabbits and Irish hares (*Lepus timidus* subsp. *hibernicus*) are known to graze woodland, little information about their numbers or impact on regeneration is available. Many woods are subject to some level of grazing by domestic livestock, especially in winter (Hester *et al* 1998). The successful establishment of tree saplings within exclosures in overgrazed woods supports the suggestion that grazing is a limiting factor of regeneration (Telford 1977, Kelly 2000, Kelly in press).

CHAPTER 4 INTRODUCTION TO CANOPY GAPS

4.1 Disturbance in the forest ecosystem

Biological systems, composed as they are of living organisms, are dynamic in nature. The death, decomposition, regeneration and growth of plants and animals ensure constant change in the local environment on a range of scales. Influences from outside of the biotic component of the ecosystem also contribute to the non-static character of biological systems.

Events that occur irregularly and affect an ecosystem by contributing to the death of at least one individual member have been termed 'disturbances' (Morgan 1987, Pickett & White 1985). Disturbance has also been defined as 'events making growing space available' (Oliver & Larson 1990). Natural disturbance of a particular kind is a recurring feature in many ecosystems *e.g.* fire in Californian Chaparral.

While specific 'disturbances' are often easily distinguishable in space and time, *e.g.* the uprooting of a particular tree, some authors (Karr & Freemark 1983, 1985) warn that the notion of disturbance is often considered against an assumed homogenous background of 'equilibrium' or 'climax'. They argue that a 'cascade of disturbance impacts' often exist.

Disturbance has been recognised as an important feature in ecosystems world-wide. Landslides, avalanches, lava flows and floods are examples of natural disturbance. Perhaps the most widely occurring and most intensively studied natural disturbance is the effect of wind.

Gaps in forest canopies associated with wind events have been much studied, particularly in North America (*e.g.* Runkle 1981, 1982, Young & Hubbell 1991, Rebertus & Burns 1997) and the tropics (*e.g.* Uhl *et al.* 1988, van der Meer & Bongers 1996). Reviews of the literature concerning canopy gap dynamics have been presented in Pickett and White (1985), by Attiwill (1994) and by Platt & Strong (1989).

4. 2 Woodland canopy gaps

Canopy gaps are undoubtedly a significant component of many forests. The area occupied by gaps varies from one forest to another. Brokaw (1985) reports figures (total gap area as a percentage of forest area) ranging from 3-25% for lowland tropical forests. Gap density in evergreen, broadleaved forests in warm temperate Japan was estimated at 19.6 gaps per hectare and 15.7% of forest area

(Yamamoto 1992). In mixed broadleaved old-growth forests of North America, gaps occupied 9% of the area and were randomly distributed (Ward and Parker 1989).

4.2.1 Defining the gap

In older studies, the terms 'gap' and 'opening' were used without definition and taken to be self-evident (*e.g.* Watt 1947). As research into canopy dynamics has intensified over recent decades, and comparisons between data for different sites have been made, the need for a precise definition of the term 'gap' has become apparent (Brokaw 1982). Depending on the definition used, the measured area of a particular gap may vary by a factor of two (Brokaw 1985). The structural complexity of gaps and the variety in gap shape and form makes the definition of gap area difficult.

Oldeman (1978) uses the term *chablis* to describe tree fall, 'its impact on the forest, the fallen tree and the resulting destruction'. He describes the structural zonation associated with such an event (cf. section 4.4) and gives typical areas for a one-tree chablis (between 10m x 20m and 20m x 40m) but does not explain how this area was delimited.

Runkle (1981) defines a gap as 'the ground area under a canopy opening extending to the bases of the canopy trees surrounding the canopy opening'. He reckons that most gaps are at least roughly elliptical in shape and thus estimates the gap area as: $A = \pi LW/4$, where L is the longest length in the gap from edge to edge and W is the longest length at right angles to L.

Brokaw (1982) defines a gap as 'a hole in the forest extending through all levels down to an average height of two m above ground' *(sic)*. A minimum gap size should be established such that gaps are readily distinguishable from canopy conditions, but this will vary from forest to forest. He suggests measurement of the gap area by estimating the hole contained by the edge of the gap, that being 'along the line directly beneath the edge of the surrounding foliage'. However, the delineation of this in the field is a complex matter. From what height is 'surrounding foliage' relevant? How accurately can one draw the edge line, and subsequently measure the enclosed area? Brokaw has done this by scale mapping and measurement of the area contained within adjacent triangles with corners at the gap centre and at the gap edge.

4.2.2 Hemispherical canopy photography

The 'Hill' camera (Hill 1924), which allows photography of the entire hemisphere (sky) using a fish-eye lens, was originally developed to investigate cloud formation. Evans and Coombe (1959) later applied this to the study of the light environment in woodlands. Hemispherical canopy photography (HCP) reduces the complex, three-dimensional canopy to a two-dimensional image (the hemiphot).

The angular height of the canopy is proportional to the radial distance on the image. In the early days of this technique, images were manually interpreted. Characteristics such as Leaf Area Index (LAI), canopy cover and size of canopy gaps could be measured, and light regimes (direct and diffuse radiation - site factors) were estimated by superposition of solar tracks onto the image. However, these interpretations proved very time consuming and repeatability of analysis was poor both between and within investigators (Garvey 1998). The development of computer programmes (*e.g.* SOLARCALC - Chazdon & Field 1987) which automatically score images and calculate various outputs has allowed for faster and more consistent analysis of hemiphots.

The development of HCP has provided more standardised methods of calculating gap area. To estimate gap area *sensu* Brokaw, photographs are taken and the height of surrounding canopy at eight or more points is noted. Digitised images are then analysed using computer programmes such as Winphot (ter Steege 1996) which automatically calculate the gap area.

HCP also allows for the calculation of 'canopy openness'. The digitised image is automatically divided into 'canopy' and 'non-canopy' pixels, and thus the exact area *not* covered by canopy (*i.e.* the gap) is estimated as a proportion of the entire hemisphere. This leaves little room for variation in procedure between investigators. Some authors (*e.g.* Leibermann *et al.* 1989) argue that focusing on gaps as 'holes' in the canopy is not appropriate, as solar radiation is actually the determinant of variation in the environmental conditions of interest to ecologists. Whitmore *et al.* (1993) investigated different measures of gap size in tropical rainforest and correlated these with four microclimatic variables of importance to plant growth. They concluded that physical measures of gap size (including the Brokaw method) were poor indicators of gap conditions. However, site factors (direct and indirect radiation as a proportion of that incident in open conditions, Anderson 1964) and canopy openness calculated from hemiphots were closely correlated. Whitmore *et al.* (1993) showed that for asymmetrical gaps, and those on steep slopes or at high altitudes, canopy openness is the best indicator of gap size and conditions. Site factors should not be compared between woodlands, as the incidence of radiation in the open is rarely the same between different locations. Thus, canopy openness is the better measure of gap size when comparing gaps from a variety of woodlands. Use of this variable in the study of canopy gaps is becoming more common (*e.g.* Valverde & Silvertown, 1997).

4.3 Gap formation

4.3.1 Mode of gap formation

Canopy gaps are formed when trees or parts of trees die, fall or are cut down. Wind often plays a role, sometimes as the main agent, uprooting or snapping healthy trees. Alternatively, wind may work in

conjunction with other factors such as root pathogen and bark beetle infection, blowing over standing dead trees, or snapping rotten trunks (Spies & Franklin 1989). Species differ in the probable type of damage suffered (Hubbell & Foster 1986). Whitbread (1991) suggests that the shedding of large limbs, as widely observed in *Quercus* spp and *Aesculus hippocastanus* during the 1987 Great Storm in south-east England, might be a survival mechanism, as such individuals offer less wind resistance and so are less susceptible to windthrow or snapping. However, loss of limbs may predispose trees to decay, thus rendering them more vulnerable to the effects of subsequent storms. Spies and Franklin (1989) reported that >70% of Douglas fir and western hemlock in the Cascade Range (North America) died standing or from stem breakage. Runkle (1982) found that wind was involved in the formation of 90% of gaps in American old-growth forests, with 19% owing to uprooting, 58% to snapped trunks and 13% to loss of canopy branches. Beech and chestnut were most often uprooted, hemlock usually snapped, and ash and maple prone to loss of limbs. Repeated defoliation of oak by gypsy moths (*Lymantria dispar* L.) in New Jersey resulted in mortality of 30% of the oak population and gap formation (Ehrenfeld 1980).

Multiple or composite gaps, *i.e.* where more than one individual (gap maker) is involved in gap creation, can be formed in a number of ways. Strong winds may fell neighbouring trees independently of each other. A group of individuals may be affected by defoliators or pathogens. Trees may display a domino situation, one blown tree knocking another as it falls (Poore 1968, van der Meer & Bongers 1996). This may result in the fall of the entire knocked tree or simply a part of its crown. In tropical forests, several crowns 'attached' by lianas may be pulled down together (Putz 1984). The uprooting of large trees may result in smaller individuals, rooted among the roots of the larger tree, also being toppled. A multiple gap may be formed over a prolonged period, when trees around the edge of an existing gap die, fall or are damaged (Lang & Knight 1983).

4.3.2 Frequency of gap formation

The frequency of gap formation is dependent on a number of factors, and can be expected to vary from region to region and even from one woodland to the next. The function, k, disturbance rate, has been used to describe the gap régime in woodlands (White & Pickett, 1985). This is the proportion of the forest area opened to new gaps each year. Disturbance rates for a variety of forest types over a wide geographical range have been reported to be within the range 0.5-2% (Runkle 1985) with an average of ~1%.

The wind climate of a region influences the gap régime present. Areas prone to hurricanes (*e.g.* large parts of the Tropics and parts of North America) can experience gap creation on a vast scale, where thousands of hectares of trees are snapped or over-blown during a single storm (Spies and Franklin

1989). The periodicity of gap formation may have implications for the response of the woodland community. Peak frequency of treefall in lowland tropical forests of Panama occurs during the gusty winds of the rainy season, while in montane forest in Costa Rica, dry season winds cause most gaps (Brokaw 1985).

Gap formation is irregular from one year to another even at sites in the same general area (Runkle 1982), an indication that a complex suite of factors are involved in gap formation.

4.3.3 Factors affecting gap formation and gap structure

Rainfall affects gap creation. Wet trees are more susceptible to the effects of wind, as they are less streamlined (Gloyne 1968), and the weight of rainwater on trees in leaf adds to the strain imposed on the trunk and branches. Wet soil also allows for less effective grip by roots than dry soil. Saturated soil may result in landslides which can cause treefall and gap formation, independent of wind.

Attributes of the stand of trees and of individual trees affect susceptibility to wind effects. Older stands containing large canopy branches and often rotted parts of the trunk/crown are more vulnerable to the effects of wind than younger populations with more compact and elastic crowns (Whitbread 1991). Trees growing in open conditions are more resistant to windthrow (Foster 1988) as they have larger crowns along which the wind force may be distributed. Such trees generally possess well-anchored root systems, having been established and matured in unsheltered conditions (Zimmerman and Brown 1971).

Crown characteristics as affected by species and growth history are also important. Where crowns are long and narrow (*e.g.* in woodland where the trees have grown under wooded conditions) gaps tend to be linear in shape. Alternatively, where the canopy matured in relatively open conditions (*e.g.* silvi-pasture) broad crowns result in more rounded gap shapes.

The timing of storms relative to species-specific growth cycles may have an impact on gap formation. The Great Storm of 1987 in England, occurred in October, when ash had dropped its leaves but oak had not. Thus, oaks were more vulnerable to the effects of wind and rain than ash (Whitbread 1991). Location of the tree is a factor that affects the liability of the tree to wind damage. Trees that have grown to maturity in exposed conditions are more resilient to wind than are recently exposed trees. This is often illustrated when stands have been thinned. Local topography tempers the effect of wind on stands of trees. For example, during the Great Storm 1987, it was observed that trees on leeward slopes were often unaffected while those on the windward side suffered significant wind damage

(Peterken 1996). Narrow valleys can protect trees from the effects of wind if the wind direction is perpendicular to the valley length, but otherwise wind may be funnelled and intensified.

Species which typically die standing, gradually dropping limbs, form only small gaps while species prone to uprooting tend to form larger gaps (Brokaw 1985). The density of trunk wood affects the liability of a tree to snapping (Putz. 1983) and so species which suffer from infections which weaken the trunk (*e.g.* Birch) may be more prone to snapping than others.

Some species are naturally shallow rooting (*e.g.* beech and spruce) and thus more prone to uprooting than others (Peterken 1996). Trees growing in areas where the water table is high or where the soils flood in winter, may also be shallow rooted, and thus less effectively anchored in the soil. Ninety percent of gaps in wet forest in Costa Rica were caused by uprooting, and gaps were more frequent in the swampy lowlands than the dry uplands (Hartshorn 1980). Conversely, trees anchored in the bedrock (*e.g. Taxus baccata* on limestone pavement in Killarney National Park) are rarely uprooted (personal observation).

Tanaka and Nakashizuka (1997) found that for temperate deciduous forest in Japan, the spatial distribution of new gaps was biased towards the edges of old gaps. The reportedly high occurrence of canopy disturbance at the margins of existing gaps has been attributed to several factors. These include increased wind exposure (Gray & Spies 1996, Foster & Reiners 1986), damage caused by the original gap maker (Putz & Chan 1986), crown asymmetry in gap margin trees (Young & Hubbell 1991) and the spread of root pathogens (Gray and Spies 1996). Runkle and Yetter (1987), working in temperate forests of North America, calculated that subsequent disturbances occurred within 10 years of initial gap formation at 59% of all gaps. This was calculated to be within the natural disturbance rate and they concluded that the probability of death at the edge of a gap is not significantly higher than in any other part of the forest. However, in high altitude forests, tree mortality occurs more frequently among gap edge trees (Sprugel & Bormann 1981) because of the increased severity of the environment adjacent to gaps.

4.4 Gap Structure

Gap structure is primarily the result of how the gap was formed, and thus is affected by all the previously discussed factors which affect gap formation. The diversity of structure found in gaps is a result of the many causes and circumstances of gap formation.

One of the most commonly reported aspects of gap structure is gap size. Gap size is influenced by the number of trees that contribute to the gap, and by the size of these trees (Brokaw 1982). The crown shape of the gap maker will also affect gap size and gap shape. The location, shape and orientation of a gap and the height of adjacent canopy also contribute to gap structure, thus influencing conditions within the gap. Environmental conditions within a small gap in tall or open canopy will not differ much from those beneath the surrounding canopy (Collins *et al.* 1985). The ratio of gap diameter (D) to height of the adjacent canopy (H) (Geiger 1965) has been found to correlate with light conditions within gaps. Light levels increase with increasing D/H ratio and plateau off when D/H ~ 2 (Berry 1964, Minkler & Woerhide 1965). Slope and aspect are factors that will affect the amount and intensity of solar radiation received by gaps, particularly those at higher latitudes, where the sun tracks low in the sky for much of the day.

Much significance has been attributed to the heterogeneity of environment that occurs within gaps (Aubreville 1937, Grubb 1977). The structural diversity that results from canopy disturbance offers a range of microclimates that may contribute to species diversity in the system (Grubb 1977). Various classifications of gap 'zones' have been proposed (Oldeman 1978, Bazaaz 1983, Orians 1983, Brandani *et al.* 1988), but all recognise the same basic regions within gaps. These are the root zone (comprised of pit and mound), trunk zone (comprised of the fallen bole and a largely undisturbed area), and crown zone (where fallen crown debris lies).

Root Zone: Pits and Mounds

The uprooting of trees generates pit-and-mound topography. The extraction of tree root systems from the soil results in transfer of subsoil to the surface and, often, burial of old soil surfaces. Mounds can be up to several metres high. A pit tends to be shallower and often have gently sloping edges as material from the disturbed soil washes/falls in and accumulates. Beatty and Stone (1986) found pits in old-growth stands, in New York, of 5.1m^2 and up to 32cm deep. The area of forest floor occupied by pits and mounds varies from site to site. Reported values range from <1% (Crozier & Boerner 1984, Thompson 1980) to 9% for pits and 7% for mounds (Henry and Swan 1974). Given the variation in frequency and type of gap formation between sites, this range is unsurprising. Conditions for plant growth in pits and on mounds differ to those on the forest floor. Pits contain a greater accumulation of organic matter and litter, show less seasonal variation in temperature and are wetter than undisturbed soil (Beatty & Stone 1986). Mounds are drier, experience greater variation in temperature and have less litter and organic matter than undisturbed sites.

Trunk Zone:

The trunk zone of a gap contains the fallen bole and the surrounding area. This is often largely undisturbed but exposed to higher light intensities owing to the removal of canopy from directly above. Thus the general attributes applied to the gap environment (increased soil temperatures, lower humidity, high light intensities) often apply here. The bole itself has been described as 'the primary source of nutrient input' into a gap (Brandani *et al.* 1988) but the release of these nutrients will depend on the rate of bole decay, and is likely to be slow.

Crown Zone:

This area is that part of the gap where the fallen crown lies. It is often the area of maximum disturbance to understorey vegetation, which may be damaged or killed by falling debris. The fallen crown can impose shade on the forest floor so that this part of the gap may be cooler and damper than other areas (Brokaw 1985). The decomposition of fallen debris may result in a nutrient flush in this area, and the debris may also act as a barrier to browsing animals.

4.5 The gap environment

Gaps differ in environmental quality from areas under intact canopy. The determinants of environmental conditions include gap size, orientation, height and patchiness of adjacent canopy, local topography and gap shape (Collins *et al.* 1985). The effects of canopy gaps on environmental variables are not contained within the gap edge *sensu* Brokaw (1982) (see section 4.2.1). For example, increased light will reach the forest floor in an area surrounding the gap, and an intermediate situation between 'gap' and 'canopy' conditions will exist (Canham 1988, 1989, Leiberman *et al.* 1989). Increases in resource availability following gap formation may be temporary (Canham & Marks 1985). Resource availability will also vary within the gap, for example, as one moves from the gap centre towards canopy.

The most obvious difference between gaps and intact canopy is in the light environment. A gap receives higher light intensities and for longer periods than adjacent shaded woodland floor (Denslow 1980, Chazdon & Fetcher 1984), and this light differs in quality to that which has been filtered by canopy. Germination of some species is inhibited by a low ratio of red to far red light (Vazques-Yanes & Smith 1982, Silvertown 1980) that occurs under canopy. Thus, light quality in gaps can be as important as light intensity in affecting vegetation.

Increased solar radiation results in greater extremes of temperature in gaps than under intact canopy. Thus, gaps may experience lower humidity and higher evapotranspiration, which could lead to drying

out of the soil at least in some parts of the gap. However, as gap size decreases, humidity increases, wind speed decreases and temperatures fluctuate less (Geiger 1965). Despite increased evapo-transpiration, soil water may be higher (at least initially) due to reduced absorption from tree root systems (Vitousek & Denslow 1986). Soil moisture in wet tropical forest increased after gap formation, but this was not related to gap size or light levels (Denslow *et al.* 1998).

Decay of tree-fall debris and increases in soil temperatures may result in a nutrient pulse after canopy disturbance. The effects of this may be localised within the gap, with higher nutrient availability in areas strewn with debris (Bazaaz 1983). Anderson and Swift (1983) suggest that the fallen trunk of the gap maker may immobilise nutrients in tropical rainforest gaps. However, analysis of soil properties in 4 month-2 year old gaps in Costa Rica found that, while mineralisation of nitrogen and phosphate was lower in the root zone, there were no significant differences between soils of the crown zone, trunk zone and under intact canopy (Vitousek & Denslow 1986). The authors suggest that this may be due to high backround rates of mineralisation at this site, and that the effects of disturbance on soil nutrients may be detectable only soon (in the first 6 months) after gap formation. Denslow *et al.* (1998) found that nitrate increased significantly after gap creation at wet tropical forest, and peaked after 40-60 days, levelling off to below-canopy levels within a year. In the same study, phosphate behaved similarly.

Soil disturbance associated with the uprooting of trees is necessary for the germination of some (especially small-seeded) species (Putz 1983a).

The variation of environmental conditions within gaps is not regular, and depends largely on gap structure (Brokaw 1985). Light conditions varied at different sites within gaps in mixed deciduous forest in New England, USA (Ashton & Larson 1996). The northern part of gaps received up to 4 times more irradiation than the southern part. The regeneration of three oak species was related to this, with more growth flushes and higher height increments occurring in seedlings at the gap centre and northern end of the gap. However, the light is not the only factor that affects regeneration success, and drought sensitive species may be more successful in the shadier parts of gaps or in smaller canopy gaps (Gray & Spies 1996).

The existence of such resource gradients (both from canopy to gap and within gaps) is the basis for the gap-partitioning hypothesis (Gray & Spies 1996) which proposes that the establishment and growth of different species is related to gap size and within-gap position. Such resource gradients may also prevent single species from achieving dominance within gaps (Denslow 1980). However, while such patterns have been demonstrated (Runkle 1982, Brandani *et al.* 1988), other factors such as understorey characteristics and the distribution of certain substrates (*e.g.* disturbed soil) play a role in species distribution (Ehrenfeld 1980, Veblen 1989, Uhl *et al.* 1988).

Gaps experience higher activity of mammal species than closed canopy and fleshy fruits in gaps are more likely to be eaten by birds (Evans & Barkham, 1992). Increased exposure of litter to extremes of temperature and moisture associated with canopy openings can reduce the population of litter arthropods present (Schowalter, 1985), while an increase in the amount of dead wood present will accommodate a rise in the detritivore fauna. The rapid and lush growth of the field layer that sometimes follows gap formation can act as a 'honeypot' attracting high numbers of grazing deer (Gill 1992a, Putnam 1994). Vigorous growth of shrub species such as brambles in gaps created by the 1987 Great Storm in south east England, resulted in increased use of the area by warblers and wrens (Fuller *et al.* 1994).

4.6 Response to canopy gaps

4.6.1 Community level

Two broad categories of response to canopy gaps have been proposed (Marks 1974, Ehrenfeld 1980, Evans & Barkham 1992). The first involves *reorganisation* of vegetation already present, and includes the lateral expansion of canopy adjacent to the gap and growth of suppressed seedlings and saplings already present at the time of gap formation. If the gap maker survives the disturbance it may play a role in vegetating the gap created. Many species can resprout vigorously when damaged and many windblown trees remain partially rooted and capable of further growth (Whitbread 1991). The second response to gap creation involves *new establishment* of individuals from buried seed and from propagules, which arrive after gap formation. A combination of these two responses may be expected at gap sites. The prevalence of one response over another is determined by factors such as gap-size and the size of advance regeneration at gap formation (Runkle & Yetter 1987). Evans and Barkham (1992) point out that initial conditions following gap formation are important in determining the response of the woodland community and the eventual composition of the gap *e.g.* the timing of gap formation with respect to mast crops of certain species may allow/disallow that species to colonise the gap. However, many species are capable of establishment in areas which eventually prove unsuitable for survival (Schmida & Wilson 1985) and the species composition in canopy gaps in some forest types has been found to vary with gap age (Poulson & Platt 1989, Spies *et al.* 1990). Thus, one can conclude that while initial colonisation following gap formation will affect the later composition of the gap vegetation, other factors have also a role to play.

Ehrenfeld (1980) examined woodland in North America where gaps were formed by tree deaths following defoliation of *Quercus* spp. by gypsy moths (*Lymantria dispar* L.). She found that responses

of the understorey vegetation to gap formation affected the growth of tree regeneration, and postulated that the density of regeneration of canopy species would be inversely related to the density of understorey vegetation, as the two competed for space and other resources.

The ultimate response of any community to the sudden increase in availability of resources (space, light, nutrients, water) which accompanies gap formation, is exploitation of these and subsequent filling of the vacated space. Closure of small gaps is most often achieved by lateral extension of canopy at the gap margin (Runkle 1985) whereas larger gaps often depend on the growth of saplings (Runkle 1981). There is an obvious limit to the extent to which canopy branches can extend. Closure of gaps occurs at an exponential rate *i.e.* closure is fastest initially after gap formation and the rate of closure decreases as gap size decreases (Valverde & Silvertown 1997, Horvitz & Schemske 1986). After formation of large gaps in Panama, the density of seedlings and saplings rose sharply and then levelled off or declined (Brokaw & Scheiner 1989).

Various times for complete gap closure have been reported. Runkle (1981), defining gap closure time as the time taken for gap regeneration to reach a height of 10-20 metres, gives 10-40 years for old growth mesic forest in Appalachians. Valverde and Silvertown (1997) reported a canopy closure time of 9 years for gaps in deciduous woodlands in Britain, and closure of canopy was achieved in only two years for gaps in moist tropical forest (Lorimer 1989). However, gaps in coniferous forest in Oregon, USA, took 50-100 years to close (Gray & Spies 1996).

Canopy closure, by whatever means, may be 'arrested' by factors such as overgrazing, lack of germination sites or competition from non-canopy vegetation. Colonisation of large openings in Scottish woodland by woody species was found to be impeded by the dense growth of bracken (*Pteridium aquilinum*), which shaded and smothered tree seedlings (Humphrey & Swaine 1997). Similarly, gaps in old-growth tropical forest on Barro Colorado Island, Panama, were colonised by liana species, prohibiting the colonisation of gaps by canopy tree species (Schnitzer *et al.* 2000). Competition from vegetation surviving canopy disturbance was found to be most pronounced in larger gaps (Kennedy and Swaine 1992). (Gap area measures ranged from 5-30% canopy openness.)

Local conditions such as the type and extent of disturbance, species present, availability of propagules, and success of seedling establishment and sapling growth will ultimately determine the nature of gap closure and the time taken to achieve this. In addition, the response of the existing non-arboreal vegetation to the increased light availability may also affect the rate of colonisation of gaps by tree species (Humphrey & Swaine 1997, Taylor & Zisheng 1988).

4.6.2 Species level

It is proposed that forest trees may be regarded as members of one of two major groups, according to their behaviour in response to canopy gaps (Swaine & Whitmore 1988, Whitmore 1984, Brokaw 1985). 'Pioneer' (also 'intolerant' (Peterken 1996), 'early successional' (Kozlowski 1991)) species are those which require relatively high light intensities for seed germination and establishment. They tend to be short-lived, fast growing species, which mature quickly, producing large amounts of small, widely dispersed seed and casting only a light shade (Peterken 1996). Seed dormancy is more prevalent among members of this group (Brokaw 1985). 'Primary' (Brokaw 1985) (also 'intolerant' (Peterken 1996), 'non-pioneer' (Swaine & Whitmore 1998) and 'late successional' (Kozlowski *et al.* 1991)) species are those that can withstand shade, at least for a limited period, and tend to be long-lived, with slow growth rates. They achieve maturity later than pioneer species, and produce large seeds on an irregular basis (Peterken 1996). These groups represent extremes in a continuum of behaviour and strategy, and many species exhibit characteristics intermediate between these extremes.

The response to gap formation varies between these groups. Pioneer species are quick to colonise gaps soon after formation, maximising the benefits of increased light availability, which may trigger the germination of dormant seed (Vazques-Yanes & Smith 1982). Seedlings of non-pioneer species that existed in the understorey as 'advance regeneration' may also take advantage of increased resource availability and it is widely accepted that such species ultimately require gap conditions in order to reach the canopy (Hartshorn 1980).

Optimum conditions for growth varies between species and it is proposed that such conditions vary with gap characteristics such as size (Whitmore 1984, Denslow 1980). Thus, variation in gap size within a forest may have consequences in terms of the future canopy composition in such gaps (Tanaka & Nakashizuka 1997, Runkle 1982, Abe *et al.* 1995). Small gaps, in old-growth forests of the eastern USA, where the increase in light levels was quite small, were dominated by shade-tolerant trees (Poulson & Platt 1989) presumably because light levels were not sufficient to allow colonisation by light demanding pioneer species.

4.7 The role of canopy gaps in the forest ecosystem

The dynamics of afforested ecosystems have been described as a regeneration cycle composed of several phases (Watt 1947; Whitmore 1975; Cousens 1974; Whitmore 1984). These include a *gap phase,* where old trees shed branches or fall, creating openings in the canopy; a *building phase* where open areas are colonised by cohorts of seedlings or filled by the release of suppressed seedlings already present; and a *mature phase* where saplings mature to old age and the system returns to the gap phase

again. Thus, forests and woodlands may be considered a mosaic of these phases, coexistent and varying spatially and temporally.

Brokaw (1985) remarks that treefalls are central to the structure and function of the tropical forest because the majority of canopy tree species require the presence of a gap in order to grow to maturity. The high species diversity among the canopy trees of forests has also been attributed to the presence of canopy gaps (Strong 1977). This may be due to a number of factors. Connell (1978) and Huston (1979) attribute this to the fact that disturbances, such as the creation of treefall gaps, prevent any single species from attaining dominance, and thus competitive exclusion of other species is avoided. The mosaic created by the co-existence of various gaps, differing in age, size and composition of colonising species, results in heterogeneity and thus contributes to high species diversity within an area of forest (Aubreville 1937).

The varied nature of gap formation contributes much to diversity of structure within a forest. Even within a single gap, many different 'regeneration niches' (Grubb 1977) are created, each offering a different set of conditions for colonisation, and thus allowing a diversity of species to establish (Denslow 1980).

4.8 Conclusion

The literature demonstrates that gaps are an integral part of natural woodland dynamics, and may be especially important in the regeneration of natural and semi-natural woodlands. Many studies, particularly in the tropics, illustrate the various processes involved in the canopy disturbance regime, and the responses of the woodland community to such events. However, the limited amount of information on forest canopy dynamics in Britain and Ireland, is insufficient to allow assessment of the role of gaps in woodland dynamics, particularly with respect to natural regeneration, in these regions.

CHAPTER 5 METHODOLOGY

5.1 Selection of study sites

In order to examine the nature of canopy gap dynamics and regeneration in gaps in Irish woodlands it was first necessary to select woodlands and canopy gaps for study. To this end, a questionnaire was circulated among all wildlife officers (Dúchas, The Heritage Service) and foresters (Coillte, the state forestry body) – 177 individuals in total. It had been envisaged that a large number of woodland gaps could be located in this manner, and that a sample could then be selected to allow the detailed study of a range of gap types. However, it was soon apparent that little specific data existed, even locally, about gaps within woodlands and that study sites would be most efficiently located by the field survey of chosen woodlands.

A list of woodlands for survey was compiled. This included areas of woodland already known to the author and her supervisors, and woodlands listed in the Natural Heritage Area database held by Dúchas, The Heritage Service.

Woodlands were chosen based on extent and semi-naturalness. Woodlands with a high forest structure and that were not under intensive management were sought and larger stands were preferred. Wet woodlands, coniferous plantations and recent secondary woodland were avoided. A list of approximately 40 woodlands resulted. As time did not allow for the study of all of these woodlands a sub-sample was made, attempting to include woodlands located in all regions of the country.

Given the time constraints, 'point' sampling was chosen over ongoing detailed monitoring of permanent plots. It was intended that study of a range of gap types and ages would give an indication of gap processes in Irish woodlands. Selected woodlands were visited and, if deemed suitable for inclusion, were surveyed in two ways. Data about the frequency and characteristics of canopy gaps were obtained using randomly located belt transects in selected woodlands. Vegetation and regeneration in canopy gaps was investigated by the selection of a number of gaps for detailed study.

5.2 Belt transects for sampling the woodland disturbance regime

A primary aim of this study has been to describe the frequency and characteristics of canopy gaps in some Irish woodlands. Belt transects (Kent & Coker 1992) were chosen as the sampling method for a number of reasons. They are relatively easy to demarcate, and 'fit' well into woodland of any shape and size. Barden (1989), comparing the transect method with complete census of areas chosen from aerial photographs, comments that the latter tends to result in underestimation of gaps, as small gaps are easily missed. On the other hand, he suggests that the transect method might overestimate gap numbers, as the researcher attempting to follow a compass line over rough terrain might unintentionally deviate towards gaps. This was not a problem in Irish woodlands, as the mid-line of the transect was laid out in advance, and terrain was usually relatively easy.

Transects were randomly located in blocks of woodland using random number tables and a compass. Roads (and edges along same), conifer blocks and areas of heavy infestation with *Rhododendron ponticum* and *Prunus laurocerasus* were avoided. Several transects were sampled at each site, the number depending on the length of individual transects, and the size and shape of the woodland. Transects were 10 metres wide and as long as possible to a maximum of 100 metres. The fragmented nature of many woodlands resulted in some transects being shorter than 100m in length.

Each transect was laid out with tapes and then surveyed. The length was walked and all canopy disturbance events were noted. For each such event, the nature of the disturbance, the species and size (height and DBH) of tree involved, and the resultant gap (if present) was measured. While some disturbances may have resulted in gaps in the past (which had closed since gap formation), these events were counted as disturbance events but not as gaps. However, the method of closure, if apparent, was noted. Closure by canopy extension was inferred if dead wood was present and replacement trees (*i.e.* younger than the gap maker) were absent or if the adjacent individuals had obviously grown in the direction of the gap. In some instances, groups of pole stage regeneration had filled previously existing gaps. Disturbance events were classified as Crown Damage (CD), Uprooting (U) or Trunk Snapping (S). The extent of crown damage was estimated and a class assigned to each CD event: I indicated loss or die-back of <24% of the crown, II loss of 25-49%, III loss of 50-74% and IV loss of >75%. In the case of uprooted and snapped trees, direction of treefall was noted. It was also determined whether events were single or multiple, and, if multiple, whether a domino effect was observable or not. The gap area (proportion of transect within gaps) was estimated by comparing the length of transect in gaps, (along the axis parallel to the transect) with the total length of the transect (after Runkle quoted in Barden 1989).

As the aim of this procedure was to describe the gap regime in selected woodlands, the general vegetation response to disturbance events was only briefly considered. The general nature of the vegetation within gaps was noted and assessed relative to that under the canopy in general. The species and abundance of seedlings and saplings was noted, and regeneration at gap edges was recorded.

5.3 Natural regeneration in woodland gaps

5.3.1 Selection of gaps

In order to examine natural regeneration in woodland gaps, a selection of gaps was chosen from a range of woodlands around the country (see Table 6.1). Gaps were subjectively chosen to be representative of those present in each woodland, and gaps which had formed naturally, and from which the fallen branches/uprooted trees had not been removed, were preferred. Woodland rides were avoided. Gaps from 13 woodlands were studied. Where enough gaps were present, 4-6 gaps were studied from each wood.

5.3.2 Gap structure

Each gap was sketched and the position of the gap makers, fallen wood and adjacent trees (both trunk and canopy edge) depicted. Details of gap formation were noted, and any relevant information (*e.g.* the presence of wood weakening fungi in snapped trunks) gathered. The species of the gap makers, their condition, girth, height (length), and canopy length were noted. Any pit and mound present was noted and its dimensions recorded.

Each gap was divided into zones, depending on the mode of formation of the gap. Where the gap was a classical *chablis*, i.e. an uprooted tree, the gap was divided into the area of the pit, the mound, beneath the fallen canopy, along the fallen bole and other areas (referred to here as the periphery). Gaps formed in other ways were divided along similar lines depending on the particular situation.

5.3.3 Gap age

A decay class was assigned to fallen trees/branches (after Rebertus and Burns 1997): 1- fine twigs still present; 2- fine twigs absent and tree bole mostly intact; 3- bole decaying; 4- only stump base visible; and 5- only mound or depression visible. However, the corresponding gap age for each

class, as defined by Rebertus and Burns, was unsuitable for application in Irish woodlands. It had been devised for use in an area with a continental climate, and thus different conditions for wood decay. It was necessary to use additional information to approximate the time since gap formation. Factors considered included the age of saplings and epicormic shoots present on fallen trunks and root-plates and the degree of colonisation of mineral soil in the pit.

5.3.4 Gap area

The gap area was measured by fitting the ground area to an ellipse (Runkle, 1981) and calculated from the formula:

$$A = \frac{\pi . L . W}{4}$$

where A denotes the Gap Area, L is the length of the longest axis of the gap, from canopy edge to edge, and where W is the perpendicular width at the widest point.

Hemispherical canopy photography (HCP) was also used to calculate canopy openness. Hemi-phots were taken at the centre of each gap, located by eye. Kodak TriX 400 monochrome film was used. The tripod height was 1.3 m, and the camera top was aligned to magnetic north and the camera fully leveled for each shot. The lens was focused to infinity, and several different exposure times bracketing that indicated by the camera's light meter were used. Ideally, the sky should be uniformly overcast when hemi-phots are taken. This reduces under-estimation of canopy caused by light reflections on leaves and branches. Occasionally, such conditions were not available, so weather was noted, and reflections later corrected on the digital image. The films were developed to negatives using Ilford Multigrade Developer and Ilford Hypam Rapid Fixer. Negatives were digitised using a flat-bed scanner and edited in a graphics package (Corel Photopaint) so that the image was black and white, and any bright patches owing to reflection of sunlight were removed and replaced with canopy. These images were then converted to 'pcx' format and imported into the analysis programme Winphot (ter Steege 1996), which allows for the calculation of canopy openness.

5.3.5 Gap Vegetation

Vegetation was identified according to Webb *et al.* (1997). The general vegetation of each gap was noted, and any saplings present inserted on the gap structure map and their species and height

recorded. The trees at edge of the gap were listed, and any potential parent trees in the vicinity noted.

Vegetation was sampled by the location of quadrats in a stratified random manner. Within each zone (see above), a number of randomly located quadrats were taken. Quadrats were 1 metre x 1metre, except in the case of the root plate zones (pits and mounds). In this instance, the entire zone was sampled. The area (typically ~2m x 2m) was measured so that vegetation and regeneration data could be compared with that from other quadrats later.

Every species of fern and vascular plant present was listed and cover estimated to the nearest 5%. Where a species cover was less than 5%, the Domin scale was applied. A single, small individual was assigned '+', a species which was scarce '1', one with scattered cover '2', and one with frequent cover '3'.

Special attention was paid to regeneration of canopy and sub-canopy species. Regeneration was classified as follows.

One year old seedlings (no woody tissue) S1

Seedlings > 1 year, < 25 cm in height S2

Seedlings > 25 cm tall & < 10cm gbh Sapling

The number of individuals of all tree seedlings and saplings present was counted and their heights recorded. The tallest sapling in each gap was deemed the 'leader'.

For each quadrat, the total cover of canopy, shrub, herb and ground layer was estimated, as was the cover of bare soil, rocks and boulders, and litter. Altitude was approximated from the relevant Ordnance Survey map, aspect from the map and compass, and slope using metre sticks and protractor.

5.3.6 Gap soils

Sampling

Soils were sampled from 16 gaps in four woodlands, two near Killarney, and two near Tullamore. Soil samples were taken from each quadrat using a 3 cm-diameter aluminium corer. Soil was taken up to a depth of 20 cm. Several samples were taken from each quadrat, and bulked for analysis. Soils were immediately air dried and sieved, and stored in the dark and at room temperature until analysis.

pH

pH was determined using a Jenway 3310 metre with a glass electrode, at room temperature. A paste was made using air dried soil and distilled water at a ratio of 1:2. This was mixed with a glass rod and allowed to settle for 30 minutes before a reading was taken. The mean value of two replicates was used for each sample.

Organic Matter

Organic content of the soil was estimated by the method of loss on ignition (Allen, 1989). A known weight (approximately 1 gram) of oven dry soil was added to a crucible, and the weight of the soil and crucible together was noted. This was placed in a furnace and the temperature set to 150°C. The temperature was gradually increased to 550°C over 4 hours and left at this temperature for a further 3 hours. The crucibles were allowed to cool in the furnace overnight and then to room temperature in a desiccator. When at room temperature, the crucibles were re-weighed. % Loss on ignition was calculated from the following equation.

$$\frac{\text{Wt. Of soil before ignition - Wt. Of soil after ignition}}{\text{Wt of soil before ignition}} \times 100$$

Phosphate

Soil Phosphate was extracted as orthophosphate ions into solution, and then estimated by the Molybdenum Blue method, adapted from Murphy and Riley (1962).

Soil samples were ignited at 550°C for one hour, and orthophosphate extracted into 1M Sulphuric acid at 90°C. This was allowed to cool, before being filtered and diluted. A mixed reagent containing antimony, sulphurous acid and molybdenum was added. The orthophosphate ions reacted with molybdate, forming a yellow colour in the solution. These were then reduced by the addition of ascorbic acid, yielding a blue coloured solution, the intensity of which was a measure of the phosphate present. This was measured using a spectrophotometer (Hitachi U 1100) at 887 nm, and a standard curve obtained by use of standard solutions.

Nitrogen

Total soil nitrogen was estimated by the Dumas method using an elemental analyser (LECO CNS 1000). Before analysis in the LECO, inorganic carbon was removed using a method adapted from Verado *et al.* (1990). Soil samples were oven dried at 60°C overnight. A ground sub-sample of ~1g was added to a beaker (whose weight had been determined to 0.0001g) and weighed to 0.0001g. A drop of distilled water was added to dampen the sample. 5 mls of sulphurous acid was added slowly and under a fume hood, and the samples dried on a hot plate. Any samples which had fizzed (owing

to the presence of carbonates) and continued to fizz after all 5 mls of acid had been added were treated with a further 5mls, and the process repeated until no more fizzing occurred. For each sample, the total amount of acid added was noted. After the sample was completely dried it was cooled to room temperature in a desiccator and reweighed. The increase in weight observed in some samples (due to the formation of sulphate salts) was corrected for after elemental analysis. The sample was re-ground to ensure thorough mixing and stored in a sterile screw cap bottle while awaiting elemental analysis.

A 0.2g sub-sample of the prepared soil was weighed to 0.0001g and added to a sterile aluminium cup. In samples which contained a high level of organic matter (>50% Loss on ignition) only 0.1g was used. The samples were then analysed in the LECO CNS 1000 analyser in which samples are combusted under oxygen at a temperature exceeding 1000°C. The combustion gases pass through several reaction columns to produce CO_2, N_2 and NO_x. Infra red and thermal conductivity detectors are used to estimate the concentration of these gases present. The samples are calibrated against EDTA, and the output obtained is % composition for the element (in this case nitrogen) under investigation. The figures % N were multiplied by 10 to give mg nitrogen per gram of soil dry weight (mg g^{-1} dw).

5.4 Browsing and natural regeneration

Browsing by ungulates is a feature of many Irish woodlands and undoubtedly affects regeneration of tree species. Where grazing pressure is high for a prolonged period, almost all regeneration may be prevented. However, even where grazing levels are moderate, grazers' preference of one tree species over another may affect the future composition of the canopy. In order to investigate such species preferences and the responses of different tree species to browsing, a transplant experiment was carried out in two woodlands of contrasting nutrient and grazing status. The species used were oak, birch, ash and rowan, as these are the common canopy trees in the woodlands investigated in this study. Beech was also used as it has successfully invaded some Irish oakwoods, and its apparent disfavour among browsers as well as its tolerance of shade, may play a role in its success.

5.4.1 Site Description

Tomies Wood is a sessile oakwood on stony podzolic soil over Old Red Sandstone and is a part of the Killarney National Park, Co. Kerry. The woodland is described in Chapter 6. The experimental site was a canopy gap formed by the removal of several oak trees in the early 1970s. heavy browsing by sheep (until 1996), sika and to a lesser extent red deer has maintained the open gap conditions here. Irish hares (*Lepus timidus* subsp. *hibernicus*) have been observed at the site (P. Dower *pers comm.*) and the remoteness of this woodland and its proximity to open mountain suggests that it is a suitable habitat for hare activity. The field layer is species poor and dominated by *Luzula sylvatica*. *Pteridium aquilinum* is also present and is quite dense in patches. The gap measures c. 30 m x 40 m and canopy openness (cf. 5.3.4) here is 47%. See Plate 1.

Charleville Estate contains a pedunculate oakwood on deep glacial till over Carboniferous limestone at Tullamore, Co. Offaly. The woodland is described in Chapter 6, and see Plate 2. The experimental site consisted of two adjacent canopy gaps, each formed by the removal of timber. One gap, the 'open' site, also contains a standing-dead oak that lacks any crown. Each gap measured c. 30 m x 30 m and the canopy openness was estimated at 27% and 43% for the open and exclosed gaps, respectively. The field layer is diverse and well developed with lush growth of bramble, enchanter's nightshade, violets, ground ivy, bluebell and various fern species. The wood and surrounding agricultural land are browsed primarily by a small herd of about 40 Fallow deer (*Dama dama*) (D. Hutton Bury *pers. comm.*). Rabbits and hares are also reportedly present, but in low numbers (Fuller 1990). No hard data about hare numbers are available, however, but the proximity of this site to a highly populated area may render it less suitable for a high level of hare activity than Tomies wood.

Plate 1 Charleville Wood, Co. Offaly

Plate 2 Tomies Wood, Co. Kerry.

5.4.2 *Experimental design*

In order to investigate preferences for different tree species of browsing animals, and variation in response to browsing between species, saplings were transplanted into these woodlands. Exclosures (~200m^2) were erected in gaps in each wood so that sapling growth in a non-browsed situation could be observed. The lower half of exclosures were fenced with chicken mesh so that deer, sheep, rabbits and hares were excluded. Saplings to be exposed to browsers were planted in a nearby gap in Charleville, and in the same gap (only half of which had been fenced) in Tomies.

15 saplings each of *Quercus robur, Fraxinus excelsior* and *Fagus sylvatica* were planted at both sites in May 1997, in both the exclosures and the 'open' plots. Saplings of *Sorbus aucuparia* and *Betula pubescens* were added in November 1997. Saplings were all approximately 3 years old at planting, and uniform in height and condition and growth form within species. They were planted randomly throughout the plot. Efforts were made *not* to avoid 'difficult to plant' places (*e.g.* amongst bramble) where naturally sown saplings would be likely to occur. Surrounding vegetation was disturbed as little as possible during planting, as the aim was to mimic the natural situation of saplings in woodland as closely as possible. Those saplings planted in May were watered at planting and once again, a few weeks after planting when a dry spell occurred. This was unnecessary with the November planted saplings.

The location of each sapling was mapped and each was labeled with a metal disc attached to one of two tent pegs hammered through the root-ball after planting. The tent pegs were used to prevent uprooting if saplings were later tugged at by browsing deer before the root system had anchored the plant in the soil. The location of the metal discs at ground level also reduced the chance that they might be knocked off and lost during browsing. The height of each sapling was measured at planting.

5.4.3 *Monitoring*

The sites were revisited at ~ two-monthly intervals. Saplings within exclosures were monitored only twice each year (summer and winter) in order to minimise trampling of vegetation. At the open plots, care was taken to minimise disturbance to vegetation during monitoring. This was to avoid making saplings more obvious to potential browsers, and to minimise negative effects on surrounding vegetation, which may have been competing with the saplings.

At each occasion, the height of every sapling was measured, and the type and extent of grazing and browsing was recorded. Browsing was categorised as follows:

0 No grazing

1 Grazing of leaves and side-shoots only

2 Browsing of the current year's shoots (cys)

3 Browsing of the previous year's shoots (pys)

When shoots had been browsed, it was possible to distinguish between deer and hare damage. The dental structure of deer results in a 'rough' breakage when they browse, while hares leave a neat, clean cut. While a detailed study of invertebrate grazing was not made, evidence of such grazing and its extent was noted.

5.4.5 Data Analysis

Field records were stored in Excel spreadsheets and summarised to yield the following:

- Frequency of browsing of each species at each site;
- Browse Category- the most severe category of browsing experienced by each individual over each season (Winter, Summer) during the experimental period;
- Browse Index for each species at each site- The severity of browsing was expressed numerically. Grazing of leaves only was assigned the value '1', browsing of cys was assigned the value '2', and browsing of pys assigned the value '3'. The Browse Index for a given species was calculated as the sum of the relative frequency of each browse category experienced. Thus the maximum value achievable was 100 x 3 *i.e.* 100% of saplings browsed severely (pys taken). Thus, species with high values were browsed most often and most severely.
- Frequency of browsing by hares and deer where identifiable;
- Mean change in height achieved by each species under each treatment;
- Species performance *i.e.* the height of saplings expressed as a proportion of that at planting;
- Sapling survival.

Where appropriate, data were compared by Analysis of Variance using Datadesk 5.0.

CHAPTER 6 DETAILS OF WOODLANDS STUDIED

Sites for the study of canopy gap dynamics in Irish semi-natural woodlands were chosen according to the criteria outlined in section 5.1.

Fifteen woodlands were used for detailed investigations during this research. These are listed in Table 6.1, and their locations shown in Fig. 6.1. (Woods are listed in alphabetical order.)

Table 6.1 Woodlands surveyed. The codes given are those used to identify each woodland on maps and in data analysis where use of the full woodland name is too cumbersome. *See Chapter 5.

Woodland	Code	Nature of Study*	Area (ha)	Grid Reference	County
Ardnamona	Ard	Transects & Gaps	66	G 96 84	Donegal
Camillan	C	Transects, Gaps & soils	60	V 95 86	Kerry
Charleville Castle	Cv	Transects, Gaps & soils	170	N 32 23	Offaly
Charleville Island	Is	Transects, Gaps & soils	3.2	N 32 21	Offaly
Derrybeg	D	Transects	2.4	C 01 19	Donegal
Garrannon	Gar	Gaps	22	R 49 60	Clare
Glen of the Downs	GD	Transects	70	T 26 11	Wicklow
Glengarriff	Gl	Transects & Gaps	154	V 92 57	Cork
Mullangore	M	Gaps	18	C 01 21	Donegal
Old Head	OH	Transects & Gaps	29	L 82 82	Mayo
Portlaw	P	Transects & Gaps	140	S 45 15	Waterford
Tomies	T	Transects, Gaps & soils	135	V 91 88	Kerry
Tomnafinnoge	Tf	Transects & Gaps	60	T 02 70	Wicklow
Union	Un	Transects & Gaps	28	G 68 28	Sligo
Uragh	Ur	Gaps	87	V 84 64	Kerry

Woodlands are described below on a site by site basis. Altitude and aspect are derived from the relevant O.S. Map (Discovery Series), and geology and soil data are taken from the Atlas of Ireland (Anon 1979) unless otherwise stated. Vegetation descriptions are based on field visits to the woodlands and pertain to the stands investigated. Supplementary data such as past management histories were obtained from local sources *e.g.* wildlife rangers and 'site synopses' from the survey of Natural Heritage Areas (Office of Public Works 1992-1995).

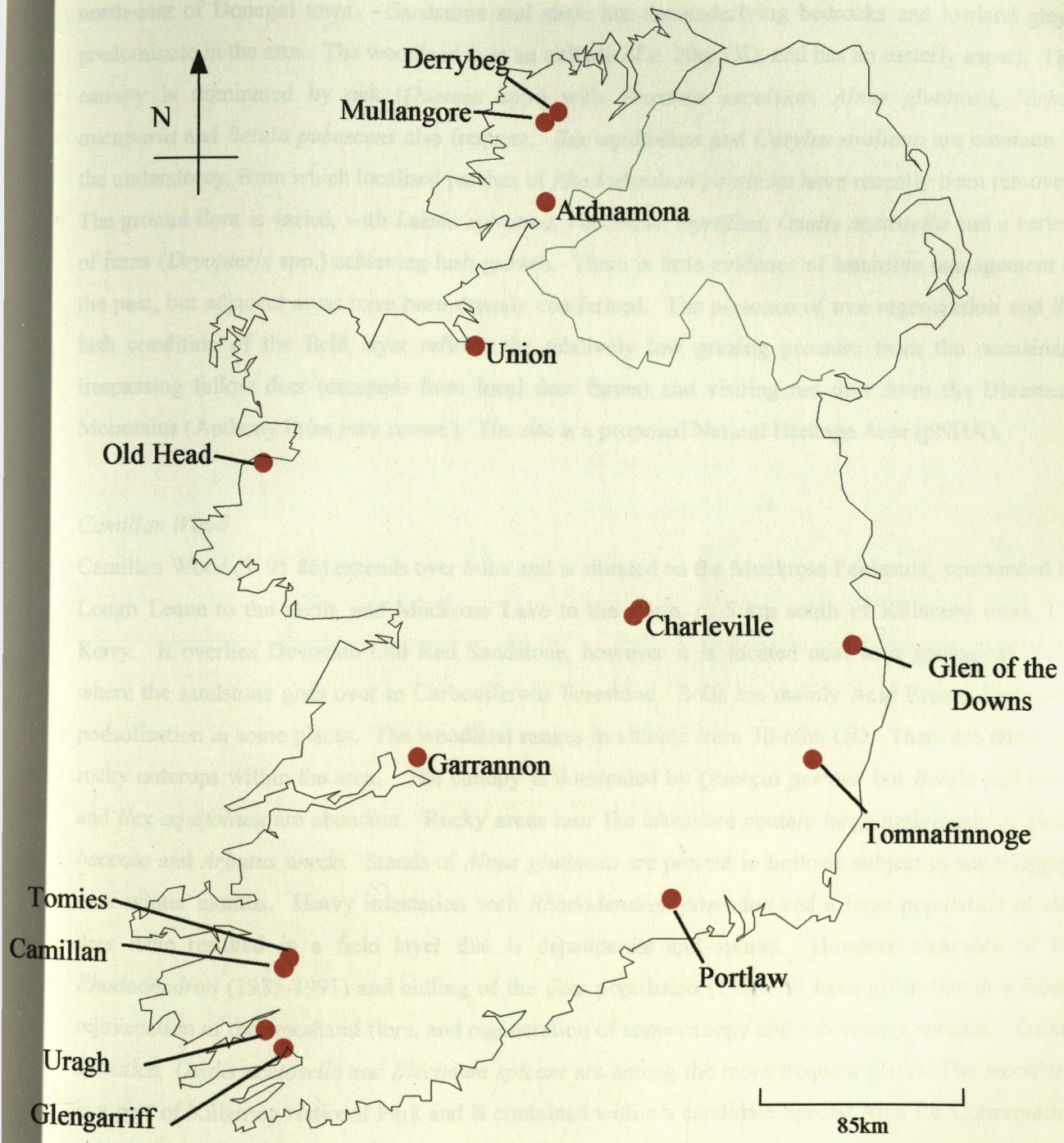

Fig. 6.1 Location of woodlands investigated in this study.

Ardnamona Wood

Ardnamona Wood (G 97 84) covers 66ha on the north-western shore of Lough Eske, c. 6 miles to the north-east of Donegal town. Sandstone and shale are the underlying bedrocks and lowland gleys predominate in the area. The woodland is at an altitude of *c.* 20m OD, and has an easterly aspect. The canopy is dominated by oak (*Quercus* spp.) with *Fraxinus excelsior*, *Alnus glutinosa*, *Sorbus aucuparia* and *Betula pubescens* also frequent. *Ilex aquifolium* and *Corylus avellana* are common in the understorey, from which localised patches of *Rhododendron ponticum* have recently been removed. The ground flora is varied, with *Luzula sylvatica*, *Vaccinium myrtillus*, *Oxalis acetosella* and a variety of ferns (*Dryopteris* spp.) achieving lush growth. There is little evidence of intensive management in the past, but adjacent areas have been densely coniferised. The presence of tree regeneration and the lush condition of the field layer reflects the relatively low grazing pressure from the occasional trespassing fallow deer (escapees from local deer farms) and visiting red deer from the Bluestack Mountains (Anthony Prins *pers comm.*). The site is a proposed Natural Heritage Area (pNHA).

Camillan Wood

Camillan Wood (V 95 86) extends over 60ha and is situated on the Muckross Peninsula, surrounded by Lough Leane to the north, and Muckross Lake to the south, c. 5 km south of Killarney town, Co. Kerry. It overlies Devonian Old Red Sandstone, however it is located near to a geological divide where the sandstone goes over to Carboniferous limestone. Soils are mainly Acid Brown Earth with podsolisation in some places. The woodland ranges in altitude from 30-60m OD. There are numerous rocky outcrops within the area. The canopy is dominated by *Quercus petraea* but *Betula pubescens* and *Ilex aquifolium* are abundant. Rocky areas near the lakeshore contain large individuals of *Taxus baccata* and *Arbutus unedo.* Stands of *Alnus glutinosa* are present in hollows subject to waterlogging over winter months. Heavy infestation with *Rhododendron ponticum* and a large population of sika deer have resulted in a field layer that is depauperate and sparse. However clearance of the *Rhododendron* (1985-1995) and culling of the deer population (1998-99) have given rise to a recent rejuvenation of the woodland flora, and regeneration of some canopy and sub-canopy species. *Luzula sylvatica, Oxalis acetosella* and *Blechnum spicant* are among the more frequent plants. The woodland is a part of Killarney National Park and is contained within a candidate Special Area for Conservation (cSAC)

Charleville Wood: 'Castle' and 'Island'

Charleville Demesne (N 32 23) is situated just south-west of Tullamore Town, Co. Offaly, and contains 170ha of woodland at an altitude of 60m OD. The area is underlain by glacial till over Carboniferous limestone and the dominant soil is a brown earth. Charleville Demesne is bisected by the N52, a National Secondary Road. The lands to the south of this route contain a man-made lake in which an island exists. In this study, the woods on the island are dealt with separately from those adjacent to Charleville Castle, north of the N52. All of the demesne woods are contained within an pNHA and cSAC.

Charleville Castle Wood

These woodlands are dominated by large, widely spaced *Quercus robur* with some large *Fraxinus excelsior*. In some areas *Acer pseudoplatanus* and *Fagus sylvatica* are present, indicative of planting in recent centuries. Past management features of this woodland include an area planted heavily with box, *Buxus sempervirens,* which is indicated as the 'Pheasantry' on 19th century maps. The woodland was managed for oak, and ground annually 'swiped' to control the undergrowth up to the 1960s (D. Hutton-Bury *pers comm.*). Consequently a dense thicket of poles of *Fraxinus excelsior* has developed, and now reaches heights in excess of 5m. The understorey includes *Crataegus monogyna* and *Corylus avellana*. *Rubus fruticosus* dominates the field layer, which is diverse and contains species such as *Hyacinthoides non-scripta, Circaea lutetiana, Glechoma hederacea* and *Hedera helix.* A herd of *c.*40 fallow deer browses the wood (D. Hutton-Bury *pers comm.*). The level of grazing is low, owing in part, perhaps, to the abundance of agricultural pasture nearby. Grey squirrels and hares are also present.

Charleville Island Wood

Charleville lake island extends over 3.16ha and originates from about 1800 when the lake was dug out from flooded callow land. Records indicate that no timber has been extracted from the island since 1800 at the latest (Hutton-Bury, 1967). Large individuals of *Quercus robur* dominate the canopy, and smaller trees of *Betula pubescens* and *Fraxinus excelsior* are also present. *Prunus spinosa, Crataegus monogyna* and *Corylus avellana* are present in the understorey, and the field layer contains *Rubus* spp., *Glechoma hederacea* and *Circea lutetiana.* The woodlands around Charleville lake have been exposed to moderately heavy grazing in the past, with upwards of 125 fallow deer grazing the area in 1940 (Fuller 1990). However poaching had reduced the population to *c.* 25 animals in 1980 (Fuller 1990). Today, the island woods appear to be more heavily browsed. This may be due to their relatively isolated status compared with the woodlands adjacent to the castle, which are quite heavily used for amenity by local people. The conifer plantations adjacent to the island may also serve as good cover for deer, concentrating their activities in this area. Grey squirrels and hares are also present.

Derrybeg Wood

Derrybeg wood (2.4 ha) is a small patch of relict woodland located on the western slopes of the Lough Beagh Valley, to the south-west of Lough Beagh, within Glenveagh National Park, Co. Donegal. The bedrock is Donegal Granite (Pitcher & Berger, 1972) from which acidic soils, dominated by peaty podsols are derived. The wood extends from 50m close to the lake shore upslope to 190m OD. The woodland has a north-eastern aspect. The woodland canopy is very open and consists mainly of *Betula pubescens* with scattered *Quercus petraea*. The woodland was fenced from grazing red deer in 1988 and contains abundant pole stage *Betula*. The field layer is dominated by *Molinia caerulea* with *Potentilla erecta, Calluna vulgaris, Dryopteris* spp. and *Lonicera periclymenum*. Sparse infestation with *Rhododendron ponticum* has been controlled.

Garrannon Wood

Garrannon Wood (R 50 61) is the largest extent of semi-natural woodland that remains of the Forest of Cratloe (Bohan, 1998) located *c.* 10km to the west of Limerick city, close to Bunratty. The soils are dominated by regosol-gleys that are derived from alluvium and Old Red Sandstone till. These 22 ha of woodland are dominated by maiden *Quercus petraea*, typically 1.3-1.6m in diameter. *Castanea sativa, Fraxinus excelsior* and *Ulmus glabra* also occur. The woodland is ungrazed, and *Rubus fruticosus* up to 1m in height dominates the field layer. Other species present include *Pteridium aquilinum, Viola spp., Lonicera periclymenum* and *Oxalis acetosella*. The woodland has a well-documented history, dating at least 1000 years (Bohan 1998), and more recently has been managed for timber. Standards of *Quercus* have been cleared from a number of coupes since 1995, leaving large artificial gaps. The site is an pNHA.

Glen of the Downs

This oak woodland covers the steep sides (40-45° slope) of a U-shaped valley in east County Wicklow, bisected by a national primary road. The woodland soils are brown podzolics and rather dry, derived from the Wicklow Granite beneath. The woodland extends over 70 ha from 100-200m OD and the eastern part (the part surveyed for this study) is south westerly in aspect. The woodland is dominated by *Quercus petraea,* which appear to be even-aged (25-32cm dbh) and form a low (8-12m) dense canopy. Some smaller individuals are also present, including coppice stools with poles of *ca.* 15cm dbh. The understorey is well developed with *Ilex aquifolium* and *Corylus avellana*. There is no apparent browse line, and little evidence of grazing. Saplings of *Quercus* (up to 5m in height) are common, with younger individuals (up to 2m tall) present along tracks. Saplings of *Fagus* and *Corylus* are occasional; those of *Sorbus* are rare. *Luzula sylvatica* dominates much of the field layer with *Vaccinium myrtillus* and *Teucrium scorodonia* present in places. Gaps are rare; space vacated by the

occasional fallen branch or standing dead tree (*c.*3m tall, <15cm dbh) has been completely filled by growth of adjacent crowns. The woodland has been designated a National Nature Reserve since 1980.

Glengarriff Wood

Glengarriff woods extend around Glengarriff Harbour to the north of Bantry Bay, Co. Cork. The woods contained within Glengarriff Nature Reserve comprise some 154 ha of Atlantic Oakwood. The woods extend from 10m to 100m OD, and are south-western in aspect. The underlying bedrock is Old Red Sandstone, and soils are dominated by Acid Brown Earths and peaty podsols. The woodlands are similar to their neighbours at Killarney, but are relatively little grazed and *Rhododendron* infestation has been successfully controlled. The canopy is dominated by *Quercus petraea* with *Fagus sylvatica* occurring locally. *Betula pubescens* and *Sorbus aucuparia* are frequent and *Ilex aquifolium* is locally dominant in the understorey. The field layer is luxuriant and is dominated by species such as *Pteridium aquilinum, Rubus fruticosus* agg. and *Luzula sylvatica. Hedera helix, Blechnum spicant* and *Oxalis acetosella* are common.

Mullangore Wood

Mullangore wood is an Atlantic oakwood contained within Glenveagh National Park. It is situated on the eastern side of the Lough Beagh Valley, on peaty podsols overlying Donegal Granite. The woodland extends over 18 ha, 2 ha of which were fenced from red deer in 1974. The remaining 16 ha were enclosed in 1984. The woodland was densely infested with *Rhododendron ponticum* in the past, but this has been largely removed, and maintenance to control reinfestation is ongoing. The canopy is rather open and is dominated by *Quercus petraea* with *Betula pubescens* and *Sorbus aucuparia. Ilex aquifolium* is dominant in the understorey. The ground vegetation is quite patchy, and includes species such as *Molinia caerulea, Agrostis* spp., *Vaccinium myrtillus* and *Luzula sylvatica.*

Old Head Wood

Located between Louisburg and Westport in Co. Mayo, western Ireland, this wood occupies the north-eastern face of a small hill on the coast to the south of Clew bay. The woodland covers 29 ha and extends from sea level to 90m in altitude. The bedrock is gneiss and the soils range from grey-brown mineral loams to peaty gleys. Gorham (1954) reports pH values of 4.44 -5.37 for samples taken in the wood. The wood is dominated by *Quercus petraea* with *Betula pubescens*, *Sorbus aucuparia* and *Fraxinus excelsior* also present in the canopy. *Corylus avellana* and *Ilex aquifolium* are present in the understorey. The oaks are typically 0.7-1.5m in girth. Occasional individuals of *Pinus sylvestris*, *Acer pseudoplatanus* and *Aesculus hippocastanum* are present, and in places *Fagus sylvatica* (up to 2m in girth) has been introduced. Ground vegetation is sparse or absent in the areas dominated by *Fagus*, although seedlings and saplings of this species are found in patches. Elsewhere, the ground flora contains abundant *Rubus fruticosus*, *Pteridium aquilinum*, *Dryopteris* spp. and *Lonicera periclymenum*. Locally, *Luzula sylvatica*, rushes (*Juncus* spp.) and sedges (*Carex* spp.) dominate. *Hedera helix* is plentiful both on trees and on the ground, and saplings of *Ilex*, *Quercus*, *Sorbus* and *Betula* are occasional. The wood has been described as an Atlantic oakwood (Dúchas, 1995) and exhibits the characteristic luxuriance of lower plants associated with such a habitat. The wood appears to be little or only lightly grazed at present, and was reported in a similar condition by Gorham (1953). No evidence of grazing ungulates was apparent during my visit. The woodland is a National Heritage Area.

Portlaw Woods

These estate woodlands near Portlaw in east Co. Waterford are the largest extent (*c.*140 ha) of mature woodland in the south east of the country. The woodlands are underlain by till derived from Ordovician and Silurian Shale and Acid Brown Earth is the predominant soil type. The woodlands extend from 30m-100m OD and have a south-southwestern aspect. Dominated by *Quercus* spp., the woodlands are managed for timber and pheasants (Marquess of Waterford *pers. comm.*), and so species such as *Betula* and *Sorbus* are lacking. Dead trees are felled and the timber removed. Some areas are planted with exotic conifer species. The woods were grazed by deer until 1910, but have been ungrazed since, and so natural regeneration of tree species is frequent. *Rhododendron ponticum* is present in patches, but has not yet achieved dominance in the shrub layer.

Tomies Wood

Tomies wood lies on the lower slopes of Tomies Mountain, overlooking Lough Leane, north of Killarney town in Co. Kerry. It is one of the most extensive of the Killarney oakwoods (135 ha), and is dominated by *Quercus petraea* on peaty podsols over Old Red Devonian Sandstone. The woods extend from 60m (at the lakeshore) to 180m OD. Adjacent areas have been planted with coniferous species, and *Rhododendron ponticum* has heavily infested small areas in the wood. However the larger part of the woodland has been only lightly infested with *Rhododendron* and regular removal of re-infestation is ongoing. The wood has a history of heavy grazing by sheep and deer, at least over the past century. The sheep have been excluded since the erection of a boundary fence in 1996, however both sika and red deer still browse the woodland. Hares are also common in the area. *Ilex aquifolium* is abundant, as pollards and coppice stools, and *Betula pubescens* and *Sorbus aucuparia* are also frequent. Much of the ground is rather bare of vegetation, owing to long sustained heavy grazing. There is a dearth of young trees outside of experimental exclosures. Bryophytes are abundant, and *Blechnum spicant*, *Oxalis acetosella* and *Luzula sylvatica* are the most common plant herbs.

Tomnafinnoge Wood

Tomnafinnoge Wood is a part of the larger ancient Shillelagh Woods, and is located c. 3km east of the town of Shillelagh in south County Wicklow. The woodland extends over 60 ha and overlies acid brown earths derived from Ordovician-Silurian Shale till. The wood ranges in altitude from 70-100m OD, and is north-westerly in aspect. The history of woodland management at this site has been well documented, (Jones, 1986). In the 18th century, the wood had a structure of *Quercus*, *Fraxinus* and *Alnus* standards with mixed underwood, which was managed as a coppice. Today, Tomnafinnoge Wood is comprised of widely spaced mature *Quercus petraea* with *Fagus sylvatica, Betula pubescens* and *Sorbus aucuparia.* In places, *Fagus* attains dominance and casts a deep shade excluding any growth of plants other than occasional small *Ilex* saplings. Elsewhere, the understorey contains *Corylus avellana* and *Ilex aquifolium* and the field layer is diverse and well developed. Species present include *Vaccinium myrtillus, Rubus* spp. and *Oxalis acetosella.*

Union Wood

Union wood is a part of the former Cooper Estate, on the eastern bank of the Ballysadare River, close to Collooney, just south of Sligo town, Co. Sligo. Twenty-eight ha of oak woodland remain of the former wooded area, which is now largely planted with commercial conifer species. The woodland ranges in altitude from 20-100m OD, and has a north-westerly aspect. The underlying rock type is gneiss, and acid peaty gleys dominate the soils. The canopy is dominated by *Quercus petraea.* Some

mature individuals of *Betula pubescens, Corylus avellana* and *Crataegus monogyna* are present. The field layer comprises *Luzula sylvatica,* which forms monospecific stands over large areas. Ferns (*Dryopteris* spp and *Blechnum spicant*) are frequent, and *Oxalis acetosella* occurs locally. Substantial herds of cattle and fallow deer have grazed the area in the past. However, deer numbers are now much reduced, and cattle are confined to fields adjacent to the woodland (Anthony Prins *pers comm.*).

Uragh Wood

Uragh wood overlooks Lough Inchiquin on the northern side of the Beara peninsula, Co. Kerry. The wood is situated over parallel ridges of Devonian Old Red Sandstone, which run down-slope towards the lough. The woodland is 87 ha in area, north-eastern in aspect, and extends from 40m at the lakeshore to 150m OD. The soil types present have been investigated by Little (1994 and 1997) and are described as ranging from acid brown-earths to podsols. Poorly drained gleys and peats occur in the hollows between the aforementioned ridges. This wood has been classified as acidophilous Atlantic oakwood (Blechno-Quercetum, Little *et al.* 1996). The canopy is dominated by *Quercus petraea* which ranges from 60-100cm in dbh. *Betula pubescens, Sorbus aucuparia* and locally *Corylus avellana* and *Fraxinus excelsior* are occasional. The field layer contains *Vaccinium myrtillus, Lonicera periclymenum, Rubus fruticosus* and *Dryopteris aemula.* Investigations into the history of this woodland (Little *et al.* 1996) suggest that the woodland experienced relatively little human disturbance in the past, until the mid 17th century, when the canopy of *Quercus* and *Betula* opened up. This was likely to have been associated with the exploitation of the woods as a source of charcoal for use in iron smelting. Little *et al.* (1996) reckon that the present canopy trees date from immediately after this disturbance. More recently, the woodland has been managed as a nature reserve. The woodland was fenced in 1973 and has since been grazed only sparsely and intermittently following breaches of the fence by sika deer. Fallen timber is not removed, and no planting into the woodland has occurred. The invasive *Rhododendron ponticum,* a common alien in other woodlands in this part of Ireland, is absent from Uragh Wood.

Table 6.2 Characteristics of Woodland Sites

Woodland	Geology	Soil	Stand structure (Age,Canopy openness)	Phyto-sociology	Dominant Species (Trees)	Principal Species (Field layer)
Ardnamona	Sandstone/ shale	Peaty gley/ Podsol	Mixed age Canopy closed	Mainly B-Q	C: *Q.p (F.e)* S: *C.a, I.a*	*L.s, V.m, D.sp*
Camillan	Sandstone	Brown podsolics	Over-mature Canopy open	Mainly B-Q	C: *Q.p, B.p* S: *I.a*	*L.s, O.a, B.s*
Charleville Castle	Limestone	Brown Earth	Over-mature with thicket	C-F	C: *Q.r, F.e* S: *C.m*	*R.f, G.h, H.h*
Charleville Island	Limestone	Limestone till	Over-mature Canopy opening	C-F	C: *Q.r, F.e* S: *C.m*	*R.f, G.h, C.l*
Derrybeg	Granite	Peaty podsol	Mature Canopy open with thicket	B-Q	C: *Q.p, B.p*	*M.c, C.v, D. spp*
Garrannon	Sandstone till	Grey-brown podsolic	Mature Canopy closed	B-Q	C: *Q.p*	*R.f, P.a, V.sp*
Glen of the Downs	Granite	Brown Earth - Brown odsolic	Sub-mature/mature Canopy closed	B-Q	C: *Q.p* S: *(I.a)*	*L.s, V.m*
Glengarriff	Sandstone	Peaty podsol	Mature Canopy opening	B-Q	C: *Q,p*	*R.f, P.a, L.s*
Mullangore	Granite	Inorganic podsol	Mature Canopy open	B-Q	C: *Q.p*	*M.c, V.m*
Old Head	Gneiss/ quartzite	Grey-Brown Mineral loam	Mixed age Canopy closed	Mainly B-Q	C: *Q.p (F.s)*	*R.f, P.a, L.p*
Portlaw	Shale Till	Acid brown earth	Mixed Age Canopy closed	B-Q	C: *Q.p*	*P.a, R.f, L.s*
Tomies	Sandstone	Peaty podsol	Over mature/mature Canopy opening	B-Q	C: *Q.p (B.p)* S: *I.a*	*L.s, P.a, B.s*
Tomnafinnoge	Shale Till	Acid brown earth	Mature Canopy closed	B-Q	C: *Q.p (F.s)*	*R.f, O.a,V.m*
Union	Gneiss/ quartzite	Acid peaty gley	Mature Canopy closed	B-Q	C: *Q.p*	*L.s, D.spp*
Uragh	Sandstone	Acid brown earth-podsol	Mixed age Canopy opening	B-Q	C: *Q.p*	*V.m, L.p, R.f*

C: Canopy; S: Subcanopy; *Q.p:Quercus petraea; Q.r: Quercus robur; F.e: Fraxinus excelsior; F.s: Fagus sylvatica; I.a: Ilex aquifolium; C.a: Corylus avellana; B.p: Betula pubescens; C.m: Crataegus monogyna. R.f: Rubus fruticosus; O.a: Oxalis acetosella; V.m: Vaccinium myrtillus; L.p: Lonicera periclymenum; D.spp: Dryopteris spp; L.s: Luzula sylvatica; P.a: Pteridium aquilinum; M.c: Molinea caerulea; B.s: Blechnum spicant; V.sp: Viola sp; G.h: Glechoma hederacea; C.v: Calluna vulgaris.* Species in brackets are locally dominant. B-Q: Blechno-Quercetum; C-F: Corylo-Fraxinetum.

Table 6.2 lists the main characteristics of the woodlands included in this study. All of the woodlands were dominated by *Quercus* spp., and collectively the sample is reasonably representative of native, high forest woodland in Ireland. Examination of the geology and soil types present in the study sites reveals a bias in the sample in that woodland on base-rich, fertile soils is rather under-represented. This is explained by the fact that many of the remaining woodlands on base rich soils in Ireland are small in extent and of low (scrubby) stature, most of the high forest having been cleared for agriculture (cf. Chapter 2). Thus high forest woodland in Ireland is concentrated in marginal areas, with lower potential for agricultural development, *i.e.* on low fertility acid substrates.

CHAPTER 7 CANOPY GAP REGIME IN IRISH SEMI-NATURAL WOODLANDS

Information about canopy disturbance in Irish semi-natural woodlands was obtained in two ways. Data about the frequency and nature of disturbance events were gathered by the use of randomly positioned belt transects, through selected woodlands. The procedure followed is described in section 5.2, and the results of this investigation are presented in sections 7.1 and 7.2 below.

Data about the structure and zonation of individual gaps were obtained by the detailed study of subjectively chosen gaps. Forty-five gaps from 13 woodlands were surveyed. These were selected to be representative of the prevalent gap type found in each of the woodlands studied. These gaps were independent of those encountered by the transect study, and while the many of the woodlands in which transects were sampled also contained gaps which were selected for study, the two data-sets are separate. The methods used are outlined in section 5.3.3. The results of this detailed survey of gaps are contained in section 7.3.

7.1 The canopy disturbance regime

Events in the canopy resulting in the removal of vegetation from a space at least 1m in diameter are termed *disturbance events* (DE). Disturbance events range from the die-back and loss of individual branches to the uprooting of entire trees

Not all disturbance events result in gap formation and, for many identifiable disturbance events, the gap that was originally created had since been filled in by vegetation. This survey aimed to present a 'snap-shot' of the gap regime in woodland, so whether or not each disturbance event was currently giving rise to a gap, was noted.

Raw data from the transect sample is presented in Appendix II. In total 119 DEs were encountered.

The frequency of disturbance events and canopy gaps varied between woodlands, ranging from 2 DE/100m to 14 DE/100m. Table 7.1 lists the frequency of disturbance events and gaps in each of the woodlands surveyed. The proportion of each transect contained within gaps is also given.

Table 7.1 Disturbance regime in selected Irish woodlands. '% Gap' refers to the percentage of each transect which was contained within one or more canopy gaps.

Woodland	Sample length (m)	DE/100m	No. Gaps/100m	% Gap
Ardnamona	60	10	3	16
Camillan	490	5	2	14
Charleville 'Castle'	250	3	2	18
Charleville 'Island'	130	8	5	24
Derrybeg	110	14	4	17
Glen of the Downs	100	2	0	0
Glengarriff	90	7	3	23
Old Head	200	7	3	16
Portlaw	65	5	5	43
Tomies	200	9	5	25
Tomnafinnoge	151	2	2	9
Union	110	6	4	31
Mean (s.e.)	*Total: 1956*	*7.2 (0.96)*	*3.5 (0.58)*	*19.5 (2.61)*

Twelve woodlands were studied and a distance of 1956m of transect (x 10m width) sampled. In total, 119 disturbance events were encountered (Table 7.2). Of these, 66 (55.4%) were causing canopy gaps at the time of survey. Thirty (25.2%) disturbance events were multiple (*i.e.* involved more than one individual tree) and of these 23 (76.6%) gave rise to gaps. Of the 89 disturbance events (74.8% of total) which involved only one tree, 48% gave rise to gaps.

Table 7.2 Disturbance events resulting in canopy gaps

		Disturbance Events → Gaps
All Disturbance Events	119	66
%	*100*	*55.4*
Multiple Events	30	23
%	*25.2*	*76.6*
Singular Events	89	43
%	74.8	*48.3*
Crown Damage	63	33
%		*52*
Uprooting	18	8
%		*44*
Snapping	37	23
%		*49*

Table 7.3 lists wind conditions for each of the woodlands surveyed. Relationships between these factors and the disturbance regime were investigated using Spearman rank correlation (Table 7.4).

Table 7.3 Wind conditions at woodlands studied.

Wood	Weather Station & distance (km) and direction from site	Mean no. gale days	Maximum Gust (knots)	mean monthly wind speed (knots)
Old Head	Belmullet- 45, N	30.5	93	13.1
Union	Belmullet - 98, W	30.5	93	13.1
C-Island	Birr - 38, NE	1.2	85	7
C-castle	Birr - 38, NE	1.2	85	7
Glen of the downs	Casement- 30, NW	20.3	81	11
Portlaw	Cork - 40, SW	15	94	11.1
Tomnafinnoge	Kilkenny - 50, SW	1.4	77	6.5
Derrybeg	Malin Head - 60, NE	57.4	98	16
Ard na Mona	Malin Head - 95, NE	57.4	98	16
Camillan	Valentia - 55, SW	11.2	88	10.9
Glengarriff	Valentia - 55, NW	11.2	88	10.9
Tomies	Valentia - 60, SW	11.2	88	10.9

Data supplied by Met Éireann, and based on data from 30-year period 1961-1990.

Table 7.4 Relationships between site factors and disturbance values (Spearman rank co-efficients).

	DE/100m	Gaps/100m	% Gap
Mean Monthly Windspeed	0.356	-0.134	-0.082
Maximum Gust recorded	0.492*	0.886*	0.132
Mean no. of Gale Days per annum	0.308	-0.194	-0.153
Aspect	-0.271	-0.152	-0.187
Altitude	-0.031	0.077	-0.023
Canopy Height	-0.207	0.231	0.298
Slope	0.058	-0.024	-0.104

* indicates a correlation significant at 95% confidence limit.

The strongest relationship is that between the number of canopy gaps per 100m and the maximum recorded wind gust. Maximum gust is also correlated (though less strongly) with the frequency of disturbance events. None of slope, altitude and aspect appears to be the principal determinant of the disturbance regimes in the woodlands studied, however there is some trend observable between topography and gappiness (Fig. 7.1), although this is not statistically significant.

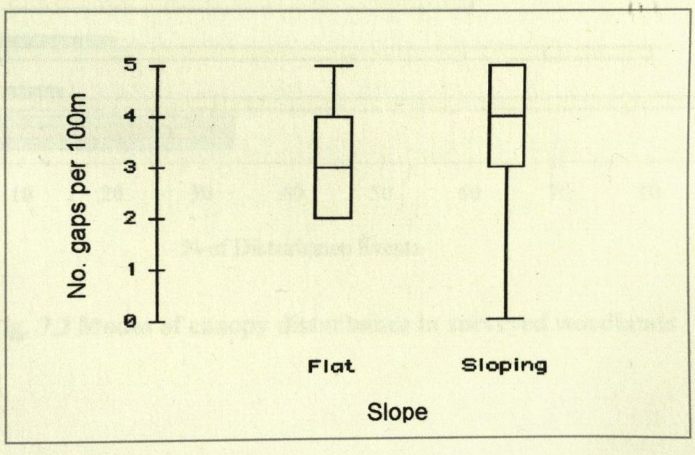

Fig. 7.1 Variation in the no. gaps per 100m and slope

7.2 Characteristics of canopy disturbance

7.2.1 Modes of disturbance

Disturbance events involving the uprooting of a tree were classified as 'Uprooted' (U). Those where the tree had fallen due to snapping of the trunk were deemed 'Snapped' (S). Those events where part of the crown was damaged were classified as 'Crown Damage' (CD), and assigned a class ranging from I to IV, depending on the proportion of the crown affected (see section 5.2).

Crown Damage was the most frequent type of disturbance event encountered and, in many woodlands was the dominant mode of canopy disturbance. Sixty-three (52.9% of all DEs) instances of CD were recorded. Uprooting of trees was the next most frequent disturbance event, accounting for 28.7% of all DEs. Trees with snapped trunks accounted for 15.9%, and cut trees for 2.5% of disturbance events. However, this overall pattern covers a variety of regimes present between woodlands. Fig. 7.2 illustrates the distribution of the different modes of canopy disturbance in the woodlands surveyed.

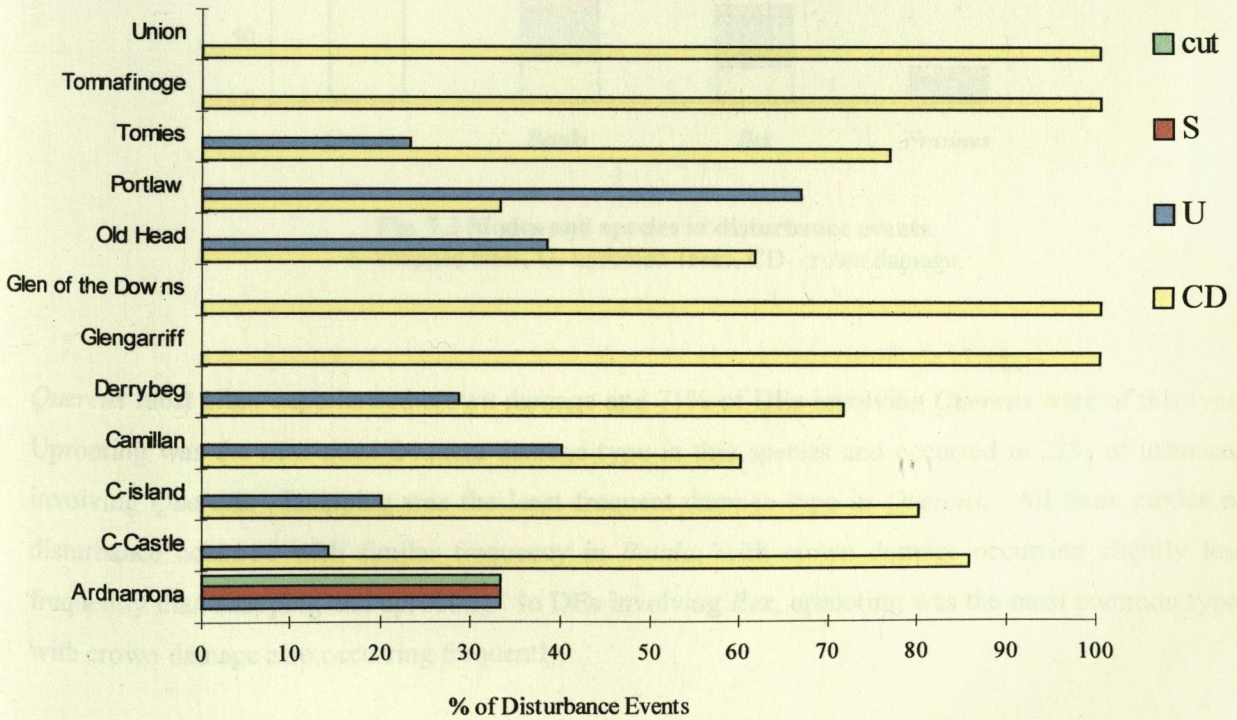

Fig. 7.2 Modes of canopy disturbance in surveyed woodlands

7.2.2 *Species involved in disturbance*

Quercus was the genus most frequently involved in canopy disturbance, and was the 'gap maker' in 52.9% of cases. This species is also the most common canopy constituent in the woodlands surveyed. *Betula* was involved in 19.3%, *Ilex* in 13.4%, *Fraxinus* in 5%, *Sorbus* in 1.7% and *Taxus* in 0.8% (one case) of disturbance events. In 6.7% of cases, the advanced state of decay prevented identification of the individual.

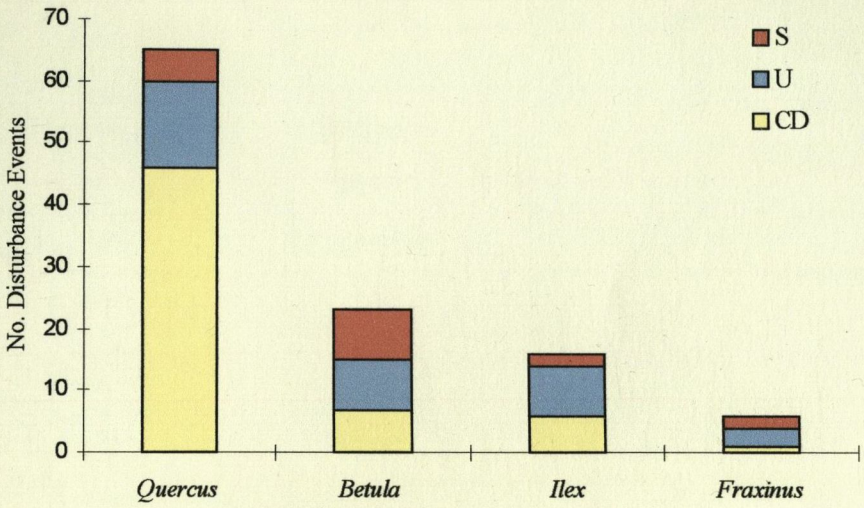

Fig. 7.3 Modes and species in disturbance events.
S- snapped trees, U- uprooted Trees, CD- crown damage.

Quercus most often experienced crown damage and 71% of DEs involving *Quercus* were of this type. Uprooting was the next most frequent damage type in this species and occurred in 22% of instances involving *Quercus*. Snapping was the least frequent damage type in *Quercus*. All three modes of disturbance occurred with similar frequency in *Betula*, with crown damage occurring slightly less frequently than snapping and uprooting. In DEs involving *Ilex*, uprooting was the most common type, with crown damage also occurring frequently.

7.2.3 Woodland Response to Disturbance

The aim of this transect survey was to gain information about disturbance in the canopy and so the vegetation response to disturbance events was not investigated in detail here. However, general notes regarding the nature of the woodland vegetation at each disturbance site was noted and these are listed in Appendix III. Many of the DEs resulted in the lateral expansion of the adjacent intact canopy into the space occupied. In some, there was evidence of saplings and seedlings, already present at the time of disturbance, growing towards the space created and availing of the increased light. However, in others, the vegetation did not appear to differ from that observed under intact canopy.

7.3 Characteristics of canopy gaps

The data presented here are derived from the study of 45 subjectively chosen gaps in 13 Irish woodlands.

7.3.1 Gap formation

Table 7.5 Gap formation and structure 'Zones' refer to the different areas of the gap which differ structurally owing to disturbance during formation of the gap: p = pit; m = mound; b =bole; fc = fallen canopy. 'dominoed' refers to the disturbance of a second tree by the initial 'gap maker'. U: uprooted; S: snapped; CD: Crown damage.

Gap Code	Age (Years)	Maker	Mode of Formation	DBH (cm) of gap maker	Height (m) of gap maker	Zones present	Orientation of gap maker
T1	1	*Betula pubescens*	U	39.5	15.7	p,m,b,fc	NW-SE
T2	3	*Quercus petraea*	U	75.5	16.3	p,m,b,fc	NW-SE
T3	1	*Q. petraea*	U	84.4	18.8	p,m,b,fc	SE-NW
		Ilex aquifolium	U (dominoed)	15.9			
T4	2	*B. pubescens*	S	54.5	16.3	p,m,b,fc	SW-NE
		Q. petraea	U (dominoed)	33.1	15.0		
T5	2	*B. pubescens*	U	63.7	15.0	p,m,b,fc	NW-SE
		Q. petraea	CD (dominoed)	44.2	18.3		
T6	2	*Q. petraea*	U	53.5	15.7	p,m,b,fc	SW-NE
		I. aquifolium	U	19.4 x 2	7.15		(gap is circular)
		Q. petraea	CD II	28.6	17.6		
		I. aquifolium	U	21.6	8.52		
		Q. petraea	CD I	25.5	17.8		
		Q. petraea	CD I	27.6	17.3		
Gl1	3	*Q. petraea*	CD III	33.4	12.0	fc	NW-SE
		I. aquifolium	U	16.6	10		
Gl2	1	*Fraxinus excelsior*	U	55.1	17.2	fc,b	SW-NE
		Q. petraea	CD I (dominoed)	84.1	18		
Gl3	3	*Q. petraea*	CD III	44.6	20	fc	n/a
		Q. petraea	S	34.4	12		gap is circular
Gl4	2	*B. pubescens*	CD IV	46.5	20	fc	n/a
		Q. petraea	CD I	33.1	20		gap is circular
Un1	7-10	*Q. petraea*	CD IV	56.3	20	fc	n/a
		Q. petraea	CD IV	?			gap is N-S
		Q. petraea	CD IV	?			
Un2	2	*Q. petraea*	CD IV	56.7	22	fc	gap is circular
Un3	15-20	*Q. petraea*	U	61.4	>14	p,m,b,fc	SW-NE
		Q. petraea	U	34.4	>14		
Un4	15-20	*Q. petraea*	U	49.0	>9	p,m,b,fc	S-N
Ur1	5-7	*B. pubescens*	U	28.7		m,b	SW-NE
		Q. petraea	CD I				
Ur2	7	*B. pubescens*	U	30.6	13.1	p,m,b,fc	SW-NE
		B. pubescens	U	36.6	8.3		
		B. pubescens	U	29.3	11.6		
Ur3	10	*B. pubescens*	S	31.5	>16	b,fc	SW-NE
Ur4	3	*B. pubescens*	S	29.3	11.2	b,fc	S-E
Gar1	2	*Q. petraea*	U	66.2	19.8	p,m,b,fc	SE-NW
Gar2	2	*Q. petraea*	S	53.2	18	b,fc	SW-NE
		Q. petraea	S	44.9	18		
Gar3	4	*Q. petraea x 20*	cut and removed			Stumps	circular gap
Gar4	3	*Q. petraea*	CD IV	54.1	>12	fc	circular gap
		Q. petraea	CD IV	48.1	>12		

Contd.//

Table 7.5 (contd.) Characteristics of canopy gaps

Gap Code	Age (Years)	Maker	Mode of gap formation	DBH (cm) of gap maker	Height (m) of gap maker	Zones present	Orientation of gap maker
Tf1	2	*B. pubescens*	S	26.1	9.8	fc	N-S
		B. pubescens	S (dominoed)	8.6 x3	6		
Tf2	2	*Fagus sylvatica*	CD III	89.1	26	fc	n/a
P1	2	*Q. petraea*	U (later cut)	119.0	25.7	m,fc	NW-SE
C1	3	*Q. petraea*	U	67.8	16.4	p,m,b,fc	NE-SW
		I. aquifolium	S	?	?		
C2	5	*Q. petraea*	S	42.9	16.4	p,m,b,fc	NW-SE
		Q. petraea	U (dominoed)	21.8	?		
		Q. petraea	U (dominoed)	?	?		
C3	3	*Q. petraea*	U	57.3	16.7	p,m,b,fc	NW-SE
		Q. petraea	U	41.4	16.1		
C4	1	*B. pubescens*	S	37.9	11.94	p,m,fc	SW-NE
		B. pubescens	U	42.0	12		
Cv1		*Q. robur*	cut	31.8	?	b,fc	?
Cv2	>5	*Q. robur*	U (later cut)	11.8	?	p,m,fc	SE-NW
Cv3	>3	*Q. robur*	CD III	90.7	27	fc	n/a
		Q. robur	CD IV	?	?		
Cv4	2	*Q. robur*	CD III	100.3	25	fc	W-E
		Q. robur	CD II	121.6	24		
Cv5	>3	*Q. robur*	CD IV	113.3	23	fc	NW-SE
Is 1	7	*Q. robur*	U	1.3	26.7	m,b,fc	NW-SE
		Q. robur	CD IV	26.1	?		
Is2	>10	*F. excelsior*	U	>25.5	>12	p,m,b,fc	SW-NE
		F. excelsior	U	>25.5	?		W-E
		?Q. robur	U	52.5	>15		N-S
M1	10	*B. pubescens*	S	27.1 x 2	>9	m,b,fc	SW-NE
		B. pubescens	U	26.7	10.3		SW-NE
		B. pubescens	S	25.5	?		SW-NE
M2	3	*B. pubescens*	U	35.0	12.1	p,m,b,fc	SW-NE
		Q. petraea	CD IV	57.3	>14		
M3	>10	*?Q. petraea*	U	>27.1	>9.30	b	SW-NE
Ard1	2	*Sorbus aucuparia*	U	33.1	9.45	p,m,b,fc	SW-NE
Ard2	1	*S. aucuparia*	U	38.5	9.4	p,m,b,fc	SW-NE
		S. aucuparia	U	27.7	10		S-N
		B. pubescens	S (dominoed)	9.5	>4		-
OH1	10	*S. aucuparia*	U	42.7	11.3	m,b,fc	NW-SE
OH2	7	*B. pubescens*	U	25.5	9.8	p,m,b,fc	W-E
		Q. petraea	CD II	35.0	18		
		Q. petraea	CD III	28.7	?		
OH3	5	*F. sylvatica*	U	48.7	14.8	p,m,b,fc	SW-NE
		Pinus sylvestris	S (dominoed)	49.0	?		
OH4	>5	*Q. petraea*	U	35.1	15.4	p,m,b,fc	NW-SE

Gaps were often irregular, but generally broadly elliptical to circular in shape, and most were on a south-west/north-east axis. Gap age was estimated from various factors (cf. Section 5.3.3). The majority of gaps studied (29/45) had been formed in the previous 5 years, almost a quarter (24%) were 5-10 years old and only 11% (5/45) were more than 10 years old. None of the gaps studied showed evidence of being more than 20 years old.

All three categories of disturbance (uprooting, snapping and crown damage) were found to contribute to some gap formation. The frequencies of these phenomena among the individual gaps studied are illustrated in Fig. 7.4. Uprooting was the most common cause of gap formation. Snapping of tree trunks was the least common type of disturbance.

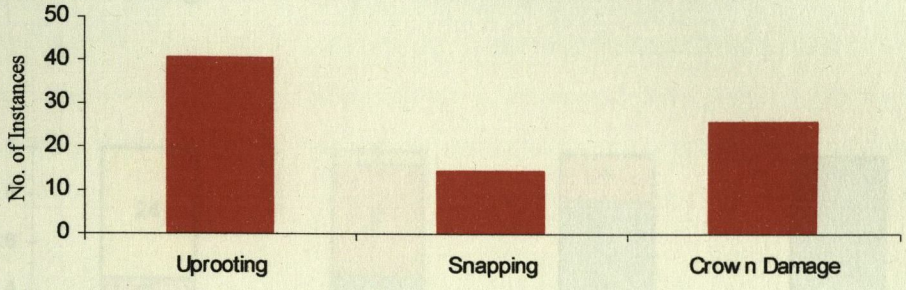

Fig. 7.4 Modes of gap formation

More than half (54%) of the gaps studied involved more than one tree. Such 'multiple' gaps often involved more than one type of disturbance within a single gap. Twenty-nine percent of multiple gaps involved a 'domino' effect, *i.e.* the disturbance of a second tree by the initial 'gap maker'. 'Domino' events resulted in all three categories of gap-forming disturbance (uprooting, snapping and crown damage). 'Dominoed' individuals were usually, but not always, smaller than the trees that knocked them.

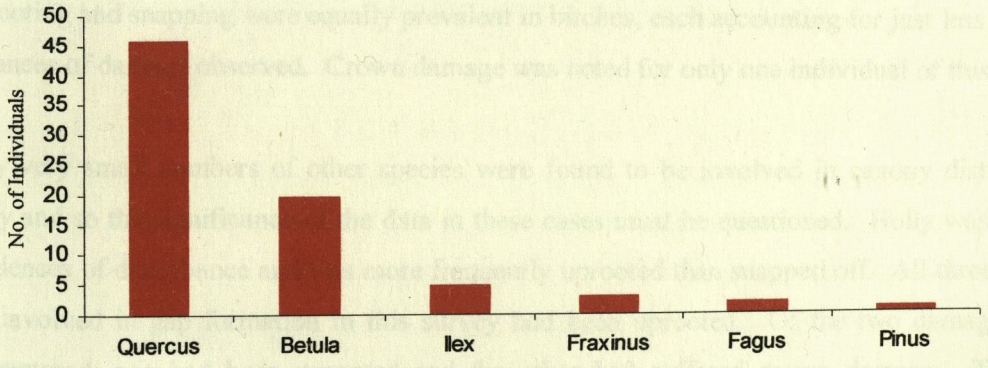

Fig. 7.5 Species involved in gap formation

The pattern of species involvement in gap formation was similar to the pattern observed in disturbance events (section 7.1). Oak and birch (which were the species most often affected by disturbance) were the most frequent gap makers, reflecting the dominance of these species in the canopies of most of the woodlands investigated. Holly frequently contributed to 'multiple' gaps in Tomies Wood, where this species is common in the sub-canopy. The frequency of each disturbance type for the more common gap makers is shown in Fig. 7.6.

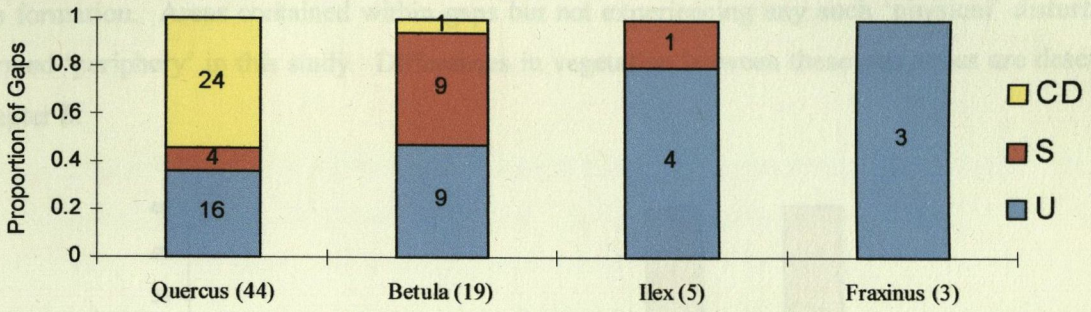

Fig. 7.6 The occurrence of different modes of disturbance for the more common gap makers. Numbers in brackets indicate the total number of DEs encountered for each species.

Crown damage was most common in oaks, and accounted for more than half of the instances of disturbance in this species. Uprooting was also frequent in oaks, and was the type of damage observed in 36% of cases. Less than 10% of gap-making oaks had been snapped off.

Uprooting and snapping were equally prevalent in birches, each accounting for just less than half of the instances of damage observed. Crown damage was noted for only one individual of this species.

Only very small numbers of other species were found to be involved in canopy disturbance in this study and so the significance of the data in these cases must be questioned. Holly was involved in 5 incidences of disturbance and was more frequently uprooted than snapped off. All three individuals of ash involved in gap formation in this survey had been uprooted. Of the two damaged beech trees encountered, one had been uprooted and the other had suffered crown damage. The single pine included in this study had been snapped off, when knocked by a falling beech tree.

7.3.2 Gap zonation: structure & soil properties

Structure

Each gap in this study was subjectively divided into zones, according to structural variation within the gap. The zones identified within gaps are listed in Table 7.5, and the frequency of each zone-type is illustrated in Fig. 7.7. Many gaps contained pits and mounds, areas along boles of fallen trees, and areas covered in fallen crown debris. The presence or absence of these zones is dependent on the mode of gap formation. Areas contained within gaps but not experiencing any such 'physical' disturbance are termed 'periphery' in this study. Differences in vegetation between these gap zones are described in Chapter 8.

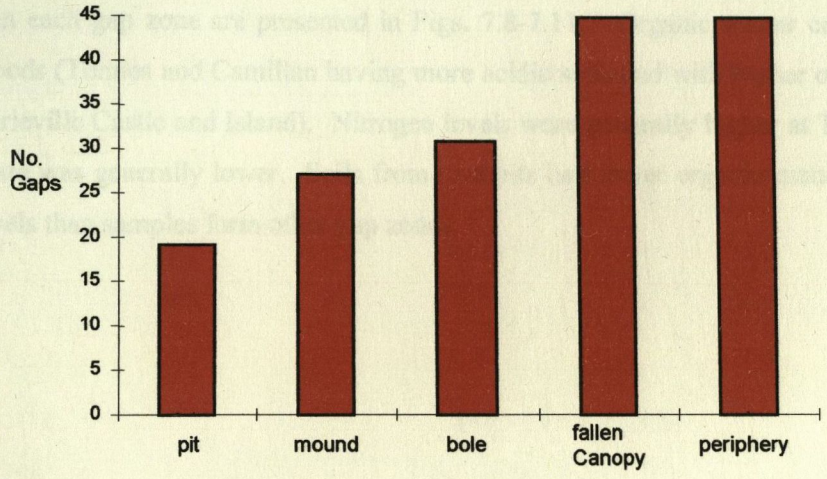

Fig. 7.7 The frequency of gap zones

Some pits were barely discernable, owing to the time lapse since uprooting occurred, while others were up to 2.3 metres deep. Mound dimensions ranged from 0.8m x 0.7m to 7.8m x 1.9m. Typically mounds were 1.5 - 4.0m x 1.0 – 2.5m in size. Fallen canopy debris was present in all of the gaps studied. The distribution of such material varied with the mode of gap formation. Where 'crown damage' was involved, fallen debris was usually located near the centre of the gap. Where uprooting or snapping of an individual was the mode of gap formation, the fallen canopy debris tended to be polarised towards the end of the gap opposite where the 'maker' had been/was still rooted. The extent and condition of fallen debris depended on the original amount deposited and the age of the disturbance event. 'Periphery' areas existed in all gaps, and typically occupied the area on either side of the maker's fallen trunk, between the mound (if present) and the fallen canopy zone.

Soil

Variation in soil properties between gap zones was investigated by sampling soil from gaps in four woodlands. Tomies and Camillan woods are located in the south-west of Ireland, over Devonian Old Red Sandstone, and are on peaty podzols. Charleville Castle and Island woods are located in the midlands on deep glacial till over Carboniferous limestone. Soil samples were taken from the different zones in gaps from each of these woodlands, and nitrogen, phosphate, pH and organic matter content were investigated (cf. section 5.3.6). Five gaps in Tomies, 4 in Camillan, 4 in Charleville Castle woods, and 2 gaps from the Island were sampled. Each zone present was sampled in duplicate. Samples were also taken form soils below woodland canopy adjacent to each gap.

The mean values for soil pH, organic matter content (by loss on ignition), total nitrogen and total phosphate in each gap zone are presented in Figs. 7.8-7.11. Organic matter content and pH varied between woods (Tomies and Camillan having more acidic soils and with higher organic matter content then at Charleville Castle and Island). Nitrogen levels were generally higher at Tomies and Camillan, but phosphate was generally lower. Soils from root pits had lower organic matter content, and lower nitrogen levels than samples form other gap zones.

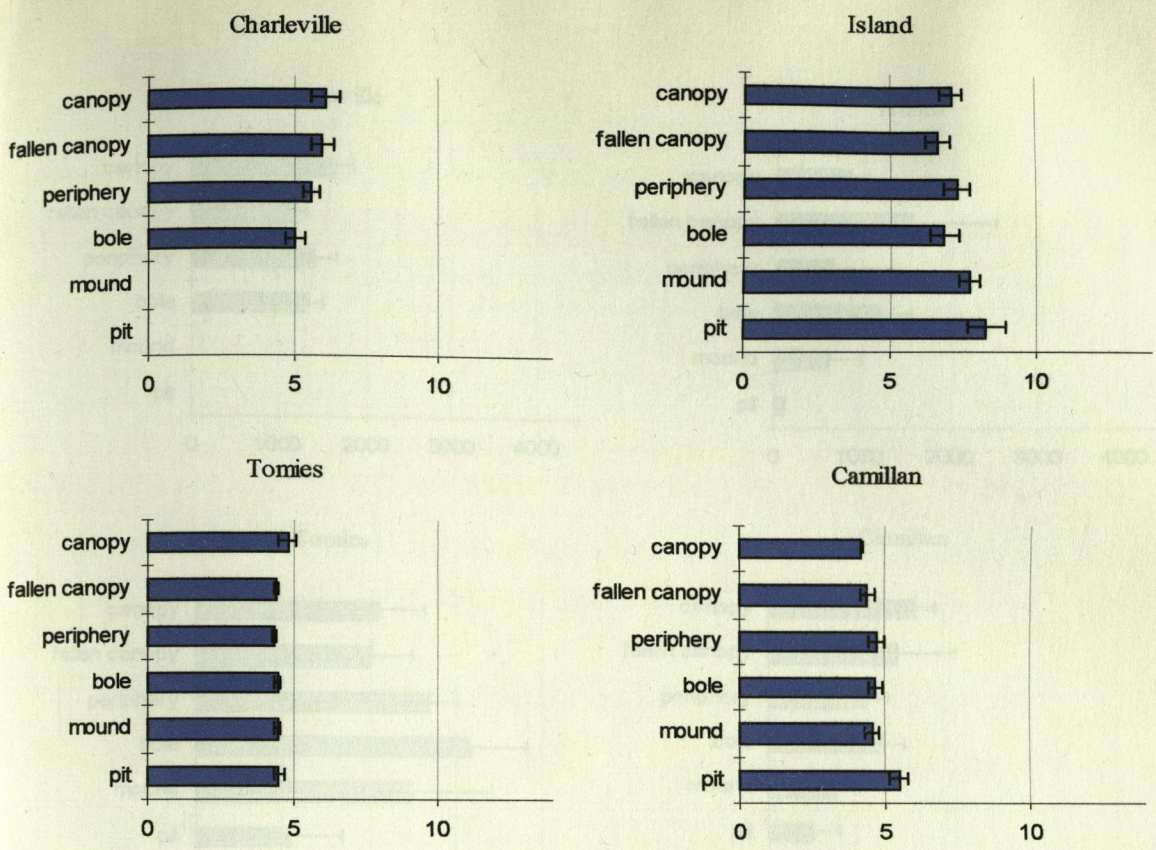

Fig. 7.8 Mean pH for soils in gap zones in four woods.

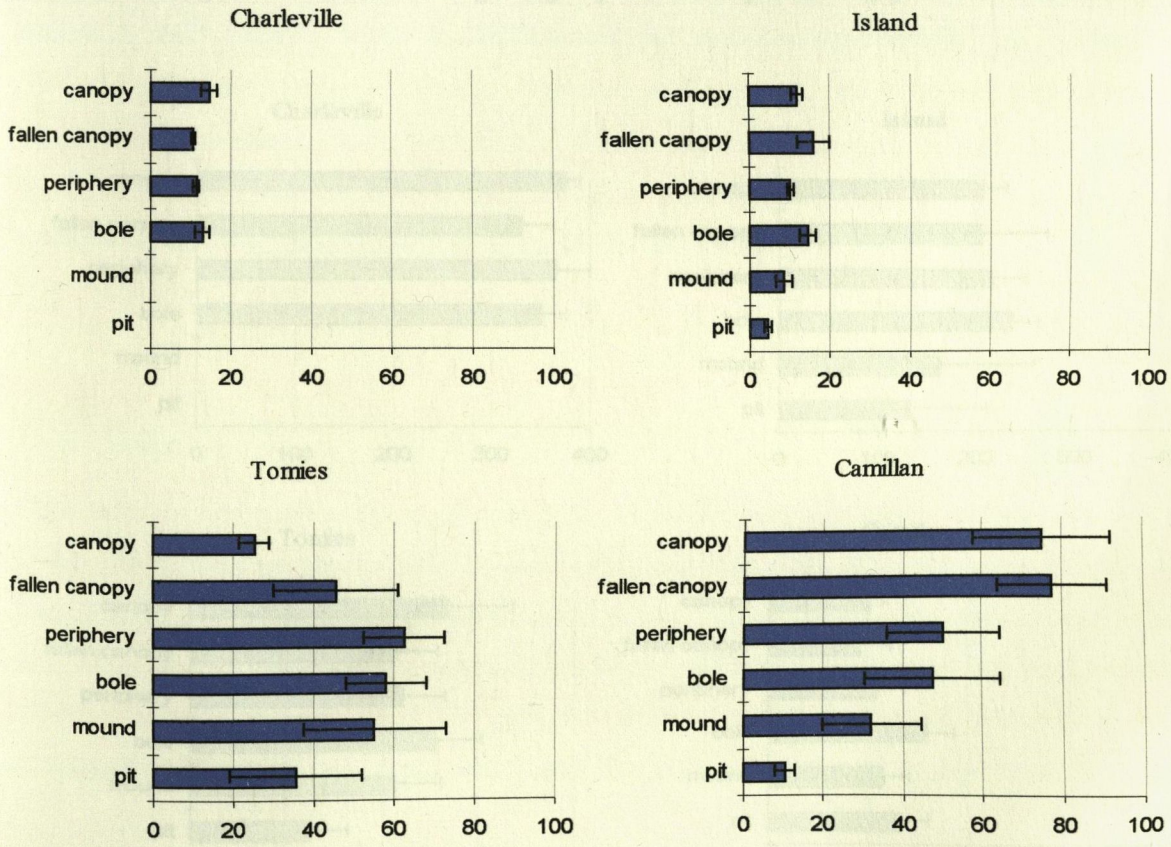

Fig. 7.9 Mean organic content (% by weight) of soils from gap zones in four woods.

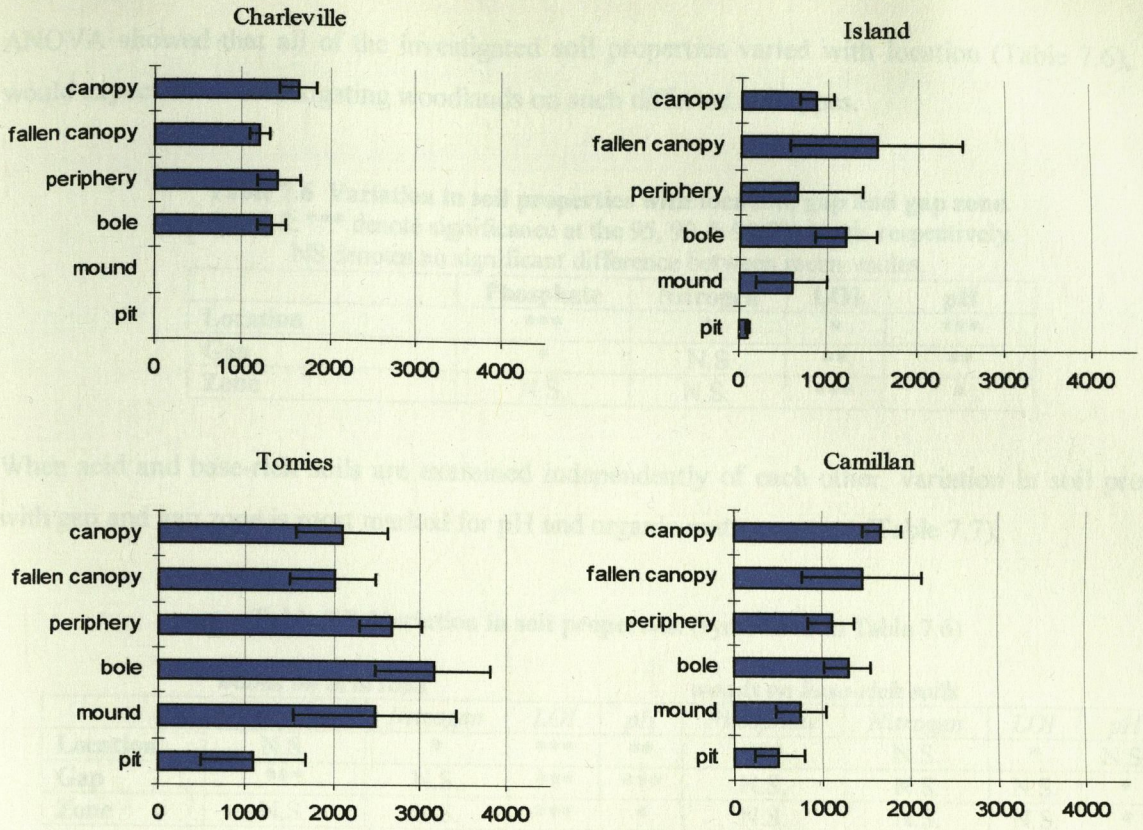

Fig. 7.10 Mean total Nitrogen (ug/ml) in soils sampled from gap zones in four woods.

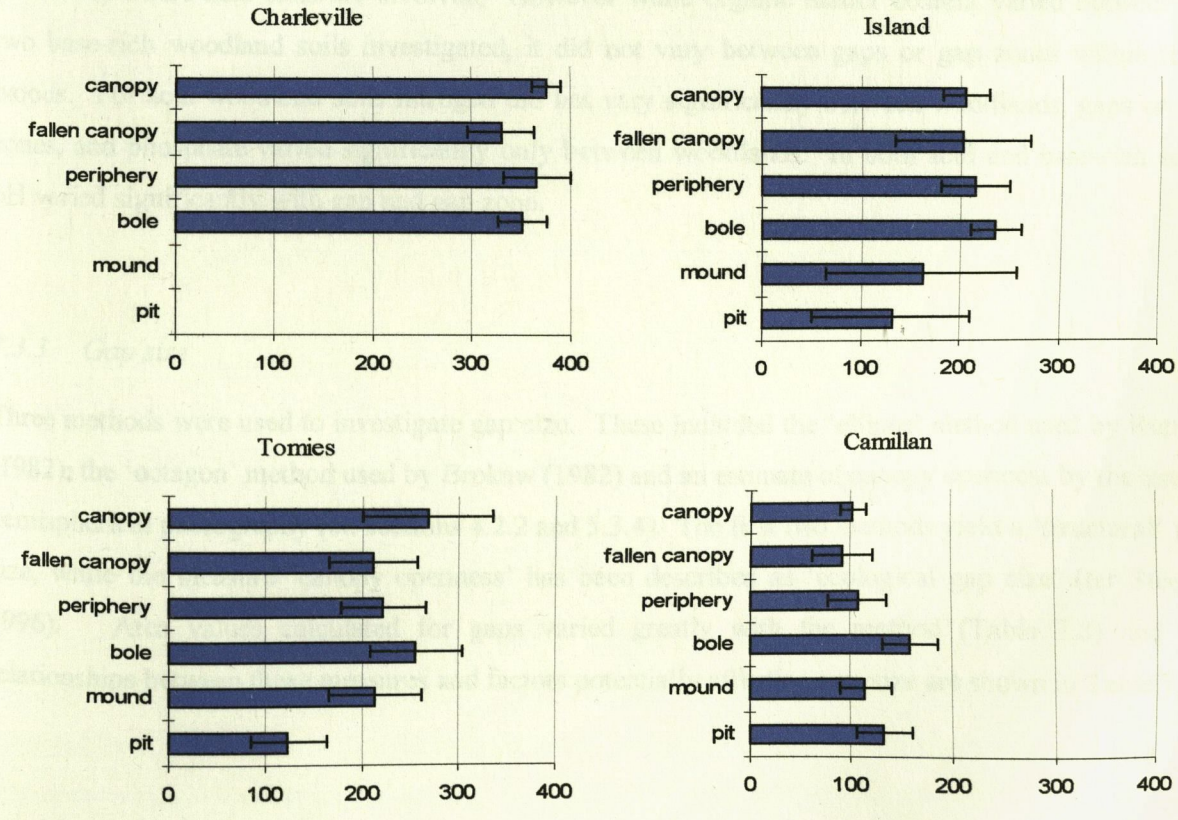

Fig. 7.11 Mean Total Phosphate (ug/ml) in soil samples from gap zones in four woods.

ANOVA showed that all of the investigated soil properties varied with location (Table 7.6), as one would expect when investigating woodlands on such different soil types.

Table 7.6 Variation in soil properties with location, gap and gap zone.
*, ** & *** denote significance at the 95, 99 & 99.9% levels respectively.
NS denotes no significant difference between mean vaules.

	Phosphate	Nitrogen	LOI	pH
Location	***	*	*	***
Gap	*	N.S	**	**
Zone	N.S.	N.S.	***	*

When acid and base-rich soils are examined independently of each other, variation in soil properties with gap and gap zone is most marked for pH and organic matter content (Table 7.7).

Table 7.7 Variation in soil properties. (symbols as in Table 7.6)

	woods on acid soils				***woods on base-rich soils***			
	Phosphate	*Nitrogen*	*LOI*	*pH*	*Phosphate*	*Nitrogen*	*LOI*	*pH*
Location	N.S.	*	***	**	***	N.S.	*	N.S.
Gap	***	N.S.	***	***	N.S.	N.S.	N.S.	*
Zone	N.S.	N.S.	***	*	N.S.	N.S.	N.S.	*

The pattern of variation in these soil properties differs between woods on acid soils and those on base-rich substrates. Organic matter content varies significantly between woods, gaps and gap zones ($P<0.001$) where acid soils are involved. However while organic matter content varied between the two base-rich woodland soils investigated, it did not vary between gaps or gap zones within these woods. For acid woodland soils nitrogen did not vary significantly between woodlands, gaps or gap zones, and phosphate varied significantly only between woodlands. In both acid and base-rich soils, pH varied significantly with gap and gap zone.

7.3.3 Gap size

Three methods were used to investigate gap size. These included the 'ellipse' method used by Runkle (1982), the 'octagon' method used by Brokaw (1982) and an estimate of canopy openness by the use of hemispherical photography (cf. sections 4.2.2 and 5.3.4). The first two methods yield a 'structural' gap size, while the measure 'canopy openness' has been described as 'ecological gap size' (ter Steege, 1996). Area values calculated for gaps varied greatly with the method (Table 7.8) and the relationships between these measures and factors potentially affecting gap size are shown in Table 7.9.

Table 7.8 Canopy gap size

'L' denotes the longest length of canopy opening, and 'W' the longest width at right angles to the measured length. % Openness is calculated from hemispherical photography from the centre of each gap (cf Section 5.3.4).

Gap	No. Makers	DBH (largest maker) (cm)	Canopy Ht (m)	L x W (m)	Ellipse (LWπ/4) (m^2)	% Openness	D:H
T1	1	39.5	22	5.7 x 5.1	23	8.3	0.2
T2	1	75.5	20	8.8 x 10.9	76	19.7	0.5
T3	2	84.4	20	35 x 12	330	21.3	1.2
T4	2	54.5	19	10.7 x 6.1	313	12.6	0.4
T5	2	63.7	20	27.1 x 14.7	296	39.7	1.0
T6	6	53.5	21	13 x 5.6	57	17.6	0.4
Gl1	2	33.4	12	6 x 18	85	16.7	1.0
Gl2	2	84.0	20	16.1 x 11	138	20.9	0.7
Gl3	2	44.6	20	11 x 9	78	8.0	0.5
Gl4	2	46.5	20	7 x 9	49	10.6	0.4
Un1	3	56.3	21	10.9 x 5.7	49	42.4	0.4
Un2	1	56.7	20	10.6 x 10.3	86	31.1	0.5
Un3	2	61.4	16	< 1 x 1	1	28.9	0.06
Un4	1	49.0	16	< 1 x 1	1	34.5	0.06
Ur1	2	28.7	16	11..3 x 7	62	52.4	0.6
Ur2	3	36.6	17	15 x 5.7	67	40.6	0.6
Ur3	1	31.5	17	15 x 5	59	55.2	0.6
Ur4	1	29.3	17	13.2 x 3.8	39	45.9	0.5
Gar1	1	66.2	18	18 x 10	141	-	0.8
Gar2	2	53.1	18	18 x 22	311	-	1.1
Gar3	20	70.2	17	50 x 50	1962	64.8	3.0
Gar4	2	54.1	15	17 x 13	173	-	1.0
Tf1	2	26.1	20	3.5 x 1.4	4	16.4	0.1
Tf2	1	89.3	27	4.7 x 2.1	8	12.6	0.1
P1	1	119	16	17 x 9	120	-	0.8
C1	2	67.8	17	14.5 x 5.7	65	40.0	0.6
C2	3	43.0	18	11.0 x 10.0	86	26.6	0.6
C3	2	57.3	17	17.2 x 12.6	170	32.7	0.9
C4	2	42.0	17	26.1 x 7.5	154	43.7	0.9
Cv1	1	31.8	23	14.7 x 27.4	285	-	0.9
Cv2	1	11.8	24	8.05 x 3.8	24	-	-
Cv3	2	90.7	28	5.6 x 9.5	41.8	19.7	0.3
Cv4	2	121.6	26	10.9 x 4.7	40	54.5	0.3
Cv5	1	113.3	26	9.0 x 7.8	55	28.3	0.3
Is1	2	26.1	27	19.2 x 15.3	231	31.4	0.3
Is2	3	52.5	28	8.5 x 5.7	38	29.5	0.2
M1	3	27.1	20	8.8 x 9.3	64	26.7	0.5
M2	2	57.3	16	4.9 x 4.8	18	28.5	0.3
M3	1	27.1	16	4.1 x 9.1	29	24.1	0.4
Ard1	1	33.0	11	7.3 x 5.1	29	59.2	0.6
Ard2	3	38.5	10	14.9 x 7.8	91	-	1.1
OH1	1	42.7	16	9.7 x 1.0	8	31.5	0.3
OH2	3	35.0	19	18.0 x 10.0	141	19.8	0.7
OH3	2	49.0	15	15.0 x 6.0	71	11.6	0.7
OH4	1	35.0	17	10.0 x 1.5	12	30.4	0.6
Mean (s.e.)	1.88 (0.14)	53.2 (3.8)			95.88 (14)	29 (2)	0.29 (.04)

Most of the gaps studied were relatively small, with 1 to 6 individuals involved in gap formation. The one exception to this was the felling coupe investigated at Garannon Wood (Gar3), from which 20 trees had been cut and removed. This gap has been omitted from general analyses of the gap size data. Gap area values ranged from less than 1 m^2 to 330 m^2 (the felling coupe was ~1962m^2). Canopy

openness ranged from ~8% to ~55% (canopy openness in the felling coupe was ~65%). Brokaw's octagon method consistently returned gap sizes at least one order of magnitude greater than those calculated with the 'ellipse' method (Runkle, 1982). Area values calculated by the ellipse method were quite closely related to the D:H ratio (r=0.754). Values obtained using Brokaw's octagon method have been dismissed from further application in this study, as the computation proved too sensitive to variation in canopy height and delineation of the gap edge.

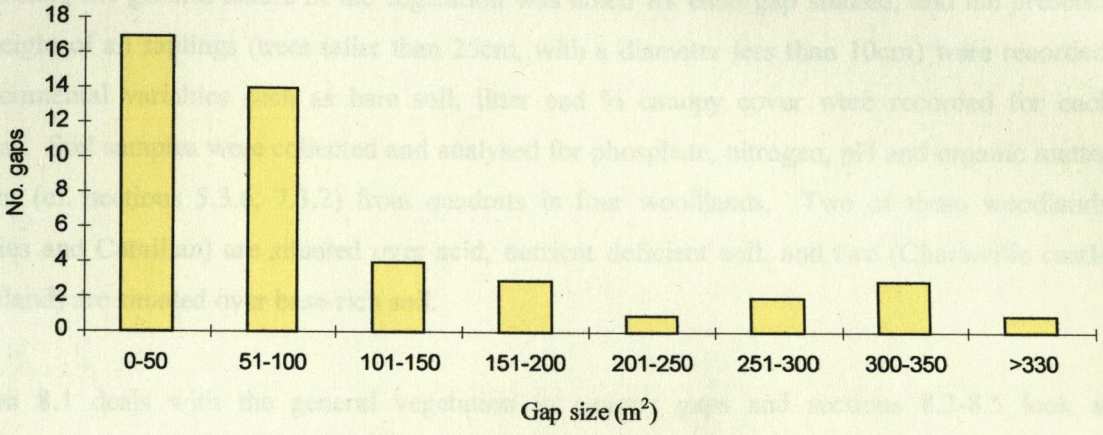

Fig. 7.12 Distribution of gap sizes. Gap area measured by Ellipse formula.

Table 7.9 Relationships between measures of gap size and related factors (Spearman rank correlation co-efficients). 'D:H' is the ratio of mean gap diameter to height of adjacent canopy; DBH is the diameter at breast height of the largest gap maker. * indicates significant correlation at the 95% confidence limit.

	% Openness	D.H	Octagon	Ellipse	DBH	No. Makers
% Openness	1.000					
D.H	0.172	1.000				
Octagon	0.761*	0.278	1.000			
Ellipse	-0.050	0.754*	0.031	1.000		
DBH	-0.117	-0.037	-0.056	0.151	1.000	
No. Makers	-0.100	0.123	-0.084	0.269	-0.005	1.000

These correlation coefficients reflect the disparate values obtained for gap size, depending on the method used. The significant correlation between the ratio of mean gap diameter to canopy height and the gap area yielded by the ellipse method reflects the fact that the same measure of gap diameter is used to compute both statistics. The relationship between Brokaw's 'octagon' area and canopy openness may stem from the fact that both measures were computed from a single hemi-phot of each gap, and so use essentially the same raw data to compute the area statistic. The low correlation between the number of gap makers and the gap area is not surprising considering the limited range, (in terms of the number of gap makers) of gaps available for study. (Note: the only gap formed by a large number of makers (50) was omitted from these analyses as it distorted the data.)

CHAPTER 8 VEGETATION IN CANOPY GAPS IN SEMI-NATURAL IRISH WOODLANDS

The vegetation of woodland canopy gaps was surveyed by the use of stratified random quadrats. Quadrats of 1 square metre were sampled from subjectively delineated zones within gaps (cf. section 5.3.5) and also from below closed canopy. In total, 273 quadrats were sampled from 45 gaps in 13 woods. Thirty-seven quadrats were sampled below closed canopy.

In addition, the general nature of the vegetation was noted for each gap studied, and the presence and height of all saplings (trees taller than 25cm, with a diameter less than 10cm) were recorded. Environmental variables such as bare soil, litter and % canopy cover were recorded for each quadrat. Soil samples were collected and analysed for phosphate, nitrogen, pH and organic matter content (cf. sections 5.3.6, 7.3.2) from quadrats in four woodlands. Two of these woodlands (Tomies and Camillan) are situated over acid, nutrient deficient soil, and two (Charleville castle and Island) are situated over base-rich soil.

Section 8.1 deals with the general vegetation in canopy gaps and sections 8.2-8.5 look at regeneration of canopy and sub-canopy species in canopy gaps.

8.1 Vegetation in canopy gaps

Forty-seven taxa (excluding bryophytes, canopy and sub-canopy species) of vascular plant were encountered during the survey. All of these occurred in gaps, none were restricted to canopy quadrats, and 15 occurred only in gaps (Table 8.1). However, the number of canopy plots sampled was very low (37) compared to the number of quadrats sampled from canopy gaps. Furthermore, examination of the distribution of those species confined to gaps reveals that they were rare species in the overall survey, often being present in a single gap, and in some cases, a single quadrat.

Table 8.1 Species occurring only in gap quadrats. The number in brackets indicates the number of quadrats in which each species was found.

Carex pendula (2)	*Arrhenatherum elatius (1)*	*Ulex europaeus (1)*
Brachypodium sylvaticum (1)	*Senecio* juv. *(4)*	*Erica tetralix (3)*
Rumex sanguineus (8)	*Crocosmia* x crocosmiiflora *(1)*	*Epilobium angustifolium (2)*
Urtica dioica (2)	*Deschampsia caespitosa (3)*	*Potentila sterilis (12)*
Viola sp. *(14)*	*Holcus mollis (2)*	*Rhododendron ponticum (9)*

The composition of ground cover in gaps varied between woodlands (Table 8.2). Litter cover were higher under canopy than in gaps ($P<0.05$) and while shrub cover was also higher in gaps, the high variability in values results in the difference not being statistically significant. Bryophyte cover was also higher under canopy than in gaps, however this difference is not statistically significant. Cover by both bare soil and herbs was higher in gaps than under canopy, but again the differences are not statistically significant.

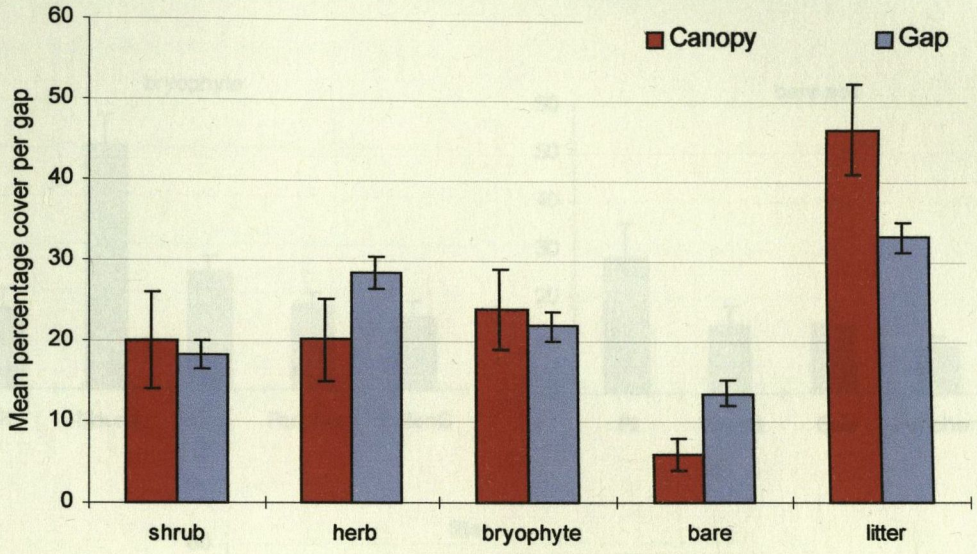

Fig. 8.1 Mean percentage cover in gaps and under canopy.

Table 8.2 Variation in cover between site, gap and canopy and gap zone. ANOVA output.

	Site	Canopy/Gap	Gap Zone
Shrub	***	*	N.S.
Herb	***	N.S.	***
Bryophyte	***	N.S.	***
Bare soil	***	N.S.	***
Litter	***	*	***

Cover varied between gap zones (Table 8.2, Fig. 8.2). Periphery quadrats had a higher cover by shrubs and herbs than other zones. Mounds generally had a high bryophyte cover, and pits were dominated by bare soil and litter. Quadrats sampled below fallen canopy also had high litter cover. Cover by herbs and shrubs was generally about 10% in pits. Litter cover was generally high (30% or higher) for all zones other than mounds.

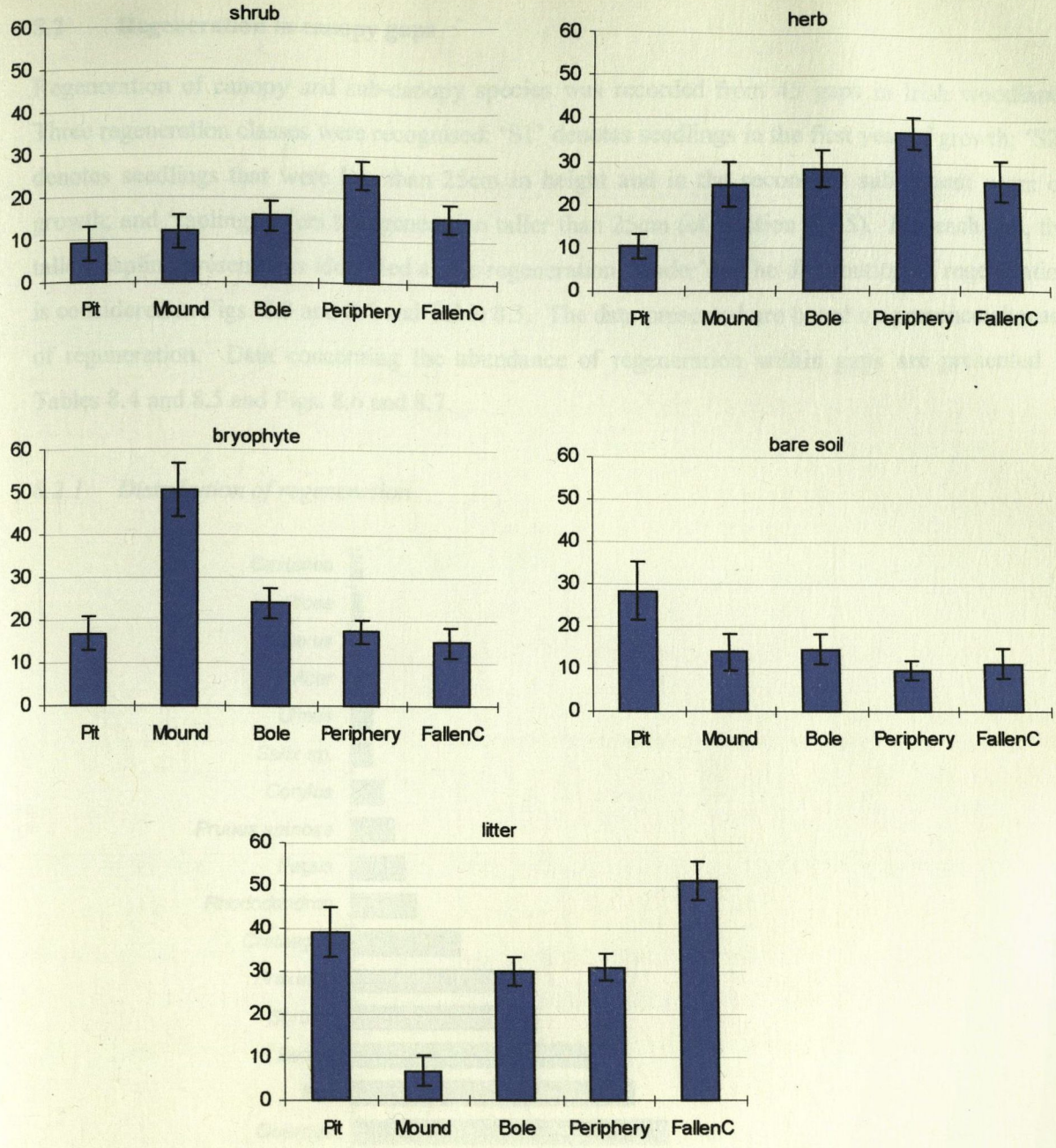

Fig. 8.2 Mean percentage cover of gap zones by vegetation groups.
(See Section 5.3.2 for description of gap zones)

8.2 Regeneration in canopy gaps

Regeneration of canopy and sub-canopy species was recorded from 45 gaps in Irish woodland. Three regeneration classes were recognised: 'S1' denotes seedlings in the first year of growth; 'S2' denotes seedlings that were less than 25cm in height and in the second or subsequent years of growth; and 'sapling' refers to regeneration taller than 25cm (cf. section 5.3.5). For each gap, the tallest sapling present was identified as the regeneration 'leader'. The distribution of regeneration is considered in Figs. 8.3 and 8.4 and Table 8.3. The data presented are based on presence/absence of regeneration. Data concerning the abundance of regeneration within gaps are presented in Tables 8.4 and 8.5 and Figs. 8.6 and 8.7.

8.2.1 Distribution of regeneration

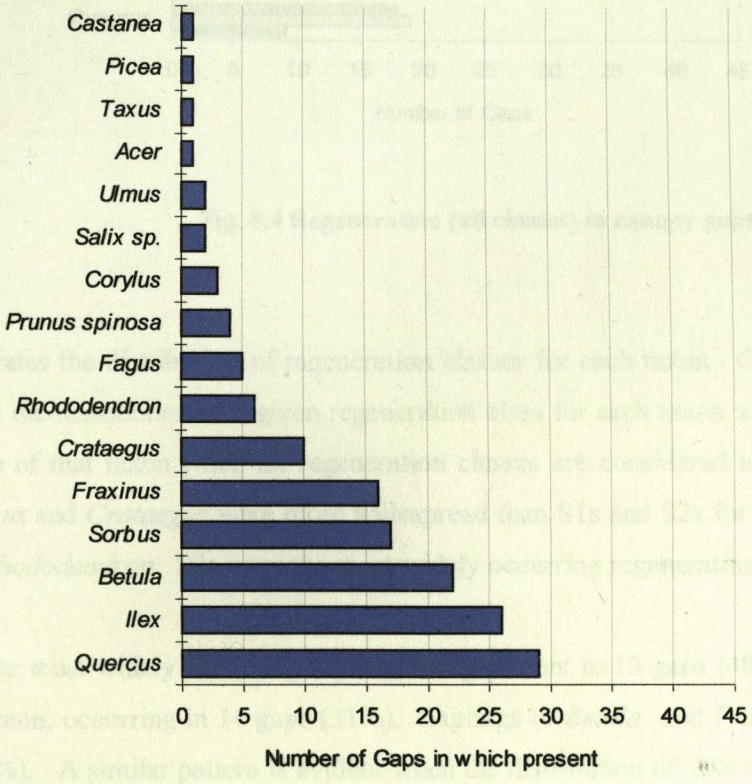

Fig. 8.3 Taxa regenerating in canopy gaps

Sixteen taxa were found to be regenerating in the canopy gaps surveyed. Three of these (*Castanea sativa, Picea sitchensis,*and *Taxus baccata*) were each represented by a single individual in a single gap. Owing to hybridisation and the difficulty in conclusively identifying juveniles, *Quercus robur* and *Q. petraea* are not differentiated here and are referred to jointly as *Quercus*.

No taxon was ubiquitous. *Quercus* was the most widespread regenerating taxon, occurring in 29 gaps (64%). *Ilex, Betula, Sorbus* and *Fraxinus* were also widespread, being present in 58%, 49%, 38% and 36%, respectively, of gaps. Eight taxa were found to be regenerating in less than 10% (less than 5) of the gaps studied.

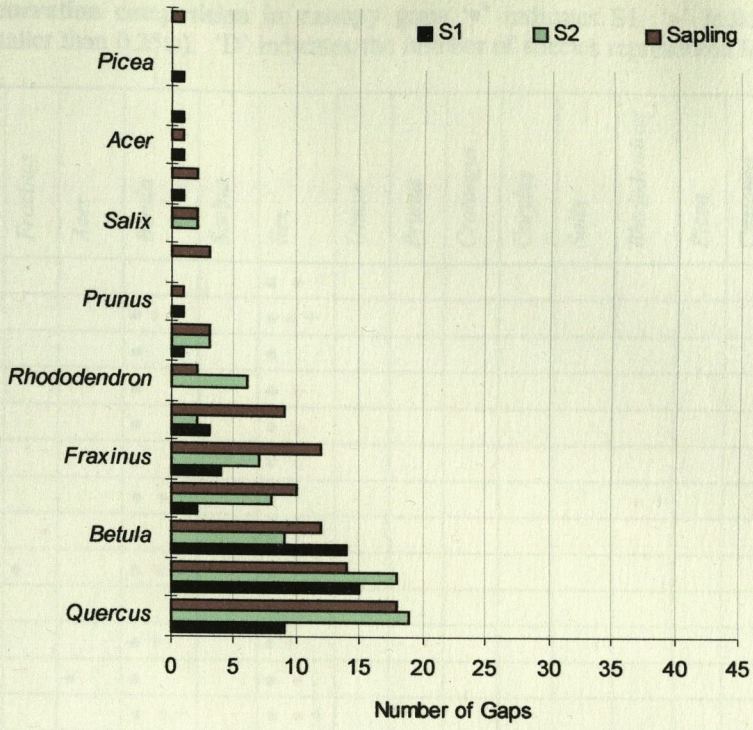

Fig. 8.4 Regeneration (all classes) in canopy gaps.

Fig. 8.4 illustrates the distribution of regeneration classes for each taxon. Comparison with Fig. 8.3 shows that the distribution of a given regeneration class for each taxon was more limited than the distribution of that taxon when all regeneration classes are considered together. Saplings of *Fraxinus, Sorbus* and *Crataegus* were more widespread than S1s and S2s for these taxa. For *Ilex, Quercus* and *Rhododendron,* S2s were the most widely occurring regeneration class.

Quercus was the most widely occurring sapling, being present in 18 gaps (40%). Saplings of *Ilex* were also common, occurring in 14 gaps (31%). Saplings of *Betula* and *Fraxinus* each occurred in 12 gaps (27%). A similar pattern is evident when the distribution of S2s is considered. Again, *Quercus* and *Ilex* were the most widespread, with S2s of these taxa being present in 19 (42%) and 18 (40%) of gaps respectively. S2s of *Betula, Sorbus* and *Fraxinus* were common, being present in 9 (20%), 8 (18%) and 7 (16%) of gaps, respectively. The distribution of S1s differed somewhat from that for S2s and saplings. *Ilex* and *Betula* were the most widespread S1s, occurring in 15 (33%) and 14 (31%) gaps, respectively. S1s of *Quercus* were relatively common, occurring in 9 (20%) of gaps.

8.2.2 Composition of regeneration in canopy gaps

Table 8.3 gives the regeneration composition (presence/absence) of each gap surveyed. Data are derived from the quadrats sampled and from the general survey of vegetation for each gap.

Table 8.3 Regeneration composition in canopy gaps '•' indicates S1, '•' indicates S2, '+' indicates saplings (stems taller than 0.25m). 'D' indicates the number of species represented for a given regeneration class.

Gap Code	*Quercus*	*Fagus*	*Fraxinus*	*Acer*	*Betula*	*Sorbus*	*Ilex*	*Ulmus*	*Prunus*	*Crataegus*	*Corylus*	*Salix*	*Rhododendron*	*Picea*	*Castanea*	*Taxus*	D S1	D S2	D Sapling	D All classes
T1	• •						• •										2	2	0	2
T2	• +				• • +		• • +										2	3	3	3
T3	• •				•		•										3	1	0	3
T4	• •				•		• •										3	2	0	3
T5					•		• •										2	1	0	2
T6					•		• •										2	1	0	2
C1	•				• • +	•	• +						• +				2	4	3	5
C2	•		•		•		• •										2	3	0	4
C3	• • +		•		• • +		• • +										4	3	3	4
C4						+	• •										1	1	1	2
M1	+				• +		• +										2	0	3	3
M2	•			•	•		• •										4	1	0	4
M3	• • +				• • +		• • +									•	4	3	3	4
Ur1	+				• +	• +											0	2	3	3
Ur2	+				•	• +	• +										1	2	3	4
Ur3	+					• +	+										0	1	3	3
Ur4	+				•	+											0	1	2	3
Un1																				
Un2																				
Un3	+				+		•										0	1	2	3
Un4	+				+	•	• +										2	0	3	4
Gl1	•				• •		•						•				2	3	0	4
Gl2	+		+		+												0	0	3	3
Gl3					+	+	+						•			•	1	1	3	5
Gl4	•					•	•						•				0	4	0	4
OH1					• •	+											1	1	1	2
OH2					+												0	0	1	1
OH3	• +	• +	•			+	• +										0	4	4	5
OH4	•	•	•				• +										0	4	1	4
Gar1	• +		+					+		+							0	1	4	4
Gar2		+	+					+		+							0	0	4	4
Gar3	• +											• +					0	2	2	2
Gar4	• +		+							+							0	1	3	3
Tf1					+												0	0	1	1
Tf2		+					+										0	0	2	2
P1	• • +						• +					+	• +		+		1	3	5	5
Ard1	•							•									2	0	0	2
Ard2	• +					+	+				+						0	1	4	4
Cv1			• +						• +	• • +							2	2	3	3
Cv2			• • +	+						+							1	1	3	3
Cv3	• +		• +							• • +							2	2	3	3
Cv4			• +							+							0	1	2	2
Cv5	•		+														0	1	1	2
Is1	• •		• • +							+	+						2	2	3	4
Is2			+							• +	+	•	•				1	2	3	5

Some tree regeneration was present in all gaps studied, with the exception of two gaps at Union Wood, Co. Sligo (Un1 and Un2). More than 70% (33/45) of gaps contained saplings. Thirty-seven gaps (82%) contained S2s, and 25 gaps (56%) contained S1s of at least one species.

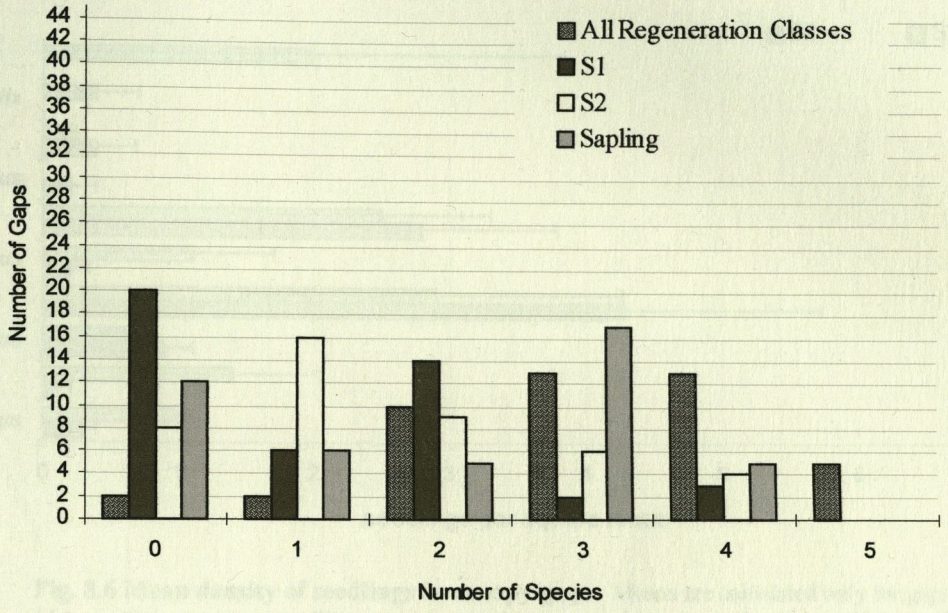

Fig. 8.5 Diversity of regeneration in canopy gaps

Fig. 8.5 illustrates the diversity of regeneration in the gaps surveyed. Five gaps (11%) contained regeneration of 5 different species. Thirty-six gaps (80%) gaps contained regeneration of 2 or more species. High diversity among saplings was the most widespread, with 21 gaps (47%) containing saplings of 3 or more species.

Table 8.3 shows the combinations of regeneration class and species that occurred in canopy gaps. Regeneration of *Ilex* and *Betula* was commonly present within a single gap. Similarly, regeneration of *Crataegus* and *Fraxinus* frequently co-occurred within a single gap. In both of the gaps in which only a single species of regeneration was present, *Betula* was the regenerating species. Rare taxa (those which occurred in only one or two gaps *i.e. Picea sitchensis, Castanea sativa, Taxus baccata* and *Salix* spp.) contributed to the diversity in those gaps that contained the highest number of regenerating taxa. Such gaps usually contained four of the more common regenerating species plus a rare taxon.

8.2.3 *Abundance of regeneration*

The abundance of seedlings (S1s and S2s) was estimated for each gap from the seedling counts made in quadrats sampled for each gap (Table 8.4). The mean densities of the commonly occurring seedlings are illustrated in Fig. 8.6.

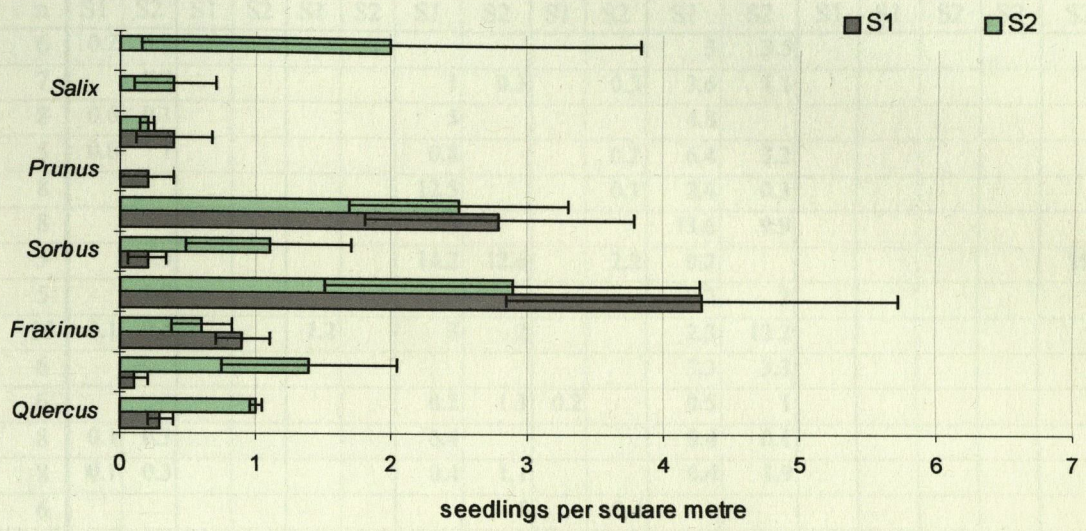

Fig. 8.6 Mean density of seedlings in canopy gaps. Means are calculated only for gaps in which seedlings were present. The mean presented represents the average density at which seedlings were present *i.e.* the average of the mean density for each gap where the species was present. Error bars indicate standard error on the mean.

S1s of *Betula* occurred at the highest density, with an average of more than 4 seedlings per square metre in gaps where seedlings were present. Seedlings of *Ilex* and *Rhododendron* also occurred at high densities. The large error values shown in Fig. 8.6 are indicative of the great variation in seedling densities that occurred even within single gaps (see Table 8.4). Densities of S1s were generally higher than densities of S2s for *Ilex, Fraxinus* and *Betula.* Conversely, S2s were more abundant than S1s for *Quercus, Sorbus* and *Fagus*.

Table 9.4 shows the mean density of S1s and S2s for all gaps surveyed. Seedling densities were less than 1/m^2 for most species in most of the gaps studied. Seedlings of *Betula* achieved the highest densities, with 14.2 S1/m^2 and 12.6 S2/m^2 present in one gap. Seedlings of *Ilex* also occurred at high densities, with 13.6 S1/m^2 and 9.9 S2/m^2 occurring in one gap. Seedlings of *Quercus* (which were among the most widespread regeneration) were generally present at low densities. *Quercus* S1s were never present at densities higher than 1 seedling/m^2. While *Quercus* S2s were often present at densities higher than 1 seedling/m^2, in 37% of the gaps in which any were present, the density was 5 S2/m^2 or lower.

Table 8.4 Mean density of seedlings (seedlings per m^2) per gap. Species that occurred only once are not included. Data are derived from the 1 x 1 m quadrats sampled in each gap. 'n' denotes the number of quadrats sampled in each gap.

Gap Code		*Quercus*		*Fagus*		*Fraxinus*		*Betula*		*Sorbus*		*Ilex*		*Prunus*	*Crataegus*		*Salix*	*Rhododendron*
	n	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S1	S2	S2	S2
T1	6	0.2	0.8									3	3.5					
T2	7		0.7					1	0.3		0.3	3.6	1.1					
T3	8	0.6	0.1					5				4.8						
T4	5	0.6	1					0.8			0.2	6.4	3.2					
T5	8							12.5			0.1	2.6	0.3					
T6	8							0.8				13.6	9.9					
C1	5		1.4					14.2	12.6		2.2	0.2						10.4
C2	5		1.2				0.2	0.2				0.2	2					
C3	10	0.1	0.3			1.2		3	2			2.3	12.2					
C4	6											3.3	3.3					
M1	6							0.2	1.3	0.2		0.5	1					
M2	8	0.1	0.3					6.4				0.4	0.1					
M3	8	0.1	0.3					0.4	1.1			0.4	1.9					
Ur1	6								5		0.2							
Ur2	6							13.3			5		1.7					
Ur3	5										0.2							
Ur4	5								0.8									
Un1	4																	
Un2	6																	
Un3	6												0.2					
Un4	6									0.2		0.5						
Gl1	4	0.8						1.3	2.3				0.3					0.5
Gl2	5																	
Gl3	3																	0.3
Gl4	4		0.3								0.8		2.5					0.5
OH1	6							1.7	0.5									
OH2	6																	
OH3	7		1		2		0.1						0.7					
OH4	7		0.3		2.1		0.1						0.3					
Gar1	5		2															
Gar2	5																	
Gar3	6		5														0.7	
Gar4	5		0.4															
Tf1	3																	
Tf2	3																	
P1	8	0.3	0.3										0.1					0.3
Ard1	8	0.1										0.1						
Ard2	8		0.1															
Cv1	5						1.2							0.2	0.2	0.2		
Cv2	4					1.5	1.5											
Cv3	8		1.9			0.5									0.1	0.1		
Cv4	8						0.3											
Cv5	8		0.4															
Is1	8			0.1	0.1	0.4	0.9											
Is2	7														1		0.1	0.1

The numbers of saplings present in each gap are given in Table 8.5. The mean numbers present are presented for those species that occurred in 3 or more gaps in Fig. 8.7. Saplings of *Ilex* frequently occurred in high numbers within a single gap: in the 14 gaps in which they were present, 9 gaps contained 5 or more saplings. Six gaps contained more than 10 *Ilex* saplings each. Saplings of *Quercus* tended to occur in lower numbers: In two-thirds (12/18) of the gaps that contained *Quercus* saplings, less than 5 individuals were present. Seven gaps each contained a single *Quercus* sapling. Saplings of *Fraxinus* occurred both in high numbers (5 or more per gap in 6 gaps) and lower numbers (less than 5 individuals in each of 5 gaps). *Sorbus* and *Betula* also demonstrated variation in this regard, while *Crataegus* was represented by a single individual in all but 2 of the gaps in which it was present.

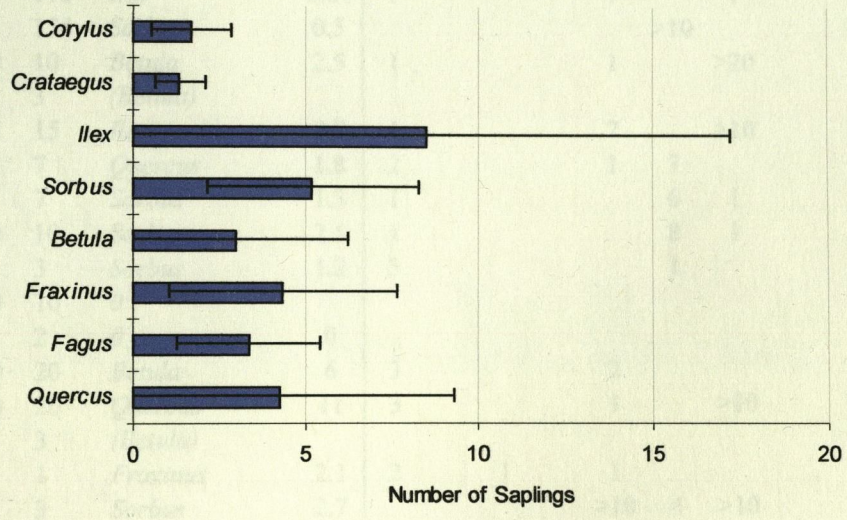

Fig. 8.7 Mean number of saplings per gap. Means calculated only from gaps in which saplings were present. Gap sizes range from $1m^2$ to 330 m^2.

Comparison of Tables 8.4 and 8.5 illustrates that the presence, and even abundance, of seedlings (S1 and S2 combined) does not guarantee the future presence of saplings in a gap. *E.g.* while four of the six gaps studied in Tomies Wood contain *Quercus* seedlings, only one gap contains a single *Quercus* sapling. Gaps in this woodland have an abundance of *Sorbus, Betula* and *Ilex* seedlings, however only one gap has saplings of *Ilex* and *Betula*, and no Tomies gap contains a *Sorbus* sapling. Conversely, two of the gaps in Union Wood (Un 3 &4) contained saplings of *Quercus* and *Betula*, but no seedlings of these species. Similarly, gaps at Garannon (Gar 1-4) contained saplings of four species, for which no seedlings were present.

Table 8.5 Numbers of saplings (regeneration >25cm in height) in canopy gaps. 'Leader' indicates the tallest sapling present. Species in brackets indicate the dominant seedlings present in gaps containing no saplings. Figures given are the total number of saplings present in each gap.

Gap Code	Gap Age (Yrs)	Gap Area (m^2)	Leader	Leader Height (m)	*Quercus*	*Fagus*	*Fraxinus*	*Acer*	*Betula*	*Sorbus*	*Ilex*	*Ulmus*	*Prunus*	*Crataegus*	*Corylus*	*Salix*	*Rhododendron*
T1	1	23	*(Ilex)*														
T2	3	76	*Quercus*	1.3	1				1		6						
T3	1	330	*(Ilex, Betula)*														
T4	2	313	*(Ilex)*														
T5	2	296	*(Betula)*														
T6	2	57	*(Ilex)*														
C1	3	65	*Rhododendron*	1					2		>30						>10
C2	5	86	*(Ilex)*														
C3	3	170	*Ilex*	0.64	1				1		7						
C4	1	154	*Sorbus*	0.5						>10							
M1	10	10	*Betula*	2.5	1				1		>20						
M2	3	3	*(Betula)*														
M3	15	15	*Ilex*	0.7	1				7		>10						
Ur1	7	7	*Quercus*	1.8	2				1	7							
Ur2	7	7	*Sorbus*	1.3	1					6	1						
Ur3	10	10	*Sorbus*	2.5	1					8	1						
Ur4	3	3	*Sorbus*	1.2	5					1							
Un1	10	10	*0*														
Un2	2	2	*0*	0													
Un3	20	20	*Betula*	6	3				2								
Un4	20	20	*Quercus*	11	3				1		>10						
Gl1	3	3	*(Betula)*														
Gl2	1	1	*Fraxinus*	2.1	2		1		1								
Gl3	3	3	*Sorbus*	2.7					>10	4	>10						
Gl4	2	2	*(Ilex)*														
OH1	10	10	*Sorbus*	4						5							
OH2	7	7	*Sorbus*	4					4	5							
OH3	5	5	*Sorbus*	1.7	5	5				4	1						
OH4	7	7	*Fraxinus*	1.6			1				1						
Gar1	2	141	*Fraxinus*	2.7	>10		2					2		1			
Gar2	2	311	*Fraxinus*	2.5		1	2					1		2			
Gar3	4	1962	*Salix*	2.5	$5m^{-2}$											$2m^{-2}$	
Gar4	3	173	*Fraxinus*	6	1		9							1			
Tf1	2	4	*Betula*	3					1								
Tf2	2	8	*Fagus*	6		4					1						
P1	2	120	*Quercus*	1	20						>10					5	>10
Ard1	2	29	*(Quercus, Ilex)*														
Ard2	1	91	*Ilex*	1.9	10					1	5				1		
Cv1	10	285	*Fraxinus*	7			>10						1	1			
Cv2	7	24	*Fraxinus*	3.8			5	1						1			
Cv3	5	42	*Fraxinus*	8	4		3							1			
Cv4	2	40	*Fraxinus*	10			5							1			
Cv5	5	55	*Fraxinus*	1			5										
Is1	7	231	*Crataegus*	1.6			1							3	3		
Is2	15	38	*Crataegus*	6			7							1	1		

The tallest sapling in each gap was noted and deemed the 'leader' in that gap (see Table 8.5). *Fraxinus* was the most frequent leader (10 gaps,) but (as a sapling) was confined to gaps in five woodlands (Figs. 8.8 & 8.9). The heights of *Fraxinus* leaders ranged from 1m to 10m. In all but two of the gaps in which *Fraxinus* saplings were present, this species was the leader. *Sorbus* was the next most frequent leader, and was the tallest sapling in eight gaps. All except one of the gaps in which *Sorbus* was the leader also contained saplings of other species. *Quercus*, the most widespread sapling, was the tallest sapling in only four of the forty-five gaps surveyed. Each of these gaps was in a different woodland, and *Quercus* leaders ranged in height from 1 to 11m. In all four gaps in which *Quercus* was the leader, saplings of other species also occurred. *Betula* was the tallest sapling in three of the gaps studied, and in one gap (Tf1) was the only sapling present.

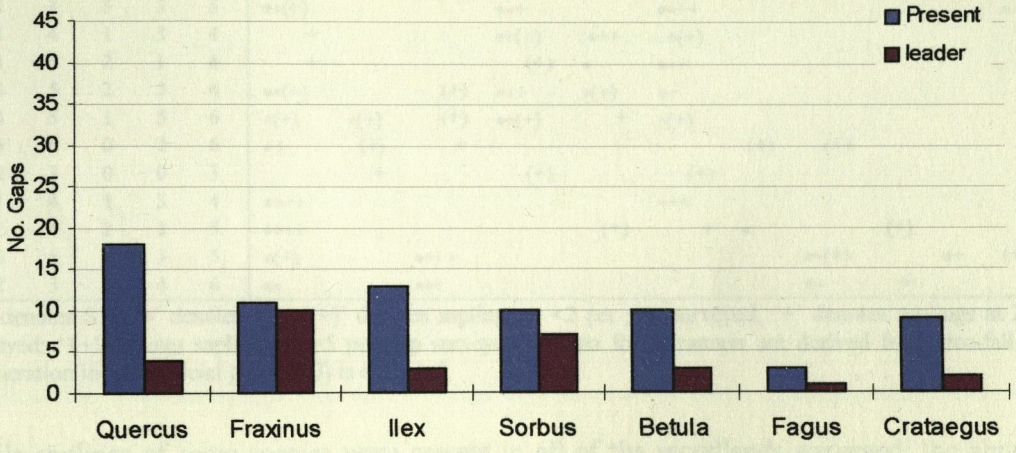

Fig. 8.8 The occurrence of saplings in canopy gaps, and their frequencies as leaders (tallest sapling present).

Crataegus was the leader in two gaps and *Ilex* in three. Both of these species occurred as leaders in gaps in which saplings of other species were also present.

Twelve of the gaps surveyed contained no saplings and for these, the dominant (most abundant) seedling present is indicated in Table 8.5. In those five gaps in Tomies wood that contained no sapling, seedlings of *Betula, Ilex* or a combination of the two, dominated regeneration. In fact, these two species (*Ilex* and *Betula*) were the dominant seedlings in all of the gaps in which no sapling occurred.

8.3 Regeneration on the woodland scale

Table 8.6 summarises the occurrence of regeneration for tree and sub canopy species in canopy gaps in the 13 woodlands surveyed. Every woodland contained regeneration of at least three species. Five woodlands contained regeneration of six species.

Table 8.6 Regenerating species in surveyed woodlands

Wood	No. Gaps	D Saplings	D S1	D S2	D All Classes	*Quercus*	*Fagus*	*Fraxinus*	*Betula*	*Sorbus*	*Ilex*	*Ulmus*	*Crataegus*	*Corylus*	*Prunus*	*Acer*	*Salix*	*Rhododendron*
T	6	3	3	3	3	•(+)			•(+)		•(+)							
C	4	5	4	6	6	•(+)			•(+)	+	•++							+
M	3	3	5	3	5	•(+)			•+		•++					•		
Ur	4	4	1	3	4	+			•(+)	•++	•(+)							
Un	4	3	2	1	4	+			(+)	•	•+							
Gl	4	5	2	5	6	•(+)		(+)	•+	•(+)	•+							•
OH	4	5	1	5	6	•(+)	•(+)	(+)	•(+)	+	•(+)							
Gar	4	6	0	2	6	•+	(+)	+				(+)	(+)					
Tf	2	3	0	0	3		+		(+)		(+)							
P	1	4	1	3	4	•++					•++						++	•++
Ard	2	4	2	1	5	•++				(+)	+	•		(+)				
Cv	5	5	3	3	5	•(+)		•++					•(+)		•+	(+)		
Is	2	3	3	4	6	••		•+					•+	+			•	•

'•' denotes S1s; '•' denotes S2s; '(+)' denotes saplings at <2 per gap surveyed; '+' denotes saplings at 2-5 per gap surveyed; '++' denotes saplings at >5 per gap surveyed. *Data for Garannon are derived from tree-fall gaps only: regeneration in the artificial gap (Gar3) is excluded.

While saplings of some species were present in all of the woodlands surveyed, the abundance of saplings varied between species and woodland. Saplings of *Quercus* were present in 11/13 woodlands, but were sparse in 6 of these, with the equivalent of less than 2 *Quercus* saplings per gap. In 3 of the remaining 7 woodlands, *Quercus* saplings were present at a density of 2-7 individuals per gap. Two woodlands contained more than 5 *Quercus* saplings per gap surveyed. Saplings of *Ilex* were present in 10 woodlands, and were abundant in many of the woodlands where it was present. *Ilex* saplings were present at more than two per gap, in six of the surveyed woodlands.

Woodland type clearly affected the species of regeneration present, with species like *Betula, Sorbus* and *Ilex* concentrated in woodlands on acid soils, while *Fraxinus* and *Crataegus* were confined to woodland over base rich substrate (Table 8.3, Fig. 8.10; see Chapter 6 for woodland descriptions). This clearly reflects the differing suitability of sites for germination and growth of different species, and also the distribution of parent (seed producing) trees.

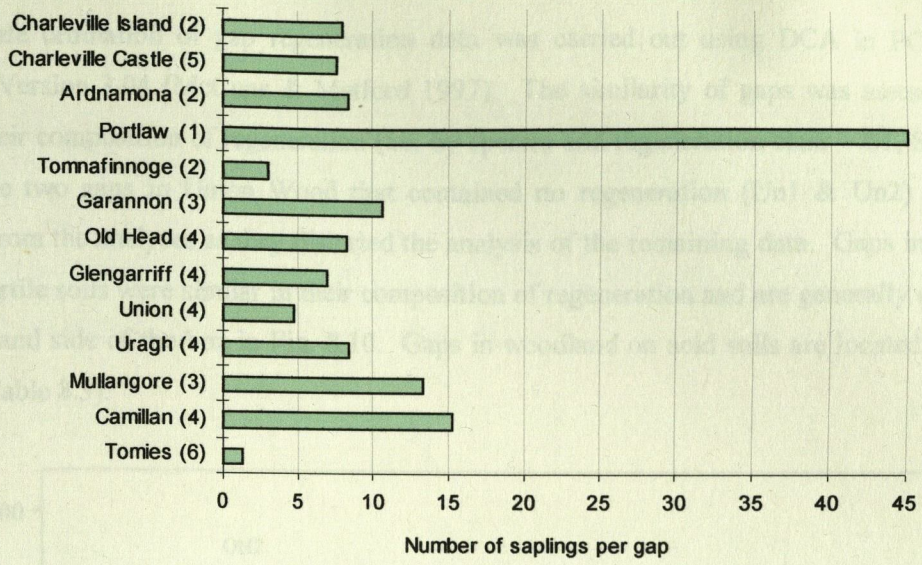

Fig.8.9 Abundance of saplings in woodlands. Numbers in brackets indicate the number of gaps sampled per woodland.

Portlaw Wood contained the highest abundance of saplings. A thicket of *Rhododendron ponticum* accounts for ten of the saplings present. However only one gap was sampled in this woodland. Tomies and Tomnafinnoge Woods contained the least number of saplings, with only 1.3 and 3 saplings per gap respectively. Tomies Wood is heavily grazed by sika deer, and has a history of sustained heavy grazing by both deer and, until recent years, sheep. The gaps surveyed in Tomnafinnoge Wood were located in a stand dominated by mature *Fagus sylvatica*, which casts a heavy shade. The other woodlands studied contained 5-15 saplings per gap.

8.4 Regeneration on the gap scale

Multi-variate ordination of gap regeneration data was carried out using DCA in PC-ORD for Windows Version 3.04 (McCune & Metford 1997). The similarity of gaps was assessed on the basis of their composition of regeneration (*i.e.* by species and regeneration class – S1, S2, Sapling (S3)). The two gaps in Union Wood that contained no regeneration (Un1 & Un2) have been excluded from the analyses as they distorted the analysis of the remaining data. Gaps in woodland on more fertile soils were similar in their composition of regeneration and are generally clumped to the right-hand side of the box in Fig. 8.10. Gaps in woodland on acid soils are located to the left (see also Table 8.3).

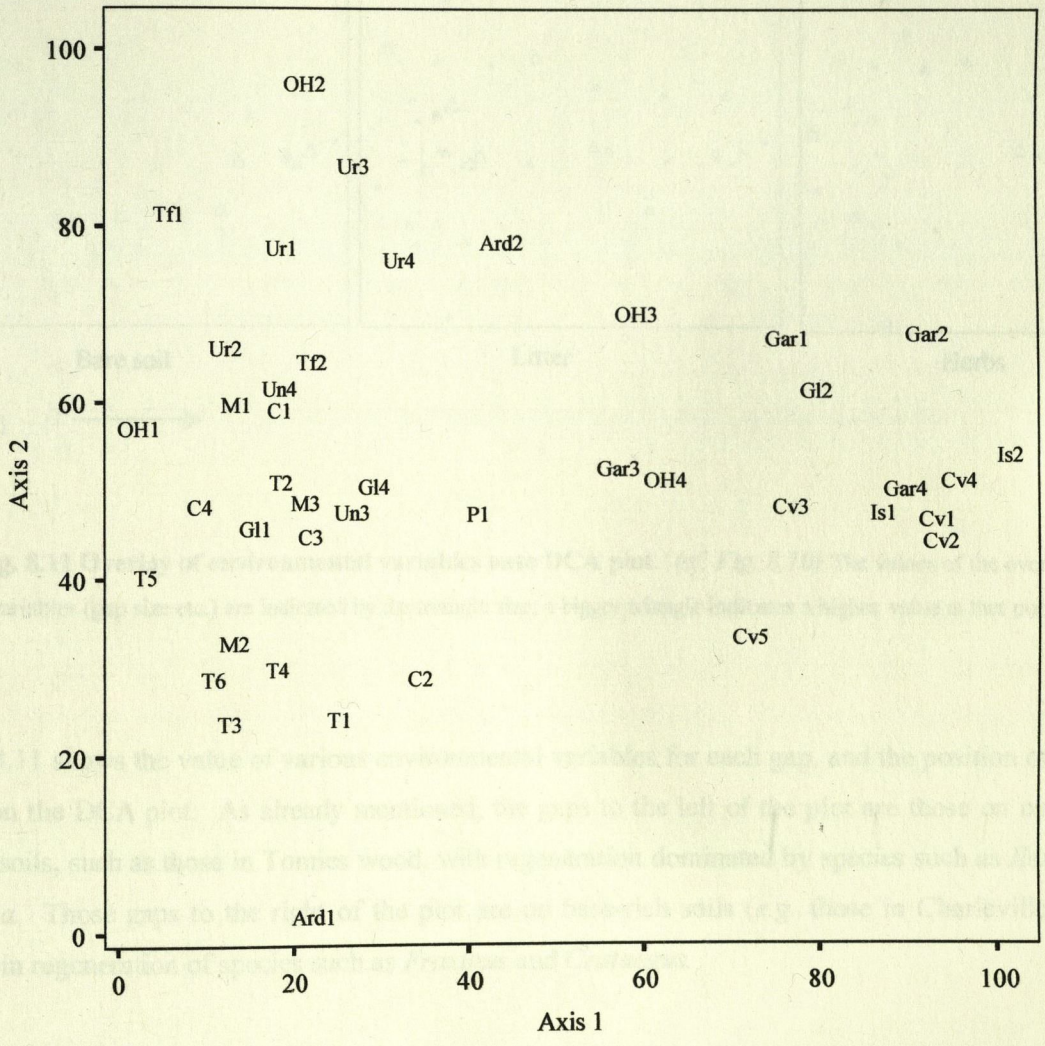

Fig. 8.10 DCA plot (Axis 1 v Axis 2) comparing gaps based upon regeneration composition (see Table 8.3).

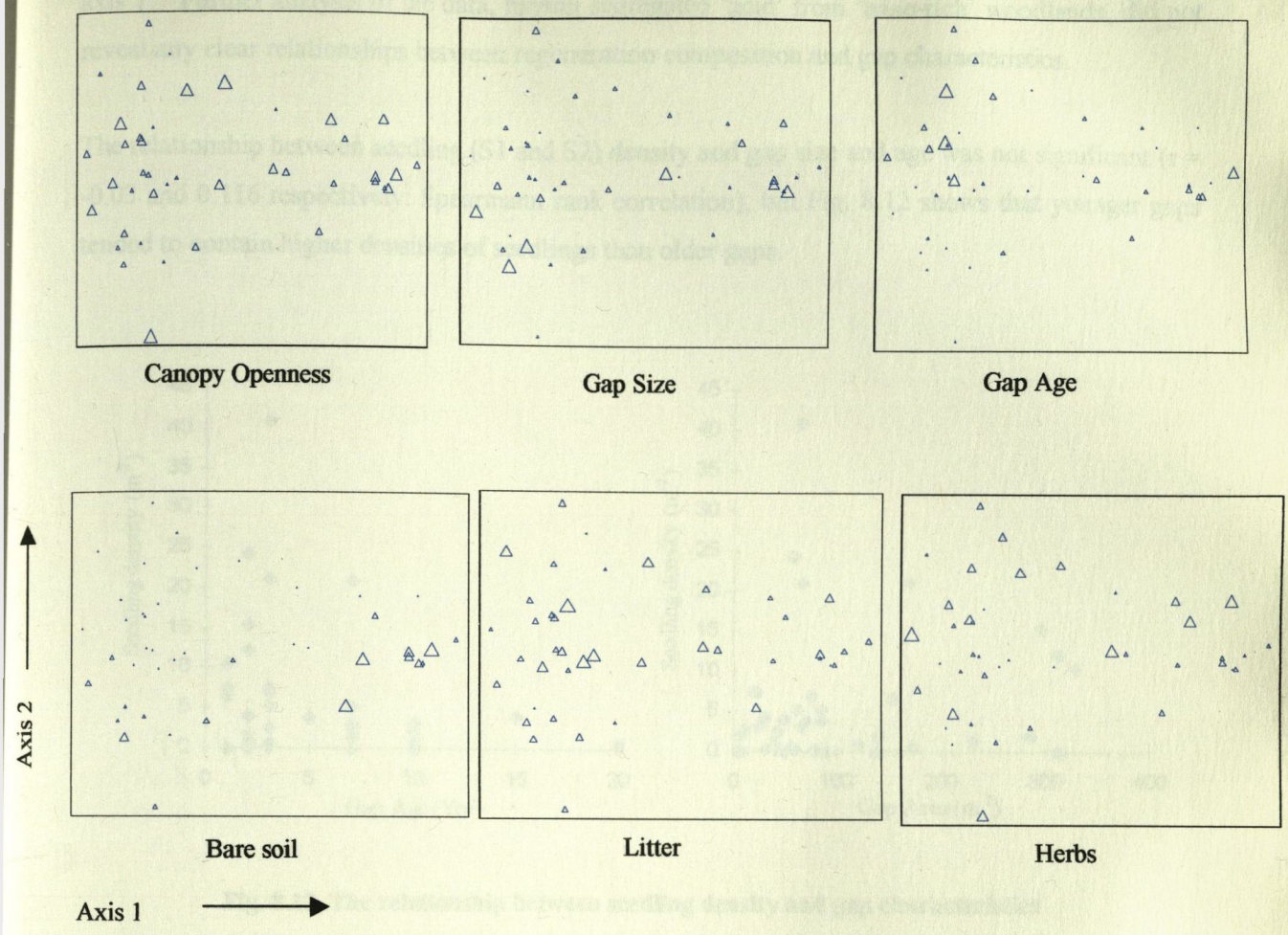

Fig. 8.11 Overlay of environmental variables onto DCA plot. *(cf. Fig. 8.10)* The values of the overlaid variables (gap size etc.) are indicated by the triangle size: a bigger triangle indicates a higher value at that point.

Fig. 8.11 shows the value of various environmental variables for each gap, and the position of each gap on the DCA plot. As already mentioned, the gaps to the left of the plot are those on nutrient poor soils, such as those in Tomies wood, with regeneration dominated by species such as *Ilex* and *Betula.* Those gaps to the right of the plot are on base-rich soils (*e.g.* those in Charleville) and contain regeneration of species such as *Fraxinus* and *Crataegus.*

The degree of canopy openness does not appear to be strongly associated with the regeneration composition of the gaps studied. Gap size however displays some pattern in Fig. 8.11, with larger gaps confined to the extreme right and left ends of the plot. This suggests an association between gap size and regeneration composition, within each woodland type. No such association is evident for gap age, with high and low values of this factor being randomly scattered on the DCA plot. Similarly, litter and herb cover appear to be randomly distributed on the plot. Bare soil cover shows a distribution similar to that for gap size, with higher values concentrated at both ends of

axis 1. Further analysis of the data, having segregated 'acid' from 'base-rich' woodlands, did not reveal any clear relationships between regeneration composition and gap characteristics.

The relationship between seedling (S1 and S2) density and gap size and age was not significant (r = -0.03 and 0.116 respectively: Spearmann rank correlation), but Fig. 8.12 shows that younger gaps tended to contain higher densities of seedlings than older gaps.

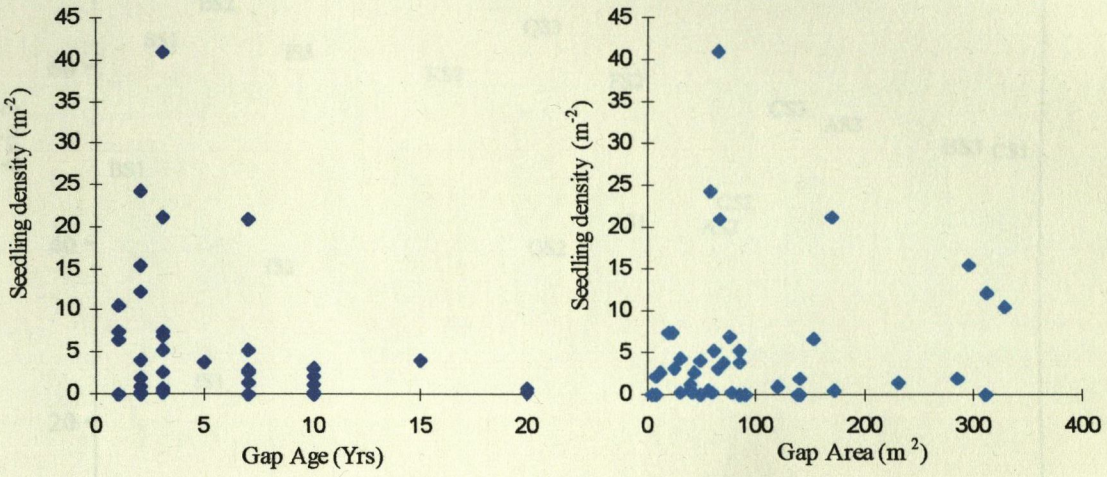

Fig. 8.12 The relationship between seedling density and gap characteristics

The DCA plot for regeneration (species and class) is presented in Fig. 8.13 and mirrors that for canopy gaps (Fig. 8.10), in that species common on base rich soils are grouped to the right hand side of the plot, while those of acid substrate tend towards the left. The species plot also suggests that Axis 2 on the gap plot (Fig. 8.10) may reflect the size of regeneration present, with saplings (denoted as S3) confined to the top of the plot, while smaller classes (S1s and S2s) are concentrated at the bottom.

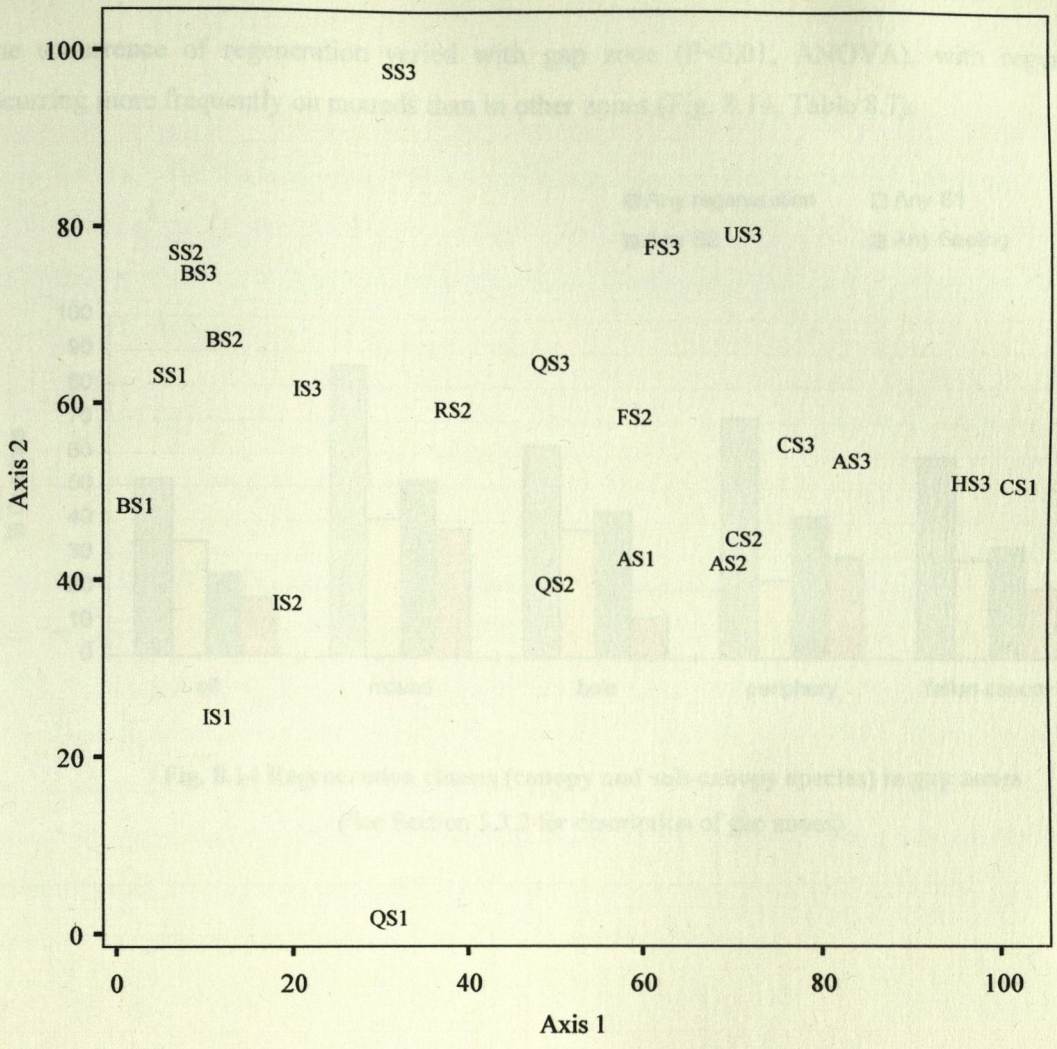

Fig. 8.13 DCA plot (Axis 1 v Axis 2) for regeneration composition of gaps, comparing the distribution of species and regeneration class.

Q: Quercus; B: Betula; A: Fraxinus; S: Sorbus; F: Fagus; U: Ulmus; C: Crataegus; H: Corylus. S1, S2, S3: regeneration classes- see section 5.3.5)

8.5 Regeneration patterns *within* canopy gaps

The occurrence of regeneration varied with gap zone ($P<0.01$, ANOVA), with regeneration occurring more frequently on mounds than in other zones (Fig. 8.14, Table 8.7).

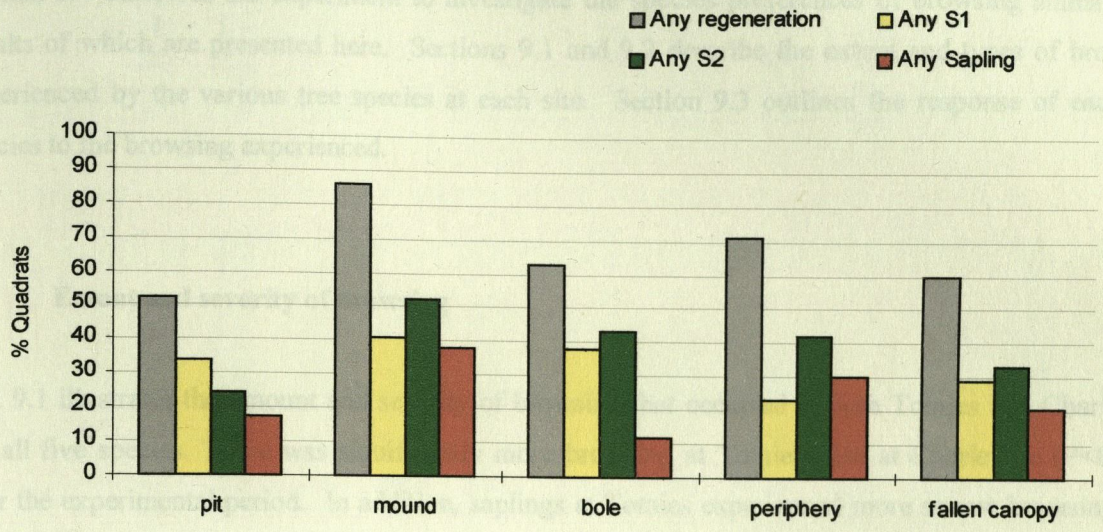

Fig. 8.14 Regeneration classes (canopy and sub-canopy species) in gap zones

(See Section 5.3.2 for description of gap zones)

CHAPTER 9 BROWSING OF TREE SAPLINGS

Section 5.4 describes the experiment to investigate the species preferences of browsing animals, the results of which are presented here. Sections 9.1 and 9.2 describe the extent and types of browsing experienced by the various tree species at each site. Section 9.3 outlines the response of each tree species to the browsing experienced.

9.1 Extent and severity of browsing

Fig. 9.1 illustrates the amount and severity of browsing that occurred at both Tomies and Charleville for all five species. There was significantly more browsing at Tomies than at Charleville ($P<0.001$) over the experimental period. In addition, saplings at Tomies experienced more severe browsing (*i.e.* more browsing of previous years' growth) than those at Charleville ($P<0.001$). The type of browsing varied between species with beech experiencing more grazing of 'leaf only' than other species, and oak experiencing significantly more severe browsing (more browsing of previous years' shoot) than any of the other species investigated ($P< 0.001$). Ash was more severely browsed ($P< 0.001$) than birch, and birch had more previous years' shoot taken than beech ($P< 0.001$).

TABLE 9.1 Effect of location, period and species on the amount and severity of browsing of saplings. Means are compared by ANOVA. N.S. denotes no significant difference; * & *** denote a significant difference in compared means at the 95 and 99.9% levels of confidence, respectively.

Factor	Any Browsing	Leaf only	cys	pys
Location	***	N.S.	N.S.	***
Period	***	N.S.	***	***
Species	***	***	***	***
Location x Period	***	***	***	***
Location x Species	N.S.	***	***	***
Species x Period	***	***	***	***
Location x Period x Species	N.S.	***	*	***

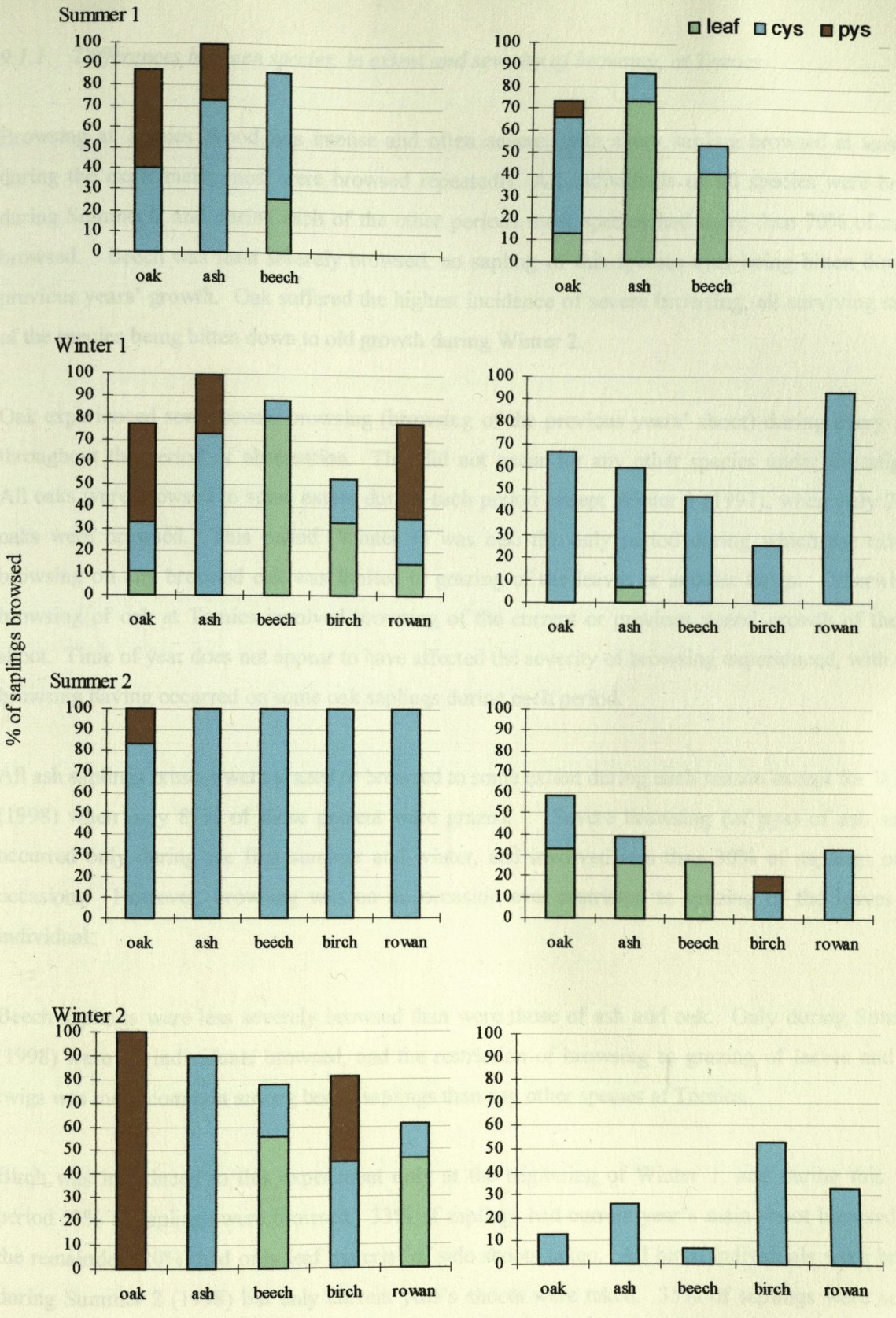

Fig. 9.1 Percentage of saplings browsed at Tomies and Charleville. 'leaf' denotes saplings from which only leafy material or side shoots were removed; 'cys' denotes saplings from which current year's growth of the main shoot was also removed; 'pys' denotes saplings whose main stems were bitten down into previous years' growth.

9.1.1 Differences between species, in extent and severity of browsing, at Tomies

Browsing at Tomies Wood was intense and often severe, with every sapling browsed at least once during the experiment; most were browsed repeatedly. All individuals of all species were browsed during Summer 2 and during each of the other periods most species had more than 70% of saplings browsed. Beech was least severely browsed, no sapling of this species ever being bitten down into previous years' growth. Oak suffered the highest incidence of severe browsing, all surviving saplings of the species being bitten down to old growth during Winter 2.

Oak experienced some severe browsing (browsing of the previous years' shoot) during every season throughout the period of observation. This did not occur for any other species under investigation. All oaks were browsed to some extent during each period except Winter 1 (1997), when only 76% of oaks were browsed. This period (Winter 1) was also the only period during which the extent of browsing on any browsed oak was limited to grazing of the leaves or smaller twigs. Otherwise, all browsing of oak at Tomies involved browsing of the current or previous years' growth of the main shoot. Time of year does not appear to have affected the severity of browsing experienced, with severe browsing having occurred on some oak saplings during each period.

All ash saplings present were grazed or browsed to some extent during each season except for Winter 2 (1998) when only 87% of those present were grazed. Severe browsing (of pys) of ash saplings occurred only during the first summer and winter, and involved less than 30% of saplings on both occasions. However, browsing was on no occasion ever restricted to grazing of the leaves of an individual.

Beech saplings were less severely browsed than were those of ash and oak. Only during Summer 2 (1998) were all individuals browsed, and the restriction of browsing to grazing of leaves and small twigs was more common among beech saplings than any other species at Tomies.

Birch was introduced to this experiment only at the beginning of Winter 1, and during this winter period 53% of saplings were browsed. 33% of saplings had current year's main shoot browsed while the remainder (20%) had only leaf material or side shoots taken. All birch individuals were browsed during Summer 2 (1998) but only current year's shoots were taken. 35% of saplings were severely browsed (pys) during Winter 2 (1998) and 44% moderately browsed (cys only).

Rowan was introduced to the experiment at the beginning of Winter 1 and during that winter period 80% of saplings were browsed. 10% of saplings had only their leaves and/or side shoots taken, 20% had current year's growth removed and 40% were more severely browsed with older growth removed. All rowan saplings had some current woody growth removed during Summer 2. Only 60% of rowans were grazed during Winter 2, the majority of which were only lightly browsed, having only leaves or small twigs taken.

9.1.2 Differences between species in extent and severity of browsing at Charleville

Generally, there was less browsing at Charleville than at Tomies wood. During no season were all individuals of any species browsed at Charleville. The highest incidence of browsing occurred during Winter 1 when 93% of rowan saplings were browsed.

Some saplings of oak were browsed during each of the periods measured, the proportion varying from 11% during Winter 2 to 74% during Summer 1. Oak was only one of two species at Charleville (the other was beech), of which individuals were browsed down to previous years' growth. However this occurred in only 7% of oak saplings (1 individual), and during only one of the four periods (Summer 1). During this same period a further 14% of saplings had leaf material only taken and 60% had current year's shoot also browsed. About 70% of oaks were browsed (cys) during Winter 1 and 60% were browsed (33% leaf only) during Summer 2. Only 14% of oaks were browsed during Winter 2, and leafy material and current year's shoots were taken.

During the first season after planting, Summer 1, more ash saplings (c.87%) were browsed than oak or beech. The main proportion had only leaf material or side shoots taken. The remainder had current year's shoot removed. This situation reversed during Winter 1, with most (>80% of the browsed ash) having main shoot removed and the remainder losing leafy material/side-shoots only. 26% of ash saplings had only leafy material removed during Summer 2, and a further 13% had current year's growth removed from the main stem. All 26% of saplings that were browsed during Winter 2 had some of the current year's main shoot removed.

As at Tomies, the beech saplings at Charleville were generally less severely and less often browsed than saplings of oak or ash. Beech at Charleville was also less browsed than rowan at Charleville. At no time was any beech sapling bitten back into previous years' growth, and the proportion of saplings browsed was always less than 60%. During each of the two summer periods, most of the beech saplings browsed had only leafy material taken (3/4 of those browsed during Summer 1 and all of those

browsed during Summer 2). Less than 10% of saplings were browsed during Winter 2 and current year's growth of the main shoot was taken from each of these.

Birch was introduced to the experiment at the beginning of Winter 1, during which winter period 26% of saplings had current year's growth of their main shoot removed. During Summer 2, 13% of birches had current year's shoot taken, and 7% were bitten down into previous years' growth. The highest incidence of birch browsing at Charleville occurred during Winter 2, when 50% of saplings were browsed, all having current year's growth of their main shoot taken.

Following its introduction to the experiment at the beginning of Winter 1, rowan was extensively browsed, with 93% of saplings experiencing browsing of current year's growth of the main shoot during Winter 1. During subsequent seasons rowan was browsed less, with 33% and 31% of saplings having current year's growth of the main shoot removed during Summer 2 and Winter 2 respectively.

9.2 Species of browser and grazer

9.2.1 Grazing by invertebrates

The extent of invertebrate grazing that occurred during this investigation was so limited compared to that by hares and deer that it was deemed to have no significant effect on sapling growth and thus was not investigated in detail. Indeed, browsing of unfenced saplings in Tomies was so severe, that little leaf material was available to any potential invertebrate grazers.

The occurrence of any invertebrate grazing was noted for fenced saplings at each site on one occasion, in mid-summer. The type of grazing was not described in detail. Invertebrate grazers were present on 5-40% of leaves. Caterpillar-type damage appeared to be the most significant type. Leaf miners were also observed. The volume of foliage removed by invertebrates was deemed insignificant in the context of this investigation and so was not investigated further.

9.2.2 Browsing by deer and hares

Deer and hares were the principal browsers at both Charleville and Tomies. Sika deer (*Cervus nippon*) are present at Tomies, and fallow deer (*Dama dama*) at Charleville. Instances of browsing by deer and hares were often identifiable (cf. section 5.4) and the amount of identifiable browsing by each is

illustrated for the entire experimental period in Fig. 9.2. Season by season data are presented for Charleville in Fig. 9.3 and for Tomies in Fig. 9.4.

There was more browsing by deer than by hares at both woodlands over the entire period of investigation. Browsing by both deer and hares differed significantly between tree species ($P < 0.001$). Deer browsing of ash at Tomies was the most frequent browse type, followed by deer browsing of oak and rowan, also at Tomies. At Charleville, oak was the species most often browsed by deer, followed by rowan and then ash. At Tomies, browsing was significantly higher in summer than during winter ($P < 0.05$).

At Charleville, hare browsing differed significantly between tree species ($P < 0.01$), with oak less often browsed than beech. There was no significant difference in hare browsing between summer and winter. Neither did deer browsing differ between the seasons. However, deer browsing varied with tree species ($P < 0.01$), with oak more often browsed than beech.

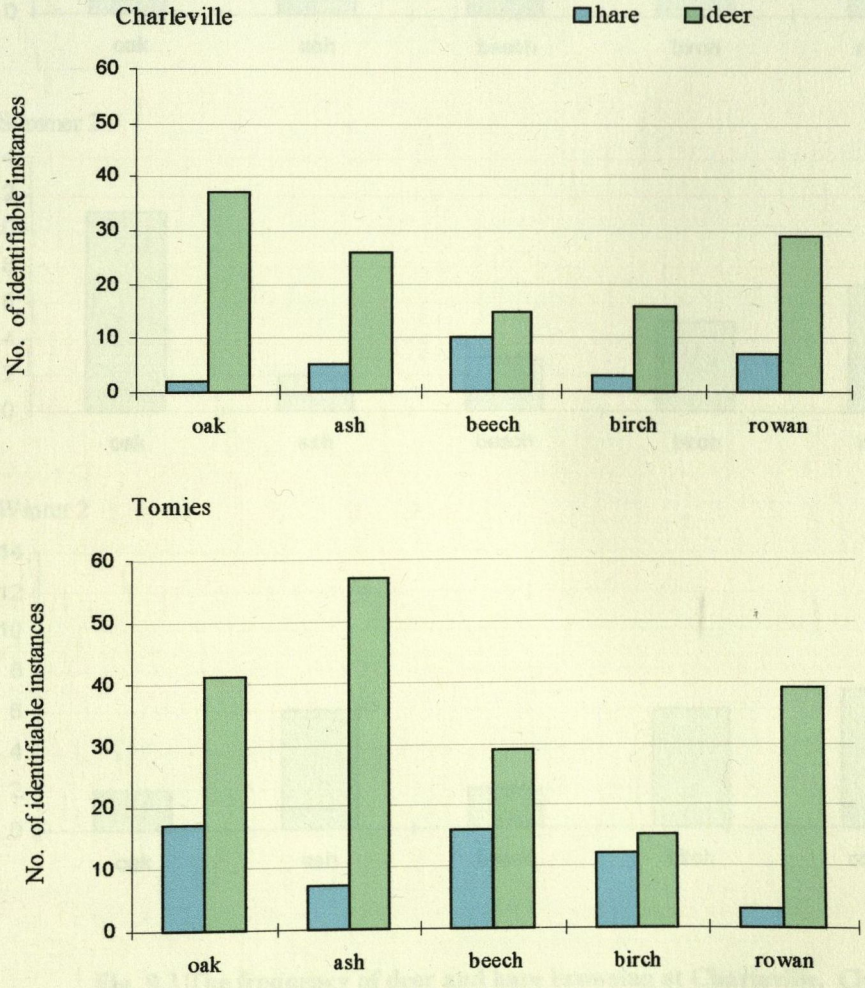

Fig. 9.2 The occurrence of browsing by hares and deer at Tomies and Charleville over the experimental period.

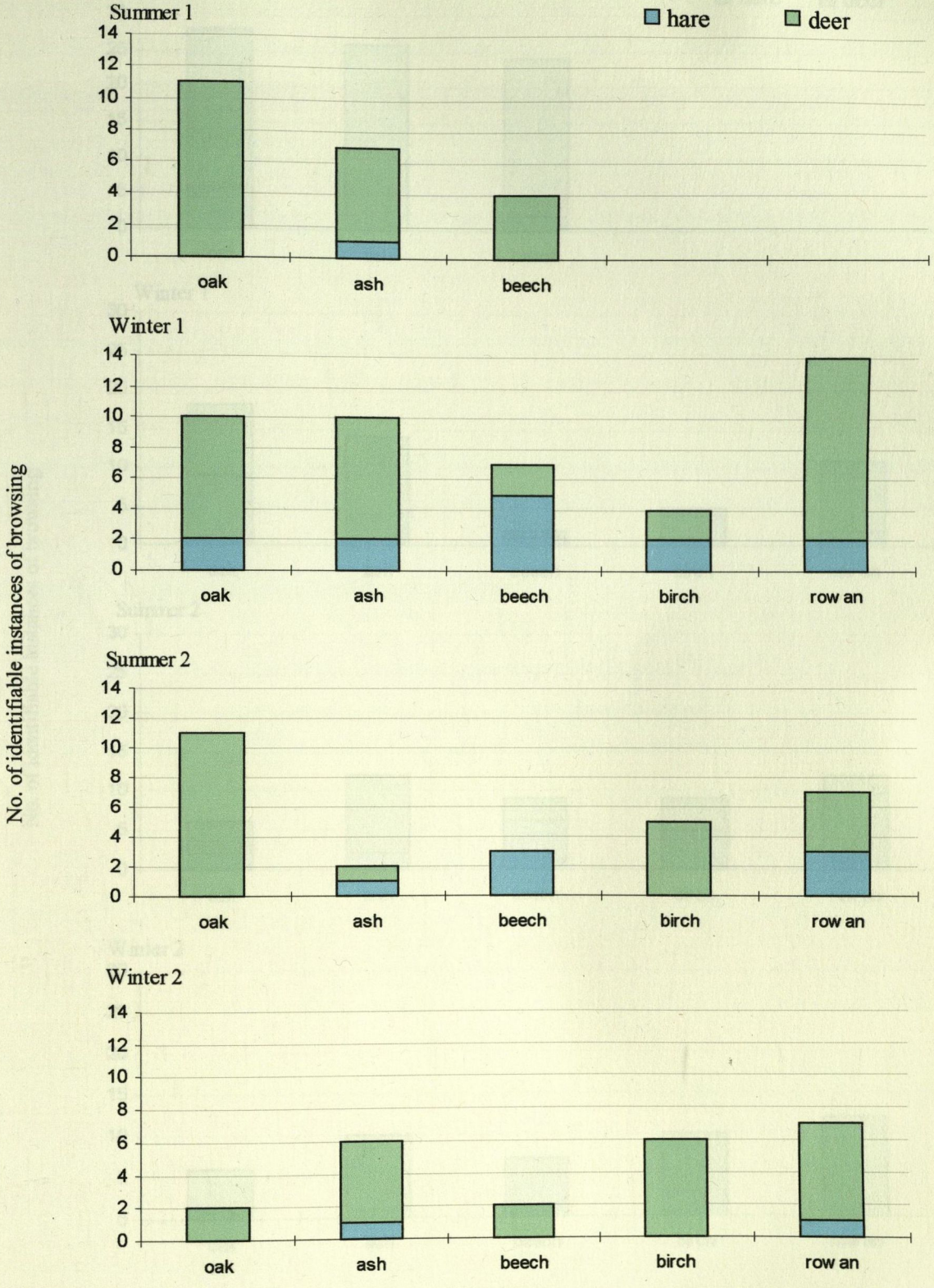

Fig. 9.3 The frequency of deer and hare browsing at Charleville. Charts indicate the number of identifiable instances of each type.

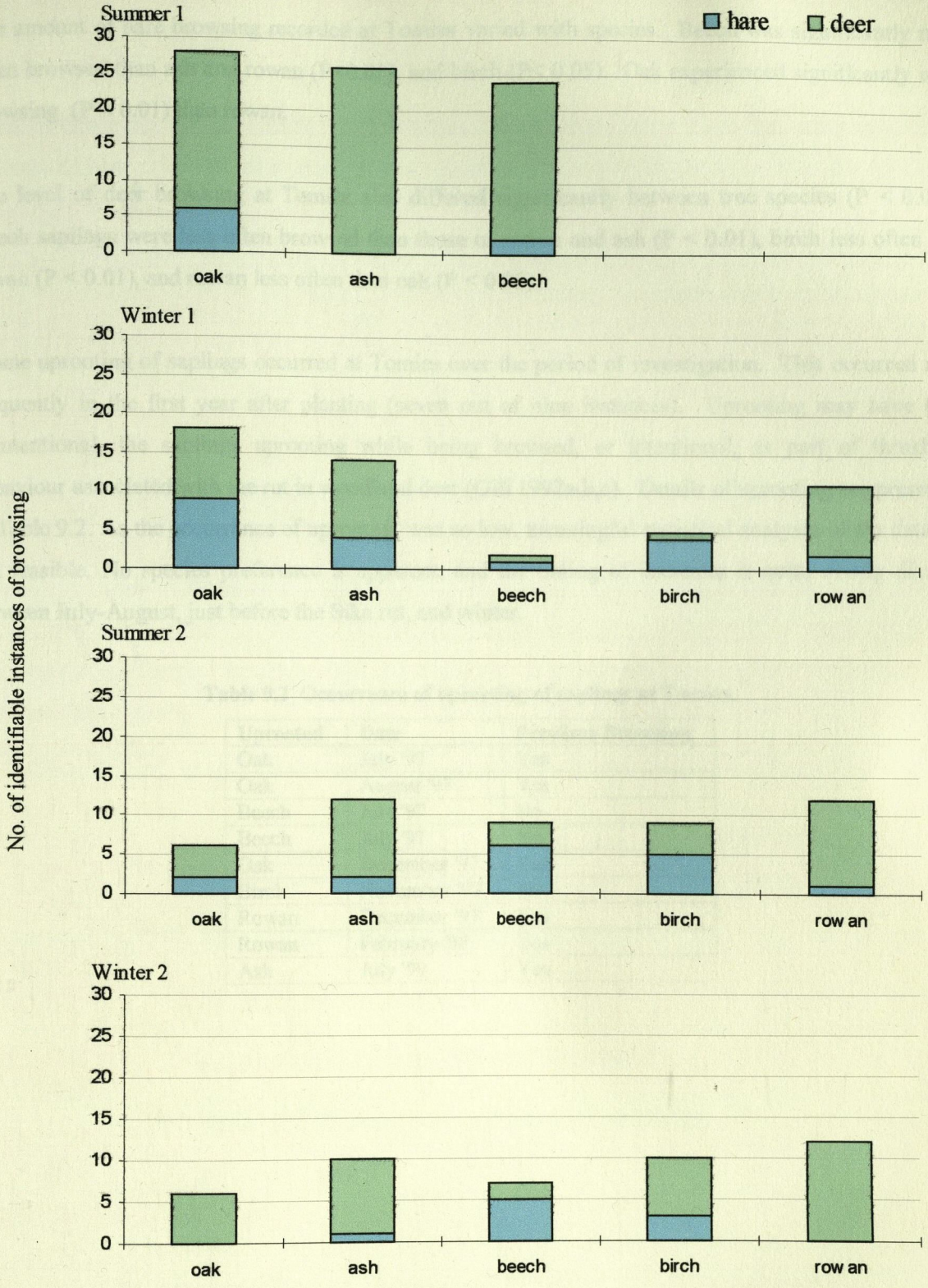

Fig 9.4 The frequency of deer and hare browsing at Tomies. Charts indicate the number of identifiable instances of each type.

The amount of hare browsing recorded at Tomies varied with species. Beech was significantly more often browsed than ash and rowan ($P<0.01$), and birch ($P< 0.05$). Oak experienced significantly more browsing ($P < 0.01$) than rowan.

The level of deer browsing at Tomies also differed significantly between tree species ($P < 0.001$). Beech saplings were less often browsed than those of rowan and ash ($P < 0.01$), birch less often than rowan ($P < 0.01$), and rowan less often than oak ($P < 0.05$).

Some uprooting of saplings occurred at Tomies over the period of investigation. This occurred most frequently in the first year after planting (seven out of nine instances). Uprooting may have been unintentional, the saplings uprooting while being browsed, or intentional, as part of thrashing, behaviour associated with the rut in woodland deer (Gill 1992a,b,c). Details of uprooting are presented in Table 9.2. As the occurrence of uprooting was so low, meaningful statistical analyses of the data are not feasible. No species preference is apparent, and the timing of instances is quite evenly divided between July-August, just before the Sika rut, and winter.

Table 9.2 Occurrence of uprooting of saplings at Tomies.

Uprooted	Date	Previous Browsing
Oak	July '97	Yes
Oak	August '97	Yes
Beech	July '97	No
Beech	July '97	No
Oak	December '97	Yes
Birch	November '97	No
Rowan	December '97	Yes
Rowan	February '98	Yes
Ash	July '99	Yes

9.3 Species preferences displayed by browsers

In order to simplify the data regarding the incidence and severity of browsing for each species, an Index of Browsing was compiled (cf. 5.4). This computes a browsing score for each species based upon the frequency and intensity at which that species was browsed (see also fig. 9.1). The scores are presented in Table 9.3.

Table 9.3 Browsing Score for saplings at Tomies and Charleville. A maximum score of 300 indicates the highest possible browse pressure for a species (*i.e.* 100% x 3 (pys)) in a given season. The overall score was calculated from the percentage of the the maximum possible score for each species (1200 for oak, ash and beech; 900 for birch and rowan) over the entire experimental period.

	Summer 1		Summer 2		Winter 1		Winter 2		**Overall Score**	
	Tomies	Charleville	Tomies	Charleville	Tomies	Charleville	Tomies	Charleville	**Tomies**	**Charleville**
Oak	215	132	240	80	200	140	300	20	**80**	**31**
Ash	230	72	200	45	225	113	180	60	**70**	**24**
Beech	140	60	200	30	95	100	90	14	**44**	**17**
Birch	/	/	200	35	70	56	245	100	**58**	**21**
Rowan	/	/	200	90	200	180	62	60	**51**	**37**

Overall, the order of preference of species differed between Charleville and Tomies. At Tomies, where pressure was generally higher, oak was the most browsed species, followed by ash, birch, rowan and beech respectively. At Charleville, rowan was the most preferred species, followed by oak, ash, birch and lastly, beech.

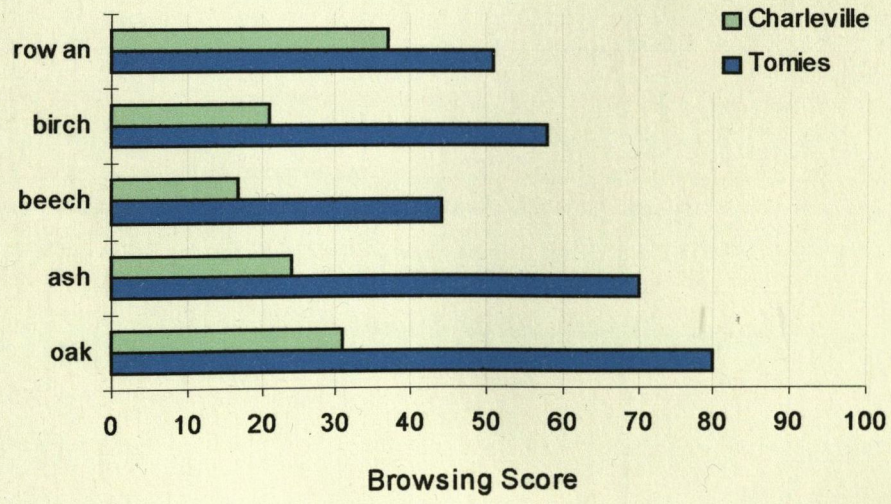

Fig. 9.5 Browsing preferences expressed by deer and hares at Tomies and Charleville Woods. Higher scores indicate more preferred species.

9.4 Browsing and sapling growth

The impact of browsing on transplanted saplings was assessed by the repeated measurement of sapling heights regularly throughout the experimental period. The mean height for each species under each treatment is presented in Figs. 9.6 and 9.7. Sapling height varied significantly with both locality ($P < 0.01$), and exposure to/protection from browsing ($P < 0.01$). Saplings exposed to browsing animals either achieved little increase in height (at Charleville) or experienced a net loss in height (at Tomies) over the experimental period (see also Figs. 9.8-9.10).

Comparison of measurements for fenced (and therefore not grazed or browsed) and unfenced saplings give an indication of the effect of browsing on sapling growth. Survival was also recorded and was affected by browsing. This is illustrated in Figs. 9.12 and 9.13.

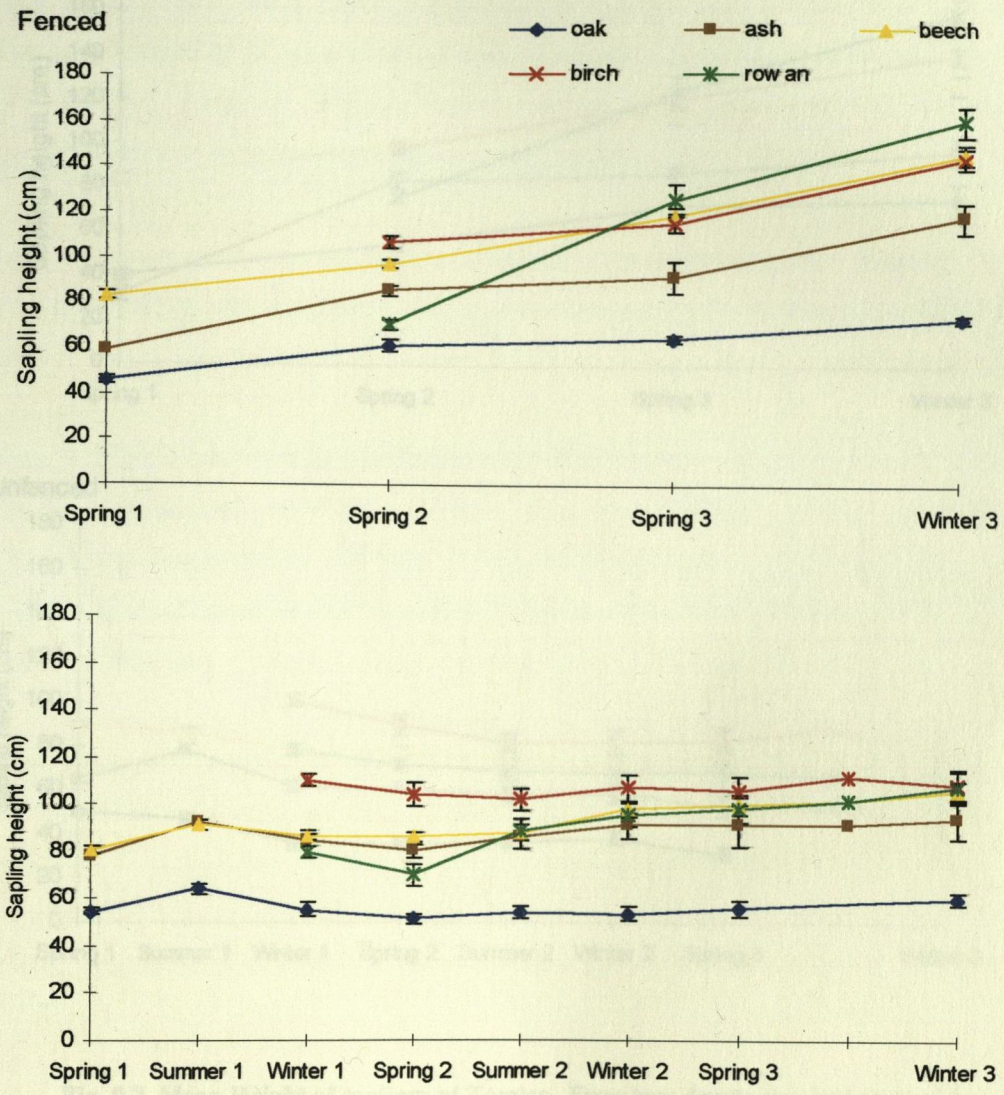

Fig. 9.6 Mean height of saplings at Charleville. Error bars denote standard error of the mean.

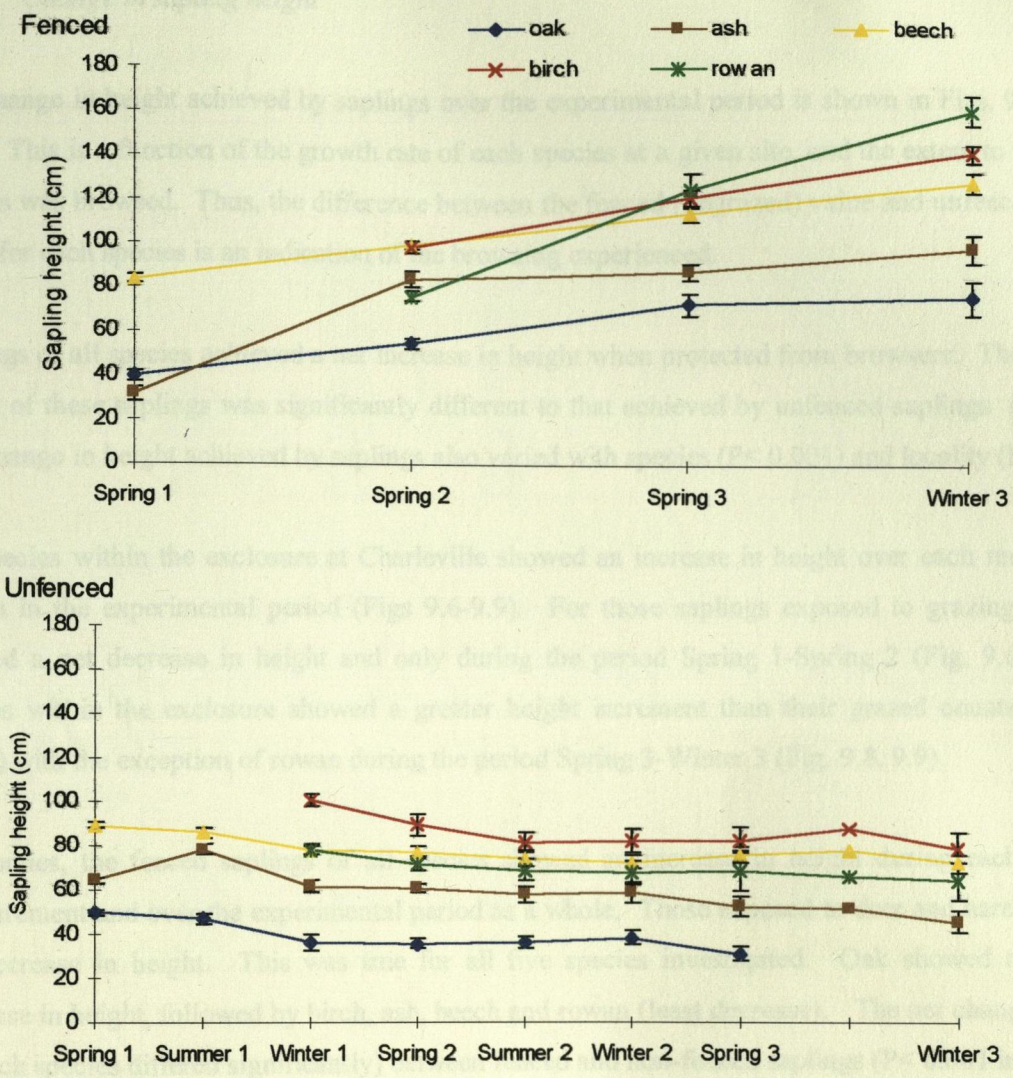

Fig. 9.7 Mean Height of saplings at Tomies. Error bars denote standard error of the mean.

9.4.1 Change in sapling height

The change in height achieved by saplings over the experimental period is shown in Figs. 9.8, 9.9 and 9.10. This is a function of the growth rate of each species at a given site, and the extent to which each species was browsed. Thus, the difference between the fenced (ungrazed) value and unfenced (grazed) value for each species is an indication of the browsing experienced.

Saplings of all species achieved a net increase in height when protected from browsers. The change in height of these saplings was significantly different to that achieved by unfenced saplings ($P < 0.001$). The change in height achieved by saplings also varied with species ($P < 0.001$) and locality ($P < 0.001$).

All species within the exclosure at Charleville showed an increase in height over each measurement season in the experimental period (Figs 9.6-9.9). For those saplings exposed to grazing, only oak showed a net decrease in height and only during the period Spring 1-Spring 2 (Fig. 9.6, 9.9). All species within the exclosure showed a greater height increment than their grazed counterparts ($P < 0.001$) with the exception of rowan during the period Spring 3-Winter 3 (Fig. 9.8, 9.9).

At Tomies, the fenced saplings of all species showed an increase in height during each period of measurement and over the experimental period as a whole. Those exposed to deer and hares showed a net decrease in height. This was true for all five species investigated. Oak showed the greatest decrease in height, followed by birch, ash, beech and rowan (least decrease). The net change in height for each species differed significantly) between fenced and non-fenced saplings ($P < 0.001$ in all cases).

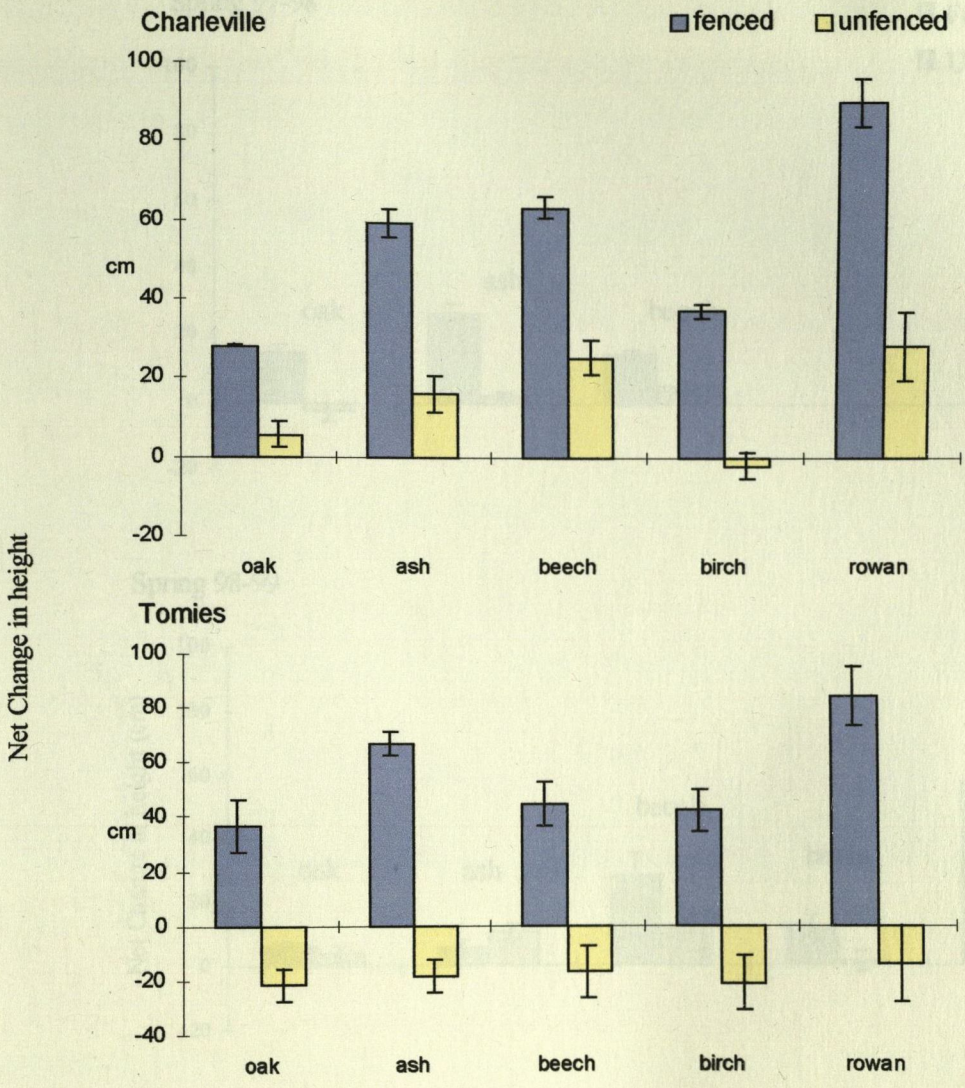

Fig. 9.8 Mean overall change in height for grazed (unfenced) and non-grazed (fenced) saplings. The period covered is Spring 1-Winter 3 for oak, ash & beech, and Winter 1-Winter 3 for birch and rowan. Error bars show standard error of the mean.

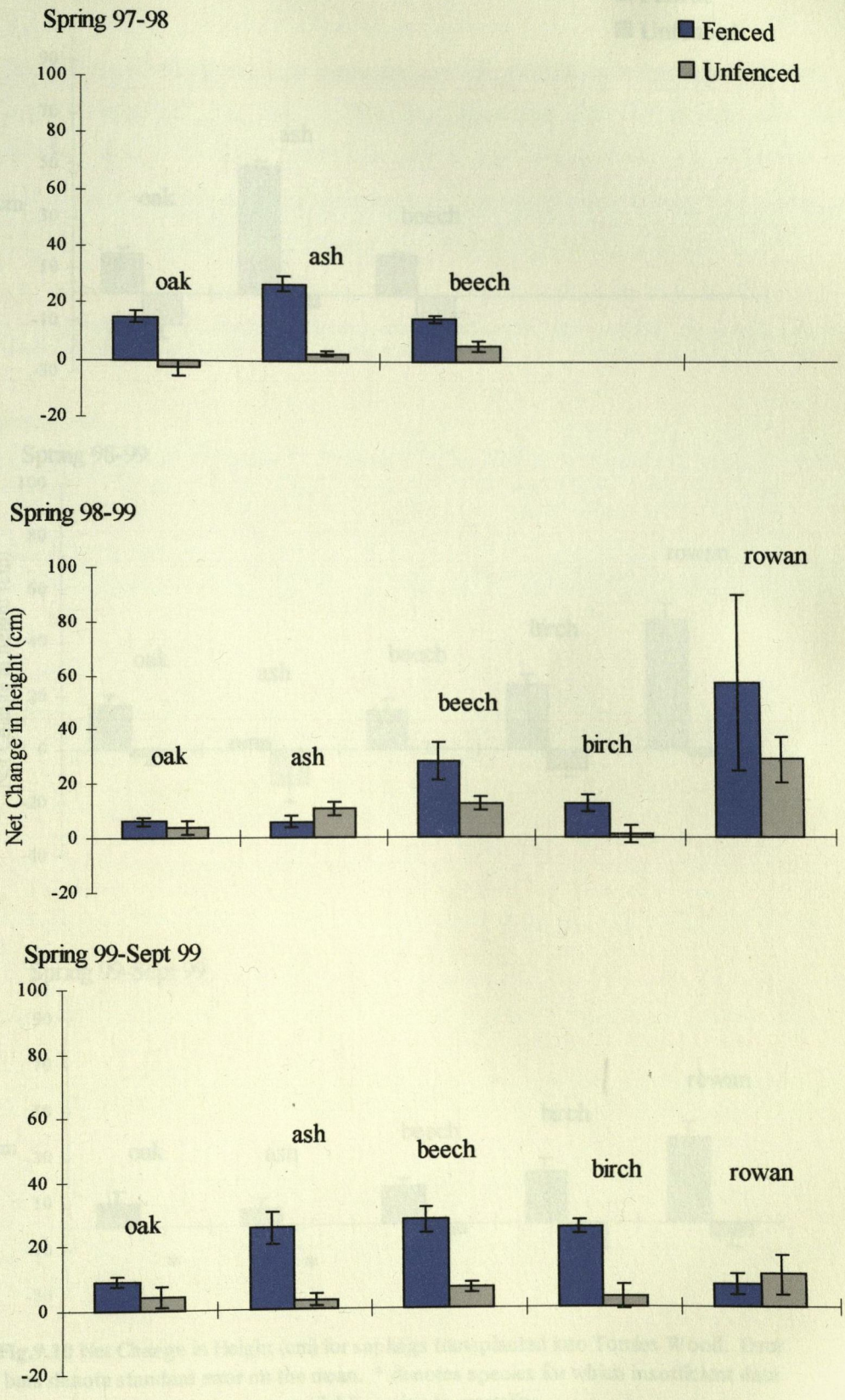

Fig.9.9 Net Change in Height (cm) for saplings transplanted into Charleville Wood. Error bars denote standard error on the mean.

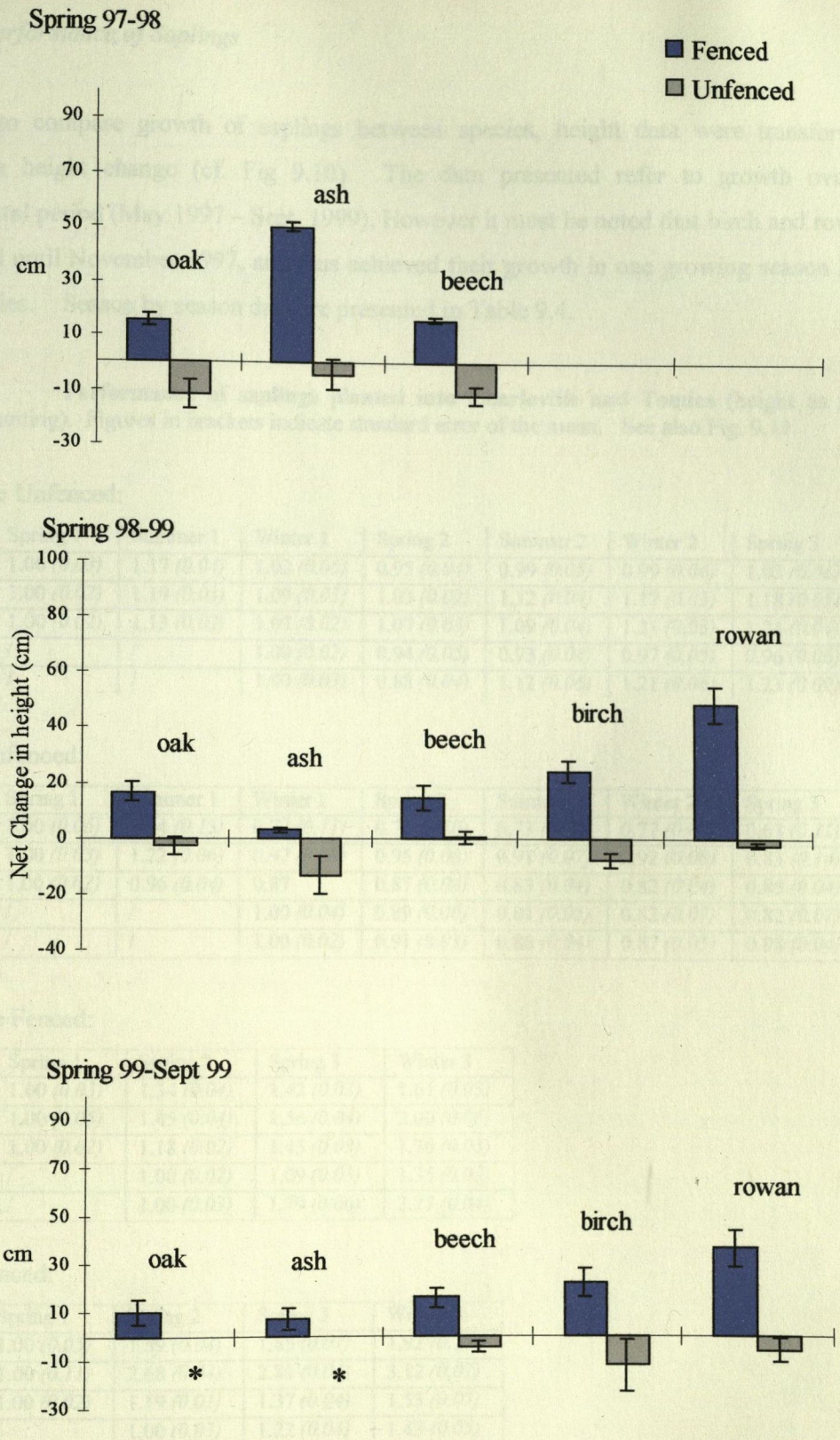

Fig.9.10 Net Change in Height (cm) for saplings transplanted into Tomies Wood. Error bars denote standard error on the mean. * denotes species for which insufficient data were available, owing to mortality.

9.4.2 Performance of Saplings

In order to compare growth of saplings between species, height data were transformed to give percentage height change (cf. Fig 9.10). The data presented refer to growth over the entire experimental period (May 1997 – Sept. 1999). However it must be noted that birch and rowan were not introduced until November 1997, and thus achieved their growth in one growing season less, than the other species. Season by season data are presented in Table 9.4.

TABLE 9.4 Performance of saplings planted into Charleville and Tomies (height as percentage of height at planting). Figures in brackets indicate standard error of the mean. See also Fig. 9.11.

Charleville Unfenced:

Species	Spring 1	Summer 1	Winter 1	Spring 2	Summer 2	Winter 2	Spring 3	Winter 3
oak	1.00 *(0.03)*	1.17 *(0.04)*	1.02 *(0.06)*	0.95 *(0.04)*	0.99 *(0.05)*	0.99 *(0.06)*	1.03 *(0.06)*	1.10 *(0.05)*
ash	1.00 *(0.02)*	1.19 *(0.03)*	1.09 *(0.03)*	1.03 *(0.02)*	1.12 *(0.04)*	1.17 *(0.05)*	1.18 *(0.05)*	1.21 *(0.05)*
beech	1.00 *(0.02)*	1.13 *(0.02)*	1.07 *(0.02)*	1.07 *(0.03)*	1.09 *(0.04)*	1.21 *(0.03)*	1.24 *(0.04)*	1.31 *(0.04)*
birch	/	/	1.00 *(0.02)*	0.94 *(0.05)*	0.93 *(0.04)*	0.97 *(0.05)*	0.96 *(0.06)*	0.98 *(0.06)*
rowan	/	/	1.00 *(0.03)*	0.88 *(0.04)*	1.12 *(0.06)*	1.21 *(0.06)*	1.23 *(0.09)*	1.35 *(0.08)*

Tomies Unfenced:

Species	Spring 1	Summer 1	Winter 1	Spring 2	Summer 2	Winter 2	Spring 3	Winter 3
oak	1.00 *(0.06)*	0.94 *(0.13)*	0.73 *(0.11)*	0.72 *(0.10)*	0.73 *(0.09)*	0.77 *(0.07)*	0.63 *(0.11)*	No data
ash	1.00 *(0.03)*	1.22 *(0.06)*	0.97 *(0.08)*	0.95 *(0.08)*	0.91 *(0.07)*	0.92 *(0.08)*	0.83 *(0.14)*	0.71 *(0.20)*
beech	1.00 *(0.02)*	0.96 *(0.04)*	0.87	0.87 *(0.04)*	0.83 *(0.04)*	0.82 *(0.04)*	0.85 *(0.04)*	0.81 *(0.06)*
birch	/	/	1.00 *(0.04)*	0.89 *(0.06)*	0.81 *(0.05)*	0.82 *(0.07)*	0.82 *(0.07)*	0.79 *(0.14)*
rowan	/	/	1.00 *(0.02)*	0.91 *(0.03)*	0.88 *(0.04)*	0.87 *(0.05)*	0.88 *(0.04)*	0.82 *(0.05)*

Charleville Fenced:

Species	Spring 1	Spring 2	Spring 3	Winter 3
oak	1.00 *(0.03)*	1.34 *(0.04)*	1.42 *(0.03)*	1.61 *(0.03)*
ash	1.00 *(0.05)*	1.45 *(0.04)*	1.56 *(0.04)*	2.00 *(0.06)*
beech	1.00 *(0.02)*	1.18 *(0.02)*	1.45 *(0.03)*	1.76 *(0.03)*
birch	/	1.00 *(0.02)*	1.09 *(0.03)*	1.35 *(0.03)*
rowan	/	1.00 *(0.03)*	1.79 *(0.06)*	2.27 *(0.04)*

Tomies Fenced:

Species	Spring 1	Spring 2	Spring 3	Winter 3
oak	1.00 *(0.05)*	1.39 *(0.04)*	1.85 *(0.07)*	1.92 *(0.10)*
ash	1.00 *(0.11)*	2.68 *(0.04)*	2.81 *(0.04)*	3.12 *(0.07)*
beech	1.00 *(0.02)*	1.19 *(0.01)*	1.37 *(0.04)*	1.53 *(0.07)*
birch	/	1.00 *(0.03)*	1.22 *(0.04)*	1.43 *(0.05)*
rowan	/	1.00 *(0.07)*	1.63 *(0.08)*	2.10 *(0.09)*

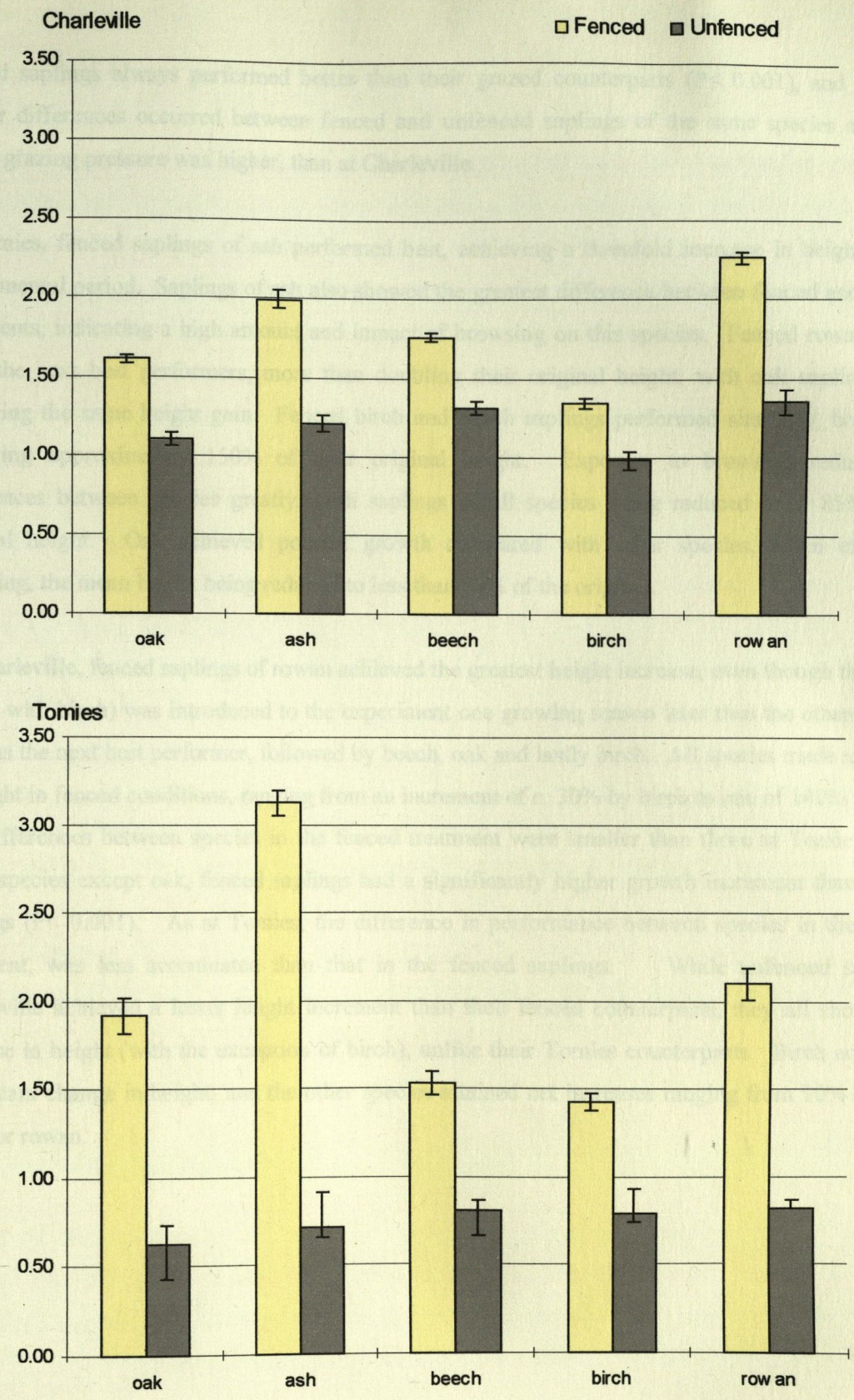

Fig. 9.11 Performance of Saplings (height as a percentage of height at planting). Figures refer to growth over the entire experimental period (Spring '97 - Sept. '99). Note that rowan and birch were not added to the experiment until Autumn '97.

Fenced saplings always performed better than their grazed counterparts ($P < 0.001$), and generally, greater differences occurred between fenced and unfenced saplings of the same species at Tomies, where grazing pressure was higher, than at Charleville.

In Tomies, fenced saplings of ash performed best, achieving a threefold increase in height over the experimental period. Saplings of ash also showed the greatest difference between fenced and unfenced treatments, indicating a high amount and impact of browsing on this species. Fenced rowan saplings were the next best performers, more than doubling their original height, with oak saplings almost achieving the same height gain. Fenced birch and beech saplings performed similarly, both species achieving approximately 150% of their original height. Exposure to browsing reduced these differences between species greatly, with saplings of all species being reduced to *c.* 85% of their original height. Oak achieved poorest growth compared with other species, when exposed to browsing, the mean height being reduced to less than 70% of the original.

At Charleville, fenced saplings of rowan achieved the greatest height increase, even though this species (along with birch) was introduced to the experiment one growing season later then the others. Fenced ash was the next best performer, followed by beech, oak and lastly birch. All species made an increase in height in fenced conditions, ranging from an increment of *c.* 30% by birch to one of 140% by rowan. The differences between species in the fenced treatment were smaller than those at Tomies. Within every species except oak, fenced saplings had a significantly higher growth increment than unfenced saplings ($P < 0.001$). As at Tomies, the difference in performance between species in the unfenced treatment, was less accentuated than that in the fenced saplings. While unfenced saplings at Charleville achieved a lesser height increment than their fenced counterparts, they all showed a net increase in height (with the exception of birch), unlike their Tomies counterparts. Birch achieved no significant change in height, and the other species attained net increases ranging from 10% for oak to 40% for rowan.

9.4.3 Survival

Survival of transplanted saplings is presented in Figs. 9.12 and 9.13. Initial survival of saplings was good. 100% of saplings of all species survived at least the first season (and most the first year), with the exception of ash in the Tomies exclosure, a quarter of which had died by Spring 1998. However, by the end of the experimental period, all species in all treatments suffered some mortality, with the exception of rowan in the Charleville exclosure which showed 100% survival.

Survival was higher in exclosures ($P < 0.001$) and was significantly higher at Charleville than at Tomies ($P < 0.001$). There was also a significant difference in survival between species ($P < 0.001$) with oak and ash both showing significantly lower survival rates than rowan and beech. Unfenced saplings at Charleville achieved significantly higher ($P \leq 0.001$) survival than their Tomies counterparts. There was no significant difference in survival of the fenced saplings between localities. However, overall survival was significantly higher at Charleville than at Tomies for saplings of oak, birch ($P < 0.001$) and ash ($P < 0.01$).

Survival of saplings at Tomies

The order of success of species (in terms of survival) was the same for both fenced and unfenced saplings at Tomies. Oak showed the highest mortality; however at the end of the experimental period almost half of the fenced saplings were still alive while only 7% (one individual) of the browsed saplings remained alive. Beech and rowan displayed the highest survival rates both in fenced and unfenced treatments, with rowan achieving 100% survival of fenced saplings and beech 87%. Forty-seven percent of unfenced saplings of both species survived. Birch and ash were intermediate in their survival.

Survival of Saplings at Charleville

Among the saplings planted at Charleville, there was no significant difference in survival between different species, or between fenced and unfenced saplings. The lowest rate of survival (63%) was in fenced oak saplings. In unfenced saplings, ash had the lowest survival rate, with 73% of saplings surviving. Both beech and rowan outside of the exclosure achieved 93% survival

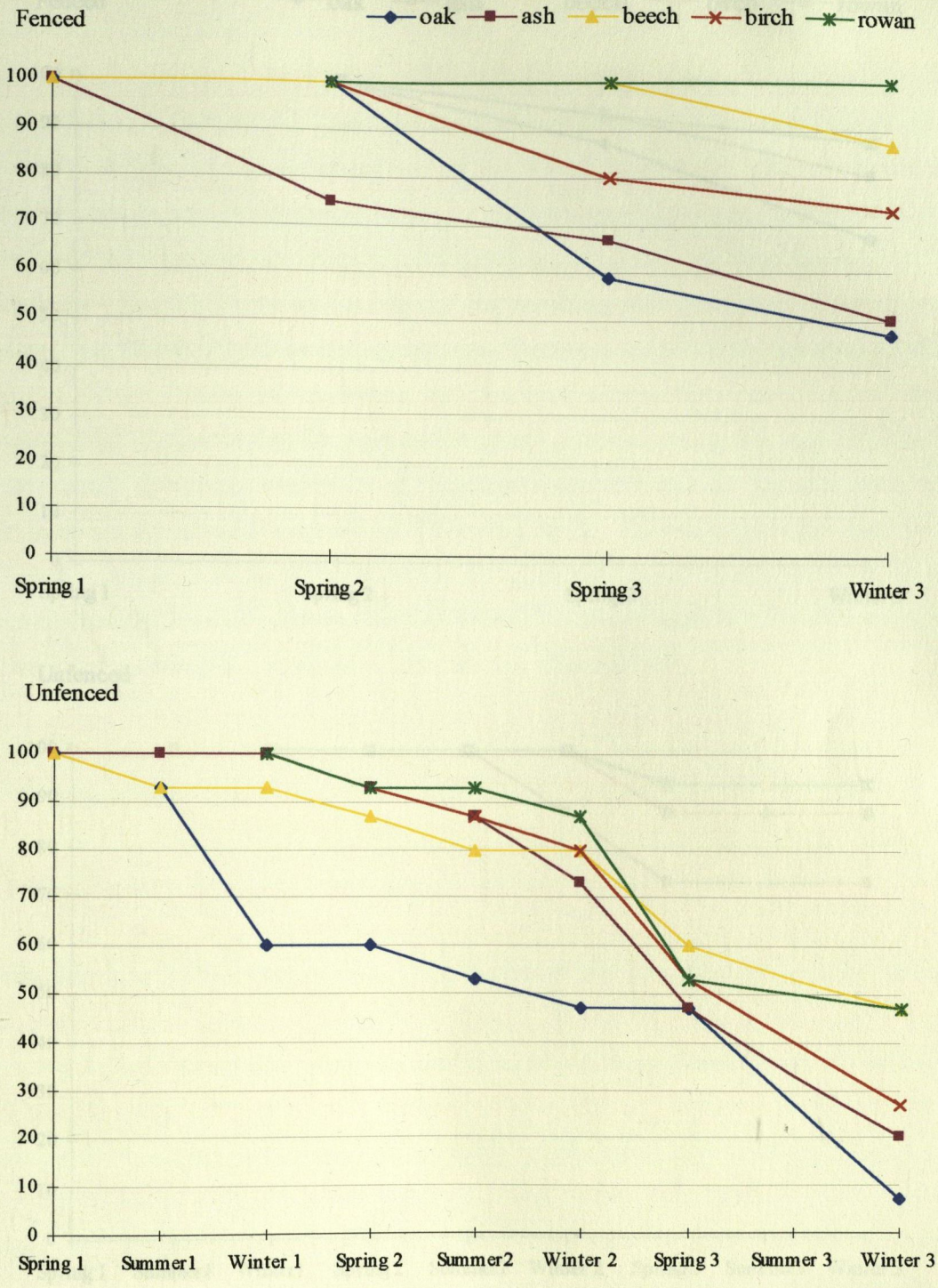

Fig. 9.12 Percentage survival of saplings transplanted into Tomies Wood

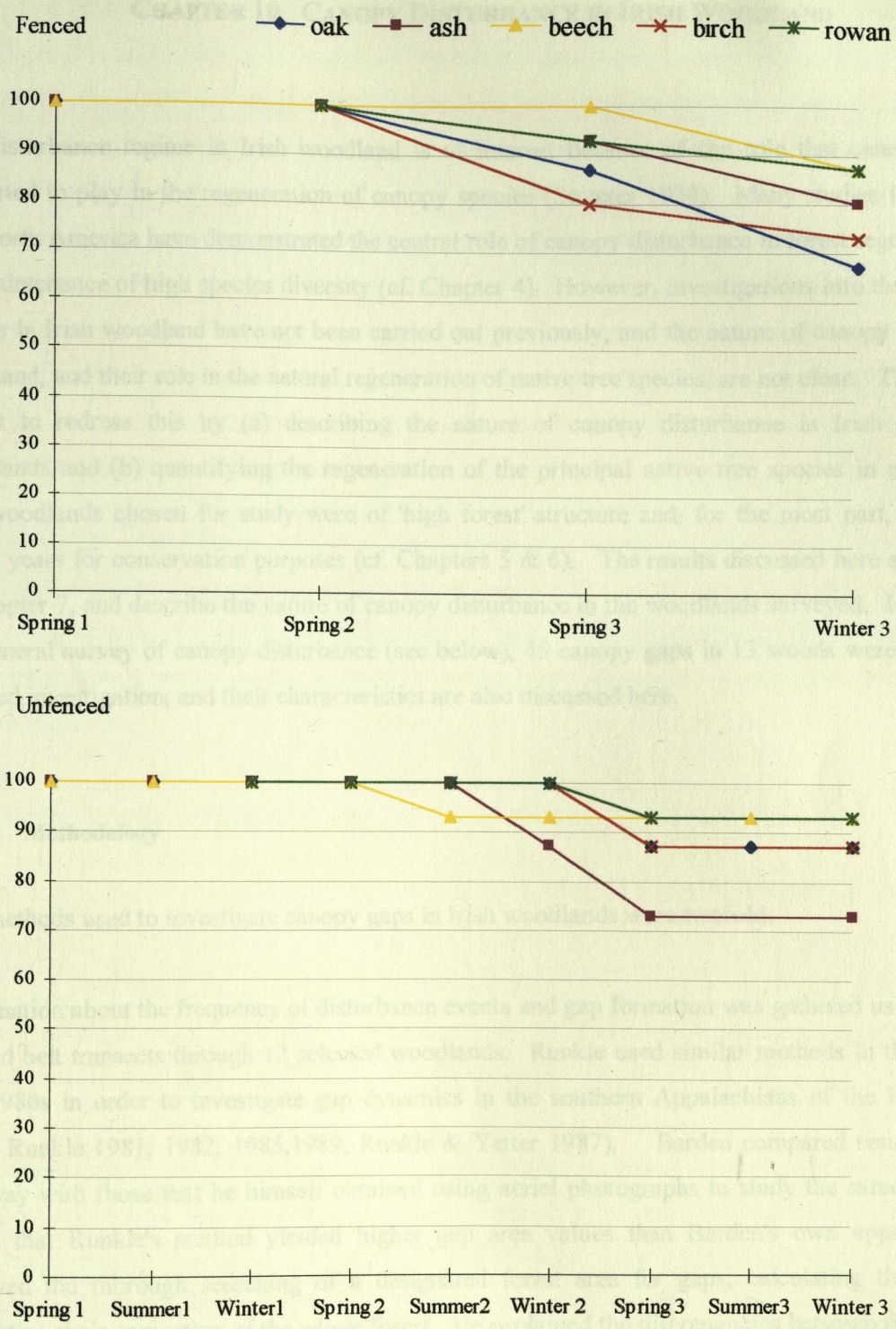

Fig. 9.13 Percentage survival of saplings transplanted into Charleville Wood.

CHAPTER 10 CANOPY DISTURBANCE IN IRISH WOODLAND

The disturbance regime in Irish woodland is of interest because of the role that canopy gaps are purported to play in the regeneration of canopy species (Streeter 1974). Many studies in the tropics and North America have demonstrated the central role of canopy disturbance in forest regeneration and the maintenance of high species diversity (cf. Chapter 4). However, investigations into the disturbance regime in Irish woodland have not been carried out previously, and the nature of canopy gaps in Irish woodland, and their role in the natural regeneration of native tree species, are not clear. This study has sought to redress this by (a) describing the nature of canopy disturbance in Irish semi-natural woodlands and (b) quantifying the regeneration of the principal native tree species in canopy gaps. The woodlands chosen for study were of 'high forest' structure and, for the most part, managed in recent years for conservation purposes (cf. Chapters 5 & 6). The results discussed here are presented in Chapter 7, and describe the nature of canopy disturbance in the woodlands surveyed. In addition to the general survey of canopy disturbance (see below), 45 canopy gaps in 13 woods were selected for detailed investigation, and their characteristics are also discussed here.

10.1 Methodology

The methods used to investigate canopy gaps in Irish woodlands were twofold:

Information about the frequency of disturbance events and gap formation was gathered using randomly located belt transects through 12 selected woodlands. Runkle used similar methods in the late 1970s and 1980s in order to investigate gap dynamics in the southern Appalachians of the USA (Barden 1989, Runkle 1981, 1982, 1985,1989, Runkle & Yetter 1987). Barden compared results gained in this way with those that he himself obtained using aerial photographs to study the same region. He found that Runkle's method yielded higher gap area values than Barden's own approach, which involved the thorough searching of a designated forest area for gaps, calculating their area and estimating their proportion of the whole forest. He explained the discrepancies between the two by the following:

(i) Over-estimation when using the transect method. A researcher might encounter difficulty in adhering to a fixed compass azimuth while pacing over rough terrain, and might unwittingly deviate towards gaps, thus overestimating the gap area.

(ii) Under-estimating the gap area when searching an area. This might occur if small gaps are missed.

In order to eliminate the possibility of deviation from the randomly selected compass direction, transects in this study were laid out with tape before the data were recorded. This method proved to be efficient for the study of a large number of woods, in that relatively large areas of forest could be covered quickly, and variation between stands within a single woodland was encompassed within the sample. The data obtained showed significant variation in gappiness between woodlands, and even within woodlands. This survey yielded a general picture of the gap regime. For a deeper understanding upon which predictions about canopy turnover might be made, long-term studies of selected sites may be more appropriate. In such cases, the use of high-resolution aerial photographs may be effective in locating all gaps, which can later be surveyed on the ground. Fox *et al.* (2000) found that errors of omission were almost 26% for searching by ground survey, compared with only *c.*5% for the aerial photograph method.

I addition to the transects, more detailed data about gap formation, structure and vegetation were collected through the study of subjectively chosen gaps in 13 woodlands. These gaps were chosen to be representative of the gap type predominant in each woodland studied, and the number of gaps studied varied with woodland (cf. Table 7.5). In some woodlands (*e.g.* Portlaw), they were the only sizeable gaps found.

10.2 The disturbance regime

The general survey of the disturbance regime in Irish woodland yielded information about the scale on which canopy disturbance occurs, the types of damage involved, the temporal and spatial variation in disturbance events and the frequency with which disturbance events resulted in gap formation. The methods used provide a 'snap-shot' of the canopy at the time of survey, from which some general conclusions about the gap regime in Irish woodlands can be drawn.

For the most part, the disturbance regime in the surveyed woods is characterised by small-scale disturbances. This is consistent with the wind climate that prevails over the island. While average wind speeds may be high (as much as 19 km/h on the west coast), violent storms and hurricanes are infrequent, and the effects of wind and exposure are most relevant in their limiting of growth in exposed sites and at higher altitudes (O' Carroll 1984). In fact, the growth of trees in a relatively windy environment may confer some resistance to wind damage, in the absence of severe conditions or other pertinent circumstances such as poor rooting or disease-weakened timber (Kozlowski *et al.* 1991 #228). However, in Ireland, individual trees or small groups of trees are damaged by wind almost every year (O Carroll 1984). Kuuluvainen (1994) reports a similar pattern of frequent small-scale gap disturbance for Boreal forests which have escaped catastrophic fires. However, the occurrence of 'the

great storm' of 1987 in south-east England is evidence that extreme wind conditions are not an impossibility in this part of the world. Indeed, severe wind storms have occurred in Ireland in the past. O Carroll (1984) lists wind storms that resulted in major damage to trees for 1839, 1903, 1955, 1957, 1961 and 1974. He notes that thousands (up to 281,000) of trees were blown down on each occasion, and as with much of the literature, refers only to the effects of storms on plantation woodlands. Whether this reflects a bias in reporting towards such stands because of their economic value or some propensity to damage (compared with natural stands) is unclear. Fuller (1990) refers to the severe wind storms of 1839 and 1902, which resulted in large-scale damage to trees in the Charleville Demesne. In 1839, the majority of trees blown were oak and lime, while those affected in 1902 were mostly beech. Thus, large-scale disturbance to woodland is a distinct possibility in the future, especially when predictions regarding climate change are borne in mind (Houghton *et al.* 1995).

10.2.1 Factors affecting canopy disturbance

The variation in the frequency of gaps and disturbance events, between and within woodlands, reflects differences in stand structure, wind regime and other site conditions, so that no one factor appears to determine the gap regime present. Woodlands on the more exposed west coast of the country did not have more disturbed canopies than those in the midlands or to the east of the country. The strong relationship between the frequency of gaps and the maximum gust recorded (cf. Table 7.4) reflects the role of severe wind events in canopy disturbance. It must be noted, however, that the wind data used here were recorded at wind stations that, in most cases, are several miles away from the woodland site in question (cf. Table 7.3). While efforts were made to obtain data from stations of similar exposure and altitude to the relevant woodland sites, local topography and other factors can have significant effects on the local wind climate, and the data used here give only an approximate view of the wind climate.

Oldeman (1978) reported gap densities for forests in Ecuador and found that they varied with altitude and slope: On flat land at 650m OD, gaps occurred at densities of 16 ha^{-1} compared with 23 gaps ha^{-1} on hillsides at similar altitudes. The frequency of gaps increased with altitude, with 33 ha^{-1} reported for forest at 1900m. In the present study, gap densities ranged between 0 /100m and 5/100m (~50 ha^{-1}). The altitudes of the woodlands studied here ranged only between 10 and 200m above sea level, and no significant relationship was found between gap density and altitude. However, insufficient data were collected to test statistically the hypothesis that altitude (or any other site factor) is the major determinant of the disturbance regime at a site. Nonetheless, a trend was evident when the gap density for fairly flat areas were compared with those on a slope (cf. Fig. 7.1). While the ranges of gap density

overlapped between the two, there was a clustering of lower gap densities for flatter sites, and conversely, of higher densities for sites on slopes. Yamomoto (1992) reported a gap density of 19.6 gaps /ha (~1.9 gaps/100m) for broadleaved forests in Japan, which is within the range of gap density calculated for the Irish woodlands surveyed here.

Hubbell and Foster (1986) reported that local differences existed in the gap regime of a 0.5 km^2 plot of tropical forest in Panama and postulated that the higher risk of damage to trees adjacent to existing gaps may have been partly responsible. Tanaka & Nakashizuka (1997), investigating mixed deciduous forest in central Japan, also report that creation of new gaps was biased towards the edges of old gaps. However, Runkle & Yetter (1987) calculated that the risk of damage to trees adjacent to canopy gaps in temperate North American forests did not differ significantly to that for other trees in the forest. Battles *et al.* (1995) found that the occurrence of canopy gaps varied with topography and elevation in spruce forests in the USA. Gaps were more frequent at higher and lower altitudes than in the mid-slope, and gaps were larger and more abundant along streamsides and ridges.

While the spatial distribution of canopy disturbance within individual stands was not actively investigated in this study, observations from the transect study indicate a degree of disturbance clustering in some places (*e.g.* the occurrence of 'multiple' gaps where damage to more than one individual result in a canopy gap). However, the nature of this survey (a linear transect) was not suited to an in-depth analysis of disturbance clustering, and while gap expansion by disturbance at the edge of older gaps was observed at some places, evidence is lacking as to whether this scenario is more frequent than isolated disturbance events.

Disturbance events were more frequent than actual canopy gaps (cf. Tables 7.1, 7.2). There were two reasons for this. In some cases, evidence of a past gap was still apparent (*e.g.* an uprooted tree) but the resultant canopy gap had been filled with vegetation. In other circumstances it appeared that the disturbance event had not resulted in a canopy gap in the first place (*e.g.* if a lower branch fell). More than 55% of the disturbance events encountered were giving rise to canopy gaps at the time of survey (Table 7.2). Resultant gaps were observed for 52% of crown damage events, 49% of snapped trees and 44% of uprooted trees. The higher percentage of crown damaged trees involved in canopy gaps partly reflects the more frequent occurrence of this damage type in multiple disturbance events. Multiple events gave rise to gaps more often than events involving only a single individual. Multiple events tend to result in larger gaps, which take longer to fill, and so are more likely to be observed in a survey such as this. Van der Meer & Bongers (1996) found that, in tropical rain forest in French Guiana, 58% of crown damaged trees, and 65% of fallen trees, resulted in gap formation. This survey was

conducted by the continuous monitoring of all trees in a 12 ha plot over a one year period, and so is likely to reflect the true rate of gap formation resulting from canopy disturbances at that site.

10.2.2 Modes of disturbance

The types of disturbance encountered in Irish woodland ranged from loss of one or more limbs (crown damage) to the snapping or uprooting of an entire tree. Crown damage was the most frequently encountered disturbance type, and accounted for more than 50% of disturbance events in 10 of the 12 woods surveyed (Fig 7.2). This is probably a reflection of the predominance of oak (which is somewhat prone to limb shedding (Whitbread 1991)) in the canopies of the woodlands studied. Jans *et al.* (1993) reported that, in tropical forest on the Ivory Coast, stands with larger trees had generally smaller gaps. This was explained by the propensity of large individuals in the canopy to die slowly, shedding limbs one by one. Thus in woodlands where the canopy dominants display such a feature, a disturbance regime dominated by frequent small gaps may be expected.

Van der Meer & Bongers (1996), in their survey of disturbance events in rainforest in French Guiana, found that 46% of disturbances involved crown damage, 33% snapping, and 21% uprooting of entire trees. The major cause of damage was other falling trees or crowns, and 83% of crown damage and 75% of uprooting/snapping was the result of this. Larger trees were more likely to initiate disturbance than smaller trees. Their study indicated that when fallen trees (uprooted and snapped) were considered, tree size did not affect whether or not a gap was created, and the authors explained this apparent anomaly by the small number of very large trees in the forest. When crown damage was investigated, branches from larger trees were more likely to result in gap formation than those from smaller trees. It was also found that crown damage was as likely to result in gap formation as felling of entire trees, possibly because of the tendency for very large trees in this forest to shed large limbs.

Runkle (1982) found that the disturbance regime in old-growth forests in the USA was dominated by snapped trees, which accounted for almost 60% of disturbance events, while uprooting was the cause of 19% and crown damage only 13%. This variation in the predominance of different disturbance types between studies, may be affected by differences in the methods used, but is also likely to reflect true differences between woodland sites *e.g.* the forests investigated by Runkle were old-growth and had a significant conifer component, thus increasing the rate of snapping among canopy trees. The dominant mode of disturbance was found to vary considerably between sites investigated here (cf. Fig. 7.2). Crown damage accounted for 100% of the disturbance events randomly encountered at some

woods (*e.g.* Union Wood, Tomnafinnoge and Glen of the Downs) while uprooting was more common in others (*e.g.* Portlaw, Ardnamona).

10.2.3 Canopy species and disturbance

The results of this survey imply that canopy disturbance is not related to particular canopy species. However, the low variation in canopy composition among the study sites may account for this apparent lack of relationship between species and disturbance. The predominance of oak in the canopy was reflected in the high proportion of disturbance events involving this species. The other species most frequently involved in disturbance events (holly and birch) are also common components in the woodlands surveyed. The small number of ash trees involved in disturbance is a reflection of bias towards woodlands on acid soils in this study. Although ash accounted for less than 10% of disturbance events overall, when the data referring to woodlands on base rich substrates are considered separately, ash is found to be involved in almost 30% of disturbance events.

However, the type of damage, and consequently the structure of resultant canopy gaps, may be related to characteristics of the species involved. Putz *et al.* (1983) investigated the variables that affect the mode of damage to canopy trees and found that wood properties, such as density and strength, were more important than factors such as girth, height, slope and buttressing. Uprooted trees had stronger, denser wood than snapped trees and disease and fungal attack contributed to wood weakening and thus snapping of trees. In the present study, birch accounted for 44% of the snapped trees encountered on random transects. This species has relatively weak wood (Grime *et al.* 1988) and is prone to fungal infection. However, birch was also frequently uprooted (22% of uprooted trees were birch), an indication of this species' characteristically shallow-rooting habit.

The high proportion of crown damage among disturbance events involving oak suggests that a high number of gaps formed by this species will lack the pit and mound associated with uprooted gap makers. Gaps formed by crown damage may be smaller than those formed by uprooting or snapping of entire trees and may be more likely to fill by lateral extension of the adjacent canopy rather than by growth of seedlings and saplings.

The response of the woodland community to canopy disturbance was not investigated in detail as part of the transect survey. However, the predicted trend of small gaps being filled by lateral extension of the adjacent canopy (Bazaaz 1993) was observed (Appendix II). Also, saplings apparently present at the time of disturbance were observed growing towards gap centres (Appendix II).

10.3 Characteristics of canopy gaps

Individual canopy gaps were studied primarily to investigate the occurrence of natural regeneration of tree species therein (cf. Chapters 8, 11). However, data about the structure of these gaps and heterogeneity within them, were also recorded. Although these data have not been gathered randomly, they provide a general indication of the characteristics of canopy gaps in Irish woodland.

10.3.1 Gap size

Gap sizes are frequently quoted in the relevant literature, however, methods of delineating the gap edge and measurement of the gap area often differ between studies, and details of these may be lacking from the publications (*e.g.* Brandani *et al.* 1988, Hubbell & Foster 1986). The delineation of the gap edge and subsequent measurement of the gap area pose problems in the field (Leiberman & Leiberman 1989) and differences in approach to these may result in significant disparities between data for similar (or even the same) sites (Barden 1989 #11).

Three main approaches to the measurement of gap size are frequently quoted, and all three were used in the present study. The simplest of these is that of Runkle (1982) which assumes that gaps are generally elliptical in shape, and calculates the length and width of the ellipse from the distances between the bases of the trees at the gap edge. Runkle applied a minimum size to the edge trees of 20 cm dbh. However, the simplification of the gap shape means that this method is less accurate when gap shapes are irregular. The second measure of gap size frequently used is that defined by Brokaw (1982). He defines a gap as 'a hole in the forest extending through all levels down to an average height of two m above ground'. The gap area is calculated by measuring the distance from the gap centre to the gap edge for 8 points or more, and summing the areas of the resultant triangles to yield an area for the gap, the shape of which is an octagon. Brokaw suggested that irregularities of outline tend to cancel out but even in a perfectly circular gap, an octagon will underestimate gap area by 25% (ter Steege 1996). The third method of estimating gap size yields, not a figure in square metres, but rather an ecological gap size, closely correlated with gap conditions such as light levels (Whitmore *et al.* 1993, Valverde & Silvertown 1997). This canopy openness (%) essentially describes the proportion of the sky which is unobstructed by canopy. Both Brokaw's octagon measure and % canopy openness can be derived from the analysis of hemispherical photographs (cf. 4.2.2 and 5.3.4) using specialised computer programs. (That used here was Winphot 5, ter Steege 1996.)

The calculation of gap size (*sensu* Brokaw) using hemiphots involved the projection of the 3-dimensional hemisphere into a 2-dimensional figure and, using canopy height at the gap edge, calculation of the areas of the triangles (with apices at the gap centre) which make up the gap. However, Winphot allowed for the insertion of only one value for canopy height, and often the canopy at the gap edge varied significantly in height. In addition, the calculations proved extremely sensitive to the canopy height value, with differences of one or two metres dramatically affecting the gap area result. Thus, this measure was not used in analysis of gap data in this study, and subsequent references to gap areas here refer to those calculated from Runkle's ellipse formula. Runkle's ellipse approach proved quite sturdy and allowed comparison, at least of the scale of gap size, between gaps. It is also easier to visualise than canopy openness, which is affected by stand characteristics other than gap size *sensu stricto*.

The sizes of naturally formed gaps ranged from $1m^2$ (the minimum recognised) to $330m^2$, with an average of $\sim 96m^2$. This compares with reported gap areas of: 1-1490 m^2, average 65 m^2 (Runkle 1981, 1982) in eastern USA; average gap area of 80.3 m^2 in western Japan (no minimum size given) (Yamamoto 1992). Most of the gaps (~2/3) measured in this study were less than 100 m^2 and more than one third were less than 50 m^2 (cf. Fig. 7.12). Yamamoto (1992) and Hubbell and Foster (1986) also reported a higher frequency of smaller gaps than large gaps. This is a reflection of the small numbers of individuals involved in gap formation. All of the naturally formed gaps studied here were formed by damage to a single or few (up to 6) trees. Van der Meer & Bongers (1996) found that the area of gaps (using a modified version of Brokaw's 1982 method where the canopy gap edge was delineated at 20m from the forest floor) was correlated with the number of makers involved and their total basal area. Runkle and Yetter (1987), studying old-growth forests in the Appalachians, reckoned that 76% of the gap area was contained within gaps less than $200m^2$ in size.

Canopy openness values (cf. 4.2, 5.3) ranged from 8% to ~60% for naturally formed gaps. Kennedy and Swaine (1992) referred to a canopy openness value of 3 % as equivalent to closed canopy, of 8% as equivalent to small gaps, and of 30% as equivalent to large gaps. However, no corresponding gap areas were published for these gaps. Canopy openness values calculated for gaps in this study ranged from ~ 8% to ~55%. Stand characteristics such as the presence of understorey vegetation, and canopy density also affect canopy openness, and the poor correlation between gap sizes calculated from the ellipse method and canopy openness values reflects the variation in stand structure, both between and within the woodlands sampled. Canopy size in gaps at higher latitudes may be of more significance than in temperate or tropical areas. Kuuluvainen (1994) reported that, in boreal forests, small gaps had light conditions similar to those under intact canopy. This is because the low solar angle resulted in standing trees casting a longer shadow than they would at lower latitudes.

10.3.2 Gap makers

The pattern of species involvement in gap formation was similar to that observed from the random transect sample of canopy disturbance events. The predominance of oak as the gap maker can again be explained by its dominance as a canopy former, rather than any predisposition to damage, uprooting or snapping. Similarly, Brandani *et al.* (1988) found that most (65%) of the gaps studied in tropical Costa Rican forest were caused by the dominant canopy tree species. Conversely, Whitbread & Montgomery (1994 #332) reported that beech trees were more often damaged than oak, both in pure and mixed stands, during the great storm of 1987 in south east England. The lack of correlation between particular species and gap formation (apart from that owing to frequency of particular species in the canopy) in this study demonstrates that the rate of gap formation cannot be predicted according to the species composition of a stand. However, other stand characteristics may play a role in determining the rate of gap formation, and the types of gaps formed.

10.3.3 Gap formation

When the different modes of gap formation are examined for each species of gap maker (cf. Fig. 7.6) oak was proportionately more often crown damaged than any other species. Lamb (1989) investigated the different types of damage experienced by various tree species in the great storm of 1987 in south east England. He found that limb shedding was particularly characteristic of oaks and proposed that this was a mechanism to avert more severe damage such as uprooting or snapping of the main trunk.

In the present study, uprooting was the most common contributor to canopy gap formation, but crown damage was also common. Foster (1988) found that soil conditions played a role in determining the type of damage most likely to occur in storms in the USA. He found that when soil was dry, rooting was more effective and so windsnap was more common than windthrow. However, wet soil reduces the grip of roots and in such conditions, therefore, the occurrence of uprooting is more likely. Because the gaps investigated here were not the result of a single storm, circumstances pertinent to the occurrence of each are likely to have varied. Among gap makers, birch was more often found to be snapped than damaged in another way. This is likely to be related to the inherent weakness of birch timber, and the susceptibility of this species to fungal infection (Grime *et al.* 1988). However, this shallow rooting species was also frequently uprooted and local conditions (*e.g.* soil type and water table depth) may have affected this.

Many of the gaps studied were the result of damage to more than one tree, and in some cases the cause of damage was the falling of another tree. Many of the uprooted hollies that contributed to gap

formation were toppled because they were rooted amongst the roots of a larger tree (usually oak), which was blown down. Van der Meer & Bongers (1996) found that, in rainforest in French Guiana, 75% of fallen trees (snapped and uprooted) and 83% of crown damaged trees, were the result of damage from another falling tree.

10.3.4 Gap age

Tanaka and Nakashizuka (1997) investigated gap formation in a mixed deciduous forest in central Japan over 15 years. Temporal variation in gap creation was observed, with peak gap formation related to successive years of more severe typhoons. The gaps investigated in my research were aged by deduction rather than from actual knowledge of their date of formation, so interpretation of their ages must be treated with some caution. The use of vegetation in the ageing of gaps (as here) carries some risk, as additional factors as well as the gap age determine gap vegetation. For example, many artificial gaps in Tomies wood (such as that used in the sapling transplant investigation - cf. Chapter 5.4) date from the 1970s and yet contain no saplings. Nonetheless, some degree of temporal clustering of gap formation was evident. All of the gaps studied in Tomies wood were less than 3 years old (cf. Table 7.5) and are likely to have resulted from a series of severe storms in the winters of the years just prior to survey. Gaps investigated in my research ranged from 1 to *c.* 20 years old. In some woodlands (*e.g.* Union wood) most of the gaps encountered were old (>10 years) and recently formed gaps were not found. This suggests a degree of periodicity in gap formation. However, it must be noted that whole site inventories were not carried out in this investigation, so the results remain somewhat inconclusive.

Kuuluvainen (1994) described the disturbance regime in forests in Northern Finland. He found that, because conifers are usually monopodial, and thus less flexible in growth form, they have a limited ability to adapt to canopy gaps and forage for light. Thus, gaps in such forests may persist for longer than those where species are adapted to quickly colonise space vacated by canopy gaps. Similarly, my findings indicate that gaps in woodlands where regeneration is inhibited by factors such as overgrazing may persist for longer than those where regeneration takes place freely (cf. Chapter 11).

10.3.5 Heterogeneity of gap structure

The structural heterogeneity that occurs within canopy gaps is the gap characteristic most credited with the important role of promoting species diversity in forests (Grubb 1977). Variation in structure provides physical diversity (*e.g.* in availability of seedbeds) and allows for variation in environmental conditions within a gap (Brokaw 1985).

The gaps studied here were subjectively divided into gap zones before vegetation and environmental variables were recorded. The zones used roughly correspond with those used by previous researchers (Oldeman 1978, Orians 1983, Brandani *et al.*1988; cf. 4.4) but with additional subdivision of the root zone into pit and mound, and of the trunk zone into bole and periphery (cf. 5.4.3). The presence of some or all of these zones in individual gaps in Irish woods illustrates the range of structural diversity to be found in canopy gaps, and the predicted link between the mode of gap formation and the presence of different zones was found to be valid (see Table 7.5).

The dimensions of treefall mounds found in Irish woodland gaps varied from 0.8m x 0.7m to 7.8m x 1.9m and pits were up to 2.3 m deep. This contrasts with pit depths reported by Beatty & Stone (1986 #198) for old-growth forests in the USA, which were up to only 32cm deep. Whether this disparity reflects differences in the root structure of the uprooted trees, or the age of pits (and hence the degree of infilling) is unclear. Buckley *et al.* (1994) reported root plates of up to 5m tall, and pits up to 1m deep for beech woods on the Wye Downs in south east England. All of the gaps investigated in Irish woodland contained fallen canopy, and two thirds contained fallen trunks. Pits and mounds were present in lower proportions (42 and 60% respectively) a reflection of the role of crown damage and trunk snapping in gap formation. Kuuluvainen (1994) identified areas along decomposing fallen trunks and branches, on pits and mounds, and on mineral soil exposed by fallen branches and debris as good sites for regeneration in Scots pine forests in Northern Finland. The attributes of these areas that provided for good chances of successful establishment were: protection from browsing; increased nutrient input through the disturbance of soil and decay of crown debris; shelter from excess wind and radiation which may render seedlings vulnerable to desiccation

Even if the area of disturbance is quite small compared with the total forest area, it may still be a significant niche within the ecosystem. Yamomoto (1992) found that even where uprooting occurred at low frequencies, it was still important as it provided the majority of suitable sites for the germination and establishment of pioneer species.

10.3.6 Heterogeneity of soils in gaps

Investigations into resource availability in canopy gaps have focused on light (Barton *et al.* 1989, Chazdon & Fletcher 1984, Poulson & Platt 1989) and nutrient cycling in gaps has been studied to a lesser extent (Bauhaus & Bartsch 1995). Bauhaus & Bartsch (1995) found that leaching of nutrients from soils was higher in gaps than within closed forest. The loss of root function (from uprooting/death of the gap maker) was found to be a major cause of disruption to the nitrogen cycle,

increasing nitrification and acidification. Bauhaus & Barthel (1995) found a decrease in microbial biomass in canopy gaps and attributed this to the loss of ectomycorrhizal hyphae that had previously been associated with the gap makers' root systems.

Denslow *et al.* (1998) also reported increased leaching of nitrogen after clear-felling and examined the effects of gap size on soil nutrients. They reported an initial increase in nitrate and phosphate immediately after gap creation, but these returned to under-canopy levels within a year.

Soil properties may be expected to vary between gap zones owing to the physical effects of fallen debris and trunks (shelter, infiltration of precipitation, shading and thus cooling influence) and of pits and mounds (exposure of mineral soil) and also the nutrient input from decay of litter and debris. The organic content of the exposed mineral soils was found to be lower in pits than in other parts of gaps studied. However, this difference was not consistent for all gaps, presumably because of the input from leaf litter trapped in older or more exposed pits. Soil nitrogen and phosphate also varied between gap zones, but the most significant differences were between different gaps, even in the same woodland. This reflects the high level of background heterogeneity in woodland soils in general. Nonetheless, the root zones tended to have lower nutrient levels than other zones, presumably because of the nature of mineral soil, and the elevated input of nutrients into the other zones (especially along decomposing boles, and below fallen canopy) from leaf and woody litter.

Vitousek and Denslow (1986) identified comparable differences in soil properties between gap zones in woodland in lowland tropical forests. Soils from root zones had lower carbon and nitrogen, and higher pH than other zones. Extractable phosphate was lower in the root zone than elsewhere. However, no significant difference in nutrient availability was found between the crown zone and beneath intact canopy, despite higher temperatures, higher water levels and input from crown debris. They suggest that the background rates of mineralisation in these relatively nutrient rich soils are too high to allow observation of increased nutrient availability from decomposition of debris, and conclude that changes in nutrient availability on gap formation are relatively small compared with changes in the light resource.

10.4 Conclusion

The results of this investigation into the disturbance regime in Irish semi-natural woodland give a general insight into the occurrence and characteristics of canopy gaps in these systems. Irish woodlands are dominated by small-scale disturbances, and the rate of disturbance and gap formation varies in time and space. However, large-scale damage to woodland trees has taken place in Ireland in the past, and is likely to reoccur. The disturbance regime is affected by multiple factors including wind events, stand characteristics and site factors such as topography. Disturbance events are not associated with particular canopy species, and the principal canopy members are represented in these events in proportion to their frequency in the woodland canopy. There is some relationship, however, between the modes of disturbance experienced and the characteristics of certain species. Irish canopy gaps exhibit a range of sizes comparable with those quoted for other temperate woodlands, and for some tropical forests. The structural heterogeneity found to be associated with canopy gaps in other studies also exists between and within gaps in Irish woodland canopy. Soil properties vary between and within gaps, and some predictable trends exist between gap zones. A more detailed investigation would involve surveys of whole woods, and calculations of forest turnover rates. It would also involve investigation of a wider range of woodland types, from coniferous plantations to semi-natural wetland woods.

CHAPTER 11 VEGETATION IN CANOPY GAPS

A general indication of the occurrence and characteristics of canopy gaps in Irish semi-natural woodlands has been presented in Chapter 7 and discussed in Chapter 10. The role of these gaps in the natural regeneration of canopy tree species was investigated by examination of the vegetation in 45 gaps (cf. 5.3.5). The purpose of this investigation was two-fold. Firstly, the extent and nature of natural regeneration in canopy gaps is of interest, because of the reported failure of woodland regeneration in Ireland. Secondly, the distribution of regeneration within and between gaps is of interest, in order to test the gap-partitioning hypothesis, and also the theory that the diversity of regeneration niches within gaps is central in promoting diversity in the woodland as a whole. Such theories have been tested in tropical forests (Pickett & White 1985), but have not previously been investigated in Irish woodland. Data were gathered by the sampling of relevés from subjectively delineated zones in 45 canopy gaps in 13 woodlands (cf. 5.3.5.). A smaller number of relevés was sampled from under intact canopy. The results are presented in Chapter 8 and individual gap descriptions are contained in Appendix III. Detailed descriptions of the vegetation present in gaps are not included here, as the focus of this study was the regeneration of tree species. A summary of the nature of the vegetation is of relevance, however, because of the potential effects of the general vegetation on regeneration in canopy gaps.

11.1 Differences between gaps and intact canopy

The response of the woodland community to canopy disturbance has been the subject of much research, especially in the tropics and in temperate forests of North America (cf. Chapter 4). Gaps differ from areas below intact canopy and so the nature of vegetation in gaps may be expected to differ from that under adjacent intact canopy.

11.1.1 The general vegetation

In this study, 15 non-arboreal taxa were found in gap relevés only (*i.e.* were absent from canopy relevés), but the significance of this must not be overestimated. The primary focus of this research was canopy gaps and the vegetation below woodland canopy was not sufficiently sampled to allow firm conclusions to be made regarding the confinement of any taxa to canopy gaps. This is illustrated by reference to the autecologies of those species found only in gaps in this study (cf. Table 8.1). Taxa such as *Viola* and *Urtica* are adapted to shade and so their restriction to light gaps in this survey is not a true reflection of their distribution in woodland habitats. However, *Ulex europaeus* and *Erica*

tetralix are intolerant of shade, and their occurrence in gap relevés only is probably an indication of their true distribution in Irish woodlands.

While the species composition of gap floras was not found to differ markedly from that under closed canopy, some differences in ground coverage were observed between the two. Litter cover was higher under canopy than in canopy gaps and cover by herbaceous species was generally greater in gaps. These patterns are easily explained by the higher direct input of leaf litter from overhead canopy, and by the increased growth of woodland herbs in response to higher resource availability (especially light) in gaps.

Overall however, there was little difference in the field layer between gaps and intact canopy. Similarly, gaps created by the Great Storm in south east England in 1987 were colonised by vegetation that was already present in the immediate area (Buckley *et al.* 1994).

11.1.2 Regeneration of tree species

Differences between the occurrence of regeneration under enclosed canopy and in canopy gaps were not investigated in detail here, as closed canopy was very under-sampled compared with gaps. Nonetheless, for all tree species encountered, regeneration of all classes was more abundant in gaps than under intact canopy (cf. Figs. 8.17 & 8.18). This was especially so for birch, which cannot establish under closed canopy, while the other main species (oak, ash, beech, rowan, and holly) can establish and tolerate shade at least for a time (cf. Chapter 3). Kelly & Kirby (1982) note the confinement of oak saplings to woodland edges and clearings. While regeneration of ash was higher in canopy gaps than under closed canopy in this study, the difference was less pronounced than in other species. This may be explained by the fact that those woodlands in which ash regeneration was most abundant (Charleville Island and Charleville Castle) are currently dominated by widely spaced oaks which cast a relatively light shade. Kelly & Kirby (1982) investigated the vegetation of native Irish oakwood over limestone, and found that saplings of ash were the most frequent (excluding hazel) in their relevés and these authors comment on the profusion of ash regeneration both under intact canopy and in gaps.

11.2 Heterogeneity of the general vegetation within canopy gaps

Subjectively delineated gap zones were found to differ in their physical and edaphic properties (cf. 5.3.2, 7, 10) and differences in the vegetation were also observed (cf. 8.2). Cover by herbs and shrubs was greatest in the peripheral areas of the gap. The vegetation in this zone is likely to have pre-dated

gap formation, as the peripheral zones of gaps generally do not experience soil disturbance or damage to the vegetation from falling debris, and thus can achieve increased growth immediately on gap formation. Bare soil was highest in the pits where upturned trees had exposed mineral soil and dragged away vegetation. Buckley *et al.* (1994) investigated the distribution of vegetation in canopy gaps in three woods, following the Great Storm in south east England in 1987. In some gaps, pits were colonised by species such as *Dryopteris* spp. and *Oxalis acetosella*, that favoured the damp shady conditions there.

11.3 Regeneration in canopy gaps

Given that woodland cover is the potential natural vegetation of many temperate and tropical areas (Ellenberg 1988, Picket & White 1985), the natural tendency is for canopy gaps to become filled by replacement trees. The specific scenarios encountered vary from one site to another and are affected by factors related to the nature of the vegetation present and features of woodland management. Nonetheless, several general mechanisms of vegetation response to canopy gaps are observed (Bazaaz, 1983). These include filling of gaps by lateral expansion of adjacent canopy branches, regrowth from the gap maker, growth of seedlings and saplings already present at the time of gap formation, and the establishment of new individuals from seed. All of these mechanisms were observed in the gaps surveyed in this study and are discussed in further detail below.

11.3.1 Factors affecting regeneration composition in gaps

Some regeneration of tree species was found in all except two of the 45 gaps surveyed. Regeneration was classified according to size, so that seedlings (S1, S2) were distinguished from saplings (cf. 5.3.5). Saplings were present in more than 70% of gaps, S2s in 82% and S1s in 56% of gaps. The distribution of seedlings and saplings in gaps depends on the occurrence of seed production, germination and establishment, and survival. Each of these steps is affected by various components of the stand structure and gap characteristics.

Seed availability

The production of seed and the resultant composition of the seedling cohort are largely influenced by the proximity of parent trees. The dominance of oak in the canopies of the woodlands surveyed here is reflected in the fact that regeneration of this species was the most widespread in the gaps studied. Similarly, the seedling composition in gaps in tropical forests and in temperate forests of North America are dependent primarily on the seed rain (Gray & Spies 1996, Brokaw 1985, Beckage *et al.* 2000). The results of the present study highlight the indirect effect of soil type on regeneration

composition in canopy gaps. Soil type was a major determinant of the parent species present and thus the availability of seed of different species (cf. Fig. 8.10). However, factors other than soil type also affect the composition of the canopy and thus of the seed producers present. For example, birch was virtually absent from Portlaw Wood because of its selective removal (Marquess of Waterford *pers. comm.*) and so it was lacking as a seedling in gaps in this woodland. The species regenerating in canopy gaps in Irish woodlands were closely related to the occurrence of potential parent individuals. Brandani *et al.* (1988) found that the distribution of regeneration within and between gaps in Costa Rican tropical wet forest was related to the non-random input of seeds as affected by the distribution of parent trees. While holly, birch and, to a lesser extent, rowan are significant components of the woodlands surveyed, their high frequency as regeneration in gaps must, at least partly, be attributed to their prolific seed production. Martinez-Ramos *et al.* (1989) point out that many species are capable of germination and establishment in sites that are unsuitable for their development to maturity. However, the presence of mature individuals of these species (the parent trees) close to these gaps suggests that growth to maturity is possible at these sites. The rarity of elm and yew in the woodlands surveyed (mostly woods over acid soils) partly explains the dearth of these species among the regeneration found in Irish woodland canopy gaps.

Germination sites

The availability of appropriate sites for seed germination can influence the presence and composition of regeneration in woodland (Brandani *et al* 1988). Some species, particularly those with very small seeds, are exacting in their seed bed requirements and may also require light for the stimulation of germination, or the breaking of dormancy (Grime *et al.* 1988). The canopy gaps in this study were found to provide a range of germination sites, from moss covered mounds and bare mineral soil in root pits to thickly littered and somewhat shaded areas below fallen canopy (cf. Table 7. 5).

In this study, seedlings of birch were more abundant on mossy mounds or on exposed soil, as cover by litter and vegetation in other gap zones prevented the short radicle of the tiny birch seedling from reaching the soil. King (1994) found that gaps created by the Great Storm, in south east England in 1987, were colonised primarily by birch. However, seedling densities were significantly lower in areas where leaf litter and woody debris amounted to a high proportion of the ground cover. In the present study, seedlings of some species were fairly evenly distributed among the different gap zones, but oak regeneration was slightly more abundant on the undisturbed soil of the bole and periphery zones, and on root mounds. King (1994) also found that oak regeneration was most successful in the parts of gaps where the soil remained intact. Buckley *et al.* (1994), also investigating post-storm gap vegetation,

found that regeneration of birch and hornbeam was associated with disturbed soil but that ash and sycamore regeneration appeared to be unaffected by seedbed.

A lack of germination sites may be the reason for the complete absence of any regeneration from seed in two of the gaps surveyed here. *Luzula sylvatica* accounts for 100% of the ground cover in these gaps (Un1 & Un2) and observation of similar coverage by this species under intact canopy suggests that the dense cover may predate gap formation (cf. Appendix III). Thus, there are no suitable sites for seed germination, even of the larger seeded species such as oak, which can generally germinate on a layer of litter. The development of such a dense mat of vegetation may be related to heavy browsing at this site in the past, and its subsequent reduction (Kelly in press). *Luzula* spp. are reported to increase in abundance under heavy browsing (Putman *et al.* 1989) and the growth form of this species may exclude access of seeds to suitable germination sites. Penetration of this blanketing field layer in the future appears unlikely unless the vegetation mat is somehow broken. Morison & Stoneman (1998) report the use of pigs to root up ground vegetation that was preventing the germination of tree species in exclosures in Scottish woodland. Mitchell & Kirby (1990) also refer to the advantages of grazing animals (cattle and sheep) in poaching the woodland floor, and thus providing suitable sites for seed germination. An increase in the number of saplings of hornbeam was found following the creation of germination sites by browsing bison in Bialoweiza (Kwiatkowska 1996).

Seedling survival

High mortality among seedlings was demonstrated in the low densities of saplings compared with that for S1s and S2s (cf. Tables 8.4, 8.5). Such a phenomenon is widely occurring, and seedling mortality in gaps has been attributed to desiccation, frost, disease and competition (Pickett & White 1985, Canham & Marks 1985).

The high mortality experienced by seedlings of all tree species explains the lower densities of saplings compared with that of seedlings generally encountered in gaps in this study. The relationship between seedling and sapling numbers is not a simple one, however, and varied between species. The high numbers of oak S2s compared with S1s illustrates the sporadic seed production in this species and the relatively low growth rate of seedlings. Conversely, high numbers of birch S1s were found relative to the numbers of S2s. This reflects the prolific annual output of this species, and the high mortality suffered during the first year of growth (Miles & Kinnaird 1979). The higher numbers of ash saplings compared with seedlings may reflect the fast growth rate of this species and also the fact that woodlands in which ash was abundant had understoreys of sapling to pole-stage ashes, and so new

seedling recruitment may not have been occurring. The low numbers of ash seedlings may also reflect the low tolerance of competition from the field layer of this species (Wardle 1959).

The absence of saplings from some gaps is more easily explained than for others. For example, saplings were absent from five of the six gaps sampled in Tomies wood (cf. Table 8.3). The presence of plentiful seedlings of many species is evidence that seed production is not lacking in this wood. Instead, the heavy grazing pressure has prevented any seedlings from achieving sapling status, and the only saplings found in this woodland (outside of exclosures) were on the rootplates of uprooted trees, which are inaccessible to browsing hares and deer. Brandani *et al.* (1988) postulated that differential rates of germination and survival between gap zones were the explanation behind the observed non-random distribution of regeneration in canopy gap zones in Costa Rican tropical forest. This is certainly true where the only saplings present in some gaps were those on mounds, which were out of the reach of browsers.

However, heavy grazing pressure does not explain the absence of saplings from all gaps. Apart from those at Tomies, the other gaps in this study that lacked saplings are distributed among many woods and, in all cases, other gaps at each site contain saplings. Each of these gaps also contains both S1s and S2s and it can be assumed that some of these will progress to the sapling stage, as seedlings at other gaps at each site have apparently succeeded in doing. Despite differential mortality among seedlings and differential competitive ability between species, it has been found that the species composition of the regeneration in a gap at a given time is a good indicator of the future stand composition in that gap (Runkle & Yetter 1987). It is also observed that mortality is higher among later cohorts of gap colonisers than among those initially present (Kennedy & Swaine 1992) and that taller seedlings and saplings are more likely to survive than shorter individuals (Brokaw 1985).

The effect of gap characteristics on regeneration

In the gaps surveyed here, stand characteristics appear to have had a greater effect than gap characteristics, on the nature and composition of regeneration present. This may have been related to the range of gap sizes included here ($1m^2$ - $1964m^2$), however size effects have been reported from other studies in which a similar range of gaps sizes was investigated (Clinton & Boring 1994). The relatively low tree species diversity in Irish woodland and the absence of strict intolerants from the tree flora may partially explain this. However other studies have also reported that site factors (such as the presence of understorey vegetation) negate the effects of gap size on regeneration (Ehrenfeld 1980).

Kennedy and Swaine (1992) reckoned that if a critical gap size exists for colonisers of rainforest gaps, it is very small (only about 5% canopy openness). Brokaw (1985) found that certain species were largely restricted to gaps above a certain size, and concluded that such species could not tolerate the environmental conditions present in smaller gaps. Kennedy and Swaine (1992) reject this conclusion, however, and suggest that the distribution of species among varying sizes of canopy reflected the abundance of the relevant species in the forest. Those species that occurred in both small and large gaps were abundant in the canopy, and so more likely to be found when only a small area is examined (e.g. a small gap). However, those species that Brokaw found only in large gaps were relatively rare in the forest, and so had a higher probability of being present within a larger sample area (a large gap). Kennedy and Swaine (1992) conclude that the question of gap partitioning remains unresolved, and can only be answered following detailed experimental investigation.

Chapman *et al.*(1999) carried out experimental investigations in canopy gaps in Uganda and found that mortality of seedlings increased in gaps larger than those created by single treefall. Conversely, Kennedy and Swaine (1992) found increased height increments in colonists in larger gaps compared with those in smaller gaps. Clearly, local conditions and the limiting factors exerting influence at particular sites affect the regeneration composition and the performance of seedlings and saplings in canopy gaps. Grubb (1977) postulates that larger gaps are likely to be filled by light demanding species, while smaller gaps will be filled by the growth of shade tolerators. Such patterns were not pronounced in this survey, however, perhaps because of the lack of clear distinction between the two species groups among the native tree flora. Brown & Whitmore (1992) tested the gap partitioning hypothesis in Malaysian forest and found that seedling size at gap creation was a more important determinant of gap composition than gap size. This was also observed in the present investigation, where seedlings that formed a seedling bank below closed canopy (*e.g.* holly) had an advantage over those that require disturbance for germination and establishment (*e.g.* birch). Brown and Whitmore (1992) postulate that shade tolerators would lose their competitive edge in more 'gappy' woodland, and light demanders might become more abundant in the canopy.

11.4 The response of Irish woodland communities to canopy gaps

Woodland canopy gaps have been much investigated, especially in tropical and in North American forests over the past few decades, and the emphasis of the research has been on the response of the tree flora (Beckage *et al.* 2000, Brandani *et al.* 1988, Canham 1988, Uhl *et al.* 1988, Whitmore *et al.* 1993). The role of gaps in the regeneration of canopy tree species has been acknowledged since the studies of Watt on British woodlands (Watt 1919, 1924, 1947). Canopy gaps are purported to promote diversity

in canopy tree species (Grubb 1977) and allow the regeneration of shade-intolerant species (Vera 2000). Indeed, the perceived failure to regenerate of the canopy dominant (oak) in many British woods over recent decades has been attributed to the absence of canopy gaps, resulting from intense management in recent centuries (Streeter 1974). The present study has sought to investigate the vegetation of Irish woodland canopy gaps, in order to elucidate the role of these in the natural regeneration of the native tree species within woodland. A wide diversity in gap characteristics and stand conditions was observed and this has resulted in a variety of responses to gap formation in Irish woodlands.

Bazaaz (1983) recognised 5 different types of response to gap formation (see above), and all of these were observed in the present study. In addition, other responses were also identified, where site conditions have 'arrested' the regeneration of tree species in gaps, and canopy gaps have remained open over long periods.

11.4.1 Vegetative replacement of canopy

The replacement of lost canopy by the lateral extension of adjacent canopy branches was observed particularly where the gaps formed were small in extent (cf. Appendix II). While this type of growth probably also contributed to the closure of larger gaps, repeated gap measurements were not made in this study and so this effect was not observable. Runkle (1985) reported that small gaps in North American forests were usually closed by the lateral expansion of existing canopy branches which can extend at rates of 4 - 26 cm per year.

In some cases, gaps caused by canopy disturbance were actually closed by regrowth of the gap maker. This occurred where growth of other branches filled the space vacated by loss of parts of the crown, where epicormic growth from partially rooted blown trees filled the gap, and where snapped individuals produced new branches. In each case, the new growth will have an advantage over individuals developing directly from seed, as substantial reserves and an effective root system are already in place, and such growth usually has a height advantage over new seedlings. More than four fifths of the trees blown down in the 1987 Great Storm of south east England were still alive and exhibiting crown regeneration seven years after initial damage (Buckley *et al.* 1994). The authors investigating post-storm dynamics in that circumstance questioned the long-term viability of such growth, but the results of the present study indicate that such regrowth can survive for at least up to 20 years (cf. Appendix III). In any case, even if such regrowth does not replace damaged canopy, completely or in the longer term, it will increase shade in the gap and render conditions less suitable for light demanding pioneer species.

11.4.2 Replacement of canopy by growth of seedlings and saplings

This is the type of response to gap creation most often discussed in the literature, and is accepted to be the primary method of regeneration of tree species within woodland (Ellenberg 1988). Several different patterns are observed within this general response type, which lead to different outcomes for the future canopy composition. Colonisation of gaps in temperate forest in the USA is usually by seedlings already present at gap creation (Kozlowski *et al.* 1990). Although this study did not involve monitoring of gaps from the date of formation, it can be deduced in some cases that regeneration composition was dominated by seedlings and saplings already present at gap formation.

Regeneration of current canopy dominants

Regeneration of the current canopy dominants was observed in most gaps, and oak was the most widely distributed seedling in the present study. The influence of the canopy composition on seedling composition increases the probability that gaps will be filled by members of the current canopy. However, oak was less frequent as a sapling than other species, and was the leader (tallest sapling) in only a small number of gaps. This suggests that this species may not always succeed in replacing itself (oak was the commonest gap maker), and that the future canopy may be more mixed than at present.

Regeneration of short-lived pioneer species

Birch and rowan were the most common short-lived pioneer species in the canopies of the woodlands investigated in this study. Both species are prolific seed producers and seedlings of these species were common in the gaps in woodlands in which parent trees were present, and birch thickets were observed in some older gaps (Plate 3). Exposed soil associated with root zones and trampled ground provided ample germination sites for birch in some of the woodlands. However, where litter cover was deep or vegetation extensive, birch seedlings were excluded.

Regeneration of other tree species

In order for the current composition of a forest stand to be maintained, gaps must have a high chance of being filled by the same species as created them. When this does not occur, a succession or a cyclical development of woodland canopy seems probable. The phenomenon of alternation between ash and sycamore is well documented for some English woods (Waters & Savill 1992). Regeneration in the gaps in Charleville Castle and Island woods was dominated by ash and it seems likely that the future canopy at these sites will include a higher proportion of ash than the present oak-dominated canopy. Emborg (1998) reports that gaps in mixed deciduous forest in Denmark were initially colonised by ash. Beech was established at the next mast year and could successfully establish among the juveniles of ash already present. This was interpreted as an early stage in the successional shift from ash to beech-

dominated canopy at this site. The tendency for beech to replace oak has been noted for some Irish Woods (Quinn 1994) and, although woodlands with exotic species were avoided in the present survey, beech was observed to be regenerating successfully in some of the canopy gaps sampled.

Regeneration of sub-canopy species

Competition from sub-canopy species can affect the regeneration of canopy trees in gaps, and gaps in high canopy may be filled with low-canopy vegetation. The dominance of holly seedlings and saplings in some of the gaps surveyed in this study suggests the potential of this species to dominate future vegetation in such places. Holly can form dense thickets which may, at least temporarily, prevent the establishment of canopy species. Such thickets have been observed in exclosures in some of the woodlands studied (Higgins *et al.* 1998) and cast deep shade, excluding the growth of any other vegetation. Peterken (1996) describes a similar situation at the New Forest, Hampshire, England. Holly thickets developed on heath on the relaxation of browsing pressure, and in some places have delayed the colonisation by canopy tree species such as oak. Replacement of the high canopy has been 'arrested' by various vegetation types in many forests from all regions. Ehrenfeld (1980) found that a dense understorey of *Cornus florida* inhibited the regeneration of tree species in gaps in mature oak forest in New Jersey. In gaps in deciduous forest in the Appalachians in the USA, a dense understorey of *Rhododendron maxima* prevented regeneration of canopy species (Beckage *et al.* 2000). In gaps in mixed stands of *Abies delavayi* and *Betula utilis* in Chinese sub-alpine forest, invasion by understorey bamboo prevented establishment of canopy species (Taylor & Zisheng 1988). Similarly, dwarf bamboo prevented regeneration of tree species in gaps in Japanese *Fagus crenata-Abies homolepis* forest (Nakashizuka, 1989). Schnitzer *et al.* (2000) found that 7.5% of the gaps in rainforest on Barro Colorado Island (Panama) were arrested by the high density of liana growth there. The oldest such gap encountered was 13 years old, but the authors postulate that gaps may be maintained in a low-canopy state for much longer.

11.4.3 Maintenance of canopy gap conditions

The closure rates reported for canopy gaps vary from c. 9 years for British woodland (Valverde & Silvertown 1997), to 40 years for North American forest (Valverde & Silvertown 1997, using data from Runkle 1981). However, such calculations may not apply to gaps where regeneration of canopy species is impeded or delayed. Out of the 45 gaps surveyed in this study, 8 gaps were encountered in which regeneration of tree species was apparently failing to occur. Two factors were identified as playing a part in this: heavy browsing and elimination of regeneration by dense vegetation.

Overgrazing

The impact of high levels of browsing by domestic and wild animals on woodland regeneration is well-established (Mitchell & Kirby 1990, Putman 1994). Overgrazed woodlands lack saplings, and seedlings present may show evidence of being bitten back. Many of the woodlands surveyed in this research showed evidence of some level of browsing (cf. Chapter 6). However, only in the Killarney woodlands (Tomies and Camillan) was the impact of browsing such that regeneration was prevented in canopy gaps. In Tomies Wood, where browsing pressure is maintained at high levels, saplings of any species are lacking outside exclosures and 'safe sites' on the mounds of uprooted trees (Plate 4). This is clearly the result of browsing, as seedlings of all species are plentiful. Heavy browsing may also affect the composition of regeneration present, as some species are more tolerant of damage than others. In Camillan, browsing pressure was significantly reduced in the years just prior to survey, and browsed seedlings of holly that survived browsing impact, are now forming low thickets in canopy gaps. This species has a competitive advantage over other species such as oak, which may not persist for as long under conditions of heavy damage.

Interference from ground vegetation

In some of the gaps surveyed, regeneration of canopy species appears to be inhibited by the nature of the ground vegetation. The complete absence of any regeneration from two gaps in Union Wood is probably due to the dense carpet of *Luzula* at this site. Dense cover by *Rubus fruticosus* agg. in other gaps (notably those at Garannon Wood), does not appear to prevent germination, but may exclude some species by competition. Oak appears to be capable of competing with *Rubus* and is reported to be so in other studies (Kelly in press). However, pioneers such as birch were absent from areas of high *Rubus* cover in this survey, and may not be capable of competing with the aggressive growth of this species in canopy gaps. Bracken does not appear to prevent germination and establishment of tree species but may inhibit later stages of regeneration by shading of seedlings and saplings and smothering with persistent litter (Humphrey & Swaine 1997). Similarly, dense growth of meadowsweet (*Filipendula ulmaria*) at woodland edges, recently released from heavy grazing pressure was found to inhibit the survival of alder seedlings, although actual germination rates were unaffected (Vinther 1983).

11.5 The regeneration status of the principal native species in canopy gaps

The characteristics of trees, with regard to their natural regeneration, is outlined for the principal species encountered here, in Chapter 3 and so are not repeated here. This survey assessed the presence

Plate 3 Birch saplings filling a gap at The Island, Charleville, Co. Offaly.

and abundance of regeneration of canopy and sub-canopy tree species in gaps in some Irish woodlands. While long-term monitoring of individual sites was not involved, the composition of the regeneration present in a canopy gap at a given time may be taken as a good indicator of the future canopy composition at that site (Runkle 1981). However, the majority of the regeneration encountered in this survey was less than 5m tall, and competitive exclusion of saplings at the thicket stage (Kozlowski 1991) will affect the future canopy composition. Nonetheless, the future canopy dominants will probably be derived from the seedlings and saplings present at the time of survey, as seedling cohorts that establish subsequent to that present soon after gap formation exhibit higher mortality (Kennedy & Swaine 1992). Thus, reasonable predictions about the future composition of the woodlands surveyed may be drawn from the results of this study.

11.5.1 Oak

The dominance of oak in the woodlands surveyed explains its widespread occurrence in the regeneration in canopy gaps. Both seedlings and saplings of the species were common. This species was more abundant as a seedling than as a sapling, a pattern displayed by all species. Oak saplings were usually present in low numbers, and were frequently outgrown (in height) by saplings of other species, being the leader in only 4 of the 45 gaps surveyed. In very heavily browsed woodlands, oak may not persist for as long as holly and rowan, so a seedling bank of this species may be less likely to exist on release from browsing. Nonetheless, the tendency to invest in the development of a substantial tap-root, allows oak seedlings to survive heavy browsing for some years (Shaw 1974) and if the timing of release from browsing were to coincide with a mast year (or soon after), this species might well dominate the seedling/small sapling cohort in canopy gaps. The ability of this species to withstand competition from ground vegetation such as brambles, which are likely to expand on release from browsing (Kelly in press) may confer an advantage on oak over other species, in this situation. The regeneration of this species in the canopy gaps surveyed appears to be sufficient to maintain the presence of oak in the future canopy of Irish woodlands. However, it is unlikely to be as frequent in the woodland canopy as in the past, as other species, notably ash on base-rich soils, are more prolific in canopy gaps.

11.5.2 Ash

Regeneration of ash was virtually absent from woodlands on acid soils (from which mature trees were also absent) but was prolific in sites where seed bearing adults were present. Unlike other species, ash was more often present as a sapling than as a seedling. This may be an indication of the rapid growth that this species can achieve on gap creation (Peterken 1996, Vera 2000). In addition, saplings of ash often occurred in relatively high numbers, with more than 5 individuals present in half of the gaps in which ash saplings were found. Ash was the most frequently occurring leader species, despite its

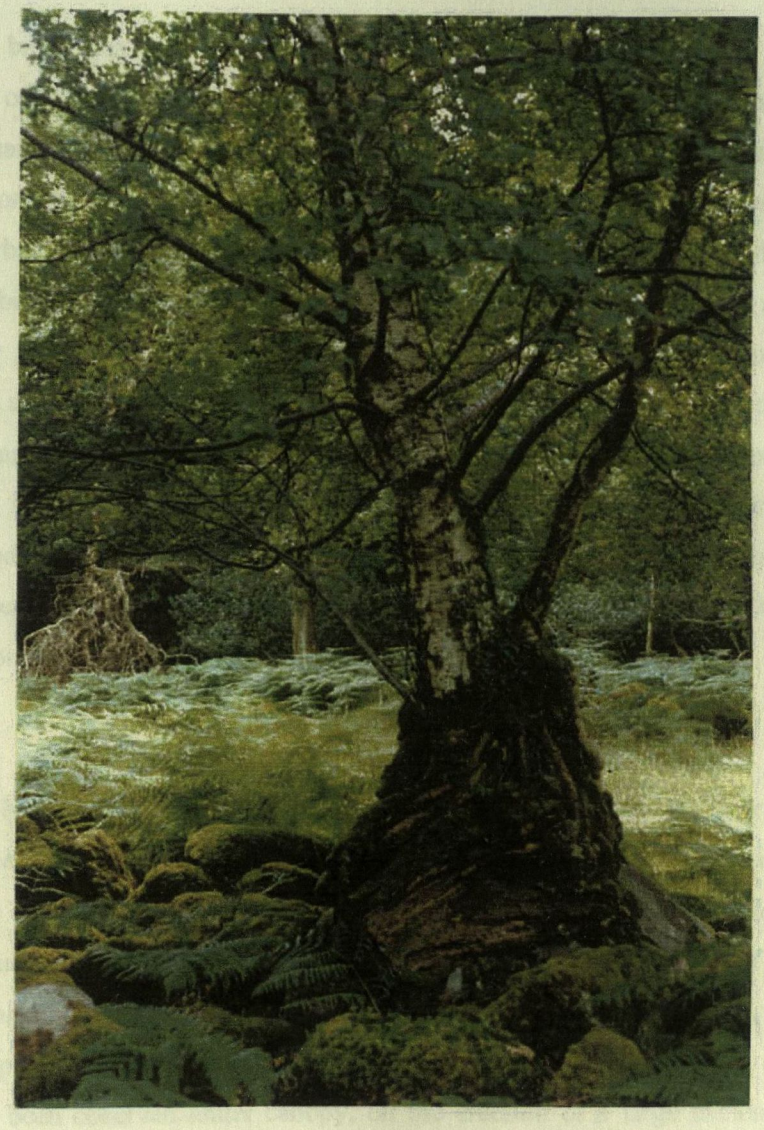

Plate 4 A young birch tree that has escaped browsing by establishing on a rootplate.

confinement to less acid soils. This species dominated the regeneration in gaps in Charleville Castle and on the Island, both in terms of height and abundance, and appears likely to replace the canopy at these locations. This situation appears similar to that reported by Rackham (1980) where ash is replacing oak in many English woods.

11.5.3 Birch

Regeneration of birch was confined to woods over acid soils, reflecting the distribution of seed producing adults of this species. However, it was lacking from some woods (Portlaw and Garannon) where it might have been expected to occur; this is explained by the management of these woods, where birch is considered a 'weed' species, and so actively removed (Marquess of Waterford *pers. comm.*). Disturbed soil or pleurocarpous moss carpets are required for the germination and establishment of birch. These sites do not appear to be lacking from most woods, as uprooting, scoring of the ground by fallen branches, and trampling by animals exposes soil for colonisation. Birch is frequently cited as a pioneer species (Ellenberg 1988), and may be expected to dominate the regeneration in canopy gaps, at least initially. This was observed by Kelly (in press), in an enclosed artificial clearing in Tomies wood. However, unlike many tropical pioneer species, a persistent seed bank is not formed (Grime *et al.*1988), and so seed must 'arrive' at a gap before colonisation can occur. Thus, where a seedling bank of shade tolerant seedlings already exists, the dominance of this species may not be as pronounced as otherwise expected.

11.5.4 Holly

Regeneration of holly was abundant in gaps in all woodlands in which mature individuals of this species were present. Holly is a long-lived tolerant species, whose prolific seed production allows it to act as a pioneer (Peterken 1996). As a seedling and sapling it displays tolerance of shade and browsing, and can achieve relatively high growth under closed canopy. All of these characteristics confer an advantage on this species both under shade and in browsed woodlands, and when conditions change (*i.e.* a gap is formed or browsing pressure relieved), holly may quickly develop into a dense thicket. This has been observed under canopy, on the erection of a large exclosure in Tomies wood (Kelly 2000). Even where such dominance by holly does not occur, its shade tolerance ensures its future in the woodland sub-canopy as it can withstand being overtopped by faster-growing and taller species.

11.5.5 Rowan

Like holly, regeneration of rowan was abundant in woodlands where this species was present in the canopy. Rowan also appears to exhibit a degree of tolerance of browsing, and can achieve rapid growth on release from browsing under high light levels. However, this species is relatively short-

lived and does not normally exceed 15-20m in height and is likely to remain a relatively small component of the woodland canopy.

11.5.6 Elm

The scarcity of regeneration of elm in the surveyed gaps can be partly explained by the low number of base-rich sites included here. However, elm is widely planted in the countryside (Webb *et al.* 1996) and is frequent in most districts, and so one might have expected to encounter more seedlings and saplings of this species. No seed bank is formed and seed remains viable for only a short period (days) (Richens 1983), but Grime *et al.* (1988) report that an abundance of widely dispersed fruits are regularly produced by this species. Elm is notoriously palatable (Mitchell & Ryan 1997, Rackham 1980) and Grime *et al* (1988) observe that predation of seeds and seedling mortality are high. Elm is self-sterile (Richens 1983) but its frequency in hedgerows in Ireland and anemophilous pollination render this factor unsatisfactory as an explanation for any dearth of regeneration of this species. The effects of Dutch Elm Disease on the status of this species may have had an impact on its regeneration. Detailed investigation into the status of this species in Ireland (a former canopy dominant), and its regeneration is required.

11.5.7 Other species

Hazel was relatively scarce in the gaps surveyed here, again, perhaps because of the emphasis of this survey on acid soils. However, even in base-rich sites the regeneration of this species was limited in distribution. In fact, seedlings and saplings of hazel were found only in gaps where a mature individual was present directly adjacent to the gap (cf. Table 8.3, Appendix III). This suggests that seed dispersal may play a role in limiting the distribution of seedlings. Dispersal of seed is dependent on predators such as rodents and birds, who may be assumed to destroy a fair proportion of the seed (Kollmann & Schill 1996). Seedlings are reportedly very tolerant of grazing, and respond with strong new growth from the roots (Sanderson 1958, cited in Vera 2000) so browsing is unlikely to be responsible for the scarcity of this species among gap regeneration. The results of my study suggest that seed dispersal and the subsequent establishment of seedlings may be limiting steps in the regeneration of hazel in Irish woodlands. However, this conclusion is merely based on incidental observation and the status of this species requires further investigation.

Yew (*Taxus bacatta*) was only a rare component of the regeneration encountered in gaps in this study, occurring in gaps in two woodlands. This species is intolerant of shade (Kelly 1975), is sensitive to browsing (Mitchell 1990) and prefers soils of base rich status. However, this does not explain the paucity of this species in the lightly and ungrazed gaps in woodlands over calcareous soil. The status

of this species requires further investigation and its ecology in Ireland is the subject of current research in this department.

Woodlands with significant amounts of introduced species were avoided as much as possible in this survey, but saplings of beech, sycamore, sweet chestnut and rhododendron were found regenerating successfully in canopy gaps. This, coupled with evidence from the literature (Cross 1981, Dierschke 1982) suggests that these species have the potential to become a significant canopy component in Irish woodlands.

11.6 Conclusion

Many types of response to canopy gaps were observed in the woodlands surveyed. Vegetative regeneration and regeneration from seed and seedlings were involved. In some cases different types of responses were observed at different gaps in the same woods. Detrended correspondence analysis grouped gaps from the same woodland reasonably close together, but by no means perfectly clustered, illustrating that while woodland did affect the regeneration composition of gaps, gap to gap differences also occurred (cf. Fig. 8.11). Such differences in the response to canopy gaps enhance diversity of structure and may result in a more diverse canopy composition in the future.

Some regeneration of tree species was found in 43 of the 45 canopy gaps sampled from 13 woodlands. The production of seed and establishment of seedlings appears to be successful for all species for which a seed source was nearby. The development of saplings was affected by browsing, competition, and seedling mortality but, in most of the woodlands surveyed, sufficient saplings are present to ensure the future of the woodland canopy.

The management of a site and characteristics of the woodland stand may predispose vegetation in some gaps to particular types of response to gap formation *e.g.* at Camillan, the history of browsing resulted in a bank of holly seedlings, which have an advantage over other species which must recruit from seed at gap formation. Management practices such as the removal of birch from some woodlands (*e.g.* Portlaw) may result in this species playing a lesser role than might be otherwise expected in canopy gaps. The presence of dense grassy swards (which may result from past browsing) may restrict germination of tree seedlings to disturbed soil. The different patterns of regeneration observed were not mutually exclusive, and in some cases are interlinked, *e.g.* overgrazing may promote the development of impenetrable grassy swards, thus keeping canopy gaps open by two means: exclusion of germination sites and inhibition of seedling growth. Canopy gaps assist the promotion of species diversity by offering structurally differing zones, with varying environmental conditions. However,

the low tree species diversity inherent in Irish woodlands, and the range of conditions present owing to management practices, means that canopy gaps may not play so significant a role in facilitating diversity in Irish woods as they are reported to do in other regions.

CHAPTER 12 BROWSING OF TREE SAPLINGS

12.1 Background

The aim of this experiment was to identify tree species preferences that may exist among browsing deer and hares, in order to elucidate potential effects of browsing on the success of regeneration in different tree species. The responses to browsing of these tree species were also examined to provide information on which to base predictions about the future canopy composition of browsed woodlands.

Saplings of five species were transplanted into two woodlands of contrasting soil type and browsing regime. Tomies wood is located over nutrient deficient peaty podsols derived from Devonian Old Red Sandstone, and is heavily browsed by sika deer and hares and, to a lesser extent, red deer. Charleville wood is situated on base-rich glacial tills over Carboniferous limestone, and is lightly browsed by a small population of fallow deer and some hares. Full site descriptions are given in Chapter 6, and the experimental procedure is described in full in Chapter 5. Results are presented in Chapter 9.

12.2 Experimental procedure

The use of experiments involving transplanting of saplings to investigate species preferences by browsers has a number of advantages. Woodlands with a history of high browsing pressure often lack saplings above a certain age or size, and saplings of some species may be less frequent or absent altogether (Mitchell *et al.* 1995, Miller *et al.* 1982). The use of planted saplings allows the investigator to control the species, size and abundance of saplings. While nursery stock may differ in quality and provenance from natural regeneration at a site, the investigator can assume relatively homogeneous nature (within species) of nursery stock subjected to the same conditions of establishment and growth prior to transplanting.

Thus, transplanting allows the investigator to carry out experimental studies under field conditions. It must be noted that the situation in Tomies wood was rather extreme in terms of the browsing pressure experienced by the transplanted saplings. Those saplings outside of the exclosure at Tomies were probably the only 75 saplings available to browsers in the wood, thus resulting in a 'honey-pot' effect.

The species investigated here were chosen for a variety of reasons. Oak, ash and birch are among the most common tree species found in the canopies of the woodlands studied. Saplings of *Quercus petraea* were unavailable, so the closely related *Quercus robur* was used, even though this

species is probably the less common of the two in Irish woodlands. While rowan is less frequent in Irish woodlands than oak, ash and birch, personal observations in heavily browsed woodlands (such as those at Killarney) suggest that this species has a relatively high tolerance of repeated browsing. Beech was included because of its alleged disfavour among browsers (Gill 1992a, Peterken 1996) and its status as a potential replacer of oak as the canopy dominant in Irish woodlands where it has naturalised (Dierschke 1982).

12.3 Incidence of browsing

12.3.1 Extent and severity of browsing

The higher frequency and severity of browsing of all species observed at Tomies Wood, compared with that at Charleville (Fig. 9.1), was not surprising. Browsing by both deer and hares was higher at Tomies. It is widely acknowledged that the incidence and severity of browsing damage is positively correlated with the density of browsing animals, and inversely related to the abundance of alternative forage (Gill 1992a, Welch *et al.* 1991). Tomies wood contains red deer, hares and a high population of sika deer. However, red deer are present only in small numbers at Tomies, and it may be assumed that the introduced sika deer dominated the browsing of saplings by deer at this site. In addition the history of sustained heavy browsing at this site (which also supported high numbers of sheep until recently) has left a very sparse field layer apart from the inedible bracken *(Pteridium aquilinum)*. The surrounding area offers little alternative forage, being mostly composed of heath and stands of coniferous forestry. Charleville wood, however, is surrounded by forage-rich pasture and agricultural land. The woodland itself, with a history of low browsing levels, has a well developed field layer, with a relatively large biomass of forage available to the small herd of fallow deer that is present.

All transplanted saplings at both sites were browsed at least once, over the experimental period, and at Tomies all were browsed repeatedly. Holloway (1967, cited in Gill 1992b) found that only new woody tissue was removed from Scot's pine saplings in woodland in Scotland, and browsed saplings were not browsed again until new growth had replaced the lost tissue. However, such a pattern is likely to depend on browse pressure and the availability of other forage. The feeding behaviour of herbivores is such that browsing damage may be clumped in distribution (Crawley 1983) and in some cases, previously browsed saplings may be preferentially selected (Danell *et al.* 1985, Welch *et al* 1991). On the other hand, browsing may induce the production of foliage with lower nutritional content and this may deter further browsing. Danell & Bergstrom (1989) found that birch saplings produced shoots of lower mineral and nitrogen content after browsing, and these effects have been shown to persist for up to 4 years (Tuomi *et al.* 1990).

12.3.2 Species of browser

Browsing by deer was more frequently recorded than that by hares, for all tree species, at both sites (Fig. 9.2). While observation of hares at both sites indicated their presence in both woodlands, no information as to their numbers or their use of the woodland for forage was available. The use of woody species as winter browse by hares is reported from some regions (Hewson 1977, Iason & Palo 1991), and hares have been cited as pests of forestry (Springthorpe & Myhill 1985). Hares and rabbits have been credited with restricting shrub and tree encroachment at woodland edges by their browsing of seedlings and saplings (Rackham 1980). However, specific investigations into the behaviour and feeding habits of hares in Ireland has been largely restricted to open habitats such as coastal grasslands and heath (Tangney *et al.* 1995, Wolfe & Hayden 1996).

In both Tomies and Charleville, hare damage accounted for a higher proportion of identifiable instances of browsing in beech compared with other species. This may have been an artefact of the experimental procedure as any hare-browsed stems that were subsequently browsed by deer may not have been distinguishable. Thus, given the higher rate of browsing of the other four species by deer, the relatively high proportion of hare-browsed beech observed may be because beech was relatively less deer-browsed, hence evidence of hare-browsing was more frequently apparent in this species. Hare browsing was more frequently recorded at Tomies than at Charleville, and oak, beech and birch were the species most frequently hare-browsed. Almost half of the identifiable instances of browsing in birch at Tomies was by hares. This accounts largely for birch's intermediate status in terms of the species preferences expressed by browsers at Tomies. Hjalten & Palo (1992) found that, when mountain hares were offered a variety of winter dormant shoots, birch was intermediate and aspen was the preferred species.

Fallow, red and sika deer all prefer broadleaved or mixed woodland as their main habitat (de Nahlik 1992). Fallow deer have traditionally been restricted to lowland woods (de Nahlik 1992), however they are increasingly found grazing agricultural land and their distribution in Ireland is increasing (R. Cardon *pers. comm.*). Woodland with well developed undergrowth is preferred, and when a wide choice of forage is available they are highly selective, preferring bursting buds and young shoots. Little information is available about the feeding habits of sika deer in Britain and Ireland. Literature from Japan, where this species is native, suggests that the diet varies with location. Jayasekara & Takatsuki (2000) report that the diet of sika deer at Honshu is dominated by forbs, especially evergreen monocotyledonous species, and that twigs and woody browse are also a significant component. Asada & Ochiai (1996) reported a similar diet for sika deer in central Japan. Yokoyama *et al.*(2000) found that diet varied seasonally, with a higher emphasis on graminoids and browse in the winter, and more dependency on forbs and agricultural crops in the spring. Penned sika deer in Korea are fed on *Quercus* browse (Kim *et al.* 1996). Burkitt (1995) investigated the behaviour of sika deer on the Muckross peninsula in Killarney National Park. He

found that the deer spent most of their time in open pasture, but use of woodland edge and thicket was also high. Sika deer are the only large herbivores in the peninsula woodlands, and the absence of a developed shrub layer and the presence of deer-browsed saplings, (mostly of holly, oak and rowan) is evidence that these tree species comprise a significant component of the diet of Irish populations of sika deer.

12.3.3 Seasonality of browsing

Both hares and deer are primarily grazers, and their diets are generally dominated by forbs and grassy species in summer, with a switch to woody browse in winter months (Hulbert *et al.* 1996, Putman 1986). Broadleaved species are most vulnerable to damage from browsing in summer months (Gill 1992b), and so any seasonal variation in browse pressure between species may affect the level of tolerance and the growth response displayed.

At Charleville, a general decline in browsing of saplings with time from planting was observed (Fig. 9.1). This may have been related to a possible decrease in the nutritional quality of the saplings as they adapted to the growing conditions in the wood, which would have been less favourable than those in the nursery. The large amount of alternative forage at Charleville would have facilitated the expression of this. In Tomies, however, where a dearth of alternative forage maintained the need to exploit the saplings as long as they offered any quality of forage, no such trend was observed.

Hares are summer grazers, feeding mostly on grasses and forbs, switching to a diet dominated by woody browse during winter months (Hulbert *et al.* 1996). Hare browsing may be partly responsible for the relatively high levels of browsing experienced by saplings, especially birch, during the winter seasons at Charleville. Miller *et al.* (1982) reported that, when alternative evergreen forage was available, browsing of birch and rowan was lower in winter than in summer.

At Tomies, where browse pressure was always higher than at Charleville, there was little difference in the frequency with which saplings were browsed between summer and winter. However, more severe browsing was experienced in winter. This may have been because: (1) as the saplings were not growing, no new shoot material was becoming available to replace that already removed; and (2) the lack of alternative forage was greater than that during summer months, and so browsers were more dependent on the transplanted saplings for food.

12.4 Species Preferences shown by browsers

The feeding strategies employed by many herbivores are relatively well understood (Crawley 1983). The dominant food type may change with season and availability of the preferred forage. Preferences in terms of vegetation types are fairly consistent, but the actual species preferences expressed by browsing animals can vary from one site to another (cf. Table 12.1). Nevertheless, such preferences, when expressed, can have a profound impact on the vegetation community involved. Consistent avoidance/exploitation of a particular species can confer a significant advantage/disadvantage on the competitive ability of that species, *e.g.* the avoidance of *Rhododendron ponticum* by ungulates may aid the invasion of woodland habitats by this species (Cross 1981).

In the present study, preference of tree species was found to vary with location. The browsing index used here was constructed in order to highlight the overall trend displayed at each site (cf. 5.4.5). While it provides insight into the general trends in browsing at each site, the browsing index blurs the picture somewhat, and detail about the pattern of browsing by each browsing species (hare and deer) is lost. Thus reference must be made to the data relating to differences between the browsers (Figs. 9.2-9.4) in order to obtain a deeper understanding of the details of browsing at each site.

At Tomies wood, oak and ash were the most preferred species overall; birch and rowan were intermediate and beech was the least preferred. However, the intermediate status of birch was strongly affected by its relatively heavy use by hares as winter browse during the experiment. At Charleville, rowan and oak were the most preferred species overall, ash and birch were intermediate and beech was again the least preferred. The disparity between the two sites may be partly explained by the lack of alternative forage at Tomies. Gill (1992a) reports that preferences of browsing deer may not be as strongly expressed when little alternative to the less preferred forage is available.

Comparison of data from the two sites shows that beech is apparently a preferred species of browsing hares. [However, the warning about the evidence of hare browsing being more likely to be observed in beech than in other species should be noted.] Inconsistencies are also present, with oak and birch apparently being preferred by hares at Tomies, but less favoured at Charleville. The increased use of these species at Tomies may perhaps be explained by the lack of alternative forage of high nutritional quality at this site compared with that at Charleville. Hewson (1977) found that mountain hares preferred willow and rowan over birch for winter browse in Scotland.

Table 12.1 Species preferences expressed by browsing animals (adapted from Gill 1992a with additions from other literature.) *S/W denotes Summer/Winter browsing.

Browser	More Preferred	Intermediate	Less Preferred	S/W*	Author, site
Red deer	*Fraxinus* *Salix* *Frangula alnus*	*Betula*	*Alnus*		Ahlén, 1965 (Sweden)
Red deer	*Juniperus* *Quercus* *Pinus contorta* *Picea abies*	*Larix* *Acer pseudoplatanus* *Pinus sylvestris* *Betula*	*Picea sitchensis* *Fagus sylvatica* *Alnus glutinosa*		Chard 1966 (England)
Red deer	*Sorbus aucuparia* *Pinus sylvestris*	*Betula*	*Pinus sylvestris* *Betula* *Sorbus aucuparia*	S W	Cummins & Miller 1982 (Scotland)
Red deer	*Salix* *Sorbus aucuparia*	*Betula* *Alnus*	*Pinus sylvestris*		Mitchell *et al.* 1982 (Scotland)
Roe deer	*Quercus* *Sorbus aucuparia* *Salix* *Fagus sylvatica* *Sorbus aucuparia*	*Alnus glutinosa* *Betula* *Populus tremula* *Fagus sylvatica* *Tilia cordata* *Carpinus* *Quercus* *Salix*	*Abies alba* *Picea abies* *Pinus sylvastris* *Sambucus nigra* *Betula* *Tilia cordata*	S W	Szmidt, 1975 (Poland)
Fallow deer	*Quercus robur* *Sorbus aucuparia*	*Fraxinus excelsior*	*Betula pubescens* *Fagus sylvatica*		This study, Charleville (based on frequency data only-cf. Fig. 9.2)
Sika deer	*Fraxinus excelsior*	*Quercus robur* *Sorbus aucuparia*	*Fagus sylvatica* *Betula pubescens*		This study, Tomies (based on frequency data only-cf. Fig. 9.2)
Mountain hare	*Salix* *Sorbus aucuparia*		*Betula*	W	Hewson 1977
Mountain hare	*Populus tremula*	*Betula pubescens*	*Alnus incana*		Hjalten & Palo,] 1992 (Sweden)
Irish hare	*Quercus robur* *Fagus sylvatica* *Betula pubecsens*	*Fraxinus excelsior*	*Sorbus aucuparia*		This study, Tomies (based on frequency data only-cf. Fig. 9.2)
Irish hare	*Fagus sylvatica*	*Sorbus aucuparia* *Fraxinus excelsior*	*Betula pubescens* *Quercus robur*		This study, Charleville (based on frequency data only-cf. Fig. 9.2)

Site differences, and the fact that the species of deer differed between Tomies and Charleville, may explain the differences, between sites, in preferences expressed by deer. At both sites birch and beech were the least preferred species. Other studies have also shown that these species are less preferred by deer (Cummins & Miller 1982, Chard 1966 re red deer). Kelly (in press) reports that sika deer which briefly accessed an exclosure in Tomies wood expressed the order of preference: rowan > oak >> birch = holly. In this study, sika deer at Tomies browsed ash most, with oak and rowan browsed to a lesser extent. The reverse was observed at Charleville, where fallow deer browsed oak and rowan most, with ash browsed to a lesser extent. This might possibly be explained by the 'food block' hypothesis (Kossack 1976). This proposes that diet selection at a given site is not so much expressed as preferences of individual species, but rather of a suite of food-types. Thus, the amount of feeding on a particular species is affected by the availability of other members of the 'block'. Ash (which was used less than rowan and oak at Charleville), is in plentiful supply among the natural regeneration at Charleville, while oak and, especially rowan, are

less frequent. The opposite is true of Tomies, where oak and rowan are relatively abundant as seedlings, while ash is absent or virtually so.

12.5 Responses of saplings to browsing

12.5.1 General trends

McKay *et al.* (1999) found that, in 1-year-old seedlings dug up and later transplanted, oak and ash were more resistant to desiccation and other potential complications than were birch and beech. Mitchell *et al.* (1995) reported high mortality in transplanted birch and found that rowan was more resistant to transplanting. In this study, precautions were taken to avoid desiccation, both prior to and after transplanting, and mortality owing to transplanting was low (cf. 9.4.3).

The responses of saplings to browsing appear to vary with the timing and severity of browsing and the age and size of the affected individual (Bergstrom & Danell 1987). Browsing can reduce growth or slow the rate of height increment (Crawley 1983, Gill 1992c). However, Cousins (1987, cited in Putman 1994) found that browsed saplings of beech and sycamore grew faster than their unbrowsed counterparts. Such a response is likely to be confined to low intensities of damage; in the case cited, only lateral shoots were removed. Repeated browsing raises the likelihood of sapling mortality.

At Tomies, where browsing pressure was high, unfenced saplings generally had low survival and achieved a net decrease in height over the experimental period (cf. 9.4.3, Fig. 9.8). At Charleville, where browsing pressure was less intense, sapling survival was higher than at Tomies, and saplings achieved a net increase in height (with the exception of birch) (cf. Fig. 9.8). The many reports of the absence of saplings from browsed woodlands are evidence of the effects of browsing on seedling growth and survival for many tree species (Gill 1992a, Mitchell & Kirby 1990, Mitchell *et al.* 1995). Van Hees *et al.* (1996) found that sapling growth and mortality in Dutch woodland were decreased by browsing.

Mortality of transplanted saplings in this study was not uniform over time (cf. Figs. 9.12, 9.13). The rates of browse-related mortality generally increased with time at both sites, but to a lesser extent at Charleville. This trend can be explained for Tomies by the increasing severity of browsing of saplings, presumably related to the lack of leafy material and current shoot material (which had been previously removed). Conversely, browsing of saplings showed an overall decrease with time at Charleville.

The growth of transplanted saplings in this experiment was affected by species specific growth characteristics, site factors such as soil type and light levels, the amount and type of browsing

experienced, and the response of each species to the browsing experienced. Height is not an ideal measure of performance; however where destructive methods are not feasible it serves as a general indicator of performance. The impact of browsing on growth may be deduced by comparing the performance of unfenced saplings with that of fenced saplings, for each species at each site.

Differences between fenced and unfenced saplings were greatest at Tomies, probably because of the higher browse pressure exerted on unfenced saplings there. When the performances of unfenced saplings of different species are compared for Tomies (cf. Fig. 9.11), a levelling effect is observed. Heavy grazing reduces the differences in growth between species. When the fenced saplings are examined however, there is a marked difference in performance between species, with ash > rowan* > oak > beech > birch*. [* Note that rowan and birch were present for one less growing season than the other species.] At Charleville, where browsing pressure outside the fence was less, differences in performance between fenced and unfenced saplings were less pronounced than those at Tomies, but evident nonetheless. The order of performance of unbrowsed saplings differed, however, to that at Tomies, and performance was generally poorer than at Tomies. Here, rowan* > ash > beech > oak > birch*. [* Again, note that rowan and birch were present for one less growing season than the other species.] These performances are somewhat surprising, as birch, a coloniser and fast growing species (Grime *et al.* 1988), performs poorly compared with slow growing species such as beech and oak. This may be partially explained by birches poor response to transplanting (Mitchell *et al.* 1995), and also by the dense ground cover at both sites. It is also conceivable that the canopy gaps in which this experiment was carried out at Charleville, were too small to provide the optimum light levels required for the rapid growth of birch which is light-demanding (Atkinson 1992). The large growth increments achieved by ash and rowan are in agreement with the high growth rates reported for these species in woodland canopy gaps (Wardle 1961, Raspé *et al.* 2000).

12.5.2 Response of oak to browsing

Saplings of oak responded poorly to the severe and repeated browsing experienced at Tomies wood. Survival was low: only one of fifteen planted saplings remained alive at the end of the experimental period (cf. Fig. 9.12). Fenced saplings at Tomies had almost 50% survival, confirming that the severity of browsing, where leafy tissue was repeatedly removed soon after production, was responsible for the high mortality outside of the fence. Comparison with browsed saplings of oak at Charleville, where survival at the end of the experimental period was almost 70%, suggests that oak is tolerant of a certain level of browsing (all Charleville saplings were browsed at least once over the experimental period). Indeed, oak is often cited as being tolerant of some degree of browsing (Crawley 1986, Shaw 1974) however this study supports the suggestion made by Mitchell *et al.* (1995) that the removal of shoot material seriously impinges on the ability

of the sapling to regrow. Repeated browsing, at the high intensity experienced at Tomies Wood, dramatically reduces survival of saplings, and clearly plays a role in the absence of oak saplings in heavily browsed woodlands.

A net loss of height was achieved by browsed oak saplings at Tomies (cf. Figs. 9.5, 9.7). Any new growth produced was repeatedly removed, and previous years' shoot was also removed so that all saplings were shorter at the end of the experiment than they were at planting. Browsed oaks at Charleville made only a small net increase in height (<10cm) over the 3 growing seasons of the experimental period. This was partly offset, however, by the observed increased production of side branches on removal of the apical bud.

12.5.3 Response of ash to browsing

Ash suffered relatively high mortality at both sites, with only 20% surviving in Tomies, and c. 70% surviving at Charleville (the lowest survival rate at this site). The high mortality at Tomies can be explained by the heavy browsing regime present and the strongly acid soils, to which ash is not suited (Grime *et al.*1988). Defoliation has been reported to affect the growth of ash in different ways, based upon the timing and extent of defoliation (Collin *et al.* 2000). Partial defoliation, especially before cessation of stem elongation, resulted in increased stem elongation. However, the severity of damage can affect the growth response. Mitchell *et al.* (1995) found that ash responded well to browsing, and was capable of replacing lost leaf material up to four times in a single growing season. In this study, ash browsed at Charleville achieved a net height gain (of almost 60 cm), displaying resilience to moderate levels of browsing, but a net decrease in height occurred at Tomies where the browsing pressure was considerably higher.

12.5.4 Response of beech to browsing

Survival of browsed beech was relatively high at both Charleville and Tomies. Whether this was due to the lower browsing experienced by this species or a high resilience to browsing is unclear. Browsed beech saplings at Tomies achieved a net decrease in height, while those at Charleville gained an average of 20 cm growth. Van Hees *et al.* (1996) found that 12 year old beech trees were more sensitive to browsing than 6 year old saplings. They also found that beech showed a lower browse-related mortality than oak and birch. However, in the same study, browsed beech saplings exhibited a greater difference in height compared with non-browsed saplings of the same age than did oak and birch.

12.5.5 Response of birch to browsing

Survival of browsed birch saplings was intermediate compared with other species. By the end of the experimental period, it was almost 30% at Tomies and almost 90% at Charleville. As with other species, this difference may be related to the differences in overall browse pressure between the sites. Miller *et al.* (1982) found that mortality in birch was positively related to the removal of previous years' shoot (pys) during summer months. They found that birches survived clipping even down to ground level in winter. Thus the high mortality in Tomies may be related to the high frequency of pys damage at this site.

Birch experienced relatively less severe browsing than other species. In spite of this, it was the only species (among the unfenced saplings) to experience no significant net increase in height at Charleville. This may have been due to the poor ability of birch to cope with competition from ground vegetation; however, comparison with the growth achieved by fenced saplings at the same site suggests that browsing was responsible. Hester *et al.*(1996) did not find that birch was more resilient to browsing than oak or ash, and considered the higher survival of birch compared with these species, to be the result of experiencing less severe browsing. The relatively low occurrence of severe browsing (cf. Fig. 9.1) and the high proportion of instances of hare browsing in this species suggest that it was less severely browsed than other species at this site. It is also relevant that birch and rowan saplings were added to my experiment some months later than the other species and so achieved the measured growth increase in a smaller number of growing seasons. Examination of the rate of height increment achieved in fenced conditions (cf. Fig. 9.5, 9.6) suggests that, at Charleville, the growth rate increased in the second season after planting. The lower growth rate in the first season may have been due to the need for a period of acclimatisation after transplanting. Harmer (1999) found that seedlings of oak, sycamore, beech and ash failed to grow in the season during which they were transplanted.

12.5.6 Response of rowan to browsing

Rowan showed the highest survival rate for browsed saplings at both Charleville and Tomies. Nonetheless, some browse related mortality was observed, with only 50% survival at Tomies (compared with 100% survival of fenced saplings) and 93% survival at Charleville. Clipping experiments carried out in Scotland concluded that rowan was particularly tolerant of severe browsing, and survived complete removal of shoot tissue, down to the lowermost bud at the shoot base, at any time of year (Miller *et al.* 1982).

Rowan achieved the greatest growth increments at both sites, despite the fact that it was present for one growing season less than the other species (except birch). Rowan was relatively heavily browsed at both sites, so these growth increments indicate a tolerance of browsing rather than

avoidance of it. They also reflect the high growth rate of this species, which displays characteristics of light demanding pioneer species (Grime *et al.* 1988). The relatively high light levels at both sites (which were canopy gaps) would have suited the growth habit of this species. Rowan is adapted to a short growing season, and completes its growth relatively early in the summer, allowing the winter buds plenty of time for development so that it is more resistant to frost damage and desiccation than are beech and oak (Barclay and Crawford 1982).

12.5.7 Browsing and sapling growth

The variation in response of different tree species to browsing may be explained by the site conditions, the extent and severity of browsing experienced, the general growth characteristics of each species, and specific growth responses to browsing. Harmer (1999) investigated the growth responses of artificially browsed seedlings in woodland in England. He suggests that the poor growth response of oak, compared with other species, may be the result of the distribution of leaves on oak seedlings. Oak leaves are generally clumped towards the tips of shoots, and so browsing is likely to remove a large proportion of, if not all of the leaves from an affected shoot. Conversely, ash produces a mixture of long and short shoots with leaves distributed among both. Thus, ash may be more likely to retain some leafy tissue, as browsing is concentrated on the ends of longer branches. Beech saplings are generally very leafy, and usually have leaves to within a few centimetres of the shoot base. Thus, removal of all leaves by a browser would be unlikely. Mitchell *et al.* (1995) explained the positive growth response of ash, compared with oak, by the former species' ability to produce new leaves at the site of browsing. Oak, on the other hand, produces new growth at the nearest node, and when sufficient shoot is removed, the capacity for the production of new leaf tissue is significantly reduced. Rowan is considered to be relatively tolerant of browsing (Miller *et al.* 1982) and was found to be so in this study. This trait is undoubtedly aided by its fast growth rate; the species has been found to lack specific defences against browsing (Kullmann 1986) such as those reported for birch (Bryant & Kuropat 1980).

12.6 Other factors affecting the growth of transplanted saplings

Some indirect effects of woodland browsing regimes were illustrated during this experiment. The higher mortality of fenced oak at Tomies, compared to that at Charleville, may be the result of two factors. On the one hand, soil conditions at Tomies were poorer than those at Charleville, and *Quercus robur* (the oak species used here) is usually found growing on base rich substrates. On the other, bracken growth in the Tomies exclosure was dense and tall, and bracken fronds smothered many oak saplings. Oak was particularly susceptible, as it was the smallest species at planting. The proliferation of bracken in Tomies, in the absence of any trampling (inside the exclosure), is an example of how the complete exclusion of browsing animals may not promote optimum conditions for the regeneration of tree species. Ash also showed relatively high mortality

in the exclosure at Tomies. It is not clear whether this was due to the effects of bracken (ash saplings were relatively tall and may be expected to be more resilient to the smothering effects of fronds) or to the unsuitability of the acidic soils for the growth of this nutrient-demanding species (Gordon 1964, Grime *et al.* 1988).

Van Hees *et al.* (1996) found that light levels did not affect the survival rates of browsed oak, birch and beech. Harmer (1999) found no differences in survival rates of clipped seedlings of ash, beech oak and sycamore under different levels of shade (varying from 0 - 80%). However, Harmer's experiment had low mortality overall, and was unlikely to reflect field conditions as seedlings were fertilised and watered and competing vegetation was removed. In addition, while the levels of shade simulated were similar to levels in open British woodlands, the artificial 'browsing' carried out involved the removal of only 1cm of shoot tissue, 7 times over 3 years. This is probably the equivalent of only very slight browsing pressure. McGraw *et al.* (1990) found that *Q. rubra* seedlings grown in shade suffered significantly higher mortality when defoliated, compared with those grown under high light intensities.

Fenced saplings at Tomies generally performed better than those at Charleville. This result is somewhat surprising, given the higher nutrient status of the soils at Charleville. However, several factors may be at play here.

The optimal edaphic conditions for the growth of the species used in this experiment may not necessarily be those at Charleville. Birch is generally associated with drier, lighter soils (Atkinson 1992) and is usually confined to substrates of low pH (less than 5 - Grime *et al.* 1988). Similarly, rowan is generally restricted to acidic soils (pH <5.5 - Grime *et al.* 1988). Beech is rarely found over calcareous strata (Rackham 1980), however it usually performs well on nutrient rich soils. Ash is rather demanding in terms of soil nutrients (Wardle 1959) although it does occur on poor soils over calcareous substrates (Grime *et al.* 1988). Its better growth in Tomies can hardly be explained by edaphic factors. Similarly, pedunculate oak is suited to damp clayey soils, such as those at Charleville, and the dominance of this species in the woodland canopy at this site suggests that edaphic factors are unlikely to be inhibitory of its growth here. Thus while edaphic factors may explain the better performance of birch and rowan at Tomies, other agents must also be involved.

Light levels at both sites were relatively high, as both exclosures were situated in canopy gaps. However, no two gaps are identical and conditions in these two differed, with slightly lower canopy openness at Charleville (43%) than at Tomies (47%). Local light conditions may also differ somewhat between the locations. Charleville occurs on the central plain of Ireland, at c. 60 m OD and 53° 15' north. The Tomies site is situated at 52° 20' north, at c. 90m OD and is north-

eastern in aspect. Thus, light levels in the exclosure at Tomies may be higher than those at Charleville, and this may explain the better performance of ash, oak and rowan at the former site.

12.7 Implications for woodland regeneration

Several studies using exclosures have demonstrated that high stocking densities of browsing animals are the primary cause of the lack of young trees and saplings in many woodlands (Pigott 1983, Linhart and Whelan 1980, Kelly 2000). Experimental data demonstrate that browsers display species preferences, and that these preferences vary with location, browser and season (Mitchell *et al.* 1990, Miles & Kinnaird 1979, Miller *et al.* 1982). Plant species that are less preferred by browsers, or show particular tolerance of browse damage, may exhibit an expansion in range and/or abundance under certain browsing levels (Putman 1994). Similarly, preferred species and those more vulnerable to negative browse impact may be eliminated from a site, or lose competitive advantage to less affected species (van Hees *et al.* 1996).

This study has demonstrated the variation in the frequency and severity of browsing of tree saplings at two Irish woodlands. Clear species preferences were expressed, although these varied with location, and the degree of expression may be reduced at particularly heavily browsed sites. Data about the dietary preferences of sika deer, fallow deer and Irish hares were obtained under field conditions in semi-natural woodland.

The expression of species preferences by browsers is not the only factor that affects species composition in browsed woodlands. Loss of biomass can be compensated for, so the impact of browsing will not be directly proportional to the amount of material removed (van Hees *et al.* 1996). This study demonstrated the variation between species in the growth response and survival after browsing.

The level of browsing at Tomies is clearly too high to permit regeneration of tree species outside of exclosures or other 'safe sites' in this woodland. The 'levelling' effect of such a degree of browse damage is such that saplings of no species are likely to survive in this woodland under the current regime. However, observations regarding mortality of transplanted saplings in the exclosure suggest that complete removal of browsers is unlikely to result in optimum regeneration. Projections about the canopy composition at such a site after a reduction of browsing pressure are complicated by other factors, such as the accumulation of a browsing tolerant seedling bank and the effects of competition from enhanced ground vegetation. These questions are discussed in Chapter 11.

The lower amount of browsing at Charleville clearly allows the growth of saplings, and yet the expression of species preferences by browsers and variation in response to same among tree species may affect the future woodland canopy composition at this site. Beech, rowan and ash performed best at this site. The success of beech is attributable to its less preferred status among browsers, and that of rowan and ash to their high tolerance of browsing and rapid growth to replace lost tissue. Oak and birch performed less well here, the former because of its preferred status and rather poor recovery from browsing, and the latter because of its light demanding nature. While the differences between species performances are relatively slight the logical conclusion from such data is that beech, rowan and ash are likely to regenerate more successfully than oak and birch at this wood. The paucity of birch, beech and rowan in the woodland canopy at Charleville eliminates them from the equation in the short-term, and simplifies the logical conclusion: *i.e.* that ash regeneration has a competitive advantage over that of oak in this woodland. In fact, this trend is already apparent, as the smaller size classes at Charleville are dominated by ash, and this species is likely to play a significant role in the future canopy at this site.

CHAPTER 13 GENERAL CONCLUSIONS

13.1 Methodology Appraisal

The aim of this research was to gain information about the disturbance regime in Irish woodlands, the distribution and characteristics of canopy gaps and the extent and nature of the natural regeneration of native tree species therein. The effect of browsing on the growth and survival of tree saplings was also investigated.

The methodology for the investigation of disturbance regimes and of the woodland response to canopy gaps comes largely from work carried out in the tropics and North America. However, such studies have usually involved the ongoing monitoring of large plots in specified forests. Such an approach was not appropriate here, because a general indication of the situation in Irish woodland was required, and so, a sample of sites was selected. Sampling carries with it the inherent danger of bias, and the results yielded by this study must be interpreted in the light of background information about the woodlands surveyed. The low representation of base-rich woodland reflects a real scarcity of broadleaved high forest on fertile, well-drained sites. This accounts for the low representation of a number of important native trees, *e.g. Ulmus glabra, Corylus avellana* and *Salix caprea* in the study. Nonetheless, the sample described in this research is representative of the high forest type woodlands present in Ireland, and a variety of stands (in terms of their past and present management) is included. Again, because a substantial number of sites were investigated, whole site inventorying was not feasible, and the time constraints imposed on this study did not allow long-term monitoring. The transect method was employed for estimation of the canopy gap regime, and whole gap studies were used to evaluate gap characteristics and the nature of natural regeneration in gaps (cf. 10.1).

The impact of browsing animals on the woodland community, and specifically the regeneration of trees has been much studied. My research sought to identify species preferences expressed by deer and hares, and the responses of tree saplings to browsing, under field conditions. Some previous investigations have involved offering penned animals a variety of foodstuffs, thus identifying their choice (Hjalten & Palo 1992, Kim *et al.* 1996). However, various field-based studies have demonstrated that factors other than inherent preferences affect the selection of forage by browsers (Gill 1992a).

13.2 Disturbance regime in Irish woodlands

The results of this study provide a general indication of the disturbance regime in Irish broadleaved woodlands. The frequency and types of disturbance varied from one site to another, but generally speaking, the regime in the woodlands surveyed can be characterised by small scale disturbances,

varying both temporally and spatially within a stand, and resulting in the asynchronous formation of a range of canopy gap types. Similar types of disturbance regime are reported from many forests (Platt & Strong 1989). However, severe wind storms have resulted in large scale disturbance to woodland in the past, and this possibility cannot be ruled out for Irish woodlands in the future.

The factors that affect canopy disturbance are many, and no single determinant of disturbance regime was identified here. However, this aspect was only incidental to the main research, and more specific investigations with a larger number of sites may identify stronger relationships between variables such as wind regime and topography and the frequency of disturbance to woodland canopies. In spite of this, the variation in disturbance frequency and the range of disturbance types encountered illustrates that many factors affect the propensity of forest stands to disturbance and gap formation.

The characteristics of Irish canopy gaps (size, presence of structurally differing zones, variation in soil properties with gap zone) were similar to those reported for gaps from other regions (Britain: Valverde & Silvertown 1997, Kirby & Buckley 1994, Lamb 1989; the tropics: Vitousek & Denslow 1986, Brandani *et al.* 1988; and North America: Runkle 1981, 1982, Runkle & Yetter 1987). Gaps and associated disturbance (fallen trees, root pits, mounds etc.) provide structural diversity within the woodland, and environmental conditions vary between gap zones.

13.3 Response of woodland to canopy gaps

Three patterns of response were observed in canopy gaps in Irish woodland. These responses were not mutually exclusive and a combination of responses was frequently observed within a single woodland, and sometimes at a single gap. The observed vegetation responses to gap formation can be summarised as follows:

1. Vegetative filling of gap by

a) the lateral extension of adjacent canopy. This was probably present in all gaps to some degree, but was most easily observed and probably the dominant form of 'gap-filling' in small gaps.

b) regrowth from the gap-maker. This was dependent on its survival after the disturbance event, and was observed in a few gaps, e.g. epicormics on boles of uprooted trees, and regrowth of crown damaged individuals.

2. Regeneration from seed/seedlings:

a) of similar species to current canopy (from seeds/ advance regeneration)

b) of pioneer species (usually from seed as these require disturbance/light for establishment)

c) of introduced species e.g. sycamore, beech

[a-c result in high woodland]

d) of non-canopy species which may arrest the succession to high canopy cover e.g. holly.

3. Maintenance of open gap conditions by

a) arrested succession through competition from ground vegetation e.g. bracken, woodrush

b) overgrazing preventing the successful development of any tree saplings.

The determinant of the response at any particular gap was a combination of factors associated with the composition of the vegetation at gap formation, the timing, composition and volume of seed input, the presence of advance regeneration and the growth conditions present.

13.4 The regeneration of trees in canopy gaps

The majority of gaps surveyed contained regeneration of tree species and there was evidence of the release of advance regeneration in many gaps. The purported role of gaps in the regeneration of canopy species appears to be valid and, for most sites, future canopy cover appears to be assured. The composition of the canopy is likely to change in many places, however, as oak was less often the 'leader' in gaps than species such as ash and rowan. Whether this 'dilution' of the oak canopy will be temporary or long-term remains to be seen. Nonetheless, all of the tree species that were adjacent to gaps as mature (and hence seed producing) individuals appear to be capable of successful regeneration in canopy gaps.

Gap zonation also plays a vital role in the promotion of regeneration, although this might be less pronounced in the species-poor woodlands of Ireland than elsewhere (cf. Brandani *et al.* 1988). The significance of gap zones was most evident in gaps where growth conditions were relatively extreme. For example, where dense vegetation prevented germination and establishment, regeneration was confined to the less densely vegetated pit, mound and bole. Similarly, where general browsing pressure was too high to permit sapling growth, saplings were confined to 'safe sites' such as the upper parts of mounds. Gap zones appear to have had less impact on the distribution of regeneration where conditions were more variable, and, seed input and chance appear to govern the distribution of regeneration in such cases.

Management plays an important role in determining the extent and nature of regeneration in woodlands. Seed availability was a major factor determining the composition of regeneration in canopy gaps and the influence of management on the canopy composition clearly affects this. On the one hand, the absence of birch from gaps in Portlaw and Garannon is the result of past and current silvicultural practices. On the other, the presence of mature planted beech, *e.g.* at Tomnafinnoge, has provided a seed source for this species, which now dominates some of the gaps present.

13.5 Browsing and regeneration

The effects of browsing on natural regeneration of trees were especially evident in the gaps at Tomies wood, where high populations of browsers are preventing regeneration. The only sapling observed in this woodland (outside of exclosures) was on the rootplate of an upturned oak. While this woodland was only one of 13 surveyed, it must be pointed out that conditions here (with regard to regeneration and browsing) are representative of some 1200 ha of woodland in the Killarney Valley, the largest tract of semi-natural woodland in the island. Some of these woods must also cope with grazing by trespassing sheep. In addition, some of the Killarney woods (particularly those in the western parts of the National Park) are among the highest in altitude and least man-modified woods in Ireland. Their stature is poor and their condition may be less than optimal for seed production (personal observation). The future of these important woodlands is seriously at risk as a result of decades of overgrazing.

Recent control of the deer population at Camillan has resulted in the development of thickets of browse-tolerant holly in some gaps. It is evident that, while reduction of browsing pressure will allow regeneration to resume, the vegetation composition is likely to have been altered significantly compared to that which existed at the onset of overgrazing.

The transplant experiment demonstrated that browsing deer and hares express species preferences and that these preferences are affected by local conditions. The less preferred status of beech confers an advantage on saplings of this species over others such as oak and ash, and may assist its establishment as a significant component of the canopy in some Irish woods. The poor response of oak to repeated severe browsing will compound this effect, and may render this species less successful in reaching the canopy in browsed woodlands. The resilience of rowan to browsing may allow this species to increase at moderately browsed sites, other factors permitting.

13.6 Implications for Irish woodland

This research has demonstrated the impact of management on regeneration in Irish woodlands. The results of the survey of vegetation in canopy gaps are on the whole reassuring, as most woodlands studied appear to be regenerating successfully. The heavy browsing levels present at some sites require reduction, if regeneration is to occur. The inheritance from past grazing regimes (e.g. the impenetrable woodrush swards dominating Union Wood) may require some intervention in order to improve structural and species diversity. However, more specific investigation and experimental trials would be recommended before any major change in management is considered.

13.7 Further studies

More detailed investigations would provide a deeper understanding of the factors that influence canopy disturbance and gap formation in Irish woodlands. A larger number of sites would require investigation, and whole site inventorying would allow for the calculation of turnover rates.

A larger scale survey of the status of Irish woodland, in terms of natural regeneration, would provide useful information for the management of this limited resource. More experimental work would provide deeper insight into the role of gap zones in promoting regeneration and diversity of tree species. The successful production of seed and establishment of seedlings ahs not been confirmed for some species, notably elm, hazel and yew, and more knowledge of the regeneration of these species would be useful.

While the general effects of browsing on woodland vegetation are understood, long-term investigations regarding the effects of different stocking densities have not been carried out in Irish woodlands (but see Kelly 2000 and Kelly in press). The total exclusion of browsers may not provide the optimum conditions for regeneration, and the ideal stocking density for Irish woodlands remains unknown.

13.8 Concluding remarks

This study has demonstrated that Irish woodlands are dominated by small scale disturbances that are affected by local factors. The resulting canopy gaps provide a suitable environment for the regeneration of tree species. Structural diversity within canopy gaps may be important in providing the only available niches for regeneration in some circumstances. Regeneration of trees is successful in most of the woodlands surveyed, but heavy browsing is preventing successful establishment of young trees at others. Browsing animals express preferences among different tree species and the response to browsing varies between tree species. Thus the regeneration success of different tree species is influenced by the extent and nature of browsing experienced.

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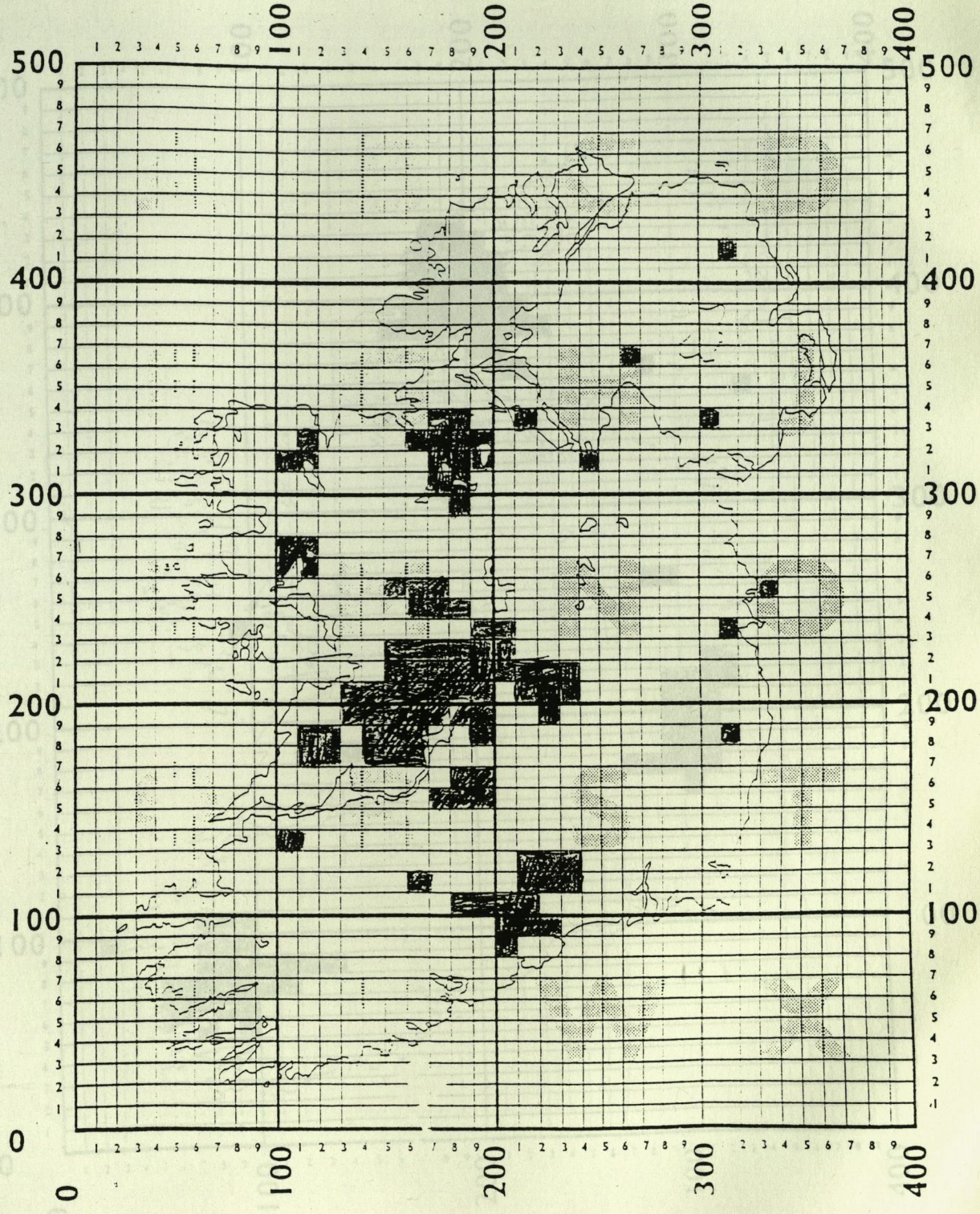
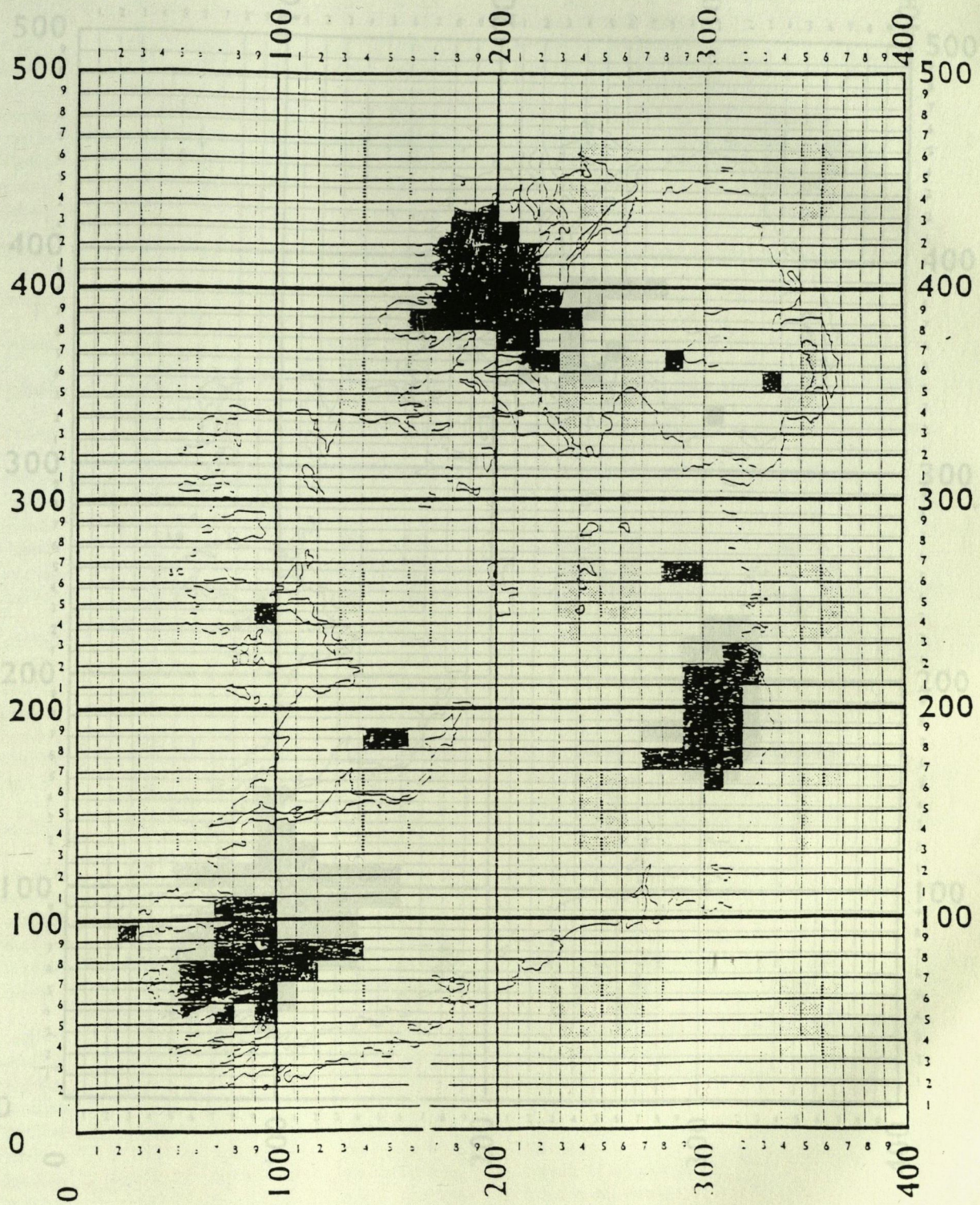
Appendix I **Distribution of deer in Ireland.**

Maps courtesy of the Deer Society of Ireland. Data represents the minimum distribution for each species.

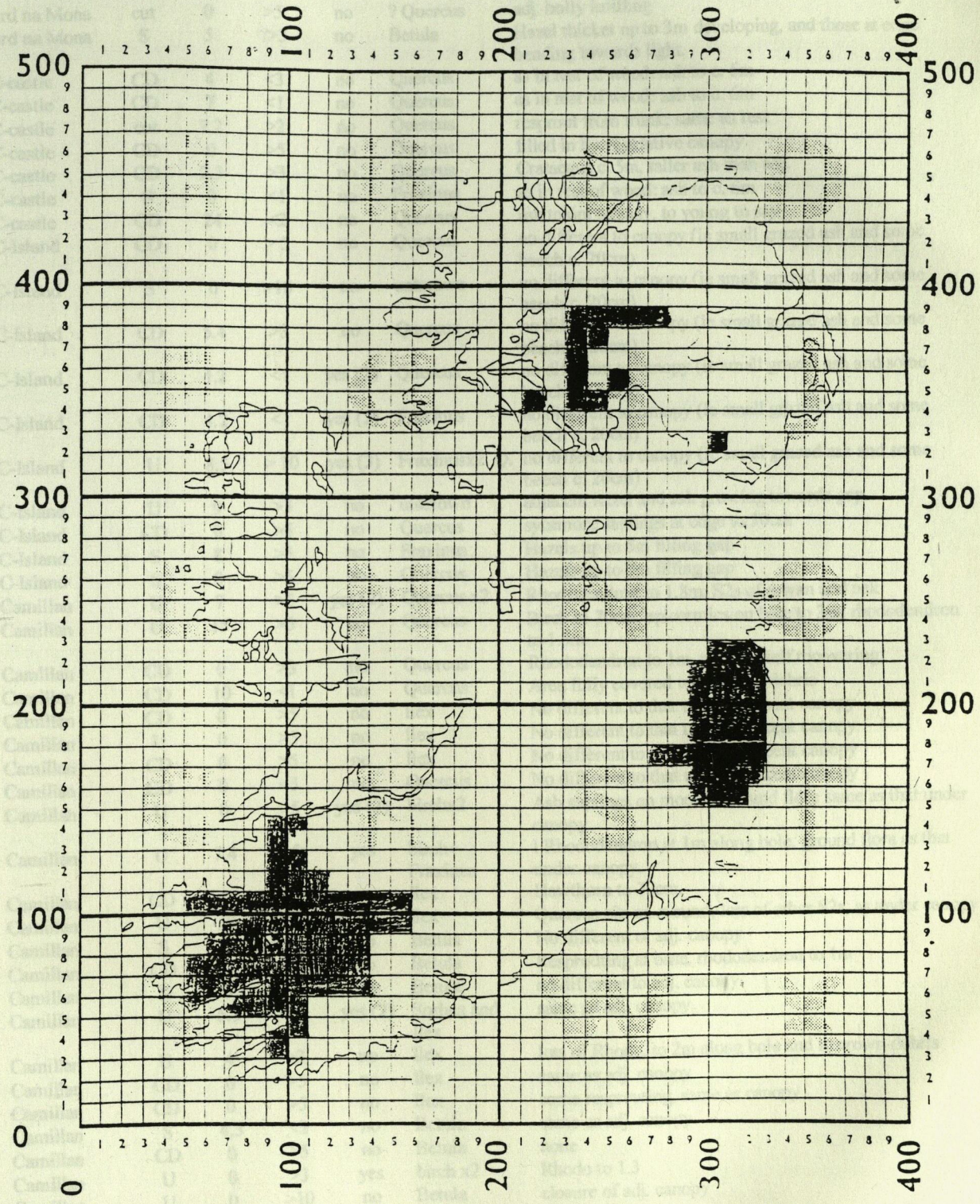
Fallow Deer



Red Deer



Sika Deer



Appendix II Details of Disturbance events encountered on random transects.

Site	D.E.	size (m)	Age (yrs)	multiple	Maker	Vegetation response to gap
Ard na Mona	U	0	<1	no	Quercus	growth of hazel and sorbus saplings towards gap
Ard na Mona	cut	0	>5	no	? Quercus	adj. holly infilling
Ard na Mona	S	5	?>3	no	Betula	Hazel thicket up to 3m developing, and those at edge bending towards light.
C-castle	CD	4	<3	no	Quercus	as in rest of wood: ash to c. 6m
C-castle	CD	7	<1	no	Quercus	as in rest of wood: ash to c. 6m
C-castle	cut	7.2	>2	no	Quercus	resprout from trunk; same as rest
C-castle	CD	0	>5	no	Quercus	filled in by vegetative canopy
C-castle	CD	2.3	>3	no	Quercus	Crataegus c. 5m, taller ash than adj.
C-castle	S	0	<1	no	Fraxinus	as in rest of wood: ash to c. 6m
C-castle	CD	24	<2	no	Quercus	ash to 6m already, to young to say
C-Island	CD	0	> 5	no	Quercus	no different to canopy (ie small grazed ash and some beech c. 20cm)
C-Island	S	0	>10	no	unknown	no different to canopy (ie small grazed ash and some beech c. 20cm)
C-Island	CD	5.4	>3	no	Quercus	no different to canopy (ie small grazed ash and some beech c. 20cm)
C-Island	CD	4.2	<1	yes (2)	Quercus	no different to canopy (ie small grazed ash and some beech c. 20cm)
C-Island	CD	4.2	<1	yes (2)	Fraxinus	no different to canopy (ie small grazed ash and some beech c. 20cm)
C-Island	U	8.5	> 10	yes (3)	Fraxinusx2, Q.	no different to canopy (ie small grazed ash and some beech c. 20cm)
C-Island	U	9	>5	no	unknown	adjacent hazel and ash growing towards gap
C-Island	CD	0	>5	no	Quercus	sycamore saplings at edge to 50cm
C-Island	S	8	>5	no	Fraxinus	Hazels up to 5m filling gap
C-Island	S	0	>5	no	Quercus	Hazels up to 7m filling gap
Camillan	U	7	>5	yes (2)	Quercus x2	Rhododendron to 1.8m, S2s of rowan and oak
Camillan	U	15	>5	no	Quercus	Birch to 70cm, epicormics on bole to 3m, rhododendron to 1.5m
Camillan	CD	0	>3	no	Quercus	Rhododendron to 1m, maker itself recovering
Camillan	CD	10	<1	no	Quercus	Area fully covered with crown debris
Camillan	CD	0	>5	no	Ilex	No different to that under adjacent canopy
Camillan	U	0	>5	no	Ilex	No different to that under adjacent canopy
Camillan	CD	0	>5	no	Ilex	No different to that under adjacent canopy
Camillan	CD	0	<5	no	Quercus	No different to that under adjacent canopy
Camillan	U	0	>5	yes (2)	birchx2	Ash saplings on mound, ground flora same as that under canopy.
Camillan	U	7.4	>5	yes	birch+ Fraxinus	1 Rhododendron at 1m along bole, ground flora as that under canopy.
Camillan	CD	0	>3yrs	no	Ilex	Hawthorn to 70cm.
Camillan	U	0	<2yrs	no	Ilex	Quercus s2s on mound, lots of other S2s, as under canopy
Camillan	S	0	<3 yrs	no	Betula	No different ot adj. canopy
Camillan	CD	0	>3	no	Betula	Resprouting at base, rhododendron to 1m
Camillan	S	5	>10	no	Betula	no different to adj. canopy
Camillan	U	5.3	>5	yes (2)	Sorbus and Ilex	same as adj. canopy
Camillan	U	4	>3	no	Ilex	lots of Rhodo. to 2m along bole and in crown debris
Camillan	CD	0	>5	no	Ilex	same as adj. canopy
Camillan	CD	0	>5	no	Ilex	some resprouting, same as canopy
Camillan	S	4.3	<2	no	Betula	same as adj. canopy
Camillan	CD	0	>5	no	Betula	none
Camillan	U	0	>3	yes	birch x2	Rhodo to 1.3
Camillan	U	0	>10	no	Betula	closure of adj. canopy
Camillan	CD	8	<2	no	Quercus	same as adj. canopy
Camillan	CD	0	<2	no	Quercus	filled by adj. holly and ivy
Derrybeg	U	0	>5	yes	Quercus x2	filled by adj birch;sorbus on mound and occasional on ground
Derrybeg	U	6	<5	no	Betula	sorbus, ilex and birch to 1.5 m

Site	D.E.	size (m)	Age (yrs)	multiple	Maker	Vegetation response to gap
Derrybeg	U	0	>10	no	Quercus	filled by adj. birch. Holly thicketingc. 1.5 m
Derrybeg	U	0	>10	no	unknown	filled by adj. oak canopy. Sorbus and Holly to 2m along bole
Derrybeg	CD	4	<3	no	Betula	Sorbus to 1m, holly c. 30cm
Derrybeg	CD	8	<1	no	Quercus	same as adj. canopy
Derrybeg	CD	0	>3	no	Quercus	infilled by adj. betula; sorbus saplings to 2 m
Derrybeg	CD	0	>5	no	Quercus	infilled by own canopy!
Derrybeg	S	0	>3	no	Betula	infilled by adj. oak canopy
Derrybeg	CD	0	>5	no	Betula	infilled by adj. oak canopy
Derrybeg	S	0	>7	no	Betula	infilled by adj. birch, sorbus, oak; and sorbus 2m on mound
Derrybeg	CD	0	>3	no	Betula	infilled by adj. oak and birch. Cluster of Sorbus 1.1m where gap was
Derrybeg	CD	0	2	no	Betula	infilled by adj. canopy
Derrybeg	CD	1	>10	no	Quercus	infilled by adj. canopy; holly and sorbus thicketing to 1.2m
Glen of the downs	CD	0	>5yrs	no	Quercus	adj. oak canopy
Glen of the downs	CD	0	>5	no	Quercus	adj. oak canopy
Glengarriff	CD	6	>2	no	Quercus	birch and sorbus to 2 m
Glengarriff	CD	8.81	>2	yes*	Ilex	oak, rowan and holly to 1m, rhodo also
Glengarriff	CD		>2	yes*	Quercus	dominated by 1995 oaks, also hollies and taller sorbus
Glengarriff	CD		>2	yes*	Quercus	as above, with birch too
Glengarriff	CD	0	>2	no	Quercus	filled in vegetatively, regen as under canopy
Glengarriff	CD	6	>2	no	Betula	dominated by hollies c. 60cm
Glengarriff	CD	0	>4	no	Taxus	vegetatively infilled, same regen as adj. canopy
Old Head	CD	3.4	>2	no	Quercus	saplings of ash, hazel, beech and sycamore
Old Head	CD	0	>10	no	Quercus	saplings of hazel and ash and vegetative fill by adj oak
Old Head	CD	0	>5	no	Quercus	vegetatively filled by adj sycamore saplings
Old Head	U	0	>10	no	Quercus	spurt of pre-existing sycamore and horse chestnut
Old Head	U	3	>3	no	Sorbus	epicormics all along bole
Old Head	U +CD	18	>7	yes	Quercusx2, betula	numerous saplings of Betula and sorbus c. 2.5-3m
Old Head	U	4	>10	no	Quercus	filled in by adj. canopy
Old Head	U	3	>5	no	Quercus	fagus saplings dense, and vegetative canopy infill
Old Head	S	0	>10	no	? Quercus	adj. young sycamore and oak infilled
Old Head	S	0	>10	no	? Quercus	canopy infill, no regen, bramble to 1m
Old Head	CD	0	>3	no	Quercus	canopy infill, large epicormics along bole
Old Head	S	0	>10	no	Quercus	canopy infill. thicket of fagus developing
Portlaw	U	10	>2	yes	Quercus +Ilex	stretch of adj. suppressed Ilex and Rhodo.
Portlaw	S	11	<2	no	Quercus	adj. young trees growing in
Portlaw	cut	7	>3	no	Quercus	adj. holly and Rhodo thicketing
Tomies	CD	0	<1	yes(C)	Quercus	None visible
Tomies	U	0	<1	yes(C)	Ilex	None visible
Tomies	U	0	>5	no	Ilex	Yes: filled by adjacent canopies
Tomies	S	1	<2	no	Ilex	Yes: filled by adjacent holly canopy
Tomies	CD	7	>2	no	Quercus	Yes: filled by adjacent holly canopy
Tomies	U	5.7	<2	yes(N)	Ilex	Yes: resprouting and infill from adjacent trees
Tomies	CD	5.7	<2	yes(N)	Quercus	Yes: resprouting and infill from adjacent trees
Tomies	CD	6.4	<1	no	Quercus	Yes infill from adjacent holly
Tomies	CD	3	>2	no	Quercus	None visible
Tomies	CD	3.4	<2	no	Quercus	None visible
Tomies	CD	0	>2	no	Quercus	None visible
Tomies	S	0	>3	no	Ilex	None visible: infilled by adjacent canopy.
Tomies	CD	1.8	>2	no	Quercus	Infilled by growth from maker
Tomies	S	6	>5	yes	Betula	None visible
Tomies	U	6	>3	yes	Betula	None visible
Tomies	CD	0	<2	no	Quercus	None visible
Tomies	CD	4.3	>3	no	Quercus	None visible

Site	D.E.	size (m)	Age (yrs)	multiple	Maker	Vegetation response to gap
Tomnafinnoge	S	1.4	?	no	Betula	infilling by adjacent canopy
Tomnafinnoge	CD	12	?	no	Quercus	adjacent beech saplings growing in
Tomnafinnoge	ride	41.6	?	no	/	saplings birch and beech to 6m
Union	CD	9.1	<3	no	Quercus	adj. canopy infilling
Union	CD	6	>5	no	Quercus	epicormics all along bole
Union	CD	0	<5	no	Quercus	adj. canopy infilling
Union	CD	0	>10	no	? Quercus	adj. canopy infilling
Union	CD	0	<5	no	Quercus	adj. canopy infilling
Union	CD	12	<3	yes	Quercus x2	adj. canopy infilling
Union	CD	7	>5	no	Quercus	adj. canopy infilling, browsed holly 62cm on mound.

Appendix III Canopy Gaps Surveyed: brief descriptions

Sites are listed in Alphabetical order

Ardnamona Wood, Co. Donegal: 2 gaps

Ard1

Formed by the partial uprooting of a rowan tree (104 cm gbh) within the previous 1-2 years. Adjacent trees include oak, rowan, birch, hazel and holly. There are epicormic shoots (to 15cm) along the bole of the gap maker. The pit is devoid of vegetation and is covered with bare soil and litter. Other gap zones are dominated by woodrush which achieves 90% cover in some quadrats. Saplings of oak and hazel are present. Seedlings of holly and oak are rare; others are absent.

Ard 2

Gap formed within a year of survey by two uprooted rowans and a snapped birch that was knocked by one of the falling rowans. Adjacent trees include oak, holly, rowan, birch and hazel and oak saplings (1.8m tall) at gap edge are growing towards the gap centre. Smaller saplings of rowan, oak, birch and holly are achieving good growth, and appear to have been present prior to gap formation. The ground vegetation is patchy, with clumps of woodrush, and wood sorrel dominant. Bare soil dominates in the root pit, but is virtually absent elsewhere, where litter cover dominates. Seedlings of oak are very occasional.

Camillan Wood, Co. Kerry: 4 gaps

C1

Gap formed by windblown oak (213 cm gbh) and independently snapped holly. The gap seems to be about 2 years old. Adjacent trees reach about 20m and are oak birch, and in the sub-canopy, holly. The ground vegetation (and that on the root mound) is dominated by bushy holly saplings (at c. 30-40 cm). Seedlings of rowan, oak, birch and rhododendron are occasional. Other vegetation is sparse, and includes ivy and purple moor grass. Litter cover is generally high (c. 60%).

C2

Gap formed by uprooted oak (100 cm gbh), and snapped oak (135 cm gbh) about 5 years previously. Adjacent trees are oak and birch and reach c. 18m in height. The pit has 100% bare soil cover and the mound, 100% moss cover. Elsewhere, litter, mosses and herbs account for the total ground cover, with purple moor grass achieving up to 40% cover in some plots. Seedlings of oak, birch, holly and rowan are very occasional, with more seedlings on the mound than elsewhere. A single ash s2 is present along the fallen bole.

C3

Gap formed by uprooting od 2 oaks (180 cm and 130 cm gbh), c. 3 years previously. Adjacent canopy trees are oak and holly and achieve c. 17m in height. A clump of Rhododendron regrowth (following initial cutting back) occurs to one side of the gap. Woodrush is the dominant vegetation in all zones except along the fallen boles. Litter cover is high throughout the gap. Seedlings of oak, birch and ash are occasional throughout, and bushy holly (up to 65cm) is widespread, especially on the mound.

C4

Gap formed by one snapped and one uprooted birch, less than a year prior to survey. All trees at the gap edge are holly or birch, and achieve 18m in height. The ground is dominated by litter (c. 60% cover) and bushy holly saplings (to 25cm). Clumps of rowan S2s are present in the periphery. Other vegetation is very sparse: shield fern is present on the root mound, and ivy is present among the fallen canopy.

Charleville Castle Woods, Co. Offaly: 5 gaps

Cv1

Formed by the felling of an oak of 1m diameter. Resprouts on the trunk are at least 2 years old. Adjacent canopy of oak and ash to 25m. Gap vegetation dominated by bramble, varying in cover from 10-90%. Ivy also abundant and bare soil varying from <5 to >50%. Regeneration of oak, ash, hawthorn and blackthorn occasional.

Cv2

Formed by the uprooting of an oak (37cm gbh) whose timber was later removed. About 5 years old. Gap dominated by ash poles, up to 6m tall and 5-15 cm dbh. Adjacent canopy includes oak, hazel and scots pine. Saplings of sycamore and hazel also present. Some bare soil present; ivy and bluebells dominating herb layer.

Cv3

Formed by crown damage to 2 oaks (285cm gbh) more than 3 years ago. Adjacent canopy of ash and oak to 23m. High cover of litter and bare soil. Bramble dominates the field layer and varies from 5-75%. Seedlings of oak, ash and hawthorn occasional.

Cv4

Formed by crown damage c. 2 years previously, to 2 oaks (315cm and 382cm gbh). Adjacent canopy of oak and young ash (<20 cm gbh). Brambles up to 1.5m cover c. 90% of the gap. Some pre-gap ash and hawthorns (c. 20cm gbh, 10m tall) still present. Seedlings of oak, ash and hawthorn are rare.

Cv5

Gap formed by crown damage to large oak (356 cm gbh) more than 3 years previously. Preexisting ash poles have grown tall and spindly (c12m tall, <17cm dbh). Ground vegetation dominated by bramble (10-75%) and bare soil and litter plentiful. Adjacent canopy composed of oak and ash. Seedlings of oak, ash and hawthorn are very occasional.

Charleville Lake island: 2 gaps

Is1

Gap formed 5-10 years previously, by the uprooting of large oak (396 cm gbh) which resulted in crown damage to a nearby oak (82 cm gbh). Adjacent canopy dominated by hazel and ash with some oak, and varying from 6 to 24 m in height. Bare soil and mosses are plentiful. Woodrush is dominant in patches, ground ivy and bramble are also abundant. Seedlings of ash are frequent and saplings of hawthorn, hazel and blackthorn are present in the gap.

Is2

Formed by the uprooting of two ash trees (> 80cm gbh) more than 10 years ago. The canopy is now fully decayed and the boles are at an advanced stage of decay. Adjacent canopy of oak, ash and hazel achieves heights of 25-30 m. Ivy and browsed brambles to c. 1m dominate the vegetation. Bare soil and litter are also plentiful. The old pits are still just discernible and are dominated by ivy with bare soil, litter and mosses also present. Seedlings of ash are frequent throughout the gap, and saplings of hazel and hawthorn are also present.

Garannon wood, Co. Clare: 4 gaps

Gar1

Formed by uprooted oak (208cm gbh) less than 2 years previously. All adjacent trees are oaks (to 20m) but elm, ash and beech are present nearby. Bracken and bramble dominate the field layer and saplings of oak, ash, elm and hawthorn are occasional throughout the gap. Bare soil is scarce except in the root pit where it is dominant (c. 70% coverage).

Gar2

Formed about 2 years previously by the snapping of 2 oaks (167 cm and 141 cm gbh). Trees at gap edge mostly oak with some ash and beech. Ground vegetation dominated by woodrush and bramble, which together cover about 90%. No bare soil visible, some litter cover present. Saplings of ash, beech, hawthorn and a single elm present.

Gar3

Artificial gap created by the removal of about 20 oaks four years prior to survey. Vegetation is up to 1.4m (not including tree saplings) and is dominated by bramble with rushes, fireweed (*Chamenerion angustifolium*), grasses and honeysuckle. Willow saplings up to 2.5 m and oaks to 1m throughout. Little bare soil visible, very occasional seedling of oak present.

Gar4

Gap formed by crown damage to 2 oaks (170cm and 151 cm gbh) less than 3 years previously. Extensive ivy growth on the crown of one of the makers (the smaller tree) may have contributed to the damage. Trees at the gap edge are oak and hawthorn. The vegetation is dominated by bramble with some patches of bracken and ivy present. Saplings of ash, hawthorn and a single individual of sweet chestnut present. Lots of bare soil and litter present (10-80% cover for each in quadrats). Seedlings of oak very occasional. No other seedlings present.

Glengarriff Woods, Co. Cork: 4 gaps

Gl1

Formed by crown damage to an oak (105cm gbh) and an uprooted holly (52cm gbh). Adjacent canopy of oak and holly, up to 12 m tall. Ground cover dominated by litter and mosses with some herbs. Cover by heather up to 95% along bole and on mound of uprooted holly. Grasses, sedges and rushes present in sparse amounts. Occasional seedlings of oak, holly and birch.

Gl2

Formed by windblown ash (173cm gbh) and crown damaged oak (by the falling ash) less than 1 year old. Adjacent canopy quite uniform at 20m, with oak and some birch and hawthorn. Bracken coverage of c. 30%, *Deschampsia caespitosa* with brambles cover about 70% of the gap area. The mound is dominated by Crocosmia sp. and the pit by bare soil. Two saplings of oak and one of ash are present in the periphery.

Gl3

Formed by snapping of one oak (108cm gbh) and crown damage to another oak (140cm gbh). About 2 years old. Dominated by thickets of holly to 2.5m and birch to 2.2m. A small clump of rowan saplings (to 2.7m) occurs at one end. Bramble to 0.5m and litter dominate the ground cover. Ivy is also plentiful

Gl4

Formed c. 2 years prior to survey by crown damage to an oak and a birch. Adjacent canopy species include oak, holly and rowan. The ground is dominated by litter and mosses with scattered seedlings of holly and rowan.

Mullangore Wood, Co. Donegal: 3 gaps

M1

Formed by wind snapped birch (> 85cm gbh x 2 stems) more than 5 years ago, and more recently an uprooted birch (84cm gbh) and a wind snapped birch (80cm gbh). Adjacent canopy of birch, holly and oak reaches c. 20m. The ground is dominated by moss covered boulders (c. 60%) and clumps of holly S2s, up to 70cm have been browsed and show bushy growth. Litter cover varies from c. 5% in the periphery to c. 65% in the shallow pit. Epicormic shoots (up to 2.5m) are present on the mound of the uprooted birch. *Agrostis* sp. dominates the periphery area. Small saplings and S2s of holly, oak, birch and rowan are occasional throughout, especially in the bole and periphery zones.

M2

Formed by partially uprooted birch (110cm gbh) (still alive), and crown damaged oak. Adjacent canopy of oak, birch, holly and rowan varies in height at gap edge from 12-16m. Patchy cover by all vegetation groups; litter, mosses, herbs and bare soil. Bramble cover up to 50% in periphery and fallen canopy zones. Plentiful birch S1s along bole, very occasional S2s of holly and oak in periphery and fallen canopy zones.

M3

Formed by windblown tree, species unknown, more than 10 years ago. Adjacent canopy dominated by oak, with single rowan, to c. 16m. Holly saplings (to 1.8m) dominate the area around the mound and bole. Litter cover 50-70% in periphery area, with heather cover up to 30% in this zone. Seedlings of rowan and oak frequent, and a single seedling of yew among fallen canopy.

Old Head Wood, Co. Mayo: 4 gaps

OH1

Formed by the partial uprooting of rowan (134 cm gbh) about 7-10 years previously. The rowan is still alive and canopy is being replaced by epicormic shoots all along the bole up to 4 m tall at time of survey. Adjacent canopy trees include oak, rowan and oak to c. 16m. The pit is dominated by litter, with only small coverage by bracken and wood sorrel. Birch seedlings dominate the root

mound. In other zones, woodrush is dominant, achieving 90-95% cover. No other regeneration is present.

OH2

Gap formed by the uprooting of a birch tree (c. 80cm diameter) and crown damage to 2 oaks. The gap appears to be 5-10 years old. The adjacent trees are oaks with a single birch also present. Saplings are plentiful at the gap edge and include birch (up to 2.8m) and rowan (up to 4m). Bracken and bramble dominate the vegetation, but total cover does not exceed c. 50% and litter and bare soil are present. Only ivy is present as a small seedling.

OH3

Gap formed by a windblown beech (153 cm gbh) and a snapped scots pine (154 cm gbh). Adjacent canopy trees include beech and oak to a height of 16m. Vegetation in the pit and the state of decay of the maker suggest a gap age of c. 5 years. Small saplings of oak, beech and rowan are present throughout (25-30 cm) and taller saplings of rowan are also present (c. 2m). bare soil and litter dominate the ground coverage, but wood sorrel, ferns and ivy are present in small amounts.

OH4

Gap formed c. 5 years previously by the uprooting of an oak (110cm gbh). The adjacent canopy of beech and oak (to 18 m) are partially filling the gap. The ground is mostly covered by litter, bryophytes and bare soil. Some bramble and ferns are present in small amounts. Seedlings of beech and to a lesser extent oak and holly are occasional in the bole and periphery zones.

Portlaw Wood, Co. Waterford: 1 gap

P1

Formed by the uprooting of a large oak (dbh: 1.19m), which was subsequently cut and its timber removed. A holly (dbh: 20cm) was snapped off by the falling oak and contributes to the gap. The gap appears to have been created in the past 2-3 years. Adjacent trees include oak, beech, rhododendron and holly, to a height ranging from 10 to 16m at the gap edge. Birch is rare/absent from the wood owing to management (Lord Waterford. pers. comm.), and young (<30 years) stands of coniferous trees. There is apparent growth on suppressed seedlings throughout the gap. Ilex saplings (to c.1m) and Rhododendron (to c. 0.8m) at edge. Bracken occasional, bramble cover c. 30% along bole, ground dominated by litter (80-100%) and bare soil.

Tomies Wood, Killarney, Co. Kerry: 6 gaps

T1:

Gap formed within the year prior to survey by the uprooting of a birch, (124cm gbh). Adjacent canopy is composed of oak and achieves 22m. The ground is dominated by litter and some bare soil, throughout. Small patches of bilberry and woodrush are present and bracken is occasional. Regeneration present is composed of S1s and S2s of holly, with occasional small seedlings of oak, birch and ivy.

T2:

This gap was created by the uprooting of a large oak (237cm gbh), about 3 years prior to survey. Adjacent canopy achieves about 20m in height and is composed of oak and holly. The ground is dominated by litter, bryophytes and to a lesser extent bare soil. Vegetation is patchy and includes foxglove, bent grass and woodrush. Regeneration is dominated by small seedlings of holly, with occasional birch, ivy and rowan also present.

T3:

This gap was formed by the uprooting of a large oak (265cm gbh), which knocked over a holly, within a year prior to survey. The adjacent canopy reaches 20m and is dominated by oak, holly and birch. The ground is dominated by bare soil, litter and some bryophyte cover. Wavy-hair grass and wood sorrel are present in patches. Regeneration present consists entirely of S1s and S2s, and oak, holly, birch and ivy seedlings are present.

T4:

This gap was created by the uprooting of an oak (1.04m gbh) and the snapping of a birch (1.71m gbh) about 2 years previously. The adjacent canopy is composed of oak and holly, to a height of c. 19m. The ground is dominated by litter and bare soil, with small patches of vegetation comprising wood sorrel and bryophytes. Few seedlings are present, and are S1s and S2s of holly, oak, birch and rowan.

T5:

Formed about two years prior to survey by the uprooting of a birch (2.0m gbh) that knocked and snapped a large branch from an oak. The adjacent trees are oaks and birch to a height of c. 20m. Bare soil, bryophytes and litter dominate the ground, and patches of vegetation include bracken, bent grass and woodrush. Regeneration is comprised of seedlings of holly, birch and rowan.

T6:

Gap formed within two years prior to survey, by the uprooting of an oak and 2 hollies, and crown damage to 3 oaks. Adjacent trees are oak and holly and reach a height of 21m. The ground is

dominated by fallen debris, leaf litter and bare soil. Regeneration present includes S1s and S2s of holly and S1s of birch.

Tomnafinnoge Wood, Co. Wicklow: 2 Gaps

Tf1

Formed by snapped birch (82cm gbh) at 1.7m, that knocked and snapped a second birch (3 stems @ 27cm gbh each). Surrounding canopy of oak, ash beech and holly to 20m. The gap seems to be 2-3 years old. Only bole and periphery present. Ground dominated by litter (30-100%) with bramble and woodrush present. Canopy cover 70-90%.

Tf2

Formed by total loss of canopy from beech (2.8m gbh) from 8m. The canopy of the gap maker is regenerating and will apparently replace the lost canopy. Adjacent trees include oak, beech, holly and hazel. Evidence of saplings at gap edge growing towards the light gap: beech (to 6m) and hazel (to 8m). Almost 100% litter cover in entire gap; some bramble and *Dryopteris* spp. present.

Union Wood, Co. Sligo: 4 gaps

Un1

Gap formed 5-7 years previously by crown damage to 3 oaks. All of the adjacent trees are oaks and the gap is dominated by woodrush, which forms an extensive mat (95% coverage), with some bracken. This mat of woodrush also exists beyond the limit of the gap and appears to predate gap formation. No regeneration is present, and the gap is being filled by lateral extension of the adjacent trees. No bare soil is present.

Un2

Gap was formed about 2 years previously by crown damage to an oak (178 cm gbh). The surrounding canopy is mostly oak, with occasional hazel and hawthorn. The ground vegetation is dominated by woodrush, bracken and male fern. Bare soil is minimal. Seedlings and saplings are absent.

Un3

Gap formed by the uprooting of 2 oaks (193 cm and 108 cm gbh) 15-20 years previously. Canopy gap is nearly replaced from growth by birches (60cm gbh) and epicormic shoots of the larger oak along the mound of the fallen tree. Woodrush and wood sorrel dominate the ground vegetation. Seedlings of oak and holly are occasional.

Un4

Gap formed by uprooted oak (154 cm gbh) about 15-20 years ago. Adjacent species are holly and oak. The canopy is being replaced by saplings of birch and oak (which may be epicormic growth) along the bole and on the mound of the gap maker. The largest of these is a birch of c. 10m in height and 66cm gbh. The ground vegetation is dominated by woodrush, with some bracken and occasional hard fern. Seedlings of ivy, holly and rowan are very occasional. Saplings of holly are present on the mound.

Uragh Wood, Co. Kerry: 4 gaps

Ur1

Gap formed by the uprooting of birch (0.9m gbh) perhaps 5 years previously and more recent crown damage to an oak. Adjacent trees are mostly birch, with holly and oak also present. The vegetation is dominated by bracken which reaches a height of c.2m (the gap was surveyed in July). Clumps of rowan saplings 30-50cm tall are present, and some show evidence of browsing. The field layer is diverse, with woodrush, bramble, honeysuckle and bilberry among the more frequent species. Bare soil is sparse, less than 5% overall (excluding that in the pit). Small seedlings are rare, S2s and saplings of oak, birch and rowan are present.

Ur2

Gap formed by the uprooting of three birches (0.96, 1.15 and 0.92 m gbh), one of which appears to have been blown c. 7 years ago, and the others less than two years previously. Adjacent trees are 16-18m tall, and are oaks and birches. The ground layer is quite diverse, with woodrush, heather, bilberry and cow-wheat among the most abundant species. There is little bare soil outside of the root pit, but bryophyte cover is generally high (20-65%). The pit and mound are dominated by birch S1s, and other regeneration in the gap include small saplings of rowan, holly, and oak.

Ur3

This gap was formed by the snapping of a birch, perhaps more than 10 years previously. Adjacent canopy height is c. 18m, and the trees are oak and birch. Rowan saplings (1.1-1.5m) are frequent, and smaller saplings of oak and holly (60-70cm) are occasional. The field layer is mixed, with bramble, purple moor grass, heather and bracken.

Ur4

This gap was formed by the snapping of a birch, about 3 years previously. Adjacent canopy reaches about 17m, and comprises holly, hazel, birch and oak. The vegetation is dominated by rather dense bracken, to a height of 1.4m, Bramble is also plentiful, with woodrush, bent grass and soft fern also present. Bare soil and litter are limited, and regeneration includes saplings of rowan (1.2m), oak (0.3m), holly (0.2m) and birch (0.25m).