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The Ecology of Yew (*Taxus baccata*) in Ireland

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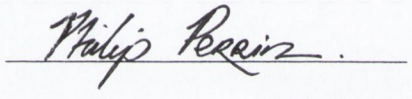

Philip Perrin

SUMMARY

This project stemmed primarily from the need for increased ecological knowledge of the development and regeneration of yew communities in Ireland. This was required to make informed management decisions pertaining to the country's last yew-dominated woodland, Reenadinna Wood, Killarney National Park, as yew woodland is classified as a priority habitat type under Annex I of the EU Habitats Directive. In addition, recent palaeoecological research has suggested that yew woodland may have been a far more important feature of the natural Irish landscape than has been thought hitherto. In view of ongoing initiatives to increase native woodland cover, it is important to understand as fully as possible the vegetation composition of this past landscape. Hence, this project was also concerned with elucidating the past distribution of the species and the reasons for its decline.

A multidisciplinary approach was taken to tackling these two main areas of research. Historical and prehistorical distributions of yew were studied by a meta-analysis of pollen diagrams produced from sites across Ireland. Surface interpolation modelling was employed to create isopollen (pollen concentration) maps for Ireland representing various times in the last 10,000 years. It is apparent that yew first expanded in Ireland around 5,000 BP in following to the elm-decline, with increments in pollen particularly notable in the west and south. However, this expansion was transient and the species soon dwindled in abundance at the majority of sites within a few hundred years, principally due to the expansion in agriculture. There was a brief and localised resurgence of yew in the Late Iron Age and place-name analysis indicates that yew woods were still widespread in the early historical period.

The successional pathway along which Reenadinna and historical yew-woods may have developed was further investigated by the compilation of a chronosequence of vegetation samples. Sites with semi-natural yew communities across south and west Ireland were surveyed and floristic data were interpreted using multivariate ordination and cluster analysis. Results indicated that yew woodland developed exclusively on limestone pavement sites, progressing from species-rich grasslands, such as are found in the Burren, through a seral scrub stage in which hazel is an important feature, to species-poor woodlands dominated by yew, or a mixture of yew and ash. Grazing levels and the presence of protective thorny scrub species appear to be influential in determining the exact path of succession. It was found that many of the remaining yew communities are threatened by invasive non-native plants such as beech and *Cotoneaster* spp. Yew also occurs in oak-holly woodland on sandstone, and ash-oak woodland on calcareous soils. Transect surveys were conducted to study the ecotonal

gradation between yew-wood stands into other habitats and highlighted their species-poor nature.

Long-term deer exclosures established in Reenadinna Wood and the neighbouring oakwood of Camillan between 1969 and 1975 were resurveyed to investigate tree stand dynamics and the effects of grazing on natural regeneration and vegetation change. Data were analysed in recombination with those from previous surveys, and revealed that deer grazing alone was not responsible for the complete dearth of yew regeneration in Reenadinna, but that yew was regenerating successfully in Camillan in the absence of deer. A field layer dominated by *Rubus fruticosus* and *Hedera helix* had developed in the Reenadinna exclosures with abundant saplings of *Ilex aquifolium*. Vegetation changes in the Camillan exclosures was variable, with some plots having developed a field layer of *Vaccinium myrtillus* and *Luzula sylvatica* and others dense holly thickets. *Rhododendron ponticum* dominated vegetation in the absence of management. In both woodland types, field layer species diversity increased rapidly after fencing as new species colonised the exclosure plots, but subsequently declined as aggressive competitors began to dominate. The pattern of mortality amongst adult yew trees in Reenadinna Wood suggests that it is currently in an aggrading phase of development.

A series of *in situ* and *ex situ* experiments were conducted to investigate additional factors that might be limiting yew regeneration. The potential for post-dispersal seed predation by small mammals, namely wood mice (*Apodemus sylvaticus*) and the introduced bank vole (*Clethrionomys glareolus*) was investigated by conducting a live trapping programme. Population estimates for a Reenadinna exclosure and a Camillan exclosure were insufficient to explain the differential rate of yew regeneration. Field germination trials in cages excluding small mammals resulted in very low rates of yew seedling establishment, but germination trials in the laboratory proved that poor seed viability was unlikely to be the cause of regeneration failure. Artificial shade experiments were conducted using shade tents on an outdoors plot at Trinity College Botanic Garden and demonstrated shade tolerance in yew, with associated growth and foliar adaptations.

The three most important management recommendations are that yew should be widely considered as a component of native woodland planting schemes, that intermediate levels of grazing pressure are required in Irish woodlands to maximise species diversity and that action should be taken regarding non-native species in Irish yew-communities.

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Terms and Conventions

Species nomenclature

For angiosperms and gymnosperms nomenclature follows Stace (1997). Pteridophyte nomenclature follows Webb *et al.* (1996).

In the body of the text common names are used to refer to following native tree and shrub species:

yew	*Taxus baccata* L.
ash	*Fraxinus excelsior* L.
hazel	*Corylus avellana* L.
holly	*Ilex aquifolium* L.
hawthorn	*Crataegus monogyna* Jacq.
blackthorn	*Prunus spinosa* L.
birch	*Betula pubescens* Ehrh.
alder	*Alnus glutinosa* (L.) Gaertn.
rowan	*Sorbus aucuparia* L.
spindle	*Euonymus europaeus* L.
sessile oak	*Quercus petraea* Matt. (Liebl.)
pedunculate oak	*Quercus robur* L.
Scots pine	*Pinus sylvestris* L.

Abbeviations

BP	=	radiocarbon years before present
gbh	=	girth at breast height (1.3 m)
PAR	=	photosynthetically active radiation
se	=	standard error

Tree size classes

Adult	=	gbh $\geq$ 10 cm
Juvenile	=	gbh < 10 cm
Sapling	=	gbh < 10 cm and height $\geq$ 25 cm
Seedling	=	height < 25 cm

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CHAPTER 1

INTRODUCTION

1.1 Rationale

Yew (*Taxus baccata*) is a dioecious gymnosperm that occurs across Europe. It typically grows as a scattered understorey tree or shrub in broadleaved and mixed woodland, or clinging to cliffs and crags where it is inaccessible to browsing animals. Despite its widespread distribution, it has been reported as declining across its range and is now rare or extinct in many parts of Europe (Bugała 1978; Lewandowski *et al.* 1995; Svenning & Magård 1999). This decline has been attributed to general deforestation, selective felling, and sensitivity to grazing (Bugała 1978; Czartoryski 1978a; Tittensor 1980; Sarmaja-Korjonen *et al.* 1991). Poor rates of natural regeneration have also been reported from many populations (e.g. Kelly 1975; Król 1978; Tittensor 1980; Lewandowski *et al.* 1995; Hulme 1996). Although widely cultivated and planted as an ornamental, the conservation status of natural yew populations has thus become a cause for concern (e.g. Czartoryski 1978a; Lewandowski *et al.* 1995; Svenning & Magård 1999; García *et al.* 2000).

Furthermore, although yew is rarely the dominant tree in woodland, in Ireland and Britain it can form almost pure stands, characterised by heavy shade and a striking paucity of ground flora (Rodwell 1991). These yew dominated woodlands (hereafter termed "yew-woods") are of international scientific and conservation importance and are designated as priority habitats in Annex I of the EU Habitat's Directive, under the category "*Taxus baccata* woods of the British Isles (Corine code 91JO)" (European Commission 1999). They almost invariably occur on calcareous substrates: chalk downland in southern England and limestone pavement in Ireland and northern England. The development of yew-woods on chalk downland in southern England has been investigated by Watt (1926) and Tittensor (1980). They have been shown to be of relatively recent origin, developing on grazing land that was abandoned *c.*1820-1860, through a juniper (*Juniperus communis*) or hawthorn (*Crataegus monogyna*) scrub stage that served to protect the establishing yew trees.

The origins, dynamics and ecology of yew-woods in Ireland are far less well understood. Only one extensive site remains, Reenadinna Wood, which covers an area of approximately 25 ha on Carboniferous limestone outcroppings in the Killarney National Park, Co. Kerry. The flora has been described by Kelly (1975, 1981). Palaeoecological investigations have suggested that this wood has never been cleared for any great length of time and has been dominated by yew for the last 5000 years (Vokes 1966; Mitchell 1990a). The current lack of ecological information, however, means that management prescriptions for this site cannot be underpinned by a sound knowledge base. Of particular importance are the effects that chronic heavy grazing by introduced sika deer (*Cervus nippon*) has been having on vegetation and natural regeneration, as yew is known to be highly sensitive to deer grazing (Mitchell 1990b). To address this problem, long-term grazing exclosures were established in the yew-wood and a neighbouring oakwood between 1969-1975.

At a broader scale, recent pollen studies from several other sites in the west of Ireland have also indicated an expansion in yew *c.*5000 BP (e.g. Watts 1984a; O'Connell *et al.* 1987; O'Connell *et al.* 1988; Hannon & Bradshaw 1989; Huang 2002), but at these sites the species subsequently declined during a period of increasing woodland exploitation. It would appear that yew-woods may once have been a far more important feature of the natural Irish landscape than has previously been supposed. Of particular note are the striking similarities in the geomorphology of the limestone outcroppings on which Reenadinna Wood stands, and the vast expanses of limestone pavement in the Burren, Co. Clare. Yew still occurs in this area, but is restricted to cliff-faces or as stunted shrubs amongst the scailps, due to the high browsing pressure from feral goats. The pollen diagram from Gortlecka, Co. Clare, (Watts 1984a) confirms that yew was once abundant in the south-eastern Burren.

This potential underestimation of the occurrence of yew and yew-woods in the natural landscape must be seen against the backdrop of the current situation regarding native woodlands. Ireland has one of the lowest native woodland covers in Europe, presently less than 1% of the land area (Cross 1998), but is recently experiencing something of a native woodlands renaissance. State funded grant schemes are now in operation to promote native woodland conservation and planting, and research is progressing on re-creating woodland in National Parks (e.g. Smith 2002). A target has been set of increasing Ireland's total forest cover to 17% by 2030 (Department of Arts, Heritage, Gaeltacht and the Islands 2002); increasing native woodland cover is to be an important component of this national strategy. If these new woodlands are to be

representative of the past natural landscape, it is important that basic information on the former distribution and abundance of native tree species is available.

1.2 Aims and structure

The study of woodlands, and particularly the study of woodland dynamics, is restricted by the longevity of arboreal species (Mitchell 1990). Peterken (1996) lists six approaches that are appropriate for such research: chronosequences, stand characteristics, pollen profiles, historical records, permanent plots and modelling. Each approach has its advantages and disadvantages. This project aims to investigate several aspects of the ecology of yew in Ireland by taking a multidisciplinary approach and will utilise the first five of the above methods. The objective of the thesis is to provide ecological information relevant to the management of yew on a local scale (at Reenadinna Wood) and at a national level. This will be achieved through the following primary aims:

i) to investigate the past distribution of yew in Ireland, and the factors affecting its expansion and decline through analysis of historical and palaeoecological data;
ii) to survey the plant communities in which yew currently occurs in Ireland;
iii) to investigate the factors governing the establishment of yew-woods;
iv) to examine the effects of deer grazing on the natural regeneration and vegetation within Irish yew-woods through survey of long-term deer exclosures;
v) to investigate aspects of the autecology of yew and how they may pertain to natural regeneration.

The thesis is structured as follows. The remainder of Chapter 1 forms an introduction to the study species and relates the salient points of its general biology; more detailed aspects of yew ecology will reviewed and discussed later in the thesis at the relevant points. Chapter 2 collates the available palaeoecological and historical data for yew in Ireland and presents an insight into its past distribution. Chapter 3 comprises a survey of the Irish plant communities in which yew currently occurs and an introduction to the yew-wood of Reenadinna, Killarney National Park. Chapter 4 consists of a survey of the long-term deer exclosures on the Muckross Peninsula, Killarney National Park, and the natural regeneration of yew therein, together with an analysis of exclosure data collected since 1969. The next two chapters deal with further factors that might be

influential in the natural regeneration of the species: in Chapter 5 the potential of post-dispersal seed predation by small mammals is examined, whilst in Chapter 6 a series of *ex situ* experiments are presented, investigating shade tolerance, seed viability, allelopathic potential and simulated browsing. Finally, in Chapter 7, general conclusions are drawn on the ecology of yew in Ireland, and areas for future study are highlighted.

1.3 Background to the species

1.3.1 Taxonomy

The common yew (*Taxus baccata*) belongs to the Taxaceae, the yew family. The genus *Taxus* is composed of several closely related species found across the northern temperate region (Table 1.1). However, morphological and chemical analyses of several of these species (Dempsey & Hook 2000) have suggested that there are insufficient interspecific distinctions to warrant the status of separate species. Existing taxonomic divisions may therefore represent geographic variants of a single species, according to Welch and Haddow (1993), although Dallimore and Jackson (1966) state that they are best regarded as distinct species on the basis of their well-defined natural geographical areas.

Table 1.1 Species and distributions of the genus *Taxus*, following Rushforth (1987).

Species	Native distribution
Taxus baccata Linnaeus	Europe, western Asia, North Africa
Taxus brevifolia Nuttall	western North America
Taxus canadensis Marshall	eastern North America
Taxus chinensis (Pilger) Rehder	China
Taxus cuspidata Siebold & Zuccarini	Japan
Taxus floridana Chapman	Florida
Taxus globosa Sclechtendal	Mexico
Taxus mairei (Lemee & Leveille) S.Y. Hu ex Liu	China
Taxus yunnanensis Zuccarini	China
Taxus wallichiana Cheng & L.K. Fu	Himalayas

There are two recognised interspecific hybrids: *Taxus* x *media* Rehder, (*T. baccata* x *T. cuspidata*); and *Taxus* x *hunnewelliana* Rehder, (*T. canadensis* x *T. cuspidata).* In addition, there is a vast number of cultivars bred largely for their ornamental value (Dallimore & Jackson 1966; Bugała 1978; Welch & Haddow 1993). Of particular note is *Taxus baccata* var. *fastigiata* (Ldl.) Loudon, the so-called Irish yew, which is derived from two female yews, found at Carraig-na-madadh near Florence Court, Co. Fermanagh around 1740 (Nelson 1993). This mutant form consists of upright vertical shoots, with little lateral branching and hence forms a distinctive

columnar tree. It has been vegetatively propagated by cuttings and grafting and is one of the most widely planted cultivars of yew in Ireland.

The common yew (*Taxus baccata*) is the only species of *Taxus* native to Europe and, alongside juniper (*Juniperus communis*) and Scots pine (*Pinus sylvestris*), one of only three coniferous species native to the British Isles.

1.3.2 Description

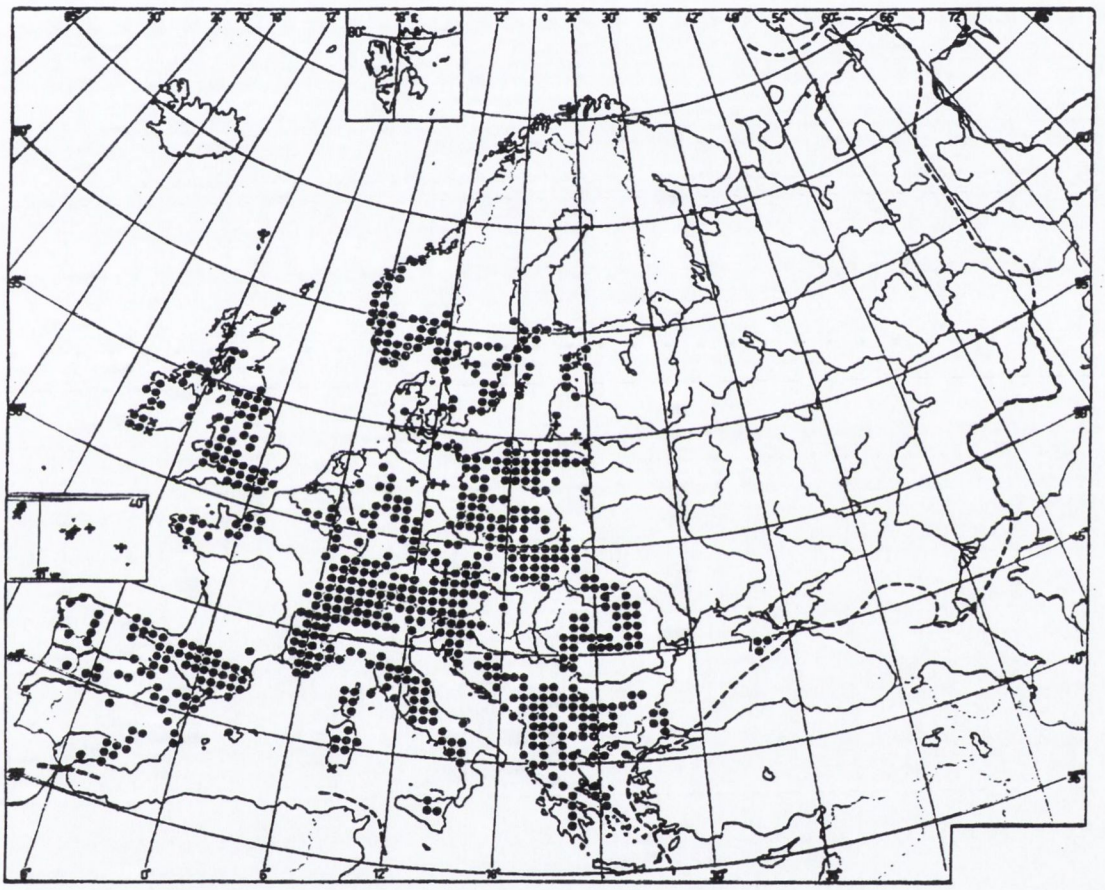
The yew is an evergreen, non-resiniferous conifer, usually dioecious, rarely monoecious. It grows as a large bush or, more typically, as a tree to a height of 20 m, exceptionally to 28 m, with a rounded crown of dense branches and dark foliage. The bark is thin, smooth and reddish-brown, peeling off in strips. Often multi-stemmed when young, but can form a massive, fluted trunk at maturity (>3m diameter). Branches are spreading, twigs are irregularly alternate, buds are green in winter. Leaves are soft, linear, shortly stalked, 10-30 mm long, 2-3 mm wide, with prominent midrib and recurved margins, spirally arranged and spreading all round on vertical shoots, but twisted on lateral shoots so as to appear in two uniform ranks, dark green with two pale green stomatiferous stripes on lower surface. They last about eight years before being shed.

Male cones (strobili) are small (*c.* 5 mm diameter), yellow, globular, arise from the axils of the leaves on the underside of branchlets of the previous year's growth, with 6-14 stamens on short filaments and with peltate anther scales, each bearing 5-9 pollen sacs. Female reproductive structures are 15-20 mm long, green, consisting of a single ovule, not in a cone, clasped by scales at base, borne in leaf axes, terminal on very short lateral shoots. Seeds are ovoid (*c.* 6 mm long), shiny brown, with thick seed coat, borne and mostly enveloped in a fleshy, scarlet, cup-shaped aril (*c.* 10 mm long), ripening in first year and falling when mature (Dallimore & Jackson 1966; Webb *et al.* 1996; Stace 1997).

1.3.3 Distribution

Yew occurs widespread across Europe (Fig. 1.1). In the north its range extends to 63°N on the Norwegian coast, 61°N in southern Sweden and the Åland Islands, Finland (Sarmaja-Korjonen *et al.* 1991) and to 56°N in Scotland, although its native status in Scotland is a point of debate (Mitchell 1974; Dickson 1994). Its range in the north appears to be limited by winter temperatures, following fairly closely the -5°C January isotherm (Godwin 1975; Król 1978; Mitchell & Ryan 1997), although Melzack & Watts (1982a) demonstrated that yew is particularly

Figure 1.1 Distribution of *Taxus baccata* in Europe (from Jalas & Suominen 1973): ● indicates native occurrence, + indicates extinction, x indicates possible extinction, ? indicates uncertain record.



susceptible to late frosts in the spring. In the east, yew reaches as far as the Gulf of Riga and its range extends down through Białowieża Forest in Poland to the Carpathians. The limitation of its occurrence in eastern Europe appears to be due to its intolerance of continental climates (Bugała 1978). In the south, it occurs around the Mediterranean, including north Africa, southern Spain, Greece and the Middle East. Whereas in the north (Britain, Ireland and Scandinavia) yew is typically a species of the lowlands, in the south it is primarily a montane species. It occurs to heights of 1100-1400 m above sea level in the Alps, 1500 m in the Caucasus, 1660 m in the Carpathians, 1800 m in Macedonia, 1700-1950 m in southern Spain and 2300 m in Asia Minor (Bugała 1978; Król 1978; Garcia *et al.* 2000). Hulme (1996) attributed this difference in altitudinal range to sensitivity to frost in the north and sensitivity to drought in the south. Whilst its natural distribution is wide, yew has become locally extinct or reduced to small isolated populations in many parts of Europe during the last 4000 years (Svenning & Magård 1999).

In Ireland and Britain, the native distribution of yew is obscured, not only by the extensive clearance of woodland, but by the widespread introduction and planting of the species. Preston *et al.* (2002) were unable to distinguish between native and introduced records and hence treated all records as if they were native (Fig. 1.2). The distribution of yew in Ireland, however, is undoubtedly underrepresented by this map, due to a less intensive level of recording in many areas; also to differences in the extent to which recording included trees that had clearly been planted. The probable native distribution of yew in the British Isles was estimated by Tittensor (1980; Fig. 1.3). In Britain, yew is native to the chalk downs of south and south-eastern England, the Welsh borders, and the limestones of Cumbria and the Peak District, with outlying populations in Scotland. In Ireland, Tittensor (1980) proposed that yew is native to Cos. Kerry and Cork in the southwest, the Burren and Connemara in the mid-west, and Wicklow in the east, with a few scattered populations throughout the north. Scannell & Synnott (1987), however, afforded yew native status over most of western Ireland with possible native status in central and eastern counties (Fig. 1.4). It is clear from these conflicting distribution maps that the past and present occurrence of native populations of yew is poorly understood, and worthy of further investigation. The contemporary altitudinal limit of yew in the British Isles is a height of 470 m above sea level, on Purple Mountain, Killarney National Park, Co. Kerry (Preston *et al.* 2002).

Figure 1.2 Distribution of *Taxus baccata* according to the New Flora of Britain and Ireland (Preston *et al.* 2002). Colours indicate time of last recording: dark green = 1987-1999; mid green = 1970-1986; light Green = Pre-1970.

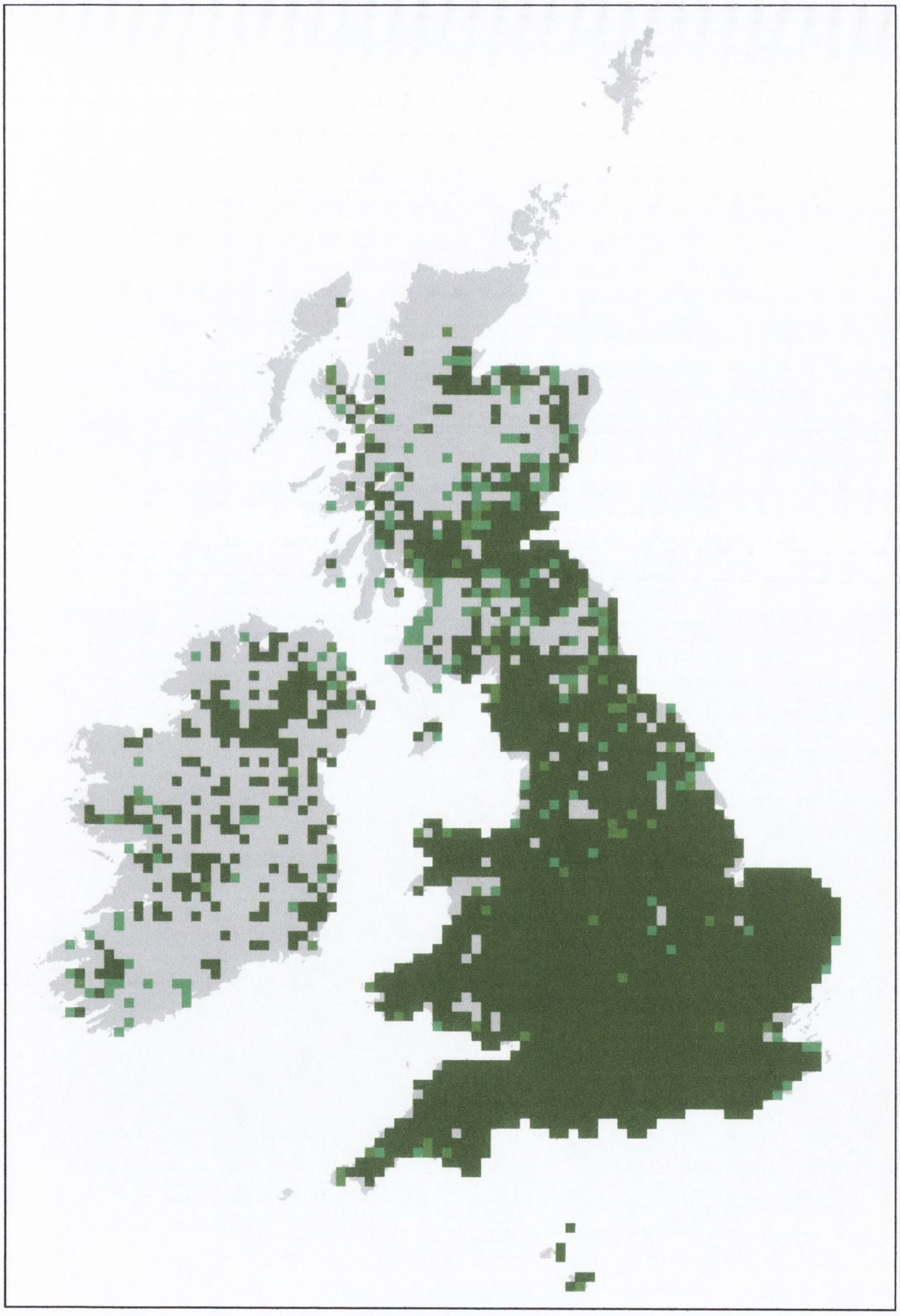


Figure 1.3 Probable native distribution of *Taxus baccata* in Ireland and Britain (from Tittensor 1980).

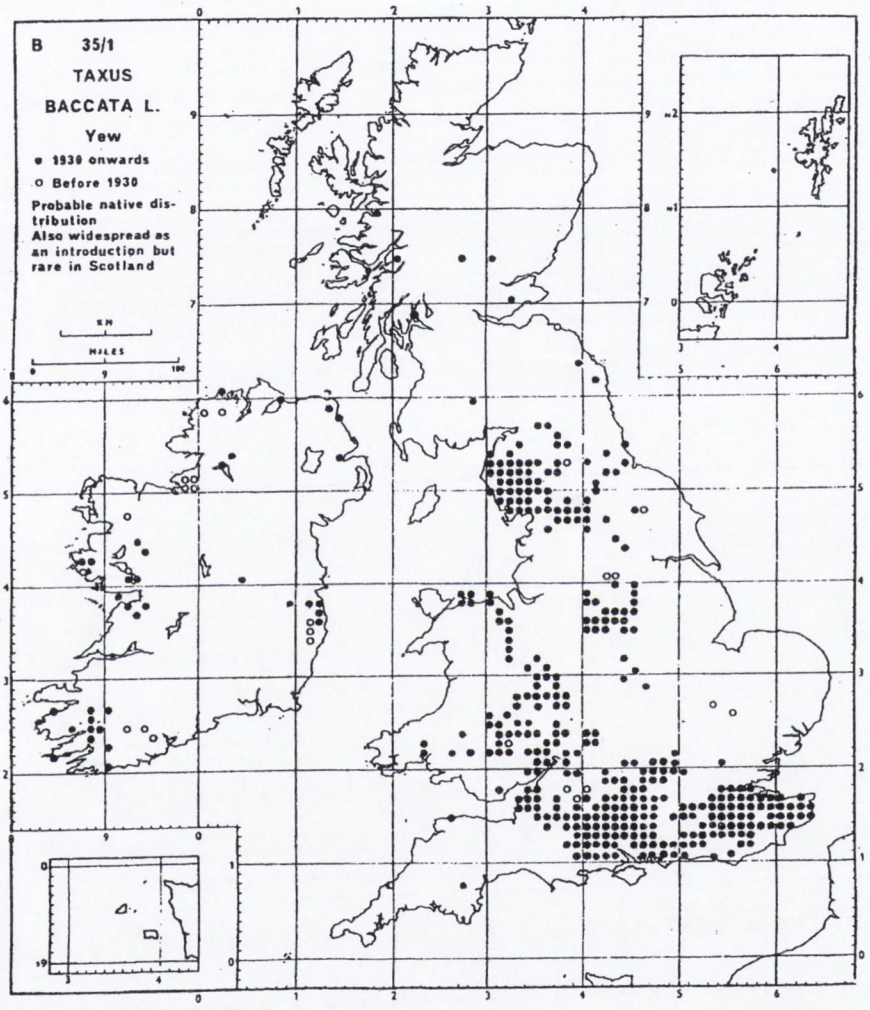
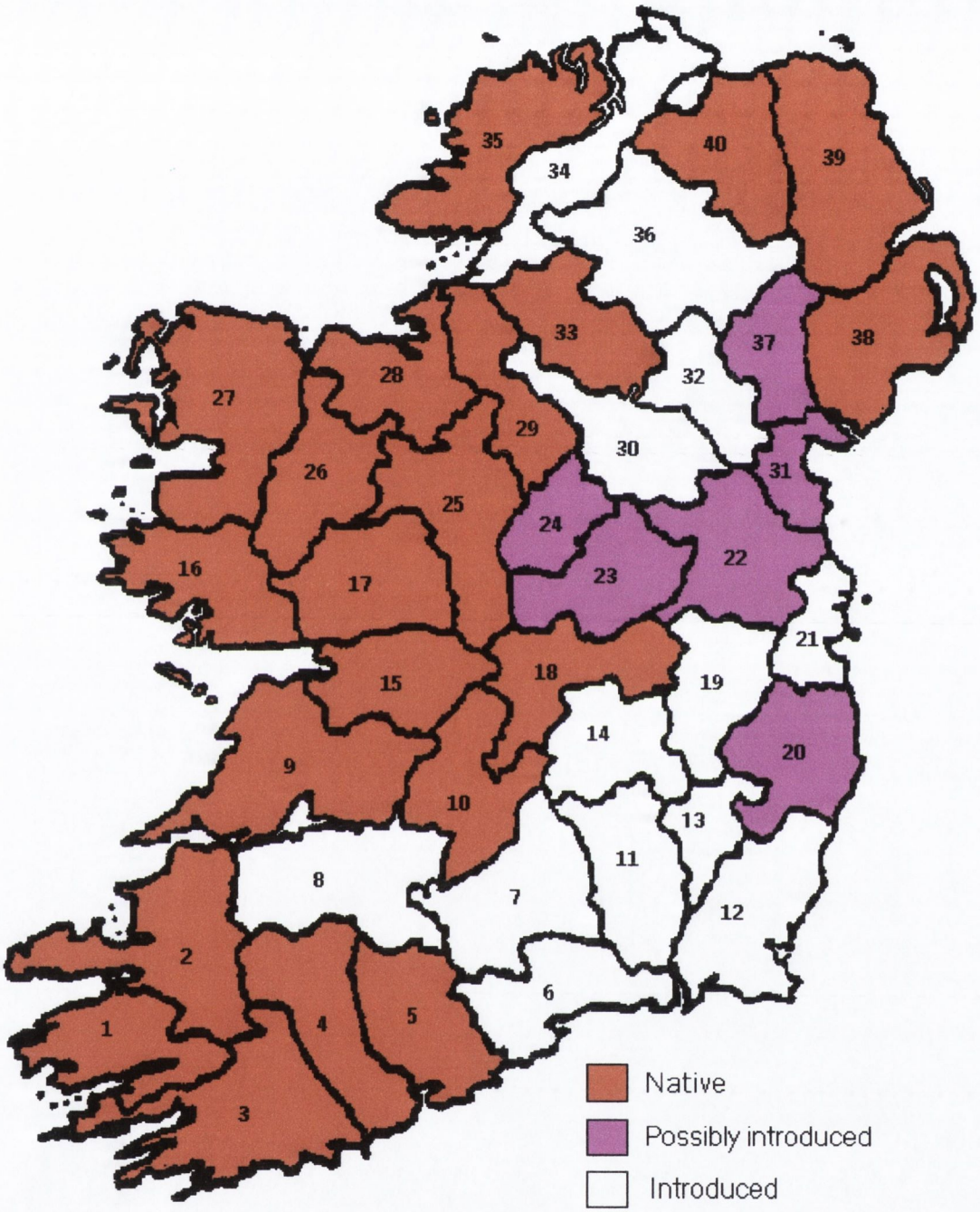


Figure 1.4 Native distribution of *Taxus baccata* in Ireland by vice-county, according to Scannell & Synnott (1987).



Key to vice-counties:

1. South Kerry
2. North Kerry
3. West Cork
4. Mid Cork
5. East Cork
6. Waterford
7. South Tipperary
8. Limerick
9. Clare
10. North Tipperary
11. Kilkenny
12. Wexford
13. Carlow
14. Laois
15. South-east Galway
16. North-west Galway
17. North-east Galway
18. Offaly
19. Kildare
20. Wicklow
21. Dublin
22. Meath
23. Westmeath
24. Longford
25. Roscommon
26. East Mayo
27. West Mayo
28. Sligo
29. Leitrim
30. Cavan
31. Louth
32. Monaghan
33. Fermanagh
34. East Donegal
35. West Donegal
36. Tyrone
37. Armagh
38. Down
39. Antrim
40. Derry

1.3.4 Reproduction

Yews are slow to reach maturity and only start seed production after about 70 years in woodland conditions, after which point seed is produced every year (Brzeziecki & Kienast 1994). Flowering occurs between February and April in Ireland. Female structures are wind-pollinated, although Milner (1992) reports that honeybees have been observed visiting them. Fertilization occurs six weeks to three months after pollination (Hejnowicz 1978). Arils ripen throughout the summer and are shed from late July / early August through to January and February the next year, with most seed being shed between October and December. There can be considerable year to year variation (Smal & Fairley 1980a).

Birds are the chief dispersers of seeds and are attracted by the bright scarlet colour of the arils which stand out against the dark green foliage. Snow & Snow (1988) observed ten species of birds feeding on yew in southern England. Thrushes (*Turdus* spp.) appeared to be particularly important to seed dispersal, consuming the fruit but excreting or regurgitating the seeds. Two of the species, however, greenfinch (*Carduelis chloris*) and great tit (*Parus major*) were seed predators. Post-dispersal seed predation by woodmice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) has been studied by Smal & Fairley (1982) and Hulme (1996,1997). Germination of surviving seeds typically occurs the second spring after seed-fall (Melzack & Watts 1982b).

1.3.5 Phytochemistry

Since the isolation of the important antitumour drug Taxol (paclitaxel) from the bark of the Pacific yew (*Taxus brevifolia*), *Taxus* spp. have been the focus of considerable biochemical research, with *Taxus baccata* being no exception, for example, Griffin & Hook (1996), Hirasuna *et al.* (1996), Vanek *et al.* (1996), Zobel *et al.* (1996), Das *et al.* (1998), Gabetta *et al.* (1998), Vesela *et al.* (1999), Laskaris *et al.* (2000), Goleniowski (2000), Navio-Osorio *et al.* (2002) and Fornale *et al.* (2002). A wide variety of taxane derivatives have now been isolated and are reviewed by Parmar *et al.* (1999). One of the most important outcomes is the production of Taxotere (docetaxel) a semisynthetic taxane derived from the leaves of *Taxus baccata* (Vaishampayan *et al.* 1999), as foliage is evidently a more sustainable source of chemical precursors than bark.

Yew is highly resistant to attack by insects due to taxane chemicals with very strong antifeedant activity (Daniewski *et al.* 1998). This may help account for the exceedingly low number of insect herbivores associated with the species in Britain, in comparison to other native tree species (Strong

1974). Taxanes are present in every part of the yew except for the arils, rendering the plant potentially toxic to herbivore browsers, but there appears to be considerable variation in susceptibility to yew poisoning. Connevin (1892 cited in Williamson 1978) experimentally determined lethal oral doses of yew leaves (per kg of animal) as: horse 2g; ass or mule 1.6g; pig 3g; dog 8g; cow or sheep 10g; goat 12g; rabbit 20g. Resistance to poisoning appears to develop with constant access (Hæggström 1990; Williamson 1978). Sheep freely roamed the yew-wood at Kingley Vale, West Sussex, for many years without suffering toxic effects from the foliage (Williamson 1997) and still do so at Ashford Hangers, Hampshire (D. Ball, pers. comm.). In Killarney, Co. Kerry, deer appear to browse yew with relative impunity (Larner 1977; Kelly 1981) and Mitchell (1990b) showed that it is also susceptible to browsing by cattle.

1.3.6 Growth and longevity

Yew is a slow growing and long-living species which, after several centuries, can form trees of moderate height, but of exceptionally large girth. The age of these ancient yew trees, often found in churchyards, has attracted a great deal of speculation regarding growth rates and longevity as far back as Lowe (1897). Some British trees can be dated at least as far back as 1152 A.D. on the basis of documentary evidence alone (Milner 1992). However, accurate ageing of yew trees by the usual silvicultural technique of increment coring is hampered by the exceedingly dense wood, non-concentric growth (which manifests as a fluted trunk) and the fact that very old trees are invariably hollow. Several authors have therefore proposed numerical relationships between girth and age based on cross sections from younger trees, repeat measurements from old trees, or measurements of trees of known planting date, for example, Allen Meredith (data cited in Milner 1992), Pigott (1995), Tabbush & White (1996), Tabbush (1997), White (1998) and Moir (1999). These relationships are largely based upon a model whereby, initially, there is a linear relationship between age and girth (Pigott 1995; Moir 1999), but once optimum crown size has been reached, annual rings decrease in width each year. This is because a constant annual volume of new wood is then being produced which, as the circumference of tree increases, must be lain down ever more thinly (White 1998). The remarkable feature of yew, and the reason for its extreme longevity, is that trees persist in good health after annual radial increment becomes barely discernible. For example, the ancient yew at Totteridge, Hertfordshire, still has the same girth (8 m) as when it was measured in 1677 (Milner 1992). Most tree species barely survive once annual ring width is ≤ 0.5 mm, according to White (1998). In comparison, Newbould (1960, cited in Tabbush & White 1996) found that ring width of yews at Kingley Vale ranged from 0.13 mm to 2.54 in younger trees, but fell to 0.051mm in older trees.

A considerable amount of variation exists between the proposed growth models, and it is apparent that growth rate is greatly affected by environmental conditions such as soil fertility and canopy cover, which should be taken into account when interpreting age from girth measurements. Williamson (1978) mentions a group of five yews at Kingley Vale, all 80 years old, but which varied in diameter from 5.08 cm (mean radial increment = 0.32 mm $year^{-1}$) to 39.37 cm (mean radial increment = 2.46 mm $year^{-1}$); the smallest tree had been severely shaded by its competitors. A yew trunk found in a bog in Co. Laois, reported by Adams (1905), displayed a markedly eccentric growth from, probably due to poor drainage (cf. Godwin 1975). At their narrowest, 74 of the annual rings in this specimen measured only 7mm in total (mean radial increment = 0.094 mm $year^{-1}$). Grazing may also severely retard growth; Watt (1926) found a yew plant at Kingley Vale only 18cm high but with 55 annual rings. Furthermore, where plants have been grazed or otherwise damaged right back to base, subsequent vegetative regeneration may mean that the diameter of existing stems bears no relation to the absolute age of the individual (Tabbush & White 1996). Yew also displays an ability for stems growing close to one another to coalesce. A single, outwardly seamless, trunk is formed, the origin of which is only revealed upon examination of a cross section (Williamson 1978). Due to these difficulties and other plastic growth characteristics, such as layering, yew is according to White (1998) the most difficult of native trees to date with any degree of confidence

These accuracy problems notwithstanding, it is clear that yew is the longest-living plant species native to Ireland and Britain. The Fortingall Yew, Perthshire is reported to have had the immense girth of 52 ft (16 m) in 1769. Although little of this tree remains, the age of the surviving fragments has been estimated at between 5,000 and 8,000 years old (Milner 1992). One of the largest existing yew trunks is that at Llangernyw, Abergele, North Wales, with a girth of 11.00 m; it is potentially 5,600 years old according to Allen Meredith's growth curve (Milner 1992). A database of the largest yews in Ireland has recently been collated for the Tree Register of Ireland. The largest known existing tree is at Ballyrankin, Co. Wexford and has a girth of 6.74 m (A. Fennell, unpublished data). According to Meredith's growth curve (Milner 1992), this tree is probably over a 1,000 years old. It is followed by a tree at Ballyfin College, Co. Laois, with a girth of 6.62m, whilst third is a yew at Glencormac, Co. Wicklow, with a girth of 6.48 m (A. Fennell, unpublished data). There is historical evidence of larger yews in the past: for example, Ledwich, writing in 1790 (quoted in Simon 2000), details an ancient yew near the cathedral at Glendalough, Co. Wicklow, three yards in diameter (2.74 m, or 8.60 m in girth) and potentially 2,000 years old.

CHAPTER 2

THE HISTORICAL ECOLOGY OF YEW IN IRELAND

2.1 Introduction

2.1.1 Overview

This chapter deals with the role that yew (*Taxus baccata*) has played in the vegetational history of Ireland since the last glaciation. The first part of the chapter is based largely on palynological research whilst the latter parts focus on evidence from archaeological records, historical literature and place-names.

2.1.2 Background to palynological evidence

Identification of pollen grains preserved in the gradually accumulated peat of Irish bogs began over 60 years ago with the work of Jessen & Farrington (1938). Since then pollen diagrams have been produced for numerous sites across Ireland, enabling past vegetation communities to be reconstructed and regional variations to be detected (Watts 1985). Increasing use has been made of lake sediments (e.g. Craig 1978; O'Connell *et al.* 1987; Huang 2002) and radiocarbon dating (see Edwards 1985), whilst sampling from small woodland hollows has permitted vegetation dynamics to be investigated at a finer spatial resolution (e.g. Mitchell 1988; Mitchell 1990a,b; Little *et al.* 1996). However, yew pollen has received universal recognition only relatively recently and its importance in Irish woodland dynamics has been previously underestimated (Mitchell & Ryan 1997; Mitchell 1990a). By drawing on data from recently compiled pollen diagrams a review of the palaeoecology of yew is now possible. The locations of Irish palaeoecological sites mentioned in this chapter are detailed in Table 2.1 and Fig. 2.1.

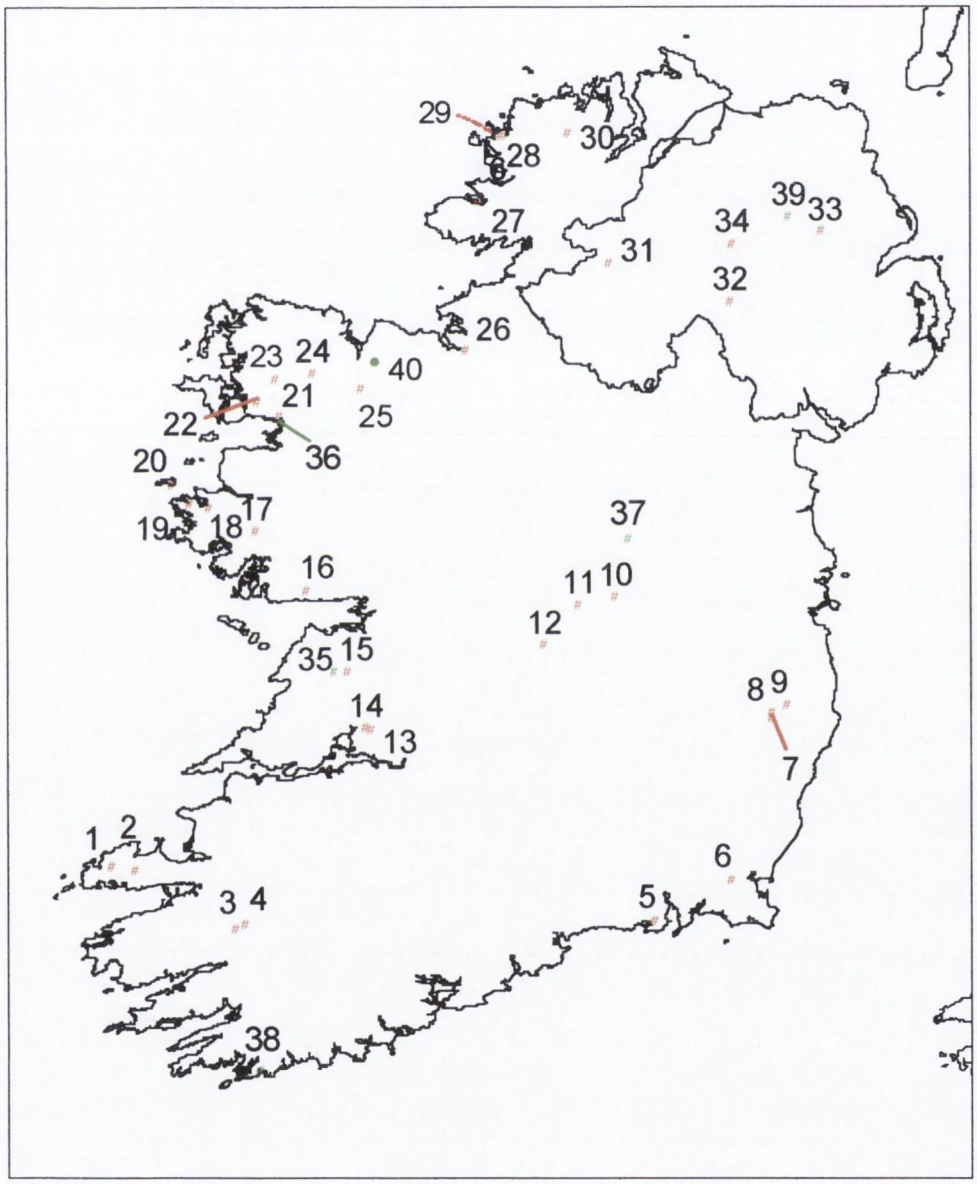
2.1.3 Background to historical and place-name evidence

Archaeological records and historical literature can supplement the picture presented by the pollen record, particularly with regards to human influence and the utilisation of woodland resources. Place-name (toponymical) data can also assist in reconstructing the wooded landscape of the historical period, although it must be cautiously interpreted. Historical ecology research of this nature was pioneered in the Britain by Rackham (1980, 1986, 1990) who has also considered some of these aspects in Ireland (Rackham 1995). Ireland is particularly well suited to the toponymical approach, as its townlands system of land division combines a high degree of spatial

Table 2.1 Palaeoecological research sites mentioned in this chapter. For locations see Fig. 2.1. Sites 1-34 only were used in compilation of the isopollen maps.

	Site	Reference
1	Ballinloghig Lake	Barnosky (1988)
2	Camclaun	Dodson (1990)
3	Doo Lough	Cooney, unpublished data
4	Sheheree Bog	Cooney, unpublished data
5	Belle Lake	Craig (1978)
6	Coolteen	Craig (1978)
7	Kelly's Lough	Cole, unpublished data
8	Arts Lough	Bradshaw & McGee (1988)
9	Glendalough	Maldonado, unpublished data
10	Cornaher Lough	Heery (1998)
11	Clara Bog	Connoly (1999)
12	Black Lough	Heery (1998)
13	Caherkine Lough	O'Connell *et al.* (2001)
14	Mooghaun Lough	O' Connell *et al.* (2001)
15	Gortlecka	Watts (1984)
16	Lough Namackanbeg	O'Connell *et al.* (1988)
17	Lough Maumeen	Huang (2002)
18	Connemara National Park	O'Connell *et al.* (1988)
19	Lough Sheeauns	O'Connell *et al.* (1988)
20	Church Lough	O'Connell & Ní Ghráinne (1994)
21	Lough Aisling	Browne (1986)
22	Lough Annafrin	Browne (1986)
23	Corslieve Lough	Browne (1986)
24	Lough Clevala	Browne (1986)
25	Lough Doo, Mayo	O'Connell *et al.* (1987)
26	Union Wood Lake	Dodson & Bradshaw (1987)
27	Lough Mullaghlahan	Fossitt (1994)
28	Lough Nabraddan	Fossitt (1994)
29	Altar Lough	Fossitt (1994)
30	Lough Nadourcon	Telford (1977)
31	Meenadoan	Pilcher & Larmour (1982)
32	Killymaddy Lough	Hirons (1983)
33	Sluggan Bog	Smith & Goddard (1991)
34	Ballynagilly	Pilcher & Smith (1979)
35	Rinn na Mona	Watts (1984)
36	Lough Kilnabinnia	Browne, unpublished data
37	Scragh Bog	O'Connell (1980)
38	Ballyally Lough & Lough Ine	Buzer (1980)
39	Newferry	Smith (1984)
40	Carrownaglogh	O'Connell (1986)

Figure 2.1 Locations of palaeoecological research sites mentioned in this chapter. For site names and references see Table 2.1. Sites marked in red were used for compilation of the isopollen maps. Other sites are marked in green. Scale 1: 3,000,000



resolution with a high degree of historical retention. The latter part of this chapter will attempt to collate such information as pertains to yew in Ireland in the historical period.

2.2 The late-glacial period

The general vegetation changes of this period, which may be regarded as an aborted interglacial cycle, have been discussed by Watts (1985) and Mitchell & Cooney (in press). They are briefly detailed here as background to the ensuing vegetation cycle of the post-glacial period in which yew features. Following withdrawl of the ice about 13,000 BP a snow-patch vegetation of sorrel (*Rumex acetosa / acetosella*), dwarf willow (*Salix herbacea*), grasses and sedges established across Ireland. Approximately 12,400 BP, juniper (*Juniperus*) increased markedly in response to a warming of the climate, dominating eastern and central parts of the country (e.g. Craig 1978; Heery 1998), whilst on acidic substrates in the west, crowberry (*Empetrum*) also expanded around this time (e.g. Telford 1977; Barnosky 1988; Fossitt 1994). An expansion in birch (*Betula*) woodland at this time seems to have been restricted to more sheltered areas, such as the Killarney Valley (Watts 1963) and Glendalough (Maldonado, unpublished data).

Between about 12,000 and 11,000 BP a slight cooling in the climate and an increase in grazing pressure from giant deer (*Megaloceros giganteus*) and reindeer (*Rangifer tarandus*) were probably responsible for the end of this scrub-woodland landscape (Bradshaw & Mitchell 1999; Mitchell & Cooney in press). Grasses now became dominant although crowberry remained abundant in the west. Around 11,000 BP a more severe cold phase known as the Nahanagan Stadial began and vegetation across the country reverted to one similar to that present at the beginning of the late-glacial period. A tundra-like landscape formed with sedges and dwarf willow prevalent amongst the sparse vegetation. Mugwort (*Artemisia*), a cold-tolerant genus, is characteristic of this phase at some sites (e.g. Craig 1978; Browne 1986; Maldonado, unpublished). Erosion increased significantly during this period as glaciers reformed in corries at higher altitudes resulting in high rates of coarse sediment accumulation (Watts 1985).

2.3 The early post-glacial period

The post-glacial period (or Holocene) began 10,000 BP as changes in North Atlantic circulation patterns, which had originally caused the Nahangan Stadial, shifted again, replacing cold polar waters near the Irish coast with warmer oceanic waters and resulting in a rapid increase in temperature (Watts 1985; Mitchell & Cooney, in press). A swift sequence of succession ensued,

initially similar to that of the early late-glacial period. Immigration of what may be regarded as the modern Irish flora was now limited not by climate but by the distance that species needed to spread from their warmer southern refugia (Mitchell & Cooney, in press). A peak in sorrels, sedges and grasses preceded a brief rise in crowberry in acidic areas. A second juniper phase followed, but this scrub was subsequently invaded by tree birch and tree willow around 9,500 BP, and under the increased shade juniper declined rapidly. Ferns (Filicales) were abundant at several sites at this point, including Lough Annafrin and Lough Kilnabinnia (Browne 1986), and guelder rose (*Viburnum opulus*) was frequent at Gortlecka in the Burren (Watts 1984).

Yew appears to have been present in Ireland at low frequencies from a fairly early point in the post-glacial period. The low levels of pollen detected, however, indicate that it was probably a widely scattered understorey tree. For instance, at Lough Nabradden in western Donegal, Fossitt (1994) detected low levels of yew pollen at 9,500 BP, and the profile for the Dingle Peninsula produced by Barnosky (1988) indicates the presence of yew pollen as far back as 9,800 BP. However, unlike most of the other main tree species, the arrival of yew in Ireland was not quickly followed by an expansion in its abundance.

Hazel (*Corylus avellana*), for instance, expanded dramatically around 9,100 BP and is subsequently the major component of the pollen profile from most Irish sites, commonly contributing 60-80% of the pollen sum at its maximum. Its actual abundance in the vegetation, however, is probably exaggerated by the relatively high levels of pollen this species produces. Nevertheless, for a brief period much of lowland Ireland was possibly covered by large expanses of hazel scrub and hazel-birch woodland (Watts 1985).

Oak (*Quercus*), pine (*Pinus*) and elm (*Ulmus*) were the next major tree species to reach Ireland around 8,900 BP. The order in which they arrived and expanded varies considerably between sites. In the west, pine was the leader, establishing soon after hazel at Clare Island (Coxon 1987), Lough Annafrin (Browne 1986) and Lough Maumeen (Huang 2002) and practically simultaneously in the Burren (Watts 1984). At Belle Lake in the south-east, oak expanded first (Craig 1978), whilst at Scragh Bog in the fertile east midlands, elm dominance preceded expansion in pine and oak (O'Connell 1980). By this point ivy (*Hedera*) had also become a widespread component of the woodlands which still contained lesser amounts of birch, willow and hazel.

Around 7,000 BP the climate appears to have became markedly wetter permitting the invasion and expansion of alder (*Alnus*) across Ireland (Watts 1985). As with the expansion of the main forest tree species, the timing of this event varies considerably between sites (Smith & Pilcher 1973; Smith 1984). It is likely that alder previously had a meagre distribution in river valleys and around lake margins, but it now became an important component of the lowland oak-elm-hazel woodlands. Pine values start to decline at this point as it became restricted to the poorer soils of the uplands (Mitchell & Ryan 1997). Bradshaw & Browne (1987) concluded that blanket peat formation replaced pine in the uplands, whilst alder replaced pine in the lowlands as waterlogged conditions increased; pine is able to grow in a broad range of edaphic conditions but is a poor competitor. The prevalence of pine stumps in upland bogs certainly indicates that these were once sites of extensive pinewoods.

By 5,500 BP Ireland was therefore covered in a mosaic of woodland types determined chiefly by geology, hydrology and altitude. Bennett (1989) derived a map of dominant woodland types for this period by extrapolating palynological records in relation to these factors. Pine was persisting in the extreme west and north and also in the uplands of Wicklow and Tipperary, where areas of birchwood may still have occurred at the higher altitudes. Oakwoods dominated much of the south-east and north-east on the non-calcareous soils, whilst the central limestone plain was covered in a mixture of hazel and elm dominated woodland. This forest cover has been termed "wildwood" – almost wholly natural vegetation virtually untouched by humans (Rackham 1986). With the increase in rainfall, however, sizeable unforested areas had begun to develop; raised bogs in the midlands and blanket bog in the uplands of far west. Neolithic humans were having a greater influence on the Irish landscape than their Mesolithic forebears but this effect was still fairly minimal (Mitchell & Ryan 1997).

2.4 The elm decline

Around 5,100 BP, there is a decrease in elm pollen concentrations at sites across Ireland, and indeed north-west Europe, indicating a sudden decline in the abundance of elm. The elm decline is of particular significance because it is following this major disturbance in the Neolithic woodlands that yew expands for the first time. The event is fairly synchronous between sites in comparison to other horizons in the Irish dataset (Smith & Pilcher 1973; Mitchell & Ryan 1997). The decline is most precipitous in areas where elm was abundant; for example, it fell from 28% to 3% of the pollen sum at Scragh Bog, Co. Westmeath (O'Connell 1980). In areas where elm was

less common, however, the horizon is barely discernible, for example, on the Dingle Peninsula (Barnosky 1988).

A number of theories have been advanced to account for this decline and have been discussed by Mitchell & Ryan (1997), Rackham (1986), Molloy & O'Connell (1987) and Peglar (1993). Anthropogenic reasons were originally favoured. Neolithic culture had spread to Ireland by this time, and clearance of woodland to create open areas suitable for pastoral and arable farming (Landnam clearances) would have logically targeted the fertile lowland soils favoured by elm. Pollarding of elms in order to feed the highly palatable foliage to cattle could have exacerbated the decline in pollen levels; this practice was still widespread in Ireland in historical times (Kelly 1997). The initiation of pollen curves at this juncture for ribwort plantain (*Plantago lanceolata*) and cereals, indicators of human disturbance and arable land, also supports the idea of early farming clearances being responsible. Rackham (1986), however, highlights two problems with this theory. Firstly, he estimates that elm covered about one-eighth (12.5%) of the British Isles at this time and in Ireland this proportion was probably even higher due to the lesser number of potential competitors, such as lime (*Tilia*). There simply could not have been enough Neolithic farmers present to fell or pollard such a vast number of trees. Secondly, in areas where elm was anything less than abundant, other trees such as hazel would need to have been felled in order to clear sufficient land for agriculture. However, in such areas there was still a selective reduction in the elm population only. O'Connell *et al.* (1988) found reduced rates of sedimentation during the elm decline interval in Connemara, whereas the contrary would be expected if a major clearance event had occurred. Furthermore, at sites such as Mooghaun Lough, Co. Clare, the response in the ribwort plantain curve to an appreciable decline in elm is minimal, suggesting a scattered disturbance in the woodland cover rather than large scale clearances (O'Connell *et al.* 2001). Finally, there is some evidence that Neolithic farming predated the elm decline in certain areas by several hundred years without any discernable reduction in elm pollen (Molloy & O'Connell 1987; O'Connell 1987). Humans were certainly still present when elm levels recovered to their former abundance which may have taken as little as a few decades (Watts 1985).

Climatic change is also an unlikely explanation due to the suddenness and transience of the decline (Mitchell & Ryan 1997; Molloy & O'Connell 1987). In addition, Rackham (1986) points out that elms were reduced throughout their climatic range, not just in marginal areas. The climatic shift required to cause such an event would therefore have been considerable, and exceedingly unlikely to selectively affect elms alone.

The hypothesis now widely accepted is that the elm decline was primarily caused by disease. This would account for the synchroneity, scale and selectiveness of the event (O'Connell *et al.* 1987). That a disease could wipe out elms with such rapidity over a large area is amply demonstrated by the wave of Dutch Elm disease that flared up in north-west Europe in the 1960s and 1970s. The pathogen is a fungus, *Ceratocystis ulmi,* which is transmitted from tree to tree by two elm bark beetles, *Scolytus scolytus* and *S. multistriatus*. Rackham (1986) details the progress of the disease in England from its outbreak in 1965. It spread at a rate of approximately 8 miles a year and by 1983, over 90% of English elms (*Ulmus procera*), the most susceptible species, had been killed in southern and central England. It is highly plausible that a similar disease was responsible for the elm decline. Small scale farming activity may have facilitated the rapid spread of the disease as pollarded trees are more susceptible to infection, as are trees of woodland margins (Rackham 1986). Followed the break-up of the woodland the opportunities for pastoral and arable farming would have increased. It may be postulated therefore that the elm decline was a stimulus for Neolithic Landnam, rather than a result of it. The recovery of elm numbers probably indicates the development of disease resistance (Watts 1985). At some sites a series of elm declines, initiating around 5,100 BP, are evident – Connolly (1999) identified five separate events at Clara Bog – and these may represent periodic resurgences of the pathogen.

2.5 The yew expansion

2.5.1 Site accounts

The elm decline resulted, directly or indirectly, in an opening up of the woodland canopy. This would have increased the levels of light penetrating the understorey, permitting the promotion of yew to the canopy layer. Enhanced light levels would also have favoured increased flowering and seed production (Svenning & Magård 1999) and consequently resulted in a rise in the population. However, the exact pattern of response of yew to the elm decline varies considerably between sites. Brief descriptions of the pollen records from sites where yew prominently features follow to elucidate these variations.

The pollen profile for Mooghaun Lough, Co.Clare (O'Connell *et al.* 2001) demonstrates several of the features of yew in the late postglacial period. Yew expanded rapidly at about 4,250 BP to become the second most important woodland tree after oak, reaching 16% of the pollen sum This seems, however, to be in response to a second elm decline, the first having occurred around 5,100 BP. In the intervening period yew pollen was low (< 2%) but rising. This may reflect yew

building up from very low numbers in response to the first woodland disturbance. It was then able to fully exploit the second decline. Ash (*Fraxinus*), another species which only expanded in Ireland following the elm decline, was able to respond more quickly to the first event. Following the yew peak, total arboreal pollen dropped as woodland clearance increased. Yew appears to have declined particularly rapidly, however, and O'Connell *et al.* (2001) proposed that the toxic nature of yew foliage to cattle may have caused its selective removal from the woodlands. Yew would also have suffered more directly from increased grazing pressure; as will be shown later (Chapter 4), yew seedlings are very sensitive to browsing. A Late Bronze Age Landnam between 2,900 and 2,570 BP finally reduced yew to minimal levels. It remained rare through to present times with the exception of a brief resurgence to about 8% during the Late Iron Age Lull of 1,985 to 1,720 BP. This is a period of canopy tree expansion characteristic of the west of Ireland, reflecting a downturn in agricultural activity.

A similar sequence of events occurred at the nearby site of Caherkine Lough (O'Connell *et al.* 2001). Yew briefly contributed 24% of the pollen sum around 4,250 BP and was therefore more important in the woodlands here than at Mooghaun Lough. Furthermore, although yew declines rapidly after this peak it remains an important feature at around 5% until after the Late Iron Age Lull when it is only represented by the occasional pollen grain.

Watts (1984) found a comparable story in the samples from Gortlecka in the Burren. Yew rose to 20% of deposited pollen at 4550 BP following post elm decline expansion. Subsequently it slumped dramatically as overall woodland cover in this area of limestone pavement decreased; prehistoric tombs in the vicinity indicate an influx of humans to the eastern Burren around 4000 BP. A brief recovery period again followed, but it is poorly dated. Subsequently yew is virtually absent from the profile. At Rinn na Mona, a nearby lake site, the profile is very similar but undated. The elm decline is not apparent here, but a sudden peak of 20% in yew correlates with the start of the ribwort plantain curve. It also coincides with a sudden crash in pine and it may be conjectured that this disruption in the woodland partly stimulated the increase in yew. The later transient recovery in yew is far more pronounced at this site, reaching around 17%.

In Connemara, O'Connell *et al.* (1988) found evidence that yew expansion occurred largely in the south-east of the region. In cores from Lough Sheeauns and the Connemara National Park in the north-west, only trace levels of yew pollen were found after the elm decline, whereas at Lough Namackanbeg a sudden spike in the profile occurred at 4250 BP when yew reached

approximately 26% of the pollen sum. The familiar crash (to about 5%) soon followed and yew gradually petered out; there was no later resurgence at this site. The sudden decline in yew coincided here not only with rises in grasses, ribwort plantain and bracken (*Pteridium*), but also the onset of major bog formation with increases in sedges, bog myrtle (*Myrica*), ling (*Calluna*) and bog asphodel (*Narthecium*). The ability of yew to expand in an area of granite bedrock is noteworthy. Blanket bog expansion also closely followed the yew decline at Maumeen Lough in the Connemara uplands (Huang 2002), where yew peaked at 12% at 4,120 BP. As at Rinn na Mona, the expansion of yew was here associated with a loss of pine. Yew apparently became extinct in this upland area around 1350 BP.

At Lough Doo, Co. Mayo a variation in the sequence occurs (O'Connell *et al.* 1987). Although yew first appears around 4,100 BP there is no significant initial expansion and it is not until much later, circa 1880 BP, that it suddenly peaks at 7% followed by a rapid decline and local extinction. There was a temporary recovery in other trees species at the same time whilst agricultural indicators briefly disappeared. These signs are characteristic of the Late Iron Age Lull. The reason for the absence of an initial yew peak is unclear, but possibly grazing pressure was too high during that period for yew to exploit the opportunity. Transient yew populations were also detected around this period at the nearby site of Carrownaglogh (O'Connell 1986). In western Mayo, yew seems to have been much rarer or absent, as Browne (1986) found only low levels of yew pollen (maxima $\leq$ 2%) at four lake sites in this area: Corslieve Lough, Lough Kilnabinnia, Lough Annafrin and Lough Clevala. At the first two sites the maxima and the only consecutive sequences occur soon after the elm decline, circa 4,500 BP. At the latter two sites modest expansions do not occur until much later. These may reflect a slackening of agricultural pressure, but the date for the expansion at Lough Clevala (circa 2,200 BP) is rather too early to be synchronous with the Late Iron Age Lull of other sites. No yew pollen was identified from either of two further sites in this area, Lough Navroony or Lough Aisling.

The vegetation history of the Killarney National Park has been dealt with in detail by Mitchell & Cooney (in press) and is of particular interest as this is the location of Ireland's only appreciable remaining yew wood. An account of the area's vegetation history will be presented later in Chapter 3. In the context of the current discussion, the salient features are a massive post elm decline expansion of yew in the area, peaking at around 55% in the profile for Doo Lough, a small lake within 1 km of the extant yew wood (Cooney, unpublished data). As might be expected, high levels of yew pollen are maintained in several regional diagrams for this area up to

the present day (Vokes 1966; Mitchell 1990a; Mitchell & Cooney, in press; Cooney, unpublished data).

Two sites of interest in Co. Westmeath were investigated by Heery (1998). Yew first appeared in the profile for Cornaher Lough at 4,400 BP, but remained at relatively low levels (< 5%). At the nearby site of Black Lough, yew was present prior to the elm decline, first appearing around 6,200 BP. It did not expand, however, until after the fall in elm pollen, and never achieved representation greater than 5%. This tallies with the findings of Connolly (1999) for Clara Bog, Co. Offaly. Nevertheless, as Heery (1998) points out, yew is underrepresented in regional pollen diagrams and these levels may reflect a relative abundance in the area, possibly in woodlands on local esker ridges. Today, however, yew is absent from most esker woodlands in Ireland (Cross 1992). At Clara Bog, the Late Iron Age Lull was clearly evident and yew pollen increased temporarily before disappearing completely from the profile.

At Kelly's Lough, in the Wicklow Mountains, Cole (unpublished data) found yew to be present almost continuously between 5,430 BP and 300 BP, but always in low amounts. Nearby at Glendalough, yew was clearly more abundant, contributing around 5% of the pollen rain from 4,750 BP to around 500 BP (Maldonado, unpublished data). At both sites yew is again detectable in small amounts (< 1%) just prior to the elm decline.

Elsewhere in Ireland, sizable post-elm decline expansions of yew are absent. At three sites in western Donegal, Fossitt (1994) detected yew fairly frequently between 5,000 and 2,000 BP but at minimal levels. Only a few grains were found by Coxon (1987) on Clare Island, Co. Mayo and by Smith (1984) at Newferry in Co. Antrim. Barnosky (1988) concluded that the low levels of yew pollen around 4,100 BP on the Dingle Peninsula were probably from sources far distant from site. Buzer (1980) reported no evidence of yew along the coast at either Lough Ine or Ballyally Lough in Co. Cork.

2.5.2 Isopollen sequence

Evidently, there was considerable regional variation in the timing and magnitude of the yew expansion and its subsequent decline. This can be effectively summarised graphically by construction of a pollen map. There are two main methods of mapping palynological data: isopollen maps and isochrone maps. Isopollen maps consist of contours which link sites of equal pollen abundance at a given time and a sequence of maps is therefore required to display temporal

as well as spatial variation. This technique was first employed in Poland by Szafer (1935). Isopollen maps have been employed at a range of geographical scales, for example, the British Isles (Birks *et al.* 1975), Europe (Huntley & Birks 1983; Huntley 1988), China (Ren & Zhang 1998) and Ireland (Bradshaw 2002). In isochrone maps, contours connect sites at which pollen-stratigraphical events occurred at the same time (Birks 1989). These horizons are typically the arrival, expansion, decline or extinction of particular species. Isochrone maps displaying the gradual spread of tree species have been produced for the British Isles by Birks (1989), and for Ireland by Mitchell (2000). The difficulty in producing isochrone maps is arriving at a meaningful criterion, generally a fixed percentage, which defines the event to be mapped (Faegri & Iversen 1989). Due largely to this problem, an isopollen sequence was chosen to visualise the spatial and temporal patterns in the abundance of yew in Ireland during the post-glacial period.

A series of thirty-four regional pollen diagrams (Table 2.1) were selected on the basis of geographical spread, inclusion of radiocarbon dating and coverage from 6000 BP to 500 BP. Due to the fairly recent universal recognition of yew pollen, diagrams published prior to 1977 were excluded to reduce the chances of introducing false absence data. Values for yew as percentages of total land pollen were derived from the diagrams at ten time intervals: 6000, 5000, 4800, 4600, 4400, 4200, 4000, 3000, 1900 and 500 BP. This irregularly spaced sequence was chosen to concentrate around the period of the elm decline and the Late Iron Age Lull, when changes in yew abundance were at their greatest. It is important to note that radiocarbon dates are not absolutes but have a degree of error attached (Smith & Pilcher 1973; Edwards 1985). For example, the radiocarbon samples analysed by Huang (2000) produced dates which were 80-120 years out in either direction. To reduce the relative importance of these errors, isopollen data are usually taken at 1000 year intervals (e.g. Huntley & Birks 1983). However, due to the transient nature typical of the yew expansion events, a decision was taken to derive data at only 200 year intervals for part of the sequence; 1000 year intervals or the use of maximum pollen values would have obscured the most important features.

Isopollen maps were constructed from the resultant data using the inverse distance weighting method of surface interpolation (ArcView GIS 3.2 / Spatial Analyst 1.1, Environmental Systems Research Institute). Inverse distance weighting is the simplest method of spatial interpolation and has been used for a variety of purposes, for example, to map fungal spore dispersal (Wu *et al.* 2001), heavy metal pollutants (Berlekamp *et al.* 1998, Leenaers *et al.* 1990) and soil properties (Schloeder *et al.* 2001). More advanced methods, particularly kriging and co-kriging, have been

shown to be superior for some purposes (Zimmerman *et al.* 1999) but require more information on the system being modelled. Inverse distance weighting requires the user to define two parameters: weighting power and neighbourhood size. Weighting power determines how quickly interpolated values decline with distance from an observed data peak; low powers, such as 1, result in a rapid decline, whilst high powers, such as 4, result in a slower decline. A weighting power of 2 was applied to the interpolation model of yew pollen; this is the most commonly used value and meant that the influence of pollen peaks declined fairly rapidly with distance from the site. This represented the relatively small landscape area from which regional sites derive their pollen, approximately 20 km in radius (Jacobson & Bradshaw 1981). Neighbourhood size determines how many data points are included in the calculation of an interpolated value for any given point, and can be specified in terms of radius or number of points. After experimentation, the twelve nearest data points were specified; other settings resulted in gaps in the interpolated surface or undue influence of distant points, due partly to the non-uniform distribution of the sites.

The resulting maps are shown in Fig. 2.2; note that a non-linear set of contours has been employed so as to differentiate clearly between the low levels of pollen that cover much of the country. The maps illustrate the sequence of events that has been described above in the site accounts. At 6,000 BP yew was rare across the country. It expanded significantly in the south and west between 5,000 and 4,000 BP in response to the elm decline, with lesser populations in the midlands and northwest. Possibly, this is a reflection of a preference by yew for a more oceanic climate, although it must also be pointed out that there was a higher density of sample sites in the west. As mentioned above, it is also important to bear in mind that due to dating inaccuracies there is likely to be some overlap between consecutive maps in this part of the sequence. Hence, the apparent progression of expansion events from the midlands, to Co. Clare, to Co. Kerry, may be an artefact of this; these occurrences may be more synchronous. Nevertheless, the brief nature of the expansion events at each site is clearly evident. By 3,000 BP, pollen levels in the mid-west had declined. A modest recovery occurred at some sites around 1,900 BP, the time of the Late Iron Age Lull, but by 500 BP yew was again rare across the country with the exception of Kerry, the location of the only extant yew wood. The apparent absence of yew from Northern Ireland throughout this entire period is particularly noticeable. This may be a reflection of an actual distribution pattern or an artefact of the available data; most of the pollen profiles available for this area were from the early 1980s, and it is possible that the analysts overlooked any yew pollen that was present. Evidently, this dataset can be improved by the addition of future pollen profiles,

Figure 2.2a Isopollen maps for *Taxus* in Ireland: 6,000 – 4, 600 BP. Scale 1:2,000,000

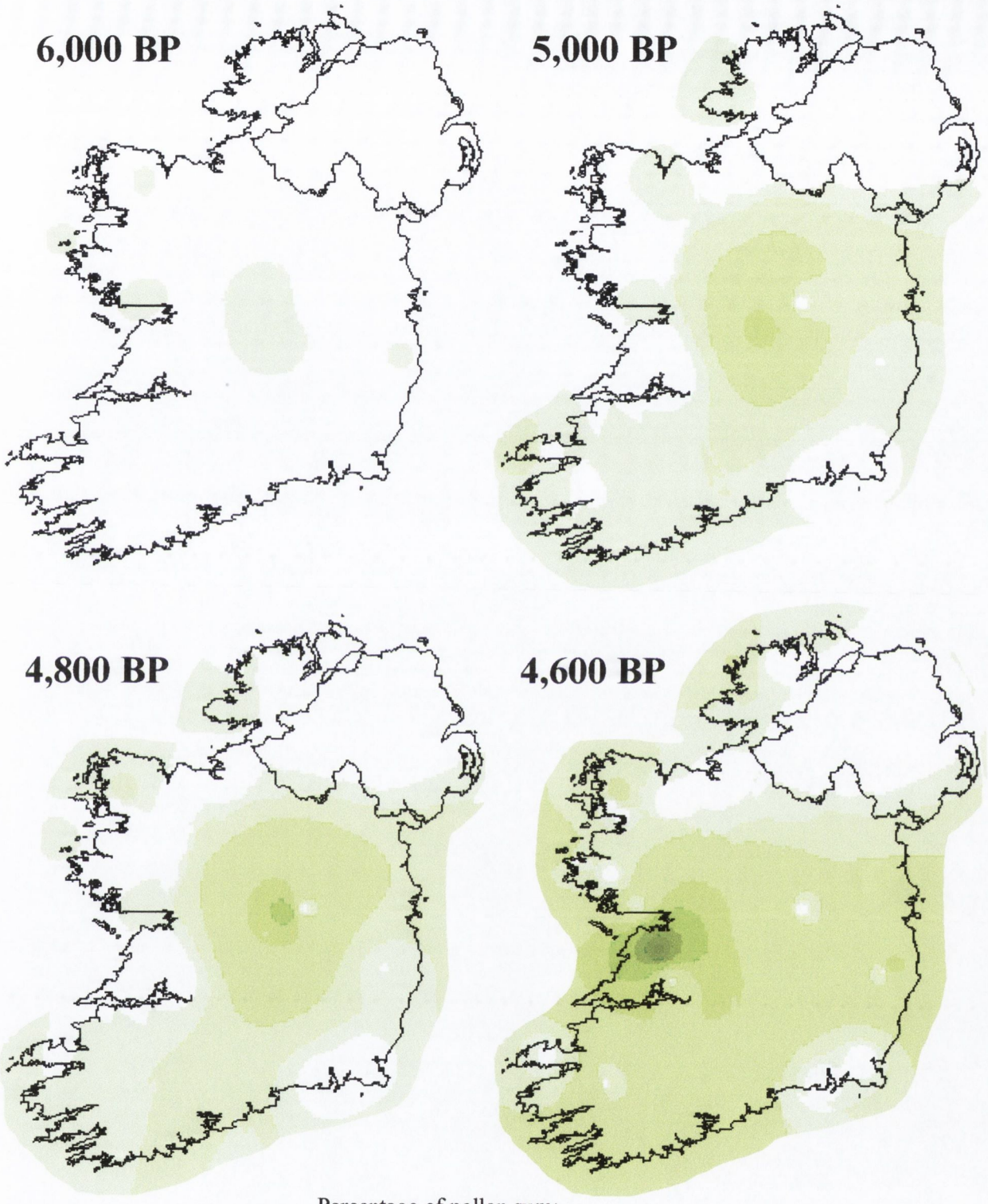


Figure 2.2b Isopollen maps for *Taxus* in Ireland: 4,400 – 3,000 BP. Scale 1:2,000,000

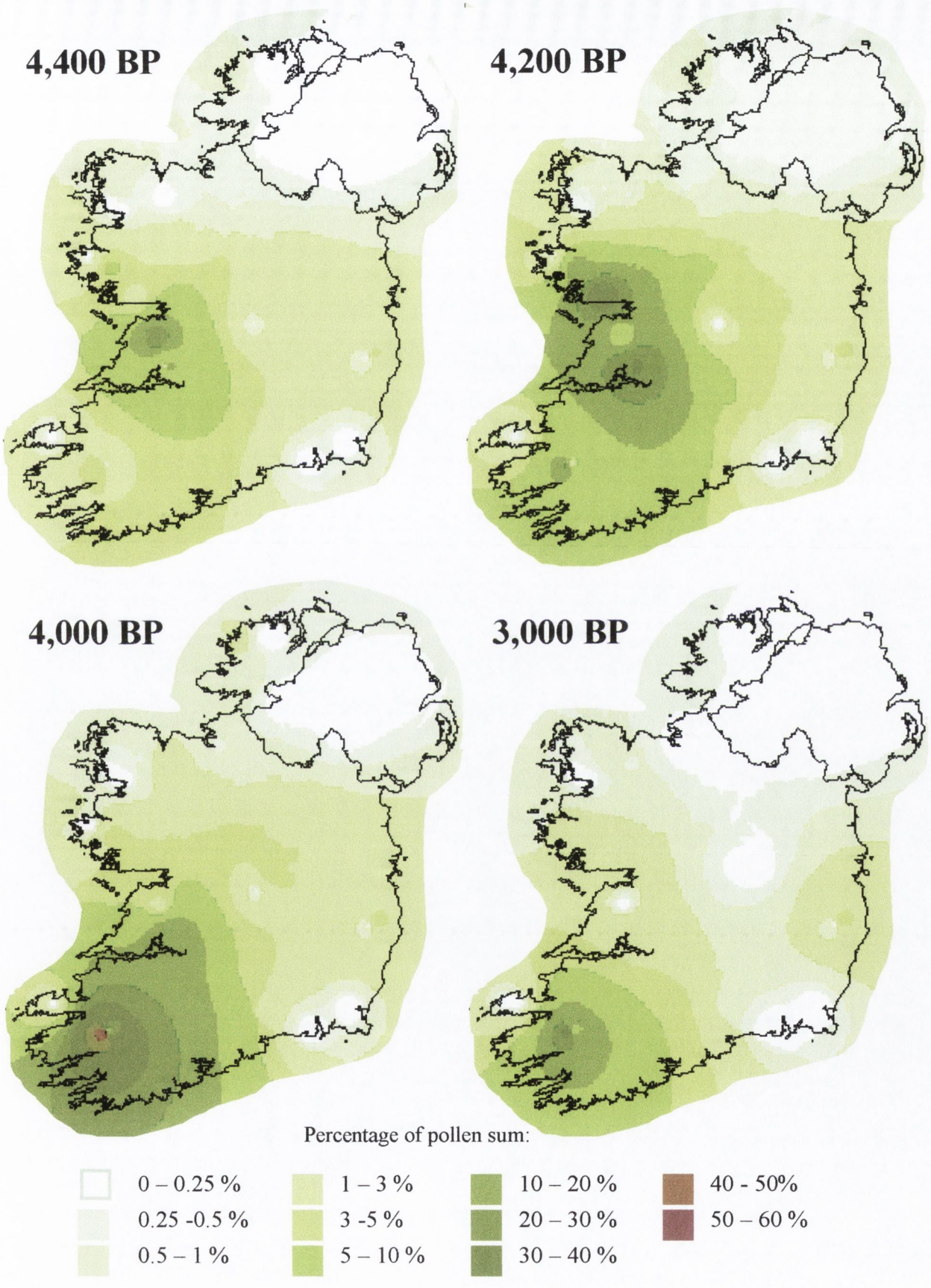
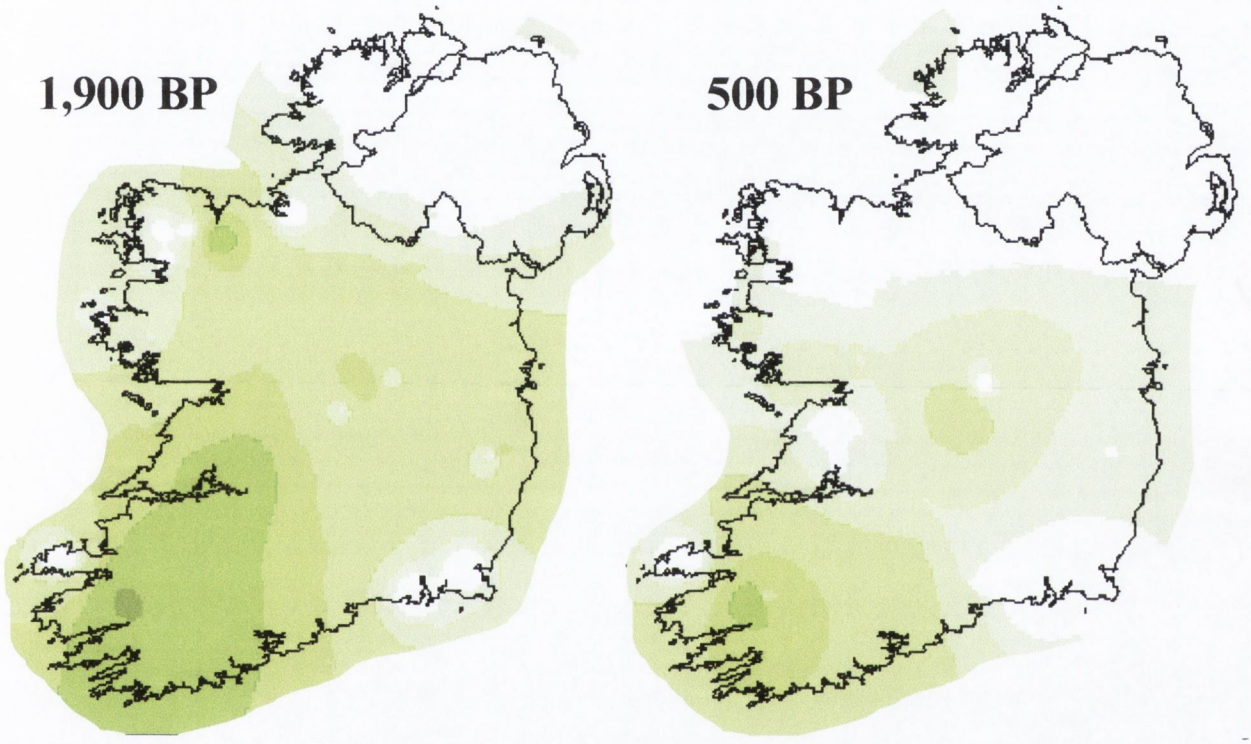


Figure 2.2c Isopollen maps for *Taxus* in Ireland: 1,900 - 500 BP. Scale 1:2,000,000



particularly from the north and east of the country, but it still clearly illustrates the main spatial and temporal patterns in yew abundance.

2.5.3 Yew in southern England

Yew rarely appears in British pollen diagrams, but features in those of a cluster of sites on the chalklands of south-east England and East Anglia. A brief consideration of these is appropriate here with a view to evaluating to the interactions of yew with other tree species and human activity. Peglar (1993) found clear evidence of agricultural development and abandonment at Diss Mere, Norfolk. Here the elm decline was marked by a sharp expansion in hazel, peaking at 55%, and a slower increase in yew which eventually attained values of 15%. The differential rates of expansion probably reflect disparity in the initial populations, with yew building up from fewer individuals. Peglar suggested that the increase in grazing sensitive yew indicated arable cultivation by Neolithic people or low levels of livestock. This secondary yew-hazel woodland was subsequently cleared in the early Bronze Age period (3500 BP to 3000 BP). A marked increase in barley (*Hordeum*) pollen at this time indicates arable cultivation. During the late Bronze Age period (3000 BP to 2500 BP) the clearings became derelict and scrub invaded, developing into a yew-dominated woodland. This vegetation lasted only until the start of the Iron Age at 2,500 BP, when improved technology resulted in the widespread and permanent removal of the woodlands.

At Saham Mere, Norfolk, a post elm decline peak in yew pollen of around 15% also occurred (Bennett 1988). The population subsided somewhat but was still considerable at 4,200 BP. Yew pollen is present during this period at the nearby sites of Sea Mere (Bennett 1988), The Mere at Stow Bedon (Bennett 1986) and Hockham Mere (Bennett 1983), but is much scarcer despite the sites, and pollen profiles, being very similar in other respects. Bennett (1988) suggests that the abundance of yew at Diss Mere may be due to the steep, well drained chalk slopes at that site, which are favourable to the development of yew woods in southern England (cf. Watt 1926; Tittensor 1980). This does not explain the prevalence of yew at Saham Mere however; possibly grazing pressure during the post elm decline period was higher at the other three sites.

The final site in this area to consider is the Caburn on the chalklands of East Sussex (Waller & Hamilton 2000). Hazel and yew both respond to the elm decline in a similar fashion to that observed at Diss Mere, but hazel subsequently declined as it was suppressed by the formation of a

yew canopy. Later, yew seems to have returned to its status as an understorey tree as populations of lime and elm recovered.

2.5.4 Macroscopic fossil evidence

Finds of macroscopic remains of yew preserved in peat have also provided evidence of a formerly wider distribution in Ireland. For example, Adams (1914) reported on the discovery of a large yew trunk in Ballyfin Bog, Co. Laois, where bog yew had supposedly been so plentiful that it was frequently used for gate posts and roof timbers. Large trunks and roots were dug up from the fen peat on the Magilligan flats, Co. Derry, in the 1830s, before they were cleared for cultivation (Hackney 1992). Hart (1898) mentions that thick yew logs were often dug out of the peat at Glenveagh, Co. Donegal. Several finds of yew stumps have also been made at Clonsast Bog, Co. Offaly (Mitchell & Ryan 1997). Similar finds have been made in the Cambridgeshire fenlands in England; despite its contemporary association with thin, calcareous soils, yew appears to have grown well on fen peat in the past according to Godwin (1975). Yew is intolerant of poorly drained conditions, but Godwin (1975) suggested that it invaded such sites during periods when climatic dryness and marine retrogression resulted in a temporary drying out of the marginal peat land, such as occurred in the Bronze Age. A different theory, however, was put forward by Mitchell & Ryan (1997) to account for the yew fossils in Clonsast Bog. They proposed that, prior to peat formation, the landscape included areas of karstic limestone on which yew trees were already growing. Surface drainage became impeded, possibly due to bogs developing in neighbouring areas. Fen plants invaded the woodland and over a metre of fen peat developed. Subsequently *Sphagnum* communities invaded the fen and it started to develop into an ombrotrophic raised bog. Mitchell & Ryan (1997) suggest that the tremendous mass of water in the bog may have forced material (including yew fossils) up into the base of the bog via hydrostatic pressure. If this theory is correct, then, considering that most of the central lowland plain of Ireland is of limestone geology, the finds at Clonsast Bog suggest that yew may have been widespread in the Irish midlands prior to raised bog development.

2.6 Artifacts of yew found in Ireland

As has been alluded to above, agriculture and the human population expanded concomitantly throughout the Bronze Age and Iron Age, resulting in the firm establishment of the poorly wooded character of the Irish landscape, and by the Early Christian Period improvements in technology, such as ploughs with iron coulters and the horizontal mill were accelerating this

process (Stout & Stout 1997). As Mitchell & Ryan (1997) proposed, though the Romans never invaded Ireland, knowledge of their agricultural techniques had certainly permeated through the country by this time, giving rise to intensification. Later, monasteries in particular would have been foci for land reclamation and improvement.

A variety of yew-wood artifacts dating from these periods been retrieved from excavations across Ireland (Table 2.2) and demonstrate an appreciation by the ancient Irish craftsmen for the qualities of the timber. Yew is a dense and durable wood and would have lent itself to the construction of items that needed to be hardwearing and strong, such as handles, wheel dowels and weapon shafts. A testament to the hardness of the material is a criterion from the Early Christian period that metal axe blades, once tempered, should not be dented by oak or yew (Kelly 1997).

A notable number of the items that have been found are parts of small stave-built containers. Earwood (1993) surmised that oak, which was more readily available, was used for large heavy-duty containers, whilst yew with its attractive fine grain and deep colouration was reserved for finer items and tableware. Certainly, the recovery of bronze fittings (hoops, handles etc.) attached to yew vessels and references in early texts (see below) indicate that these were high status items.

There seems little evidence that the use of yew for bows was important during this period. The superiority of yew wood for the making of bows has been recognised since early times; prehistoric bows made from yew have been found across Europe, including England, Germany, Switzerland and the Netherlands. A bow-stave from Ballinderry crannog 1 has been dated to the 10th century but, due to the context of the find, is probably Viking in origin (Clark 1963).

Evidence of larger scale utilisation of yew has been found by the Irish Archaeological Wetland Unit (IAWU). The survey of raised bogs in County Longford (Moloney 1993) consisted largely of the excavation of *toghers*, wooden trackways across the bogland constructed in the late Bronze Age. Of the total number of specimen components found in the survey only 3% were of yew, suggesting that it was not a common tree in that area. This is perhaps to be expected as yew thrives best on well-drained land and the nearest yew trees are likely to have been well removed from the site of construction. Yew was also used sparingly in *togher* construction in the Blackwater area of Co. Mayo, where it constituted 1.5% of specimens (Moloney 1995). However, within the largest *togher* in the Longford survey, that at Derrindif which was dated to

Table 2.2 Wooden artifacts made from yew found in Ireland. Compiled from Coles *et al.* (1978) and Earwood (1993).

Site	Artifact	Dating
Altartate Glebe, Co. Monaghan	Cauldron handle	Early Iron Age
Antiville, Co. Antrim	Bases for stave-built vessels	8th century AD
Aughrane, Co. Galway	Knife handle	Bronze Age
Ballinderry crannog 1, Co. Westmeath	Staves	7th/10th century AD
	Bucket handle	7th/10th century AD
Ballinderry crannog 2, Co. Westmeath	Staves	Late Bronze Age
Barta Bog, Co. Donegal	Club	?
Co. Wicklow	Carved sword	?
Deer Park Farms, Co. Antrim	Staves	7th century AD
	Bases for stave-built vessels	7th century AD
	Fragments of hoops	7th century AD
	Bucket handle	7th century AD
Derreen, Co.Clare	Miniature bucket (turned) with bronze fittings	8th/9th century AD
Doogarymore, Co. Roscommon	Wheel dowels	Iron Age
Dromiskin, Co.Louth	Carved box with bronze fittings	Iron Age/ 1st century AD
Edenderry, Co. Offaly	Spearshaft	Bronze Age
Glenviggan, Co. Derry	Bullroarer (?)	Iron Age
Glyde River, Annagassan, Co. Louth	Miniature bucket (turned or carved) with bronze fittings	8th/9th century AD
Kinnegad, Co. Westmeath	Axe handle	Bronze Age
Lagore crannog, Co. Meath	Two-piece tub	7th/10th century AD
	Base of bentwood box	7th/10th century AD
	Lid (turned) with bronze fittings	7th/10th century AD
	Spindles	7th/10th century AD
	Handles	7th/10th century AD
	Pins, beads and needle	7th/10th century AD
	Handle (of box?)	7th/10th century AD
Lough Faughan crannog, Co. Down	Hoops	7th/9th century AD
Moynagh Lough Crannog, Co. Meath	Composite base (for vessel)	7th/8th century AD
	Hoop fragment	7th/8th century AD
Ralaghan, Co. Clare	Carved figurine	Iron Age (?)

1612 BC, 21% of the specimens were of yew. This perhaps indicates that yew was locally abundant here. It may also be that the builders of this particular *togher* were more selective in their choice of timber, being aware of yew's strength and suitability for load-bearing components (Moloney 1993).

2.7 Early references to yew in Ireland

Probably the earliest surviving reference to yew in Ireland is in a manuscript called *Bretha Comaithchesa*, "The Laws of the Neighbourhood", dating from around the ninth century (Kelly 1997). These laws divided the native trees and shrubs into four classes dependent on their economic value (Table 2.3) and stipulated that damaging another person's tree would result in a fine reflecting the class to which it belonged. Yew is placed in the top echelon, but whilst the other trees in this class are valued for their timber, fruit and nuts, yew is prized specifically as the preferred material for domestic vessels. Indeed, special status was afforded the craftsmen who worked in yew wood (*saí ibrórachta*) and they received three-quarters of the rations of the master builder (Kelly 1997). It is noteworthy that yew was not regarded as valuable as a source of bow-staves by the Irish at this time. The inclusion of pine in the top class of trees is puzzling; after the remnant upland populations where severely reduced by the expansion of bog blanket, pine appears to have gradually become extinct in Ireland between 4,000 BP and 1,700 BP (Mitchell & Ryan 1997). Could pine have possibly still been present in the ninth century?

Further mention of yew is made by Giraldus Cambrensis (Gerald of Wales), a historian who first visited Ireland in 1183. His travels were largely confined to Leinster and eastern Munster (Cabot 1999) and much of his writings are clearly embellished by fancy – Fairley (1984) highlights a variety of problems with regards to Irish mammals - but they do provide interesting references to yew in Ireland:

"Yews, with their bitter sap, are more frequently to be found in this country than in any other place I have visited; but you will see them principally in old cemeteries and sacred places where they were planted in ancient times by the hands of holy men, to give them what ornament and beauty they could."

(in McCracken 1971)

Table 2.3 The Old Irish tree-list from *Bretha Comaithchesa*, as interpreted by Kelly (1997)

1. *Airig Fedo* "nobles of the wood"		2. *Aithig Fedo* "commoners of the wood"		3. *Fodla Fedo* "lower divisions of the wood"		4. *Losa Fedo* "bushes of the wood"	
daur	oak	fern	alder	draigen	blackthorn	raith	bracken
coll	hazel	sail	willow	trom	elder	rait	bog myrtle
cuilenn	holly	scé	hawthorn	féorus	spindle	aitenn	gorse
ibar	yew	cáerthann	rowan	findcholl	whitebeam	dris	bramble
uinnius	ash	beithe	birch	caithne	arbutus	fróech	heather
ochtach	Scots pine	lem	elm	crithach	aspen	gilcach	broom
aball	wild apple	idath	wild cherry?	crann fir	juniper?	spín	wild rose?

Table 2.4 Tree species included in the place-name study with Irish names and forms in which they occur in place-names. Compiled from Joyce (1995).

English name	Irish name	Scientific name	Common place-name elements
Alder	Fearnóg	*Alnus glutinosa*	farnoge, varnoge
Ash	Fuinseog	*Fraxinus excelsior*	unshin, inshin
Birch	Beith	*Betula* spp.	beha, beagh, beigh, behy, baha, veagh, vehy
Blackthorn	Draighean	*Prunus spinosa*	dreen, drinaghan, arney (sloe)
Elder	Trom	*Sambucus nigra*	trim
Elm	Leamhán	*Ulmus* spp.	lavan, levane, longfield (elm-wood)
Hawthorn	Sceach	*Crataegus monogyna*	skeagh, skagh, skeha, skea, skaha, skehy
Hazel	Coll	*Corylus avellana*	cullane, coyle, quill
Holly	Cuileann	*Ilex aquifolium*	cullin, cullen, cullion
Rowan	Caorthann	*Sorbus aucuparia*	keeran
Strawberry tree	Caithne	*Arbutus unedo*	-
Willow	Saileach	*Salix* spp.	sillagh, silla
Yew	Iúr	*Taxus baccata*	nure, uragh, oghill (yew-wood)

Table 2.5 Problems with interpreting anglicized forms of Irish place-names. Compiled from Flanagan & Flanagan (1994) and Joyce (1995).

English name	Irish name	Meaning
Dernaveagh	Doire na Bhfiadh	Oakwood of the deer
Derrynaveagh	Doire na Bhfiach	Oakwood of the raven
Derryveagh	Doire Bheatach	Birchy oakwood
Cullion	Cuillean	Unbroken, sloping place
Cullion	Cuilleann	Holly (place)
Drumsallagh	Druim Saileach	Ridge of willow
Garrysallagh	Garrdha Salach	Dirty garden
Donaskeagh	Dun na Sciath	Fort of the shields
Coolnaskeagh	Cul na Sceach	Backhill of the hawthorn

"[Swarms of bees] would be much more plentiful if they were not frightened off by the yew trees that are poisonous and bitter, and with which the island woods are flourishing."

(in Cabot 1999)

The first passage provides some evidence that yew was already being widely planted during this period. Evidently, the notion that bees could in some way be poisoned by yew foliage is fantastic, but the second comment does suggest that yew was particularly abundant on lake and river islands where it could have escaped from browsing pressures, an idea not inconsistent with its contemporary distribution and regeneration ecology (Hannon & Bradshaw 1989).

2.8 Place-name survey

2.8.1 Introduction:

Ireland is divided into approximately 62,200 townlands, the smallest administrative divisions in the country. They evolved from ancient territorial divisions, such as the ballybetagh, ploughland, martland and quarter (McErlean 1983). There is written evidence that some modern townland names were in use as far back as the ninth century and some may have even older origins according to Dallat (1991). McCracken (1971) proposes that many names were probably fixed around the eighth century. Townlands are usually named after conspicuous features of the surrounding landscape. These features may be man-made (e.g. *gort*, a tilled field; *cill*, a church; *dun*, a fort) or topographical (e.g. *druim*, a ridge; *carraig*, a rock; *moin*, a bog). This latter group also includes a large variety of botanical features and a substantial number of townland names refer to specific native tree species or genera (e.g. *sceach*, hawthorn; *leamhán*, elm).

By studying the geographical pattern of place-name elements researchers have investigated the distribution of archaeological features, dialectical variations and land organisation (e.g. McErlean 1983; Flanagan & Flanagan 1994; O' Connor 2001). Similar methods can be employed to obtain information on the historical occurrence of woods and trees. Both McCracken (1971; see Fig. 2.3) and O'Connor (2001) plotted the distribution of approximately 1,600 townlands containing the anglicized element "derry" (from the Irish *doire*; an oakwood).

Yew is the only tree native to the British Isles whose Celtic name has been adopted by modern English. In Irish or Scottish Gaelic it is called *iúr* or *iubhar* and in Welsh *yw*. The Anglo-Saxon name of *heben* appears to have died out in the sixteenth century (Edlin 1965, 1970). This perhaps indicates a deep-rooted traditional association, or possible a geographical prominence of the

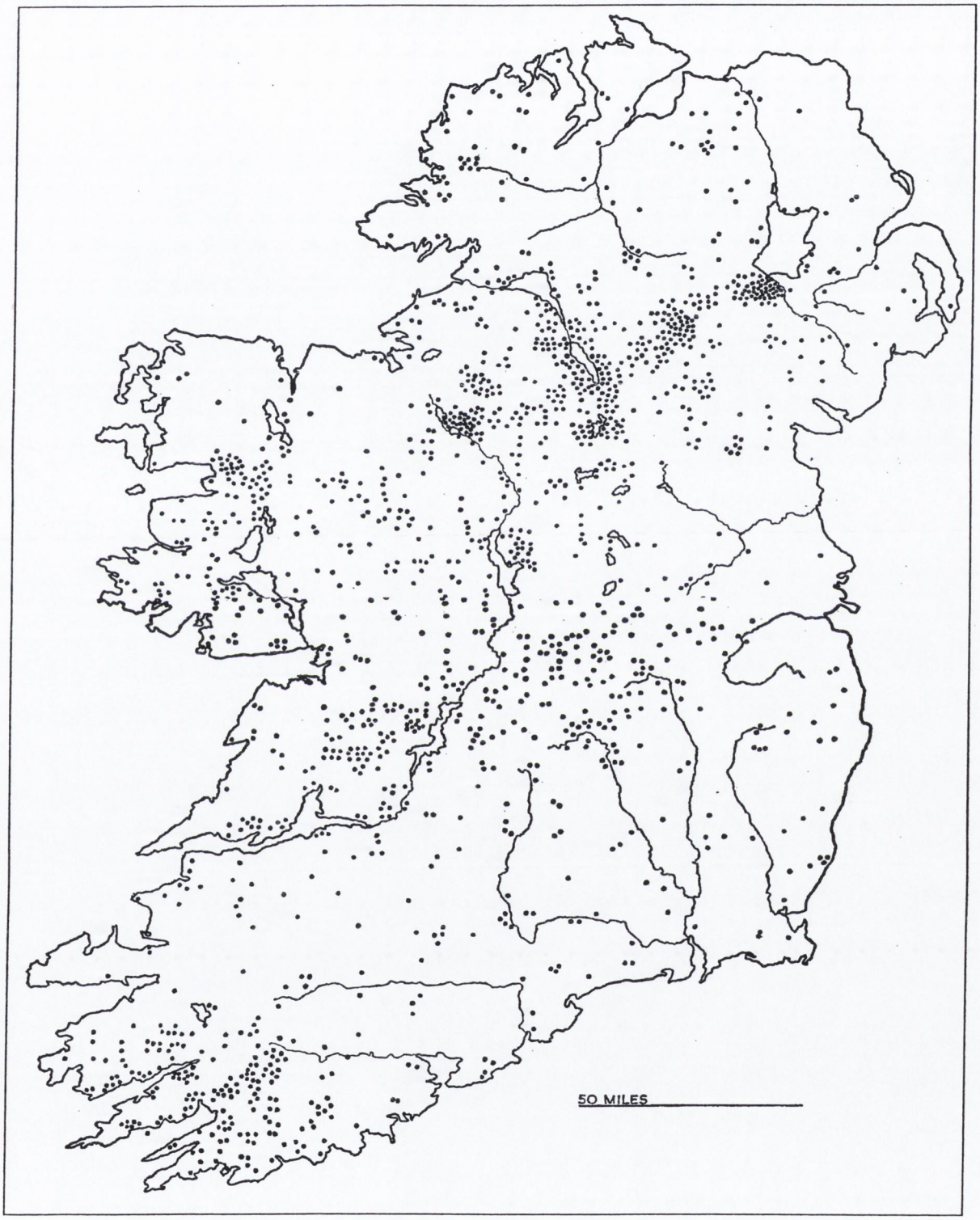


Figure 2.3 Townland names containing the word "derry" (from McCracken 1971).

species in Celtic lands. Certainly, the common occurrence of place-name elements in Ireland referring to yew has been widely commented upon and vaunted as evidence of a previously wider distribution of the species (Colgan & Scully 1898; Adams 1914; Fitzpatrick 1966; McCracken 1971; Kelly & Kirby 1982; Watts 1985; Milner 1992; Nelson 1993). Tittensor (1980) examined such occurrences in southern England but there has been no systematic study of these place-name elements in Ireland.

The aim of the present investigation was to examine the frequency and distribution of place-name elements in Ireland referring to yew and compare these data with those for other native tree species.

2.8.2 Methods:

As Mitchell (1993) points out, place-name data must be cautiously interpreted in view of the subjectivity of the original naming process and subsequent corruptions, mistranslations, renaming and ambiguities. It was therefore important that an objective methodology was adhered to as strictly as practicable in compilation of the dataset.

The *Index to townlands and towns... based on the 1851 census* (Registrar General 1984) was used as the standard source list for townlands and their spelling. Only names of townlands were included in the study – names of islands, towns, parishes and baronies were not considered.

Fourteen native tree species or genera, including yew, were investigated (Table 2.4). Apple (*aball*) was omitted as it was not possible to differentiate between references to the wild crab apple (*Malus sylvestris*) and domesticated situations. Oak (*dair*) was omitted as a large subset of the potential townlands, those pertaining to an oakwood (*doire*), have already been studied by McCracken (1971) and O'Connor (2001).

It is important to note that place-names in the *Index* are anglicized forms of the original Irish names, which were never formally catalogued, and hence their meaning is often obscured. Unfortunately, all of the species selected tend to occur as qualifying, generally secondary, elements in place-names and are therefore more prone to corruption in their anglicized form than words usually occurring as primary elements, such as *doire* which is fairly consistently anglicized as "derry" (Flanagan 1981). Hence, a variety of anglicized elements exist for each of these species. Furthermore, some of these anglicized elements are identical to corruptions from

completely different Irish words. Relevant examples of this problem are shown in Table 2.5. It was thus not possible to simply collate a list of townlands which contained the various relevant anglicized elements, as has been done for oakwoods; reliable interpretation for the names of specific townlands was needed to compile the dataset. No single comprehensive reference of this nature exists for Ireland – consequently a variety of sources were utilised (Table 2.6). Some of these sources contain a selection of translations for place-names across all of Ireland. Others provide more comprehensive coverage but only for specific regions, typically being county surveys. This inevitably introduced a bias into the dataset which must be taken into account when interpreting the results.

Where complexes of adjacent townlands occurred bearing the same name (e.g. Funshin Beg and Funshin More in Galway; Ferns, Ferns Demesne, Ferns Demesne [sic], Ferns Lower and Ferns Upper in Wexford), they were assumed to be modern divisions with the same original name source and were amalgamated into one entry in the dataset. Where alternative name origins were proposed by different sources, a decision was made based on their reliability; where doubt remained candidate sites were omitted.

The occurrence of townlands in the *Index* with purely English names, as opposed to anglicizations of the original Irish names, introduced two further problems. Firstly, some townlands have been completely renamed so that there is no connection between the English version in the *Index* and the original Irish name. Such sites were still included in the dataset, however, if suitable reference could be found to the original Irish name. For example, the Irish name for Danville in Kilkenny is *Pairc na Bhfuinsean* (field of the ash trees). The number of sites falling into this category was small however. Secondly, many of the English townland names are apparent direct translations from Irish and several of these pertain to trees. For example, there are numerous places called Ashford, Hollyhill and Birchwood. Inevitably, interpretation of these names is largely absent from the sources used and yet the possibility remains that there may be no connection between the English and Irish versions. Such sites were therefore not included in the dataset unless reference was found to the original Irish name and this too alluded to trees.

2.8.3 Results:

In total 1,667 townlands referring to native trees, other than oak and apple, were identified out of a total of around 62,200. Following amalgamation of complexes of adjacent townlands this resulted in 1,484 independent sites. The distribution of these sites is shown in Fig. 2.4 and the

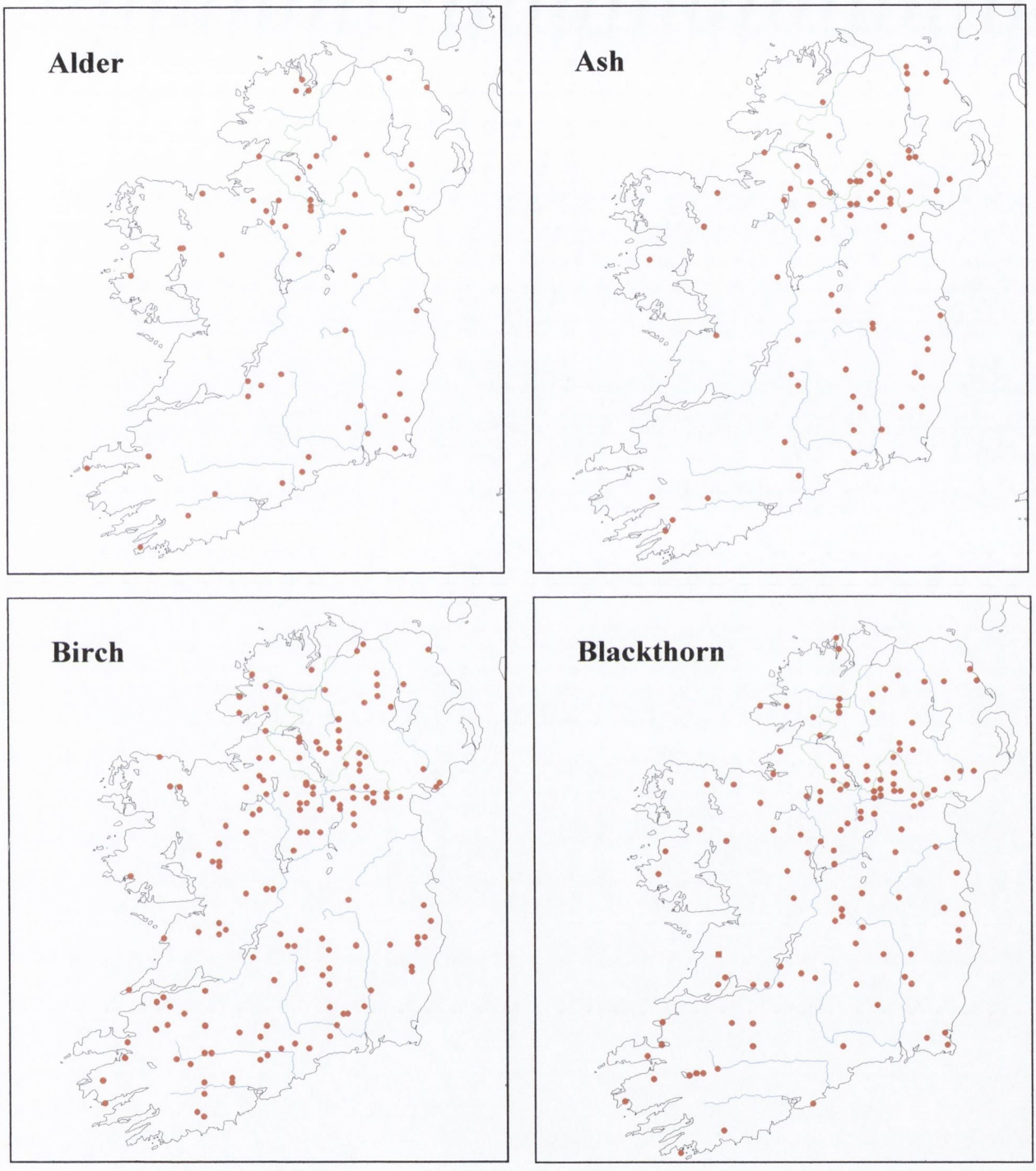


Figure 2.4a Irish townland sites with names referring to native tree species.

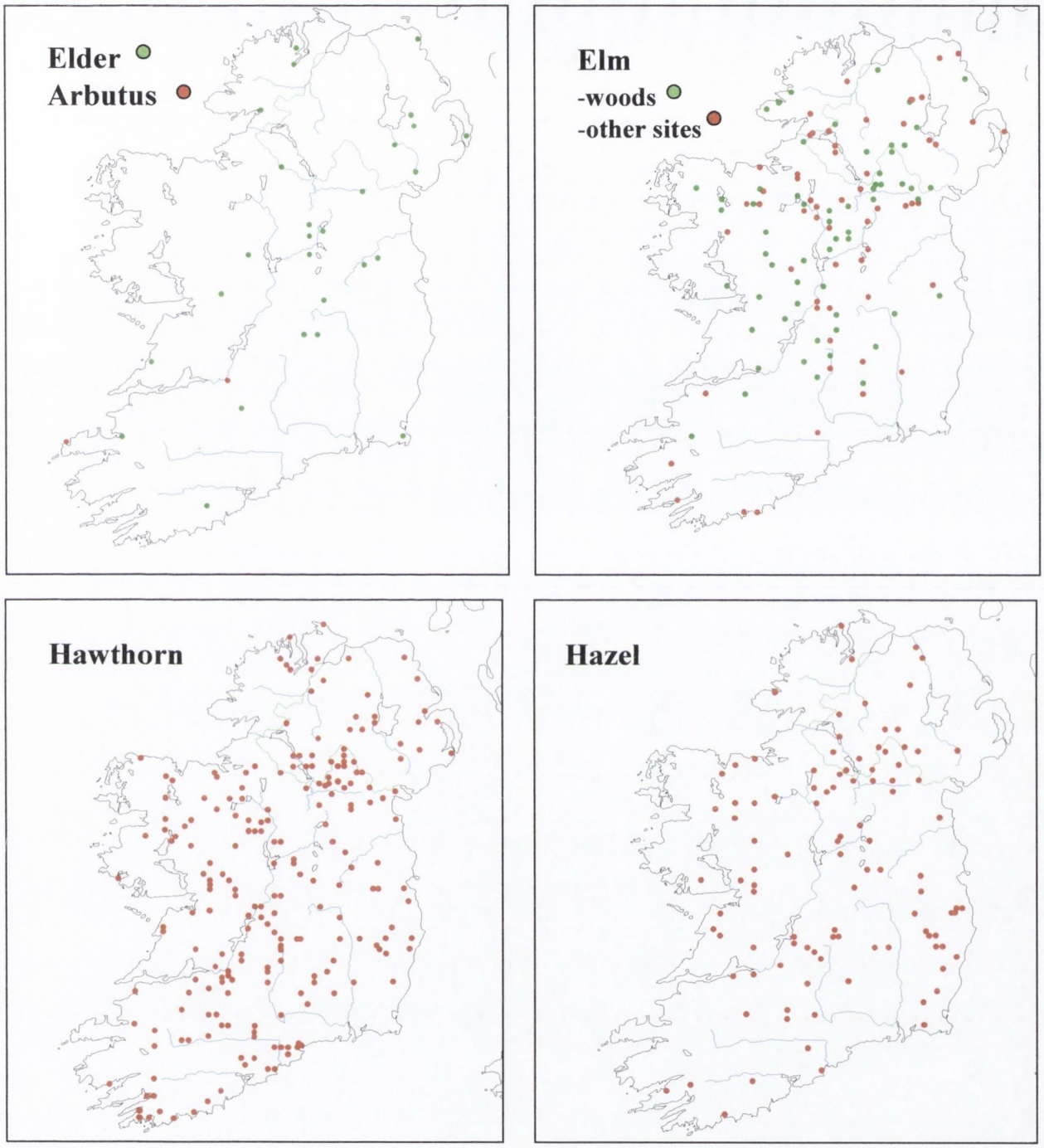


Figure 2.4b Irish townland sites with names referring to native tree species.

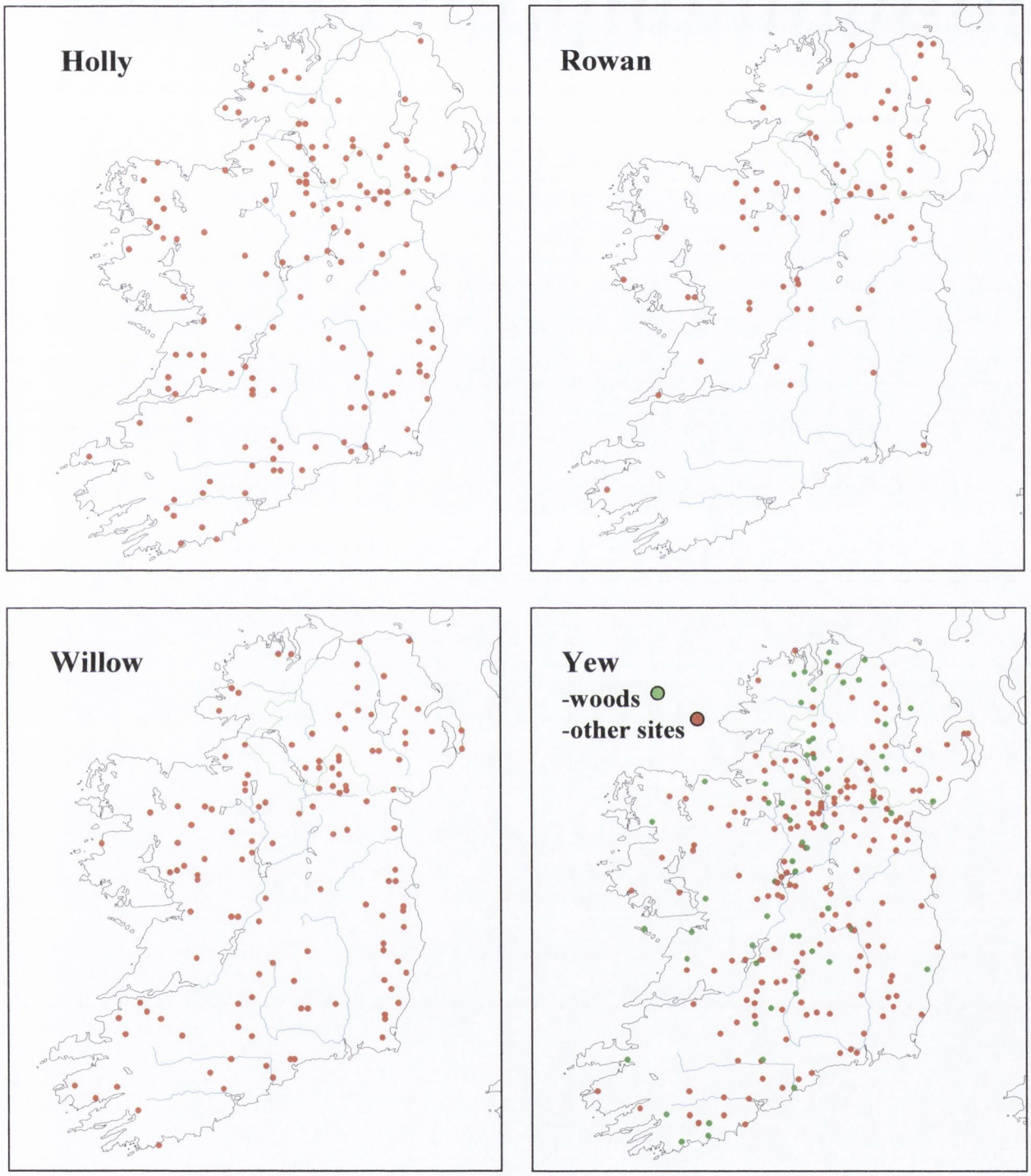


Figure 2.4c Irish townland sites with names referring to native tree species.

Figure 2.5 Percentages of townland sites identified in this survey pertaining to different native trees.

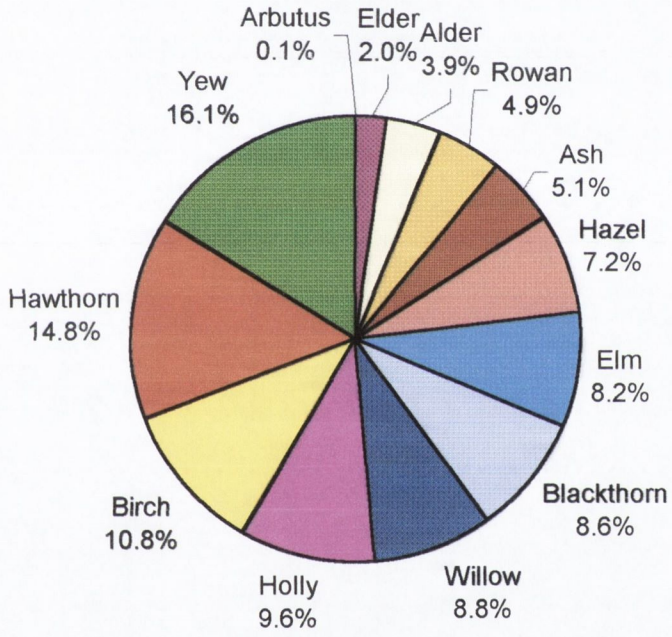


Table 2.6 Sources used for interpretation of place-names and region covered.

Source	Region covered
Room (1986, 1994)	All Ireland
McMahon (1990)	All Ireland
Flanagan & Flanagan (1994)	All Ireland
Joyce (1995, originally published 1869-1913)	All Ireland
Price (1945 - 1967)	Co. Wicklow
Walsh (1957)	Co. Westmeath
Ó Cíobháin (1978, 1984a, 1984b, 1985)	Parts of Co. Kerry
O'Kelly (1985)	Co. Kilkenny
Ó Maolfabhail (1990)	Co. Limerick
Ordnance Survey of Ireland (1991a)	Co. Louth
Ordnance Survey of Ireland (1991b)	Co. Waterford
Hughes *et al.* (1992)	Parts of Co. Down
Irish Countrywomen's Association (1992)	Co. Tipperary (North)
Toner *et al.* (1992)	Parts of Co. Down
Ó Mainnín & Stockman (1993)	Parts of Co. Down
Ordnance Survey of Ireland (1994)	Co. Offaly
Stockman & McKay (1995)	Parts of Co. Antrim
Muhr & Stockman (1996)	Parts of Co. Down
Ordnance Survey of Ireland (1996)	Co. Monaghan
Toner & Stockman (1996)	Parts of Co. Derry
Mac Gabhann & Ó Muraíle (1997)	Parts of Co. Antrim
McKay (1999)	Ulster

percentage of sites pertaining to each tree species or genus is shown in Fig. 2.5. In comparison, McCracken (1971) & O'Connor (2001), found approximately 1,600 townlands, an equatable figure, referring oakwoods alone.

Yew contributed the most sites to the dataset (16.1%, 239 sites). These are distributed across the country with a particularly high density of sites in the area of the drumlin belt, from Leitrim across to Louth. Sites are notably absent from the northeast of Ulster and the area of north Kerry / west Limerick. The subset of 61 sites referring to yew-woods exhibit a more defined distribution, being absent from much of the east and southeast and with a loose cluster running south from eastern Donegal to Tipperary.

Hawthorn (14.8%, 214 sites), birch (10.8%, 160 sites), holly (9.6%, 143 sites), willow (8.8%, 131 sites) and blackthorn (8.6%, 128 sites) were the next most common trees and exhibit similar distributions to each other, being widespread across the country with slight clustering in the drumlin belt area.

Sites pertaining to elm (8.2%, 121 sites) are restricted largely to the midlands with a conspicuous absence from east Leinster and south Munster. Almost half (60 sites) refer to elm-woods and again the subset shows a slightly more clustered distribution, still centred on the midlands. The distribution for hazel (7.2%, 107 sites) is poorly defined, but, as with yew there is a suggested absence from the extreme northeast and the area of north Kerry / west Limerick.

Both ash (5.1%, 75 sites) and alder (3.9%, 58 sites) appear to have two main clusters in their distributions: one centred on the drumlin belt area and one in the southeast of Leinster. The lack of sites pertaining to ash in the west of the country is particularly notable. Rowan (4.9%, 72 sites) has one of the most striking distributions, being exceedingly scarce in the southern half of the country. Only 29 sites (2.0%) pertaining to elder were found, sparsely spread across the country, whilst *Arbutus* is referred by only two townlands, one in Kerry and another in east Limerick.

2.8.4 Discussion:

The maps produced by this survey compliment those already produced for oakwoods to give some indication of tree and woodland distribution in Ireland around the time of the eighth and ninth centuries. A theme common to many of the distributions produced by this study is a clustering of sites in the region of the drumlin belt, which stretches across the Ulster borders from south Armagh to north Roscommon, and a similar concentration of sites is also apparent in the map McCracken (1971) produced for oakwoods (Fig. 2.3). This may in part be an artefact of the

total density of townlands in this region; the average size of a townland in Ireland is 1.3 km^2 but there is considerable variation between upland and lowland areas (Aalen 1997) and between different areas of the country. McErlean (1983) showed that townlands of Cos. Kerry, Donegal, Derry, Antrim, Down and Offaly were the largest on average (1.6-2.0 km^2) whilst those of Cos. Fermanagh and Monaghan were the smallest (0.6-0.8 km^2) and therefore most densely packed. Genuine later retention of a wooded landscape in this area is plausible, however, if one considers the edaphic conditions present. Drumlins are low, elongate hills built up of extremely dense glacial till that is rich in clay. The soils are therefore poorly drained and largely on steeply sloping ground. The low ground between drumlins is predominantly bog, rivers and lakes (Mitchell & Ryan 1997). The region is therefore very poor farmland and clearing it for agriculture would have been a particularly unattractive idea to peoples lacking modern farming technology. Contrastingly, the well-drained soils of the southeast constitute the most fertile land in the country and this area probably lost much of its original woodland cover in early times. Consequently several of the maps (e.g. rowan and oak) have a dearth of sites in eastern Leinster. The relative scarcity of sites identified in the extreme west of Ireland maybe a result of less research having been conducted for these regions (Table 2.6), but by the Early Christian Period blanket peat would have spread over much of this area, naturally denuding it of trees, although oakwoods seem to have still been common in western Galway (Fig. 2.3). The defined cluster of oakwood sites in south-west Munster, covering east Kerry and west Cork, is not reflected in the maps for other native tree species.

That more sites were found pertaining to yew than any of the other trees is noteworthy, but should not be interpreted as a comparative measure of yew's historical abundance. Many of the sites are indubitably named after single trees or small stands, often in association with churches; the evergreen nature of the tree would have been unusual and symbolic to early people making it an conspicuous feature of the landscape. The subset of sites pertaining to yew-woods probably suggests a more accurate level of abundance; 61 yew-woods compared with 1,600 oakwoods gives a ratio of approximately 1: 26. Given the historical abundance of oakwoods this ratio would still represent an impressive yew population. These yew-wood sites are largely confined to the central limestone lowlands, and less suitable underlying geology may be responsible for the lack of sites on the shales and sandstones of west Limerick, the metamorphic rocks of east Leinster and the Antrim basalt (Mitchell & Ryan 1997). Rackham (1995) has argued that while *Eochaill*, "yew-wood" may indicate a wood composed of yews, it might equally have been a hazel wood distinguished by a few conspicuous yew trees. This is certainly possible, but it might conversely

be argued just as validly that *Droim an Iúr,* "ridge of the yew", refers not to a ridge with one yew tree but a ridge covered in yew scrub. Second guessing the nature of individual sites is likely to be fruitless and analysis must be restrained to overall patterns of distribution.

There appears to be little correlation between the isopollen and townlands maps for yew. The former indicate prehistoric abundance in the west, whilst the latter indicates a more widespread occurrence with a concentration of site running down the centre of the Ireland. It is unclear whether this represents a genuine shift in distribution, or whether it is a result of data availability. The townland map for yew does, however, support reasonably well the native distribution for the species in Ireland proposed by Scannell & Synnott (1987) and depicted in Chapter 1.

The clustering of the elm sites on the central limestone plain corresponds well with the elm-hazel province of wildwood discussed in section 2.3. The subset of 60 elmwood sites compared with the 1,600 oakwood sites again gives a ratio of approximately 1:26. This indicates that elmwoods were still present during historical times, as suggested by Kelly & Kirby (1982), but that they had dwindled severely even in their zone of former dominance - they are now an extinct habitat in Ireland. The final main element of the wildwood, pine woodland, appears to have already disappeared, or at least become exceedingly rare, by this period – not a single townland was identified referring to pine or pinewoods.

Alder seems to have been restricted largely to the wet soils of the drumlin area and also the south-east where its affinity for river valleys (such as the Nore, the Barrow and the Slaney) may have permitted it to avoid the general woodland clearance. Of particular interest in the drumlin area are allusions to another lost Irish habitat, upland alder woodland. Townland names interpreted as *Greach na Fearna,* "mountain flat of the alder" occur in Cavan, Leitrim and Roscommon and may indicate historical vegetation similar to that still present in the north and west of Britain (Rodwell 1991; Latham & Blackstock 1998). Ash has a similar distribution to that of alder suggesting that, as today, it occurred alongside it in periodically-flooded alluvial woodland and permanently flushed sites (Fossitt 2001). However, ash also thrives on free-draining soils and given its present-day abundance, it seems surprisingly scarce in townland names.

There are ten species of *Salix* native to Ireland (Webb *et al.* 1996), many of which freely hybridise (Meikle 1984). Although most are associated with damp, poorly drained soils, the genus naturally covers a fairly broad range of ecological niches. The lack of a discernible pattern in the map for willow sites may therefore reflect the composite nature of this category, or it may be that

several of the major species were widespread. A few sites appear to refer specifically to osiers (e.g. *caológ*, an osier bed), as opposed to willows in general, but it is not possible to categorise sites further with any reasonable confidence. A number of place-name elements allude to sites where stems were harvested for wicker work (e.g. *gad*, a withe; *fleasc* or *slat*, a rod), but as these do not refer specifically to willow they were not included in the final dataset.

The maps for birch, blackthorn, hawthorn, hazel and holly may give some indication of the occurrence of scrubland which appears to have been widespread at this time. Although it is difficult to gauge actual abundance, hazel appears to be underrepresented in the dataset, possibly due to confusion between elements referring to hazel, *coll*, and wood, *coill*. A few sites refer to woods of birch but these are almost certainly secondary woodland rather than remnant montane birchwoods.

Arbutus is part of the Lusitanian element in the Irish flora. It is widespread throughout the Mediterranean region with a disjunct distribution along the Atlantic coasts of France and Ireland which probably reflects its sensitivity to frost (Mitchell 1993). In Ireland it occurs in a few isolated populations in Cork and Kerry, although it is frequent in the Killarney area, particularly on lake-shores and at woodland margins. An outlying population occurs by Lough Gill, Co. Sligo (Webb *et al.* 1996). A historical distribution in the southwest is supported by the Kerry site, Ardnacaithne (Smerwick), identified in this survey. The Limerick site, Cunnihee, although not an indisputable reference to *Arbutus*, tentatively suggests former populations further north, although there is no pollen data at present to indicate populations between Kerry and Sligo (Mitchell 1993).

2.8.5 Conclusions

Due to the subjectivity of this dataset it is difficult to draw detailed conclusions. Nevertheless, it is apparent that yew was much more widely distributed in the past, and that yew-woods, or at least yew-rich woods, were conspicuous features of the Irish landscape in the Early Christian Period. The species has evidently declined dramatically since then. The results also permit some general speculation on the Irish landscape. Clearance for agriculture had removed trees from much of the south and east, although woodlands may have persisted in some of the river valleys. In the west, most of the forests had gone, presumably replaced by bogland, and pine had disappeared. The drumlin belt harboured much of the remaining woodland cover, which was a

mix of oakwood, elmwood, yew-wood and scrub. Elmwoods and yew-woods were also dotted across the central midlands, whilst oak had further strongholds in the mid-west and south-west.

The quality of the dataset produced by this survey is dependant on the precision of the interpretation offered by the utilised sources. The pioneering work of Joyce (1995, originally published 1869-1913) has been particularly criticised for the number of errors it contains (e.g. O'Connell 2001, Flanagan 1981). It remains however the most comprehensive source available and the sections pertaining to animal and plant names are among the more reliable according to Flanagan (1981). Some areas of the country have also been undoubtedly underrepresented. Improvement and refinement of this view of woodland history must however await further developments in toponymical research.

2.9 The later historical period

Throughout the Viking and Anglo-Normans periods, times of disease epidemic (e.g. the Black Death of 1349) and violence allowed secondary woodland to establish on deserted farmland (Rackham 1986), but overall increases in the population caused woodland cover to dwindle further. There is little empirical data available, but the concentration of Norman settlements in the south and east of the country (Stout & Stout 1997) would again suggest that this region suffered most. During the later Middles Ages, a new selective pressure on yew populations may have been the emergence of the yew wood longbow as the most important weapon in European warfare. The considerable demand for yew wood bow-staves in Britain has been discussed by Hardy (1986). Originally bows were manufactured in England and Wales, but by the late 15th century AD there was a need to import them from abroad, as Edward IV declared "...that great scarcity of bowstaves is now in this realm, and the bowstaves that be in the realm be sold at an excessive price...". Certainly, huge numbers of yew trees were being felled on the continent during this time (Czartoryski 1978) and it is not implausible that yew populations in Ireland may have suffered as a result of this demand if they had in any way still been common. An allusion to this is made in a manuscript dating from 1584 (Anon 1906 cited in Mitchell 1990), which, describing the woods of Killarney, says: "...there also grow there many yew-trees, good for making bows".

The first of the Tudor "plantations" occurred in the mid-sixteenth century. This was the organised eviction of the native Irish people and the parcelling out of the land to English settlers. Surveys conducted at this time, quoted in Mitchell & Ryan (1997), give us some indication of the nature of the landscape. They report, for example, that extensive oakwoods still remained near Athlone

in contrast to "much small woods as crabtree, thorn, hazel, with such like", whilst in north Kerry secondary woodland consisted of "underwood of the age of fifty or sixty years filled with decayed trees of ash, hazels, sallows, willows, alders, birches, whitethorns and such like". Further plantations of people occurred in the seventeenth century and exposed the remaining woodlands to commercial exploitation.

By the time of the Civil Survey in 1654-6, woodland cover in Ireland was exceedingly scarce; Rackham (1986) made an estimate of only 3%, less than a third as much as contemporary England. During the seventeenth and eighteenth centuries, some areas of the country became rapidly industrialized, and ironworks, cooperage, tanning and shipbuilding all increased the pressures on woodland (McCracken 1971). Mitchell & Ryan (1997) illustrated how Irish oak barrel stave production rose dramatically between 1600 and 1710. Stave production then crashed and the level of foreign staves imported rose, until by 1770 domestic commercial production had ceased. The authors attribute this to over-production and exhaustion of supply but according to Rackham (1986, 1995), agriculture was still the main destroyer of woodland during this period of a dramatically increasing population. In contrast to the former pattern of clearance, it was now in the relatively industrial south-east that the remaining woodlands were a valuable resource and were afforded some degree of protection, whereas in the agricultural mid-west almost all remaining woodlands were lost. The accounts of Arthur Young, an Englishman who toured Ireland between 1776 and 1779, allude to the treeless nature of the western landscape:

"[Co. Galway] is perfectly free from trees, except around gentlemen's houses....[in Co. Limerick] the face of the country is that of desolation; the grounds are over-run with thistles, ragwort, etc. to excess; the fences are mounds of earth, full of gaps; there is no wood.."

(in Mitchell & Ryan 1997)

However, there are reports that industry was the impetus behind woodland clearance in other areas. An important statement is made by Smith (1756), who, describing the occurrence of yew in Co. Kerry, wrote:

"Rocky places, woods and mountain cliffs, rare....Grew in prodigious quantities on the mountains of all our southern baronies until it was destroyed for making coals for ironworks."

(in Colgan & Scully 1898)

Another potential factor which contributed to the decline of yew is mentioned by the botanist John Templeton in his journal for 1810, who wrote of Glenarrif, Co. Antrim:

"In the crevices of a lofty precipice on the northern side of the glen is the last remains of our native yew...for which the glen was long famous; tradition says it was once plentiful, now these stunted bushes as long as they would afford a green branch, were annually despoiled to decorate the chapels of the neighbourhood on Christmas Eve, and to procure this emblem of Eternity a person descended by means of a rope to plunder this relic of our ancient forest."

(in Hackney 1992)

There is also a tradition in Ireland of using yew foliage for "palm" on Palm Sunday (Nelson 1993; Webb *et al.* 1996). Whether this harvesting of yew branches for ritual purposes could have had a serious impact on the national abundance of yew is perhaps doubtful, but in cases such as Glenarrif, it may have sealed the fate of populations already severely reduced.

Conversely, the eighteenth and nineteenth centuries also saw the first organised planting of trees in Ireland on any real scale. Stimulated by acts of parliament, a number of the great estates instigated considerable landscaping projects, and between 1700 and 1845, around 137,000 ha were planted (Mitchell & Ryan 1997). This included many non-native species such as beech (*Fagus sylvatica*) and sycamore (*Acer pseudoplatanus*) (Fitzpatrick 1965). Yew was probably also widely planted as an ornamental during this period; the fastigiate form of the species found particular favour following its discovery around 1740, in Co. Fermanagh (Nelson 1993). Nevertheless, outside the demesnes the human population was expanding at an accelerating rate, resulting in only 10% of the woodland detailed in the Civil Survey appearing in the first series of Ordnance Survey maps in 1834-44 (Rackham 1986). The Great Famine of 1845 caused the population to crash but the agricultural economy reorganised quickly (Mitchell & Ryan 1997). Map evidence suggests that scrub established on some abandoned, poor quality, farmland in the following period (e.g. Kelly & Jeffrey 1987), but regional pollen data suggest that there was little real increase in woodland cover (Cole & Mitchell, in press).

It is apparent from a variety of floras and botanical works published in the nineteenth and earlier twentieth century that yew had become a rare species in most parts of Ireland by these times, and possibly extinct in some counties. Excerpts from these works are presented in Appendix I. Several references are made to yew being restricted to cliffs, crags and rocky ground and also to

islands in lakes or in rivers, where trees would have been offered protection from grazing animals. These situations also represent marginal land which was generally unsuitable for clearance and cultivation. Hackney (1992) proposes that steep, rocky slopes were the only habitats left where the native tree could survive, but that they should not be regarded as the preferred habitat.

The establishment of state forestry in Ireland in 1903 heralded the beginning of major afforestation. The vast majority of this, however, was composed of exotic conifer plantation, the main species being: sitka spruce (*Picea sitchensis*), Norway spruce (*Picea abies*), Japanese larch (*Larix kaempferi*), European larch (*Larix decidua*), lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) (Fitzpatrick 1965). Approximately 8% of Ireland is now covered by forestry plantations whilst semi-natural woodland, often protected as part of estate lands and heavily managed, constitutes only 1%. Of this only a small proportion is ancient woodland (Rackham 1995). Ireland currently has the lowest forest cover in Europe after Iceland (Mitchell 2000).

2.11 Summary

1. Yew was probably present in Ireland as far back as 9,800 BP as a scattered understorey tree.

2. Following the elm decline, *c.*5100 BP, localised and usually brief expansions of yew occurred being most prominent in the west and south-west.

3. Yew populations expanded again during the Late Iron Age Lull, *c.*1900 BP. Similar opportunistic colonisations of abandoned farmland have been recorded in south-east England.

4. Yew populations declined as a part of general woodland clearance for agriculture, selective felling for its attractive timber and probably due to the threat of livestock poisoning.

5. By the Early Christian Period, yew woods were present across the central limestone lowlands, with further sites in the drumlin area which still remained heavily wooded.

6. As agricultural intensification increased, yew populations in Ireland declined dramatically. In recent times it has been widely planted as an ornamental, but is now rare in semi-natural habitats.

CHAPTER 3

CONTEMPORARY YEW COMMUNITIES IN IRELAND

3.1 Overview

The first part of this chapter deals with a survey of the semi-natural plant communities in which yew currently occurs in Ireland. A comparison is made with yew communities in Britain and continental Europe and potential successional pathways for yew communities in Ireland are discussed. The second part of this chapter is an introduction to Reenadinna Wood, Killarney National Park, the largest yew wood remaining in Ireland.

3.2 Survey of Irish semi-natural yew communities

3.2.1 Introduction

Studies of the vegetation communities of Irish woodlands have largely followed the phytosociological approach of Braun-Blanquet & Tüxen (1952), for example Kelly & Moore (1974), Kelly (1981), Cross (1982), Doyle & Moore (1982), Kelly & Kirby (1982), Ferguson & Westhoff (1987) and Poole *et al.* (in press). This hierarchy based technique has allowed Irish woodlands to be classified and described in an international context (White & Doyle 1982), but is less informative about floristic and environmental gradients within study sites and the underlying processes at work. The development of ordination techniques (e.g. Detrended Correspondence Analysis) and multivariate classifications (e.g. TWINSPAN) have allowed these relationships to be more objectively and statistically investigated. For instance, using these methods, Kelly & Iremonger (1997), working with data from wet woodland sites from across the country, found ordination valuable in analysing highly variable and intergrading vegetation types. Cooper (1984) identified three main variants of hazel scrub-woodland in Co. Antrim, differentiated by drainage and elevation, and Cooper (1986) investigated the prevalence of non-native tree species in deciduous woods in Co. Down. At a different scale, Kirby & O'Connell (1981) used ordination techniques to examine saxicolous communities at Shannawoneen Wood, Co. Galway

Ordination has also been used to elucidate successional pathways by examining the relationships between vegetation samples representing a chronosequence (e.g. Bergeron 2000, le Duc *et al.* 2000, Jensen *et al.* 2001, Howard & Lee 2002). The pathway along which Reenadinna Wood has developed, and may still be developing, is unclear, although Watt

(1926) described the successional development of yew-woods on the South Downs in England. Due to its susceptibility to browsing (in this instance by sheep and rabbits) yew is unable to colonise chalk grassland directly but, following invasion of scrub composed of browse-resistant shrubs, such as hawthorn and juniper, its shade tolerance and longevity enable it to compete successfully with the other species and eventually suppress them. Hence, a wood dominated by yew is formed. Watt (1926) also differentiated between a juniper sere, where transition to pure yew-wood is relatively quick, and a hawthorn sere where the process is much longer due the lower efficiency of hawthorn at protecting yew. In the latter case, ash may play a prominent role in the intermediate stages. Whilst ash is abundant and in some places dominant in Reenadinna, the prominence of hazel and the scarceness of hawthorn and juniper suggest that some other sequence of development may occur on Irish limestone pavement sites.

By utilising ordination analysis and multivariate classification the purposes of this study were: (i) to describe the range of plant communities associated with yew in Ireland; and (ii) examine potential successional pathways of yew-wood development.

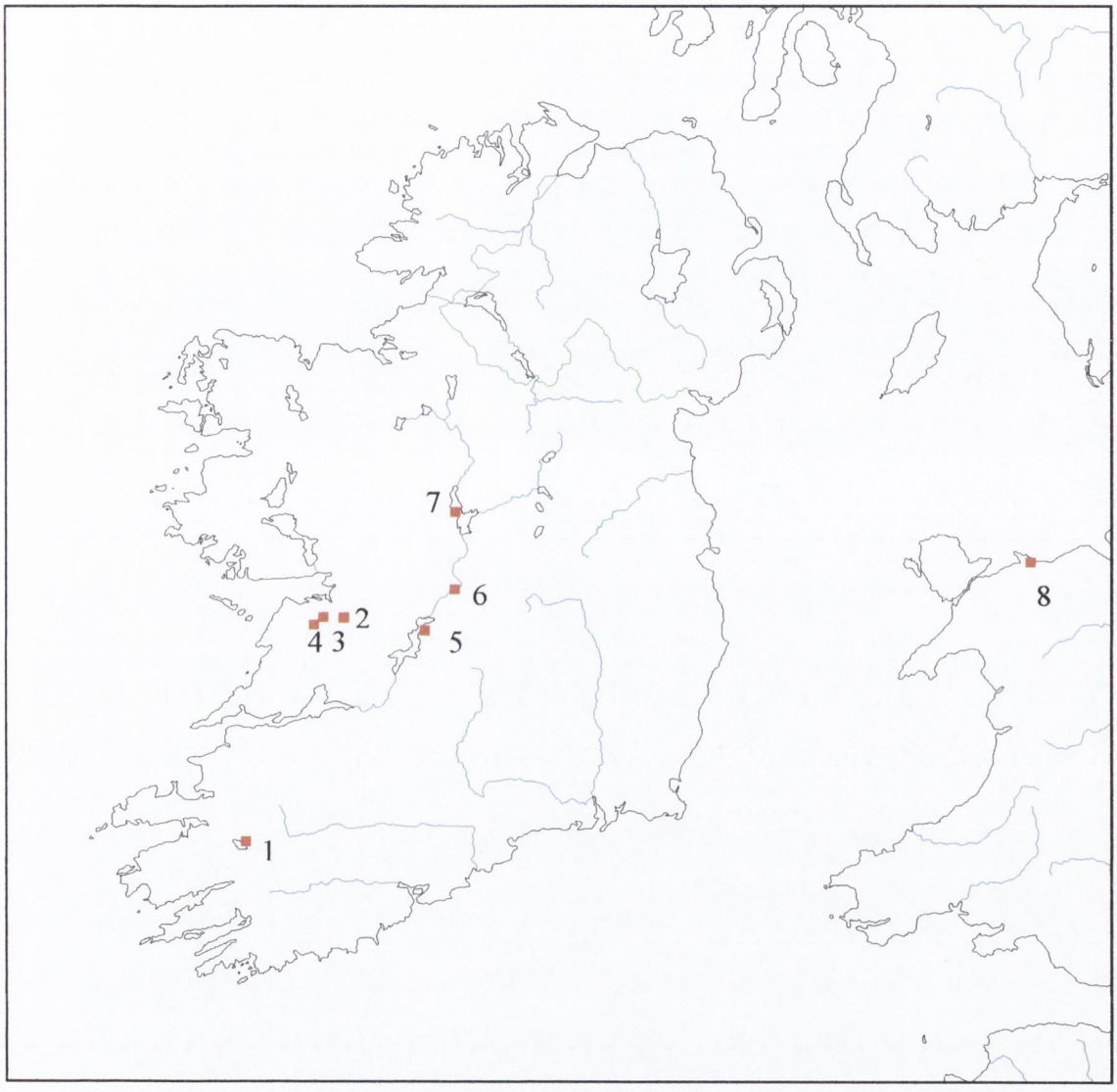
3.2.2 Methods

Survey sites

A number of the principal known localities in Ireland with native yew populations were chosen for surveying (Fig. 3.1a). They were selected on the grounds of naturalness and also to cover a range of habitat types. Hence, they included open limestone pavement, scrub and woodland sites. These sites are described here in brief.

The first five sites are all located within the Killarney National Park, Co. Kerry (Fig. 3.1b) and are therefore under state ownership. *Reenadinna Wood*, on the Muckross Peninsula, contains the most extensive areas of yew woodland remaining in Ireland. These stands, which are located on a series of Carboniferous limestone outcroppings, have been described by Kelly (1981), and wetland areas of the wood have been described by Kelly & Iremonger (1997). Further details of this area of considerable topographical and vegetational complexity are presented in the latter part of this chapter. *Monk's Wood* is located less than 1km east of Reenadinna, near to the ruins of Muckross Abbey (founded by Franciscan friars in 1448). It too lies on a series of limestone outcroppings. It is largely dominated by yew, although due to the close proximity of Muckross House and gardens, non-native species, including beech (*Fagus sylvatica*) have been planted in several areas. *Ross Island*, actually a rocky peninsula, is situated 2km north-west of Reenadinna Wood across the waters of Lough Leane. Low-lying areas support wet woodlands with birch and alder, whilst beech has been planted

Figure 3.1a Location of sites sampled for the survey of semi-natural yew communities



1. Killarney National Park
   - Reenadinna Wood
   - Monk's Wood
   - Ross Island
   - Camillan
   - Glaisín na Marbh
2. Garryland Wood
3. Slieve Carran
4. Burren National Park
   - Gortlecka
   - Loch Gailean
5. Cornalack
6. Clorhane
7. St. John's Wood
8. Bryn Pydew

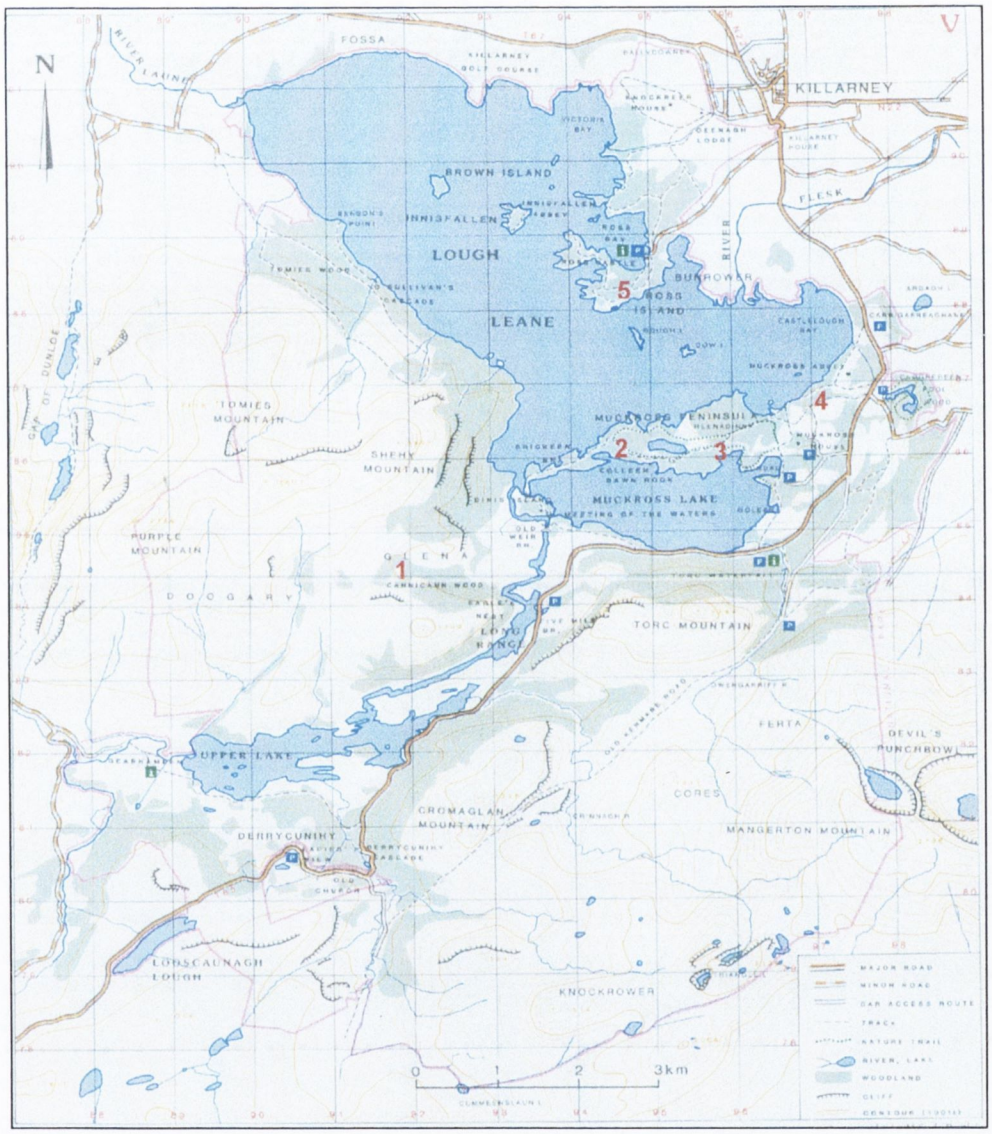


Figure 3.1b Map of the Killarney National Park. Red figures indicate: 1 Glaisin na Marbh, 2 Camillan Wood, 3 Reenadinna Wood, 4 Monk's Wood and 5 Ross Island.

extensively on higher ground. Yew occurs on the thinner soils where the limestone bedrock is at or near the surface and also on many of the lough-side cliffs. *Camillan Wood* lies to the west of Reenadinna, being separated only by an area of rough pasture known as the West Meadow and a small lake, called Doo Lough. A geological fault, running north-south, passes through the peninsula at the point of Doo Lough. Thus, whilst Reenadinna lies on limestone, Camillan stands on a bedrock of Devonian sandstone, and is dominated by sessile oak with a holly understorey; yew is occasional. *Glaisín na Marbh* is an area of upland oakwood which ascends to a height of 350 m on the sandstone slopes of Shehy Mountain, approximately 4km to the west of Reenadinna, and represents some of the highest habitat of this type remaining in Ireland; yew is infrequent.

The second cluster of sites were in the mid-west of Ireland (Fig. 3.1a). *Gortlecka*, Co. Clare, is an area of open limestone pavement within the Burren National Park at the foot of Mullagh More, whilst the rocky shore of *Lough Gailean* lies about 2km west of this site. Browsing by feral goats has a major impact on the vegetation at both sites. *Slievecarran* Nature Reserve lies approximately 10km north of Mullagh More, and comprises an expanse of open limestone pavement and an area of hazel scrub at the foot of Slievecarran hill. *Garryland Wood* Nature Reserve, Co. Galway, is part of the Coole Park estate near Gort. Its base rich soils support a canopy of oak and ash, with beech and other non-native species being locally dominant. Yew occurs on a series of small limestone outcroppings that are scattered through the wood. Browsing here is largely due to cattle and sheep.

The final set of Irish sites were woodlands in the midlands (Fig. 3.1a). *St. John's Wood* is situated on the shores of Lough Ree, Co. Roscommon; ownership is part state and part private. It is a mixed deciduous woodland on shallow soils over Carboniferous limestone which was managed for coppice until *c.*1920 according to Rackham (1995). Selective felling has removed many of big trees and it is now largely composed of hazel scrub with smaller areas of more mature woodland in which oak and ash are largely dominant. It is one of the most diverse semi-natural woodlands in Ireland, with several features of ancient woodland; Kelly & Fuller (1988) reported 30 species of native trees, shrubs and woody climbers. *The Rocks of Clorhane* is an area of outcropping limestone just above the floodplain of the River Shannon in Co. Offaly, and represents one of the only areas of karst limestone habitat in Leinster. Surveying was conducted in the southern, state-owned part of this site. Map evidence shows that this site developed from pastureland into woodland between 1838 and 1884 (Kelly & Jeffrey 1987). It presently consists of dense hazel scrub with an admixture of other shrubs and trees, including non-native species, such as beech (*Fagus sylvatica*) and Douglas fir (*Pseudotsuga menziesii*), which were planted in the 1960s (Kelly & Jeffrey 1987).

The final Irish survey site was at *Cornalack* on the shores of Lough Derg, Co. Tipperary, near Terryglass. This is a privately owned area of shattered limestone pavement containing several small disused quarries dating from the nineteenth century. It contains areas of open pavement, developing scrub and mature woodland. Map evidence also shows that the site started to develop from rough pasture to scrub between 1843 and 1901. This site has been grazed by cattle in the past but has recently been fenced off.

In addition, an open limestone pavement site with yew at *Bryn Pydew* Nature Reserve, near Llandudno, North Wales, was selected to allow direct comparison with a relatively near non-Irish site. This site is not currently grazed by livestock and the pavement area is prevented from succeeding to scrub by manually cutting back the vegetation. Adjacent areas of scrub and woodland also contain yew but were not surveyed for the present study.

Survey technique

At each site, a number (1-8) of 15x15m relevés were recorded to cover the range of vegetation present containing yew. Each relevé was positioned so as to encompass a fairly homogeneous and representative sample of the vegetation. A single size of relevé was used despite the range of vegetation structures surveyed, as it was desired to examine species richness, an area-dependent variable. In total 31 relevés were recorded.

Within each relevé the following variables were recorded using a version of the Domin scale, *sensu* Dahl & Hadăc 1941 (Table 3.1): above-ground cover of all vascular plants species, total bryophyte cover, litter, fallen wood, bare earth and bare rock. The gbh of all adult trees was recorded, as was the density of saplings for each species. Geology was recorded as limestone or sandstone and slope was measured in degrees. The growth form of yew at each site, was recorded, noting evidence of browsing, height of plants relative to the pavement surface and layering of branches.

Table 3.1 Version of the Domin scale of abundance used in this study

Cover	Domin score
91-100 %	10
76-90 %	9
51-75%	8
34-50%	7
26-33%	6
11-25%	5
4-10%	4
3%	3
2%	2
<2%	1

Data analysis

Data were analysed using the multivariate statistics program PC-Ord (McCune & Mefford 1999). Non-metric multidimensional scaling ordination (NMS) was used to examine differences in vegetation composition between sites. This method, which is an iterative ordination technique, was selected because it is particularly suitable for ecological data as it does not require normality (Legendre & Legendre 1998; McCune & Mefford 1999) and has proved superior to more widely used ordination techniques, such as DCA (Kenkel & Orlóci 1986; Michin 1987). It has previously been used, for example, to analyze vegetation data from Irish conifer clearfell sites (Smith 2002), and to classify forest vegetation in Finland (Pitkanen 2000) and Canada (Rettie 1997). The manual settings proposed by McCune & Mefford (1999) were employed: 200 iterations, 10 runs with real data, 20 runs with randomised data, an instability criterion of 0.0005, cycling down from six dimensions to one dimension. As recommended by McCune & Mefford (1999), Sørenson (Bray Curtis) distance measure was selected.

Preliminary analysis revealed that, despite attempts to choose sites with a reasonable degree of naturalness, non-native species, as classified by Rose (1981) and Webb *et al.* (1996), might be exerting considerable influence on the results. The relative importance of these species in the vegetation was therefore investigated by calculating a non-nativeness score for each relevé. This was equal to the percentage of the sum of Domin scores for that relevé that were contributed by non-native species. To investigate the importance of potential nurse shrubs a similar index was used to appraise the thorniness of the vegetation, by calculating the contribution of hawthorn (*Crataegus monogyna*), blackthorn (*Prunus spinosa*), juniper (*Juniperus communis*) and gorse (*Ulex europaeus*). Correlations between the ordination axes and the following variables were tested using Pearson's correlation co-efficient (r): bryophyte cover; bare rock; bare earth; litter; fallen wood; slope; adult tree density; total adult tree basal area; adult tree basal area of yew; total number of vascular plant species (species richness); non-nativeness; and thorniness. Flexible beta-cluster analysis (using PC-Ord, with $\beta = -0.5$) was employed to group relevés into vegetation types for which mean characteristics were calculated.

3.2.3 Results

Ordination results

The ordination yielded a two-dimensional solution (Figs. 3.2 and 3.3) with a stress value of 15.4%, and whose axes cumulatively explained 79.6% of variance. Limestone and sandstone sites were clearly segregated. Axis 1 appears to represent succession amongst the limestone

Figure 3.2 NMS ordination of the yew community relevés indicating the underlying geology: green = limestone; red = sandstone. Radiating lines indicate correlation of variables to axes 1 and 2 according to Pearson's correlation coefficient. Only variables significantly correlated to one or both axes are shown ($P < 0.05$).

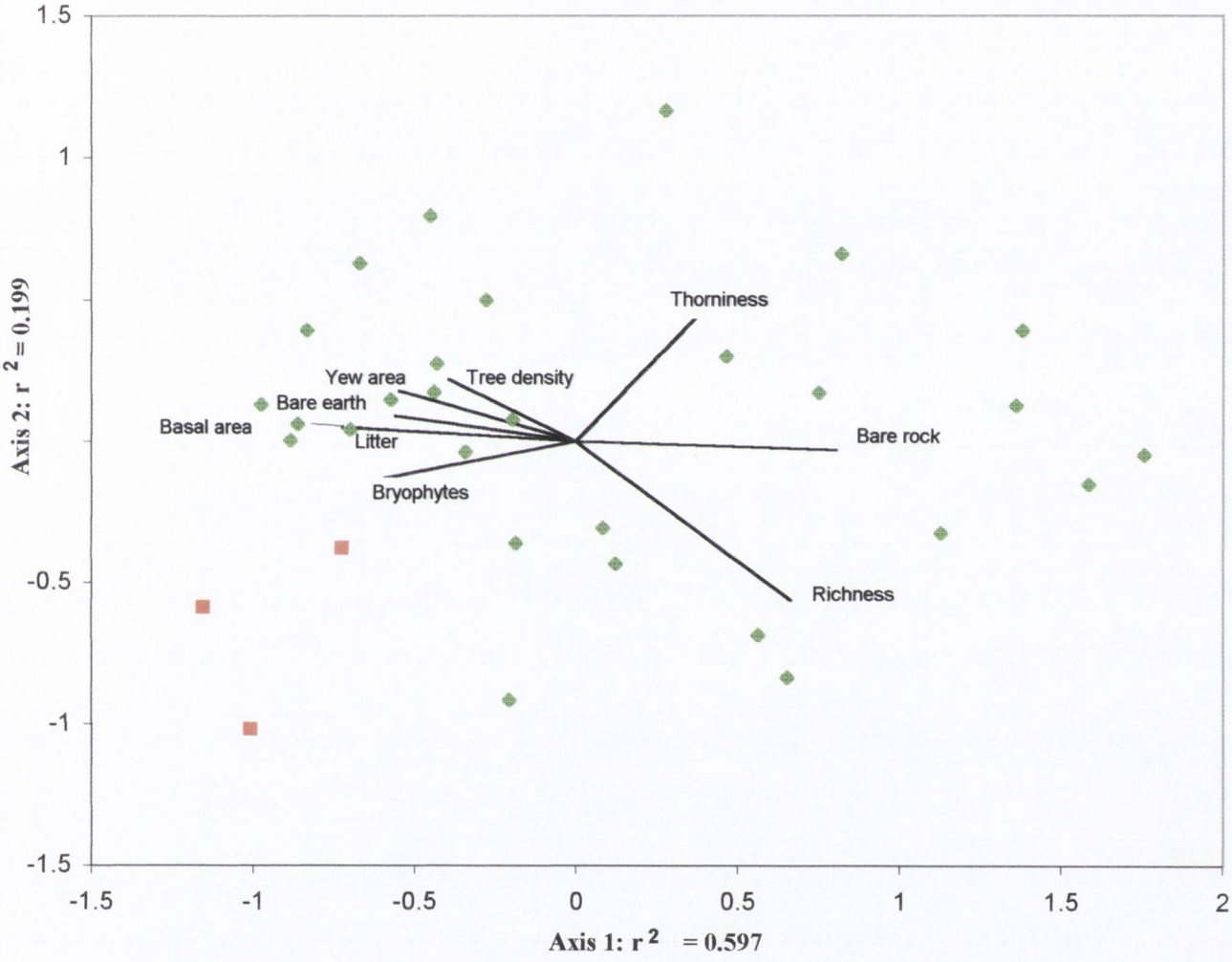
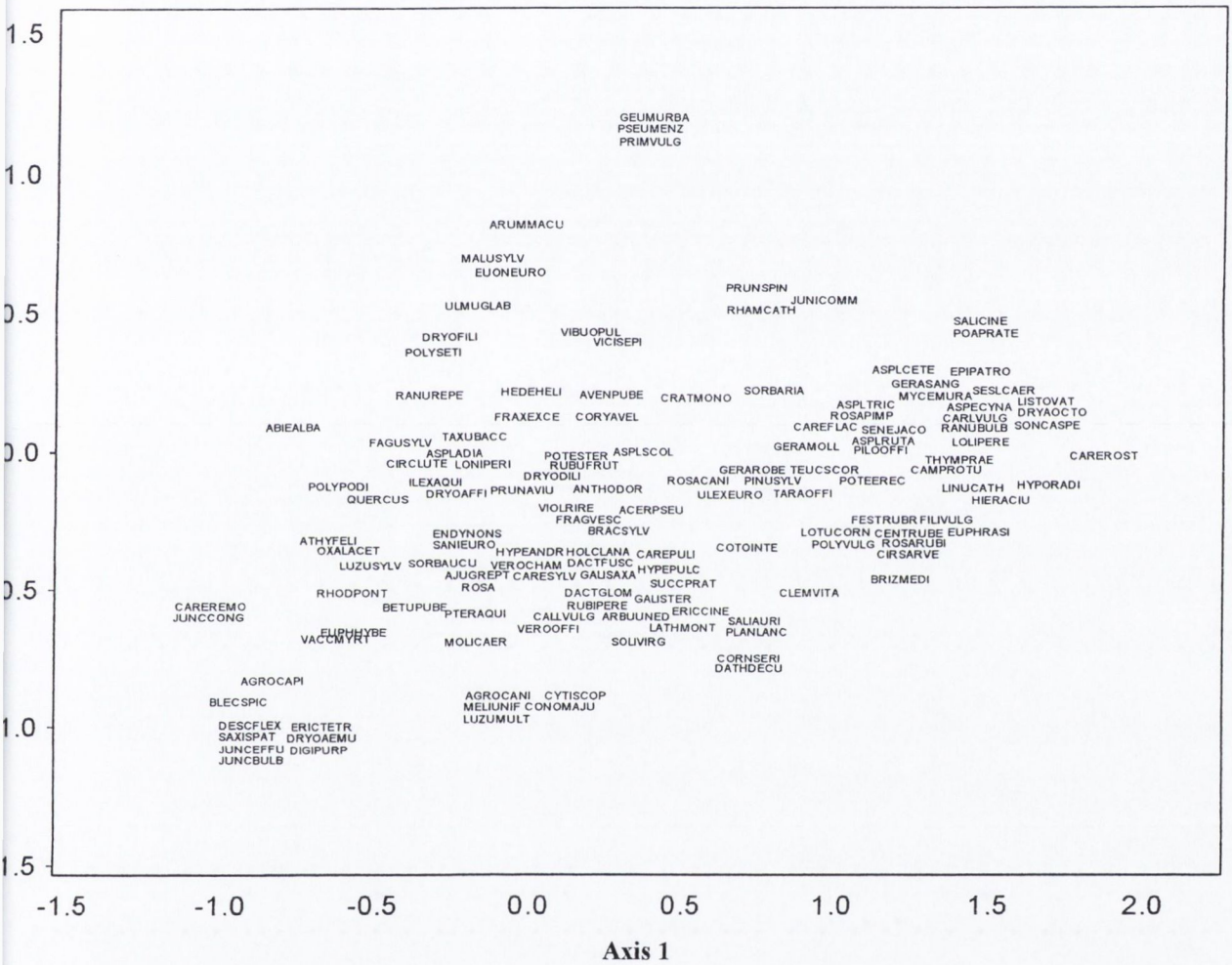


Figure 3.3 NMS ordination of the species in the yew community relevés. See Appendix II for key to abbreviations.



sites with high negative correlations with bryophyte cover, bare earth, litter, total adult tree basal area and basal area of adult yews, and a strong positive correlation with bare rock (Table 3.2). Hence, open limestone pavement sites are concentrated at the high end of this axis and mature woodland sites are at the low end of this axis. Species richness was also positively correlated with Axis 1 indicating that the number of species present declines as succession progresses, although it was also negatively correlated with the weaker second axis. This appears to be due to an interaction with the underlying geology (Fig. 3.2); in more mature woodland, species richness was higher on sandstone than on limestone. Thorniness was positively but weakly correlated with the Axis 1, suggesting a slight decline as succession progresses (Table 3.2). Thorniness was also positively correlated with Axis 2, due largely to the scarcity of thorny shrubs in the sandstone plots.

Non-nativeness did not correlate significantly with either axis (Table 3.2). Of 139 vascular plant species recorded, 10 were non-natives (Table 3.3). *Fagus sylvatica* and *Mycelis muralis* were the most frequently recorded aliens, with *Acer pseudoplatanus*, *Rhododendron* and *Cotoneaster* also prominent. Of the 31 relevés recorded, non-native species were present in 25 and contributed over 10% of the sum of Domin scores in 10 relevés (Fig. 3.4).

Vegetation types

Following inspection of the cluster dendrogram (Fig. 3.5), an eight-group level classification was decided upon. This was detailed enough to permit successional changes to be detected whilst still retaining meaningful vegetation assemblages. Mean data for each vegetation type are presented in Table 3.4. The distribution of these vegetation types in relation to the ordination axes is shown in Fig. 3.6.

***Sesleria - Teucrium* pavement:**

This is a low vegetation type of open limestone pavement sites where bare rock is the dominant feature (Plate 3.1). Vegetation is sparse, principally herbaceous and restricted largely to loess filled grykes, but species richness is high. The more abundant species include *Teucrium scorodonia*, *Rosa pimpinellifolia* and *Sesleria caerulea*. This last species may form small patches of turf where pockets of soil exist. The alien species *Mycelis muralis* is frequent as are several species of *Asplenium*. Conspicuous plants include *Lotus corniculatus*, *Geranium robertianum* and *Geranium sanguineum*. Sites with this vegetation type were restricted to the Burren, where succession to scrub is prevented by heavy grazing by feral goats. The main tree species present, hazel, hawthorn, blackthorn and yew, thus tended to occur as low or prostrate, gnarled shrubs. Yew does not exceed 2% of field layer cover.

Table 3.2 Correlations of environmental and vegetation data from yew community relevés with axes of NMS ordination of floristic data, using Pearson's correlation coefficient (r). Significant correlations are indicated by: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

	Axis 1		Axis 2	
Bryophyte cover	-0.620	***	-0.137	
Bare rock	0.805	***	-0.030	
Bare earth	-0.561	***	0.089	
Litter	-0.723	***	0.050	
Fallen wood	-0.295		-0.029	
Slope (degrees)	0.207		-0.287	
No. saplings / 225m^2	-0.064		-0.011	
No. adult trees / 225m^2	-0.395	*	0.218	
Adult tree basal area (cm^2/ 225m^2)	-0.821	***	0.062	
Adult yew tree basal area (cm^2/ 225m^2)	-0.548	**	0.177	
Species richness	0.665	***	-0.563	***
Thorniness (%)	0.399	*	0.471	**
Non-nativeness (%)	-0.022		-0.065	

Table 3.3 Frequency of non-native species in yew community relevés

Species	Frequency (n/31)
Abies alba	1
Acer pseudoplatanus	5
Clematis vitalba	3
Cotoneaster integrifolius	4
Fagus sylvatica	11
Mycelis muralis	9
Pinus sylvestris	3
Pseudotsuga menziesii	1
Rhododendron ponticum	5
Viburnum tinus	2

Table 3.4 Floristic data and environmental variables for the eight vegetation types defined by cluster analysis. Figures represent mean Domin scores except where otherwise stated. Asterisks (*) indicate non-native species. Dominant species scores (≥ 6.0) are in bold type.

	Sesleria-Teucrium pavement	*Taxus-Fraxinus* scrub/ pavement	*Corylus-Hedera* scrub	*Taxus-Corylus* scrub / woodland	*Taxus-Fraxinus* woodland	*Taxus* woodland	*Cotoneaster Calluna* heath	*Quercus-Ilex* woodland
No.of relevés	4	4	1	4	5	8	2	3
Bryophyte cover	2.5	3.0	10.0	9.0	6.6	7.6	7.5	8.0
Bare earth	0.0	1.3	2.0	1.5	2.2	1.8	1.5	2.7
Bare rock	9.0	7.5	0.0	2.25	2.0	2.6	6.5	2.0
Litter	1.0	2.5	2.0	3.3	7.0	5.8	2.0	5.7
Fallen wood	0.0	0.5	4.0	2.8	1.8	0.4	1.0	3.3
Mean species richness (spp. / relevé)	34.3	28.3	17.0	35.5	16.4	10.0	42.0	23.0
No. adult trees (ha^{-1})	13.3	349.5	2400.0	1568.9	1688.9	782.2	555.6	844.4
Adult tree basal area (m^2 / ha^{-1})	0.02	10.5	41.7	45.6	57.8	66.8	15.8	58.8
Adult yew basal area (m^2 / ha^{-1})	0.0	8.5	0.28	25.7	34.7	58.9	6.7	11.0
Non-nativeness (%)	3.7	8.4	10.0	3.1	12.0	5.8	18.0	3.4
Thorniness (%)	3.6	9.9	18.0	1.2	2.1	0.3	1.8	0.7
**Abies alba*	-	-	-	-	0.8	-	-	-
**Acer pseudoplatanus*	-	0.3	-	-	0.2	0.1	0.5	-
Agrostis canina	-	-	-	0.5	-	-	-	-
Agrostis capillaris	-	-	-	-	-	-	-	1.3
Ajuga reptans	-	-	-	0.3	0.2	-	-	-
Anthoxanthum odoratum	-	0.3	-	0.5	-	-	-	-
Arbutus unedo	-	-	-	3.3	-	-	4.5	-
Arum maculatum	-	-	2.0	-	0.2	0.1	-	-
Asperula cynanchica	0.3	-	-	-	-	-	-	-
Asplenium ruta-muraria	-	-	-	-	0.2	-	-	-
Asplenium adiantum-nigrum	1.0	1.0	-	-	-	-	-	-
Asplenium ceterach	0.8	1.0	-	-	-	-	0.5	-
Asplenium scolopendrium	0.8	-	-	0.5	0.6	0.3	0.5	-
Asplenium trichomanes	1.0	0.8	-	-	0.2	-	-	-
Athyrium felix-femina	-	-	-	-	-	-	-	0.3
Avenula pubescens	-	0.3	-	-	0.2	-	-	-
Betula pubescens	-	-	-	1.8	-	-	1.0	3.3
Blechnum spicant	-	-	-	-	-	-	-	1.7
Brachypodium sylvaticum	0.3	1.8	2.0	4.3	-	0.3	1.0	1.0
Briza media	0.3	-	-	-	-	-	0.5	-
Calluna vulgaris	0.3	-	-	1.5	-	-	4.0	1.7
Campanula rotundifolia	0.3	0.3	-	-	-	-	-	-
Carex flacca	1.8	1.3	3.0	0.5	-	-	1.5	-
Carex pulicaris	0.3	0.3	-	1.5	-	-	1.0	-
Carex remota	-	-	-	-	-	-	-	0.3
Carex rostrata	0.3	-	-	-	-	-	-	-
Carex sylvatica	-	-	-	1.5	0.2	0.3	1.0	-
Carlina vulgaris	1.0	0.3	-	-	-	-	-	-
Centranthus ruber	-	0.5	-	-	-	-	-	-
Circaea lutetiana	-	-	-	-	0.2	-	-	-
Cirsium arvensis	-	0.3	-	-	-	-	-	-
**Clematis vitalba*	-	1.0	-	-	-	-	2.5	-

Table 3.4 continued.

Conopodium majus	-	-	-	0.3	-	-	-	-
Corylus avellana	2.3	1.3	**8.0**	4.5	1.8	1.9	2.0	0.3
**Cotoneaster integrifolius*	-	1.8	-	-	-	-	**7.5**	-
Crataegus monogyna	1.3	0.8	4.0	1.0	0.6	0.1	-	0.3
Cytisus scoparia	-	-	-	0.3	-	-	-	-
Dactylis glomerata	-	0.5	-	1.5	-	-	1.0	-
Dactylorhiza fuschii	-	-	-	0.3	-	-	-	-
Dathonia decumbens	-	-	-	-	-	-	1.5	-
Deschampsia flexuosa	-	-	-	-	-	-	-	1.0
Digitalis purpurea	-	-	-	-	-	-	-	0.7
Dryas octopetala	0.3	-	-	-	-	-	-	-
Dryopteris aemula	-	-	-	-	-	-	-	0.7
Dryopteris affinis	-	-	-	0.3	0.4	-	-	-
Dryopteris dilitata	0.3	-	-	0.3	0.2	-	-	0.3
Dryopteris filix-mas	-	-	-	-	0.2	0.1	-	-
Endymion non-scripta	-	-	-	0.3	0.2	-	-	-
Epipactis atrorubens	0.5	-	-	-	-	-	-	-
Erica cinerea	-	-	-	1.0	-	-	2.5	-
Erica tetralix	-	-	-	-	-	-	-	0.7
Euonymus europaea	-	-	2.0	0.3	0.8	-	-	-
Euphorbia hyberna	-	-	-	-	-	-	0.5	1.3
Euphrasia spp.	0.8	-	-	-	-	-	1.0	-
**Fagus sylvatica*	-	-	-	2.0	4.4	1.6	-	0.3
Festuca rubra	1.3	0.3	-	-	-	-	2.0	-
Filipendula vulgaris	-	0.3	-	-	-	-	-	-
Fragaria vesca	-	0.5	-	2.3	0.2	0.3	1.0	-
Fraxinus excelsior	0.8	2.3	-	3.8	5.0	1.6	1.0	0.3
Galium saxatile	0.3	-	-	-	-	-	-	0.3
Galium sterneri	-	-	-	0.3	-	-	0.5	-
Geranium molle	-	0.5	-	-	-	-	-	-
Geranium robertianum	1.5	1.3	-	0.8	0.8	0.3	1.0	-
Geranium sanguinuem	2.0	1.0	-	-	-	-	-	-
Geum urbanum	-	-	1.0	-	-	-	-	-
Hedera helix	1.3	2.0	**8.0**	2.3	5.6	2.6	2.5	1.3
Hieracium spp.	0.3	0.3	-	-	-	-	-	-
Holcus lanatus	-	-	-	0.3	-	-	-	-
Hypericum androsaemum	-	-	-	0.5	0.2	-	-	-
Hypericum pulchrum	0.5	-	-	1.8	-	-	1.0	-
Hypochoeris radicata	0.3	-	-	-	-	-	-	-
Ilex aquifolium	0.3	2.0	-	4.0	3.8	1.9	1.0	**6.3**
Juncus bulbosus	-	-	-	-	-	-	-	1.0
Juncus conglomeratus	-	-	-	-	-	-	-	0.3
Juncus effusus	-	-	-	-	-	-	-	0.3
Juniperus communis	0.3	1.3	-	-	-	-	-	-
Lathyrus montanusa	-	-	-	0.3	-	-	0.5	-
Linum catharticum	0.8	-	-	-	-	-	0.5	-
Listera ovata	0.3	-	-	-	-	-	-	-
Lolium perenne	0.3	-	-	-	-	-	-	-
Lonicera periclymenum	-	0.5	1.0	1.3	1.2	0.5	-	1.0
Lotus corniculatus	1.3	0.5	-	0.3	-	-	2.5	-
Luzula multiflora	-	-	-	0.3	-	-	-	-
Luzula sylvatica	-	-	-	0.8	0.2	-	-	2.3
Malus sylvestris	-	0.3	-	-	1.4	-	-	-
Melica uniflora	-	-	-	0.3	-	-	-	-

Table 3.4 continued.

Molinia caerulea	0.5	-	-	-	-	-	-	1.7
**Mycelis muralis*	1.8	1.5	-	-	-	-	-	-
Oxalis acetosella	-	-	-	0.3	0.2	0.1	-	1.7
Pilosella officinarum	0.5	0.5	-	-	-	-	0.5	-
**Pinus sylvestris*	-	1.0	-	-	-	-	1.0	-
Plantago lanceolata	0.3	-	-	0.3	-	-	1.5	-
Poa pratensis	0.3	-	-	-	-	-	-	-
Polypodium spp.	-	-	-	-	0.2	-	-	0.7
Polystichum setiferum	-	-	-	-	1.6	0.1	-	-
Polygala vulgaris	0.5	0.3	-	-	-	-	1.5	-
Potentilla erecta	1.0	-	-	-	-	-	-	0.3
Potentilla sterilis	-	-	1.0	0.5	-	-	-	-
Primula vulgaris	-	-	1.0	-	-	-	-	-
Prunus avium	-	-	-	0.3	0.2	-	-	-
Prunus spinosa	1.3	2.0	5.0	-	0.4	-	-	-
**Pseudotsuga menziesii*	-	-	5.0	-	-	-	-	-
Pteridium aquilinum	0.5	-	-	0.3	-	-	-	2.0
Quercus spp.	-	0.3	-	3.0	3.0	3.9	1.0	**6.3**
Ranunculus bulbosa	0.3	-	-	-	-	-	-	-
Ranunculus repens	-	-	-	-	0.2	-	-	-
Rhamnus cathartica	-	0.5	-	-	-	-	-	-
**Rhododendron ponticum*	-	-	-	0.5	-	-	-	1.3
Rosa spp.	-	-	-	0.5	0.2	-	-	-
Rosa canina	-	0.3	-	-	-	0.1	-	-
Rosa pimpinellafolia	2.3	1.8	1.0	0.3	-	-	1.0	-
Rosa rubiginosa	-	0.3	-	-	-	-	-	-
Rubia peregrina	0.3	-	-	2.5	-	-	2.0	0.3
Rubus fruticosus	0.3	2.3	-	2.5	1.8	0.8	1.5	0.7
Salix aurita	-	-	-	-	-	-	0.5	-
Salix cinerea	0.3	-	-	-	-	-	-	-
Sanicula europaea	-	-	-	3.0	1.0	-	-	-
Saxifraga spathularis	-	-	-	-	-	-	-	0.3
Senecio jacobea	1.0	1.0	-	0.3	-	-	-	-
Sesleria caerulea	4.0	1.5	-	-	-	-	-	-
Solidago virgaurea	-	0.3	-	1.0	-	-	1.0	-
Sonchus asper	0.8	-	-	-	-	-	-	-
Sorbus aria	-	1.5	-	0.3	-	-	0.5	-
Sorbus aucuparia	-	-	-	0.8	0.4	0.1	0.5	1.3
Succisa pratensis	0.5	-	-	2.3	-	-	2.5	-
Taraxacum officinale	0.8	0.8	-	0.3	-	0.1	0.5	-
Taxus baccata	1.0	4.3	4.0	**6.8**	**6.6**	**8.1**	4.0	5.0
Teucrium scorodonia	2.5	2.3	-	2.0	-	-	1.5	-
Thymus praecox	1.8	0.3	-	-	-	-	1.0	-
Ulex europaeus	-	1.0	-	-	-	-	1.5	-
Ulmus glabra	-	-	-	-	1.0	-	-	-
Vaccinium myrtillus	-	-	-	0.8	-	-	-	2.3
Veronica chamaedrys	-	-	-	0.8	0.2	-	-	-
Veronica officinale	-	-	-	0.5	-	-	-	-
Viburnum opulus	-	0.3	-	-	0.2	-	-	-
**Viburnum tinus*	-	-	-	-	-	-	2.5	-
Vicia sepium	-	-	1.0	0.3	-	-	-	-
Viola spp.	1.3	-	1.0	4.0	0.8	1.0	2.0	0.7

Figure 3.4 NMS ordination of the yew community relevés indicating the non-native percentage of the vegetation.

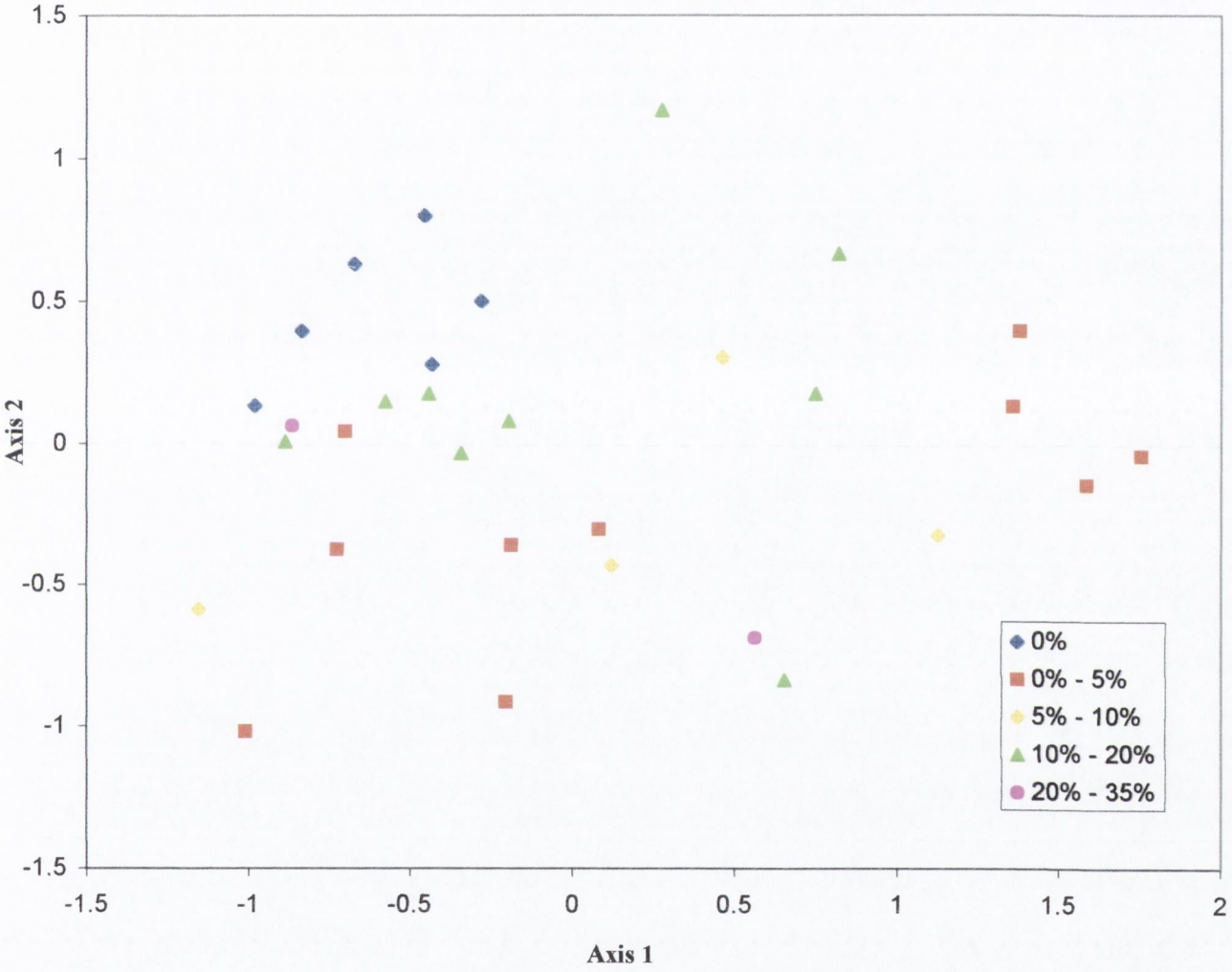


Figure 3.5 Cluster dendrogram showing the successive flexible-beta clustering of the relevé data. Colours indicate vegetation types defined by this analysis at the eight-group level.

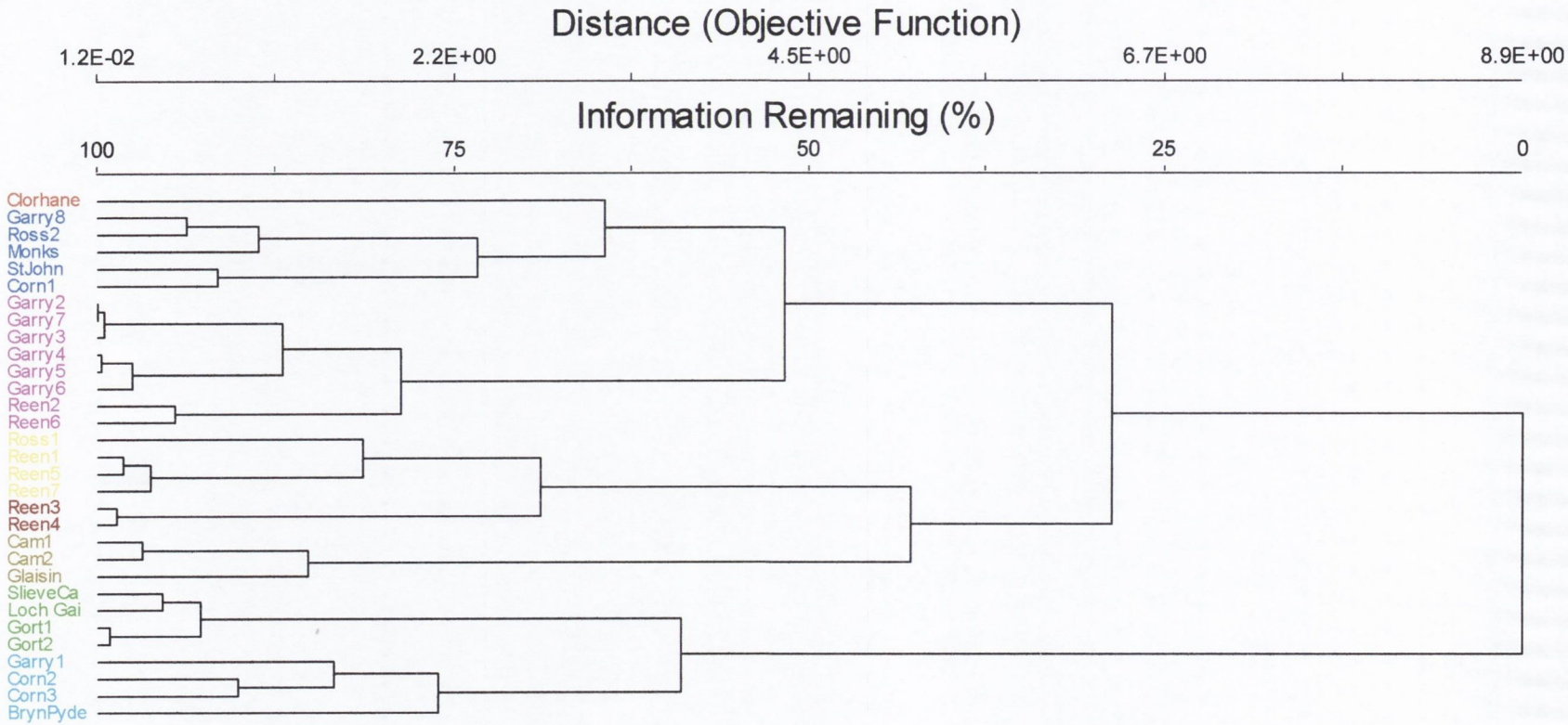
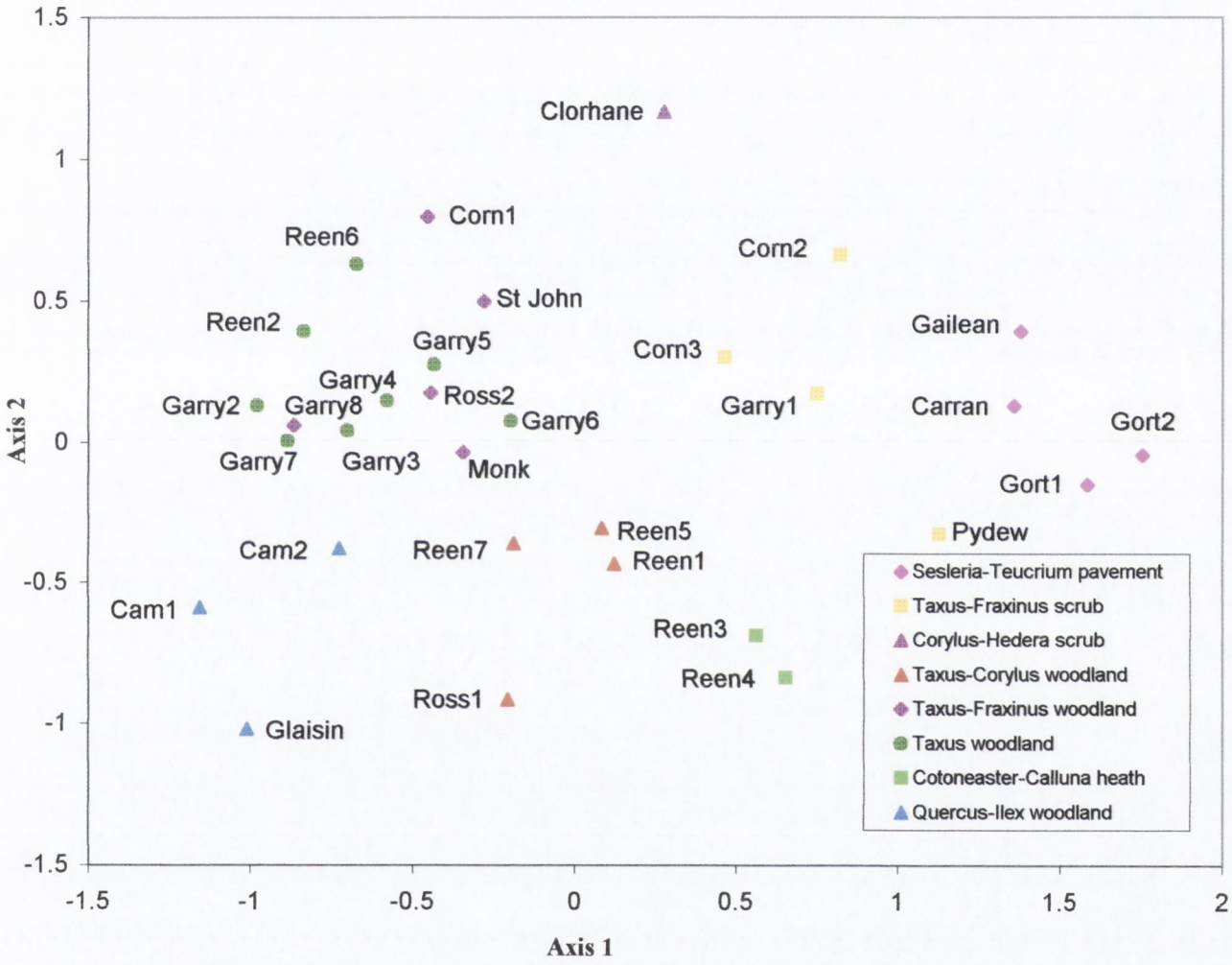


Figure 3.6 NMS ordination of the yew community relevés showing the distribution of the eight vegetation types identified by flexible-beta cluster analysis.



***Taxus - Fraxinus* scrub / pavement:**

This vegetation type, which included the Welsh site of Bryn Pydew, is similar to the *Sesleria-Teucrium* community, but is differentiated by the presence of a few adult trees, particularly yew and ash. Bare rock is still the dominant feature though and species richness is again high. Many of the herbaceous species noted in the first community also occur here, but there is an increased abundance of species more characteristic of woodland such as *Hedera helix*, *Rubus fruticosus* agg. and holly. Thorny shrubs, including juniper, gorse and blackthorn, were frequent at the Cornalack site (Plate 3.2), where the invasive alien *Cotoneaster integrifolius* was also present.

***Corylus - Hedera* scrub:**

This vegetation type was represented by only one relevé, that at the limestone outcrop at Clorhane (Plate 3.3). It may best be described as a dense hazel scrub, with a carpet of *Hedera helix* and bryophytes, and has probably been differentiated from the following vegetation type chiefly by its low species richness and the substantial presence of the non-native *Pseudotsuga menziesii*. Other trees present included hawthorn and spindle, whilst saplings of blackthorn were abundant. In and around the relevé, yew occurred as a suppressed understorey tree, although it does reach the canopy in marginal areas of the woodland.

***Taxus – Corylus* scrub / woodland:**

This is a species-rich vegetation type which, within the sites sampled, was restricted to the Killarney area (Plate 3.4). The chief tree species are yew and hazel, but pedunculate oak, ash, birch and holly are also frequent, particularly where deeper soils have developed. *Arbutus unedo* is occasional. An almost continuous layer of bryophytes covers the limestone. Common herbs include *Sanicula europaea*, *Succisa pratensis*, *Fragaria vesca*, *Teucrium scorodonia*, *Hypericum pulchrum* and *Viola riviniana / reichenbachiana*. Woody field layer plants include *Lonicera periclymenum*, *Hedera helix*, *Rubus fruticosus* and *Rubia peregrina*. Grasses and sedges, particularly *Brachypodium sylvaticum*, *Carex sylvatica* and *Carex pulicaris* may form small patches under breaks in the canopy. There is also a heath-like element to the flora with scattered occurrences of *Calluna vulgaris*, *Erica cinerea*, *Pteridium aquilinum* and *Vaccinium myrtillus*, reflecting the localised occurrence of acidic soils (cf. Kelly 1981).

***Taxus – Fraxinus* woodland:**

This is a fairly broad vegetation type which includes relevés from a number of different sites. The characteristic features, however, are a canopy of yew and ash with an understorey composed largely of hazel or holly (Plate 3.5). Oak may be also be present. Bryophytes are

not as dominant as in the previous vegetation type, with *Hedera helix* covering much of the ground, alongside *Rubus fruticosus* and *Lonicera periclymenum*. Species richness is also much lower, although ferns may be well represented, with *Asplenium scolopendrium, Dryopteris affinis, D. dilatata, D. filix-mas* and *Polystichum setiferum* all recorded. The only common herbs are *Geranium robertianum*, *Sanicula europaea* or *Viola riviniana / reichenbachiana*. This vegetation type also includes stands substantially invaded by *Fagus sylvatica*, for example the relevés at Ross Island, Monk's Wood and Garryland Wood.

***Taxus* woodland:**

This is a very species poor vegetation type with a canopy dominated by yew, although ash, beech and pedunculate oak may also occur (Plate 3.6). This is a mature stand type with low tree densities and high basal areas. The understorey tends to be non-existent or sparsely distributed trees of holly or hazel. Bryophytes are again abundant, although litter cover can be considerable where pedunculate oak or beech occur. The field layer is very scanty, with scattered occurrences of *Asplenium scolopendrium*, *Fragaria vesca*, *Lonicera periclymenum*, *Rubus fruticosus* and *Viola riviniana / reichenbachiana. Hedera helix* may also be present, but may be restricted largely to the canopy. This woodland type occurs both at Reenadinna Wood and on limestone outcroppings at Garryland Wood.

***Cotoneaster – Calluna* heath:**

This is a fairly specific vegetation type restricted to the cliff top areas on the southern side of the Muckross Peninsula (Plate 3.7). The vegetation is dominated by smothering expanses of *Cotoneaster integrifolius* which may be up to 2m in height in places. These expanses form a mosaic with patches of *Calluna vulgaris* and *Erica cinerea*, and less frequently *Ulex europaeus*. There are also sizeable areas of bare limestone which harbour many of the species typical of the *Sesleria-Teucrium* vegetation type found in the Burren, including *Euphrasia* spp., *Linum catharticum*, *Lotus corniculatus*, *Polygala vulgaris*, *Rosa pimpinellifolia* and *Thymus praecox*. Scattered trees are principally *Arbutus unedo*, yew and whitebeam (*Sorbus aria* agg.) Some areas of the pavement have also been colonised by the alien creeper *Clematis vitalba*. Despite the high non-native element to the vegetation, these sites were the most diverse in terms of vascular species.

***Quercus – Ilex* woodland:**

This vegetation type included the three sandstone relevés from Camillan and the upland oakwood of Glaisín na Marbh (Plate 3.8). The canopy in these stands is dominated by sessile oak and birch with yew and occasionally rowan. Holly forms the understorey and the field layer is largely composed of *Luzula sylvatica* and *Vaccinium myrtillus*. Other characteristic

Plate 3.1 *Sesleria-Teucrium* pavement vegetation type at Slievecarran, Co. Clare. Note *Taxus* at bottom of picture and low *Corylus* bushes (June 2002).

Plate 3.2 *Taxus-Fraxinus* scrub vegetation type at Cornalack, Co. Tipperary. Note *Sorbus aria* agg. to left of picture and *Cotoneaster integrifolious* beneath *Taxus* trees (September 2002).

Plate 3.3 *Corylus-Hedera* scrub vegetation type at Clorhane, Co. Offaly. Note *Euonymus europaeus* sapling in foreground (June 2002).

Plate 3.4 *Taxus-Corylus* scrub woodland vegetation type at Reenadinna Wood, Co. Kerry. Note *Calluna vulgaris* in foreground (July 2002).

Plate 3.5 *Taxus-Fraxinus* woodland vegetation type at St. John's Wood, Co. Roscommon (September 2002).

Plate 3.6 *Taxus* woodland vegetation type at Reenadinna Wood, Co. Kerry. Note bark damage on several of the trees (September 2001).

Plate 3.7 *Cotoneaster-Calluna* heath vegetation type at Reenadinna Wood, Co. Kerry (July 2002).

Plate 3.8 *Quercus-Ilex* woodland vegetation type at Glaisín na Marbh, Co. Kerry. Note *Molinia caerulea* in foreground (July 2002).

species include *Calluna vulgaris*, *Blechnum spicant*, *Euphorbia hyberna* and *Pteridium aquilinum*. Bryophytes were particularly abundant at the higher elevations of Glaisín na Marbh. The occurrence of wetter soils here is indicated by the presence of *Molinia caerulea*, *Juncus* spp. and *Sphagnum* spp., although individuals of yew were invariably associated with localised outcroppings of rock.

Growth form of yew

A variety of growth forms were exhibited by yew between the sites. In some parts of the Burren, yew occurs as a prostrate but exceedingly dense and well foliaged shrub (Plate 3.9). Metal cages were placed over some of these plants by staff of the Burren National Park in the early 1990s. This has resulted in an obvious increase in the height of the plants, which have grown to almost fill the cages in some cases (Plate 3.10). Evidently, browsing - presumably by feral goats - rather than exposure, is responsible for the dwarf form of yew in this area.

The ability of these plants, and those of hawthorn and hazel, to persist for long periods under heavy browsing pressure is evinced by their large basal girths in relation to their height (Table 3.5). Furthermore, in several cases a large proportion of their main stem was below the level of the pavement (Table 3.5) as these plants were often rooted at the bottom of grykes. This would afford young plants some initial protection and enable them to become established before they grow to a point where they become susceptible to browsing. Hence, they would have structural reserves to respond to browsing. There are however, distinct differences in the growth form between species (Fig. 3.7a-c). Yew grows as a compact low shrub, filling the grykes and spreading out across the pavement. Hazel forms slightly taller, less dense bushes with multiple protruding bare stems. Hawthorn and blackthorn, however, grow as gnarled and spindly plants with very little foliage.

Table 3.5 Sample measurements of seedlings and saplings growing on limestone pavement in the Burren. Data are from two 15 x 15 m relevés at Gortlecka.

Species	Height of plant above surface of pavement (cm)	Total height of plant (cm)	Girth of plant near base (cm)
Taxus baccata	13	46	15
Taxus baccata	23	66	9
Taxus baccata	38	38	12
Crataegus monogyna	58	85	22
Crataegus monogyna	22	85	13
Crataegus monogyna	20	40	10
Crataegus monogyna	38	48	8
Crataegus monogyna	68	68	13
Crataegus monogyna	27	27	11
Crataegus monogyna	50	50	17
Crataegus monogyna	67	67	27
Corylus avellana	10	34	3
Corylus avellana	12	12	<1

Figure 3.7 Growth form of species on open limestone pavement / scrub sites: (a-c) heavily browsed tree species in the Burren, (d,e) growth of central stem from broad, prostrate *Taxus,* Garryland Wood, (f) ungrazed shrub at Bryn Pydew.

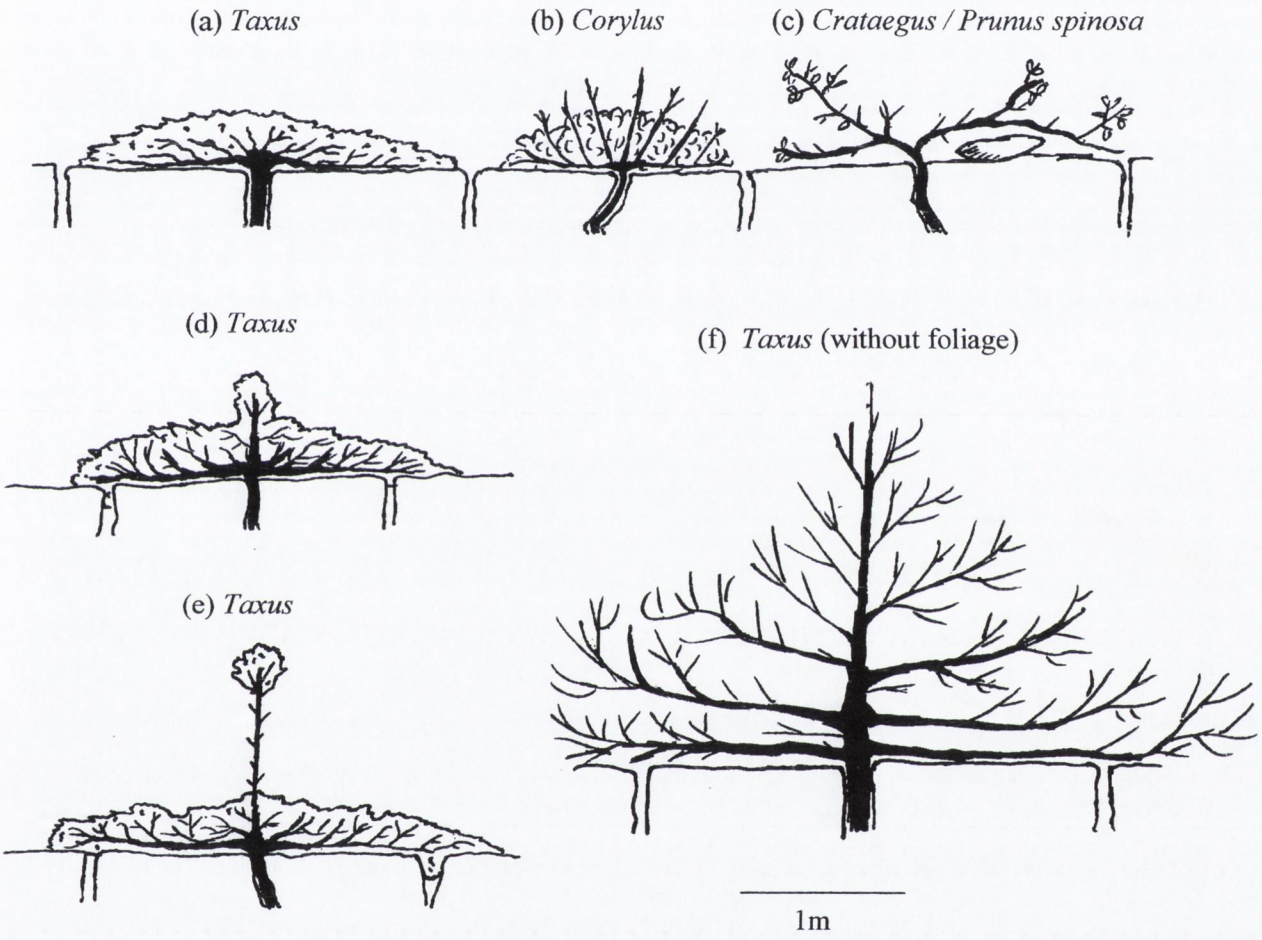


Plate 3.9 *Taxus* growing as low shrub on limestone pavement, Gortlecka, Co. Clare (June 2002).

Plate 3.10 *Taxus* released from feral goat browsing by protective cage, Gortlecka, Co. Clare (June 2002).

Plate 3.11 Broad *Taxus* shrub, approximately 1.5m high, growing on limestone pavement, near Lough Gailean, Co. Clare (June 2002).

Plate 3.12 *Taxus* shrub growing on rocky limestone outcropping in Garryland Wood, Co. Galway (June 2002).

Plate 3.13 Multi-stemmed *Taxus* tree growing on rocky limestone outcropping in Garryland Wood, Co. Galway, with heavily browsed *Taxus* in foreground (June 2002).

Plate 3.14 *Taxus* growing on limestone cliffs at Mullagh More, Co. Clare (June 2002).

Plate 3.15 Partially uprooted *Taxus* tree in Garryland Wood, Co. Galway, showing the shallowness of the root plate (June 2002).

Plate 3.16 Heavily browsed and layered *Taxus* branch, growing in deep shade in Garryland Wood, Co. Galway. Parent tree is to the right. (June 2002).

These observations also suggested a mechanism by which prostrate yew plants may eventually develop into trees despite heavy browsing pressure. As the plants grow outwards across the pavement, their breadth and the density of shoots increases to a point where central shoots become less accessible to browsing animals. A central vertical stem develops (Fig. 3.7d,e; Plates 3.11 & 3.12), which appears to be periodically browsed back, but eventually reaches a height where the leading shoots are no longer vulnerable to animals. At Bryn Pydew, a potential further stage was observed; young adult trees (gbh 10-20cm) with multiple low branches creating a spreading shrub only 3m tall, but covering an area 4-5m in diameter (Fig 3.7f.). At an open site in Garryland Wood, there were taller trees (7-8m) with multiple stems, which may represent a further stage (Plate 3.13). The vulnerability of yew to browsing was also demonstrated by the restriction of mature trees in the Mullaghmore area of the Burren to the cliff faces (Plate 3.14).

A final character worthy of note is the apparent plasticity of yew growth. Several fallen or severely leaning yew trees were observed during the course of this study, exposing the shallow root plate that develops on limestone pavement sites (Plate 3.15). Invariably however, these trees were still alive and sending up new vertical shoots from the main trunk. In a similar fashion, where low branches of old yew trees had hung down and come into contact with soil, layering was observed (Plate 3.16).

3.2.5 Discussion

It is apparent that yew is a component of several vegetation types in Ireland. Of these, some are evidently differentiated by edaphic conditions whereas others appear to intergrade and may represent stages along the same successional pathway. Grazing pressure and invasion by non-native species are also having serious impacts on the place of yew in the native vegetation.

A successional sequence for the development of Irish yew-woods is proposed by these results and is outlined here. Yew is present in species-rich open limestone pavement communities, defined in this study as the *Sesleria-Teucrium* vegetation type. It is able to persist for long periods even when heavily browsed due to the protection offered by grykes in the pavement. To grow into a tall shrub, however, it must escape from this browsing pressure. A potential morphological mechanism exists to permit this, but the use of spiny nurse shrubs as protection is likely to be more widely applicable. Watt (1926) defined two distinct seres in the development of yew-woods in southern England, dominated by either juniper or hawthorn, whilst Hulme (1996) found that an ash / hawthorn scrub stage was involved in the

development of yew communities on the Magnesian limestone of north-east England. Spiny shrubs, including juniper, were also found to be associated with yew regeneration in southern Spain (García *et al.* 2000). Kelly & Jeffrey (1987) described both gorse and blackthorn thickets as important stages in woodland succession on Irish eskers. All four of these spiny species were present in the *Taxus-Fraxinus* scrub / pavement vegetation type which appears to be the second stage in the sequence, but it is not apparent from the present data which, if any, plays the most important role

It is clear that ash, and particularly hazel, also benefit from the protection of the thorny nurse shrubs. From an exhaustive review of the European literature, Vera (2000) concluded that thorn shrub protection was a key factor in the regeneration of hazel. Hazel is a constant associate with yew throughout the successional sequence and, as it is faster growing, the next stage appears to be the development of dense hazel scrub, represented in this study by the species-poor *Corylus-Hedera* scrub vegetation type at Clorhane. At this point, under the increased shade, an extensive bryophyte layer develops. With time, yew begins to overtop the aggrading hazel stand and outcompete it due through heavy shade. A more open *Taxus-Corylus* scrub woodland vegetation type is formed. Eventually, as the yew canopy closes, the hazel component in woodland on limestone pavement is virtually eliminated. The only species which are able to persist in the *Taxus* woodland are shade tolerant plants such as holly and *Hedera helix*. The *Quercus-Ilex* woodland vegetation type on sandstone obviously lies outside this successional pathway, as does probably *Taxus-Fraxinus* woodland on deeper calcareous soils (e.g St. John's Wood).

Woodland dominated by yew to an extent such as at Reenadinna Wood and Garryland Wood is rare in Europe outside of Ireland and Britain. Hence, such vegetation has been specifically classified under the EU Habitats Directive as the priority habitat "*Taxus baccata* woods of the British Isles" (European Commission 1999). The restricted geographical range of these habitats is further highlighted by Bugała (1978) who, writing from an east European viewpoint, claimed that yew "never forms compact pure stands but occurs singly or in groups in the undergrowth of broadleaf and mixed forests". Ecologists have therefore struggled to accommodate this habitat type within essentially Continental phytosociological frameworks. Delelis-Dusollier & Gehú (1972) assigned vegetation samples from fairly species-rich yew scrub in south-east England to a *Rosa-Sorbetum ariae* which they perceived as the equivalent of the *Taxo-Prunetum mahalebis* community which occurs on chalk cliffs in France. According to Rodwell (1991), species-poor mature *Taxus* woodland in Britain is best regarded as part of the Fagion alliance, in the Querco-Fagetea alongside continental communities such as the *Taxo-Fagetum*. Kelly (1981) more specifically classified yew stands

in Reenadinna Wood as a facies of the *Corylo-Fraxinetum* association (cf. Braun-Blanquet & Tüxen 1952) within the Querco-Fagetea .

The most direct and informative comparisons to the *Taxus* woodland vegetation type defined by this study are therefore to be made with the W13 *Taxus baccata* woodland community of the British NVC (National Vegetation Classification; Rodwell 1991). These woodlands are largely confined to the chalk of the North and South Downs in southern England. No tree species other than yew is more than occasional here, although whitebeam is a characteristic associate, and indeed, where it is fairly frequent, this species defines a sub-community. Ash may occasionally emerge from the canopy and beech, pedunculate oak and sycamore (*Acer pseudoplatanus*) may be widely scattered. Beneath the heavy canopy, shrubs are rare, comprising spindly individuals of elder and less often holly, spindle, hawthorn, or dogwood (*Cornus sanguineus*). Box (*Buxus sempervirens*) may be very locally dominant. The field layer is extremely sparse with the most common species being *Mercurialis perennis* which, where more plentiful, defines a second sub-community. Occasional species include *Urtica dioica, Hedera helix, Brachypodium sylvaticum, Arum maculatum, Rubus fruticosus* agg., *Viola* spp., *Glechoma hederacea* and *Fragaria vesca*. Bryophyte cover is low, with *Eurhyncium praelongum*, the most common species, occasional at most. An outlying yew-wood community (approximately 22 ha in extent) occurs on the Magnesian limestone at Castle Eden Dene, Co. Durham. The field layer here is similarly sparse, with *Mercurialis perennis* a constant species and *Rubus fruticosus* agg., *Hedera helix*, *Sanicula europaea* and *Dryopteris* spp. usually present (R. Lamboll, pers. comm.).

Irish and English yew dominated stands would therefore appear to have several characteristic species in common (e.g. ash, *Brachypodium sylvaticum*, *Viola* spp. and *Fragaria vesca*), but also several distinguishing features. Box, for example, is not native to Ireland, whilst *Mercurialis perennis* is of dubious native status (Webb *et al.* 1996). These species are thus rare in Ireland and generally found only where deliberately introduced. Both were absent from the *Taxus* woodland vegetation type, as was whitebeam which was restricted to the more open vegetation types (Table 3.4). Remnants of juniper nurse shrubs beneath adult yew trees, a common characteristic of English yew-woods (Rodwell 1991), were not found in any of the Irish woods. There is a significant difference in bryophyte cover, which is luxuriant on the limestone rocks of the Irish stands, but is sparse in the English woods on chalk. This is probably related not only to the suitability of the substratum, but also the markedly more oceanic climate in western Ireland. The heath-like vegetation element observed on pockets of acidic soils in the Irish woods does not occur in the English woods on chalk and conversely, elder and *Urtica dioica*, two species associated with phosphorus-rich soils (Pigott & Taylor

1964), were not recorded in any of the Irish relevés. One of the most important differences, however, is the association of yew with hazel in the Irish woods. Hazel does not feature at all in the floristic table for W13 woodland (Rodwell 1991), although notably, Hulme (1996) reports it as present in the limestone yew communities in Co. Durham.

The Welsh pavement site at Bryn Pydew ordinated closely to the Irish pavement sites and was grouped in the *Taxus-Fraxinus* scrub pavement vegetation site by the cluster analysis (Fig. 6), demonstrating a close relationship between this habitat type in the two countries. Limestone pavement is a very rare habitat in Wales. A national survey by Deacon (1997) recorded only 6.7 ha of pavement habitat of varying quality, distributed between 38 sites. Notably, yew was recorded as present at 6 of these 38 sites. A yew dominated stand occurs in Scotland on the island of Inchlonaig in Loch Lomond, although this is reputed to have been planted by Robert the Bruce in the 14th century for the provision of bow staves (Mitchell 1974). The ground cover is composed of *Holcus mollis, Agrostis tenuis, Oxalis acetosella* and *Pteridium aquilinum* on the lower part of the island, with *Calluna vulgaris, Vaccinium myrtillus* and *Deschampsia flexuosa* in the upper parts (A. Carstairs, unpublished data). These species appear to represent a more open woodland structure than occurs in Ireland. Woody epiphytic species, including birch, holly and rowan, found on the Inchlonaig yews (Pilkington *et al.* 1994) were not noted during the present study or that of Kelly (1981).

Non-native species have markedly changed the character of the native vegetation at some of the sites surveyed in this study. The two important plants in this regard are *Cotoneaster integrifolius* and beech. *Cotoneaster* spp. are commonly grown in Irish gardens but, because they are bird dispersed, naturalised individuals can occur in remote places (Webb *et al.* 1996). *C. integrifolius* has become locally dominant at both Cornalack and Reenadinna, forming a dense, monospecific blanket across the limestone pavement and outcompeting native species. It has established in parts of the Burren, according Nelson & Walsh (1991). The impact of this exotic on native vegetation has probably been underestimated in the past and is worthy of further investigation. Beech featured strongly in the *Taxus-Fraxinus* vegetation type; it is largely due to this species that relevés from Monk's Wood, Garryland (Garry 8) and Ross Island (Ross 2) were differentiated from the *Taxus* woodland vegetation type relevés from Reenadinna. Beech has been widely planted in Ireland and is to able invade and dominate woodland on both acid and basic soils (Dierschke 1982), but this process has also been little investiagted. The potential for beech to dominate over yew is attested by woodland types in Britain; yew occurs as an understorey tree in both the W14 *Fagus sylvatica-Rubus fruticosus* and W15 *Fagus sylvatica-Deschampsia flexuosa* woodland communities of southern England (Rodwell 1991). Peterken (1996) has suggested that there is a weak case against allowing

beech into woods beyond its native range in Britain, as its spread across the country was originally arrested by human fragmentation of the wooded landscape. Whether beech might therefore have arrived in Ireland without being introduced is a matter of speculation, but with so little native Irish woodland left, a *laissez-faire* attitude to beech invasion can be ill afforded.

Soil depth appears be an important factor in determining whether yew is able to dominate. The remaining two relevés in the poorly defined *Taxus-Fraxinus* woodland vegetation type, at St. John's Wood and at Cornalack (Corn 1), were in areas where the limestone bedrock was overlain by soil. In these circumstances, yew appears to lose its competitive advantage and ash becomes an important element in the canopy. Watt (1926) proposed that a yew-ash wood stage would eventually succeed to mature yew-wood. This seems possible at sites such at Cornalack (Corn 1) where yew forms a definite understorey, but less likely at St. John's Wood where yew is an infrequent tree. Watt (1926) also noted that yew-woods were largely confined to steeper chalk slopes with shallower soils; in the valleys bottoms or on the plateaux above, beech or ash were more likely to dominate. The ability of yew to grow on shallow or skeletal soils holds on sandstone sites; where yew occurred in Camillan and Glaisín na Marbh it was largely associated with bare boulders. At many of its apparently native stations in Ireland yew occurs on cliffs and rocky terrain on a range of siliceous rock types (see Appendix I). Yew also occurs on bare sandstone in the High Weald of southern England and limestone cliffs in North Wales (pers. obs.). Dickson (1994) reports yew growing on cliffs of limestone, red microgranite and granodiorite in Scotland. Larson *et al.* (2000) found yew could root directly onto the rock of limestone cliffs and proposed that cliffs dominated by stunted-slowing growing yew may represent a primary forest type from which the species originally dispersed into woodland gaps created by early people. Larson *et al.* (2000) found small-statured cliff-bound yews to be in excess of 1000 years old. According to this theory, yew growing on the cliffs at Mullagh More (Plate 3.14), may therefore be remnants of ancient Irish woodland. It is appears that yew can grow on a range of underlying geologies, but gains a competitive advantage where the soils are thin and free-draining. As these conditions are usually associated with a calcareous bedrock, yew dominated communities are restricted to chalk and limestone pavement sites.

In conclusion, this study illustrates that yew occurs in several habitat types in Ireland, on both sandstone and limestone bedrocks, but yew-dominated communities are restricted to limestone pavement sites. The dataset and analysis would be improved by additional relevés, particularly from lake island communities where yew is known to be present. For example, Mitchell (1990b) mentioned the occurrence of yew on Rough Island, which is located

approximately 1.5 km north of Camillan Wood in the southern part of Lough Leane, and is composed of slightly metamorphosed Carboniferous limestone. The woodland canopy is dominated by sessile oak with invading beech, whilst the field layer is dominated by *Luzula sylvatica*. *Arbutus unedo* occurs along the rocky lake shore. Young yew trees are prevalent towards the northern end of island. Batten (1976) reported yew as present on at least three other islands in Lough Leane - Crow Island, Cherry Island and Brown Island – in association with a range of tree species including oak, holly, ash, rowan, whitebeam and beech; on Brown Island saplings up to 1 m high were noted. Turner & Watt (1939) described the vegetation community on Arbutus Island in the Upper Lake, Killarney. Here, yew occurs in mature woodland with sessile oak, rowan and birch, and also in a scrub community with *Arbutus unedo* and holly. The field layer is largely made up of *Vaccinium myrtillus*. Elsewhere, yew is also present on lake islands of Dalradian metamorphic rock in western Connemara; on Oak Island, Lough Anessaundoo, Hannon & Bradshaw (1989) reported that yew occurs in a low canopy with sessile oak, holly, rowan and sally (*Salix cinerea* ssp. *atrocinerea*), with ~~beneath~~ a field layer of *Dryopteris dilatata* and *Luzula sylvatica*. On Birch Island, Lough Derrycunlaghmore, yew was found in similar woodland, but with birch instead of sessile oak.

It would appear from the descriptions available that several of these communities may have some affinity with the *Quercus-Ilex* woodland vegetation type defined by this study, but with possibly some differentiation, including a greater prominence of regenerating yew, due to the lower grazing levels to which the vegetation is subject.

3.3 Introduction to Reendinna Wood

3.3.1 General

Reenadinna Wood (approximately 25 ha in extent) is located on the Muckross Peninsula, Killarney, Co. Kerry. Formerly part of the Muckross Estate, the wood was presented to the state in 1932 as part of the Bourn Vincent Memorial Park. Following subsequent acquisition by the state of the neighbouring Kenmare Estate, these two areas combined to form the Killarney National Park, which was designated as a UNESCO Biosphere Reserve in 1981. The area of the Muckross Peninsula has also been designated a National Heritage Area.

The wood chiefly consists of four main areas, which hereafter will differentiated by the terms North Wood, South Wood, East Wood and West Wood as indicated in Fig. 3.8. The site is bounded to the north by Lough Leane and to the south by Muckross Lake. To the west lie two open grassland areas known as the West Meadow and the Mine Paddock and a small water body called Doo Lough. It is at this point that a geological fault crosses the peninsula –

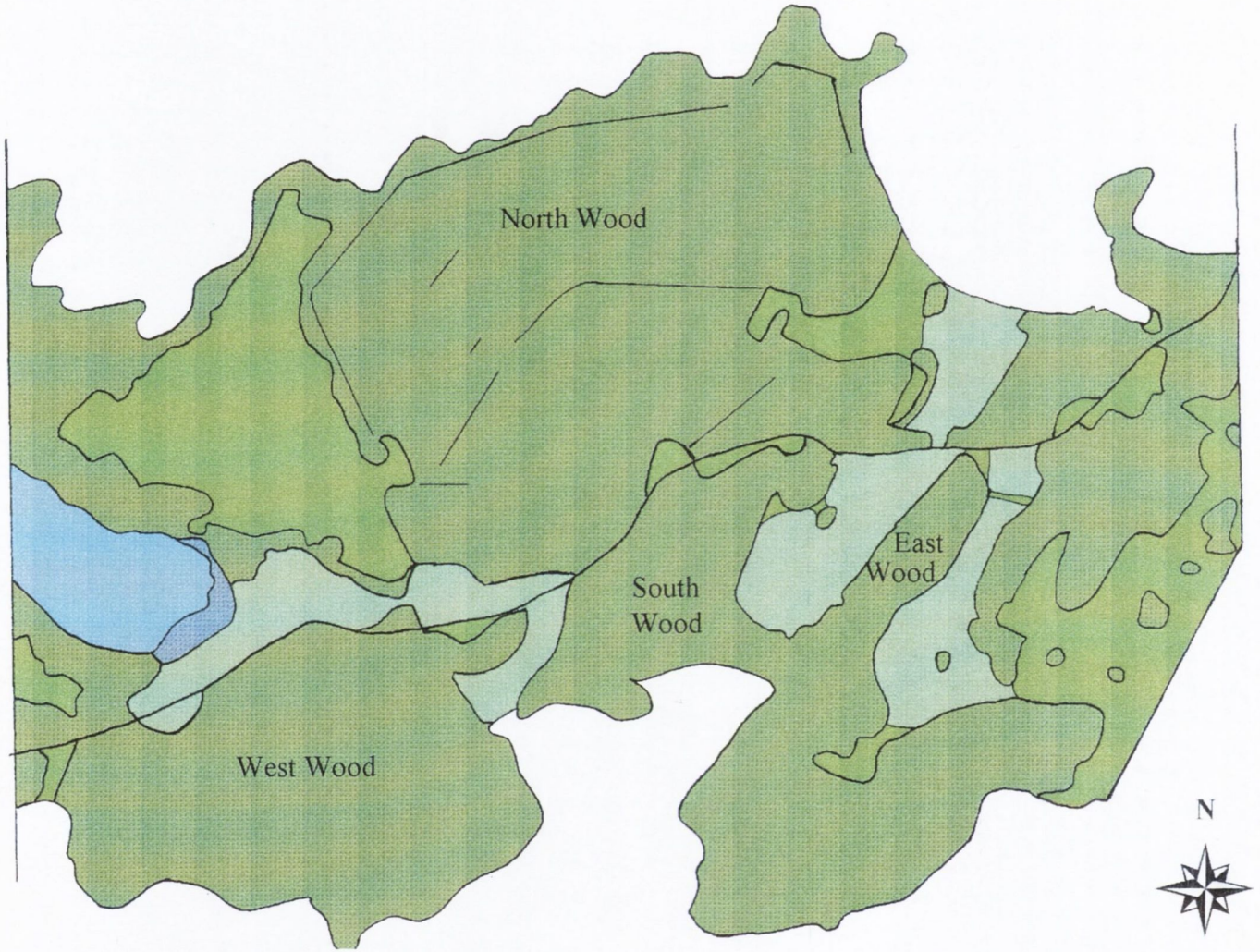


Figure 3.8 Present woodland cover at the eastern end of the Muckross Peninsula: woodland = dark green; light scrub / grassland = light green, seasonal marsh = turquoise, permanent marsh = dark blue, open water = light blue. Areas of Reenadinna Wood are labelled. Black lines in North Wood indicate remnant walls. After Costello & Cotter (1999). Scale 1: 9100

beyond this Devonian Old Red sandstone bedrock supports the oak woodland of Camillan. To the east of the site is the managed parkland and grazing meadows which surround Muckross House.

Reenadinna Wood has been the focus of several research projects in the past. Kelly (1981) described the yew dominated woodland vegetation on the limestone outcroppings, and Kelly & Iremonger (1997) described the fringing wet woodland habitat in a national context. The small mammal populations were studied Smal & Fairley (1980a,b, 1982) and the bird community has been extensively censused over several years (Batten 1976; Carruthers & Gosler 1994, 1995). McCusker (1990) lists 17 species of butterfly which occur in area. Lichens in the wood were recently surveyed by the British Lichen Society (1996) and Sanderson (1996): a species list is presented in Appendix III.

3.3.2 Palaeoecology

The Killarney valley has been intensively studied by palaeoecologists for nearly sixty years; a review of the vegetational history of the area is given by Mitchell & Cooney (in press). Regional pollen diagrams with particular relevance to Reenadinna Wood have been produced by Vokes (1966) for Muckross Bog, a small area of raised bog enclosed by the woodland, and by T. Cooney (Fig. 3.9) for Doo Lough. These diagrams show that yew first expanded around 5,000 BP, but unlike the pollen sites described in Chapter 2, yew pollen levels did not dwindle away to negligible amounts and are maintained at around 10% up to the present day. This appears to have been a fairly localised event as the regional pollen diagram from Sheheree Bog (Mitchell & Cooney, in press), just 4km to the north-east, exhibits much lower levels of yew. Confirmation of a substantial yew community having occurred at the site of Reenadinna Wood for about the last 5,000 years is provided by a pollen diagram from a small hollow at the site (Mitchell 1990a). This diagram indicates that the yew-wood developed post elm decline from a wood previously dominated by Scots pine, oak, elm and hazel. It also demonstrates succession at the stand level; as yew gradually increased, hazel declined as it was overtopped and flowering became restricted. Why the yew population here has persisted, whereas elsewhere it declined fairly rapidly after its initial expansion, is unclear. Possibly this is due to the relative inaccessibility of the limestone crags at Reenadinna to browsing animals, surrounded as they are by marshland which may have been more extensive in the past.

3.3.3 History

There is archaeological evidence of part of the wood having been cleared in the past. Mitchell (1990a) reported that there is an unexcavated souterrain (underground passage used as a refuge) in the wood, probably associated with the rath (ring fort) whose stone foundations are

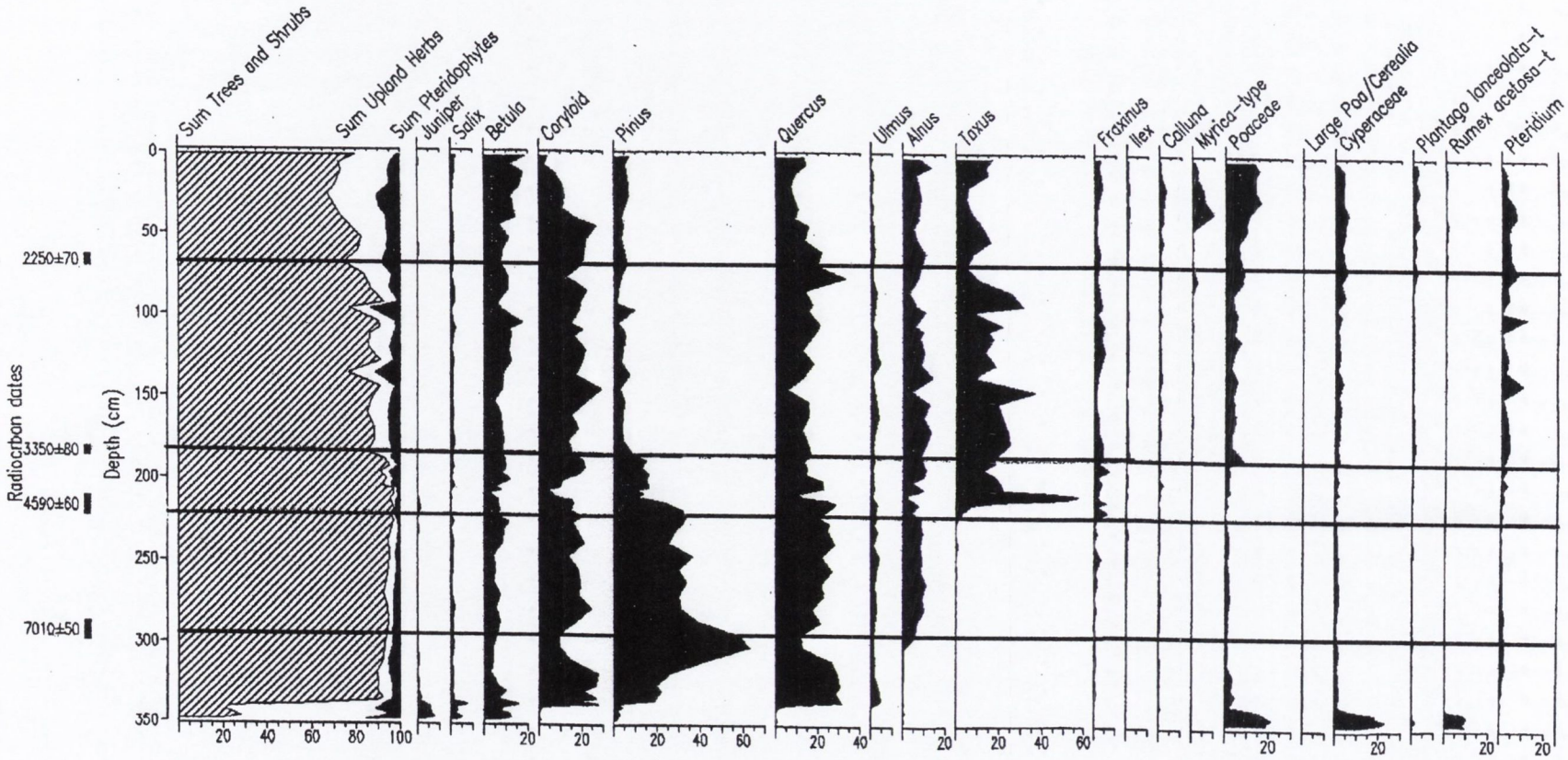


Figure 3.9 Pollen diagram for Doo Lough, Muckross Peninsula. Analyst: Tom Cooney

still discernible in the North Wood. These two structures suggest a small, defensively-minded settlement on the limestone outcropping, sometime between 500 and 1000 AD (Mitchell & Ryan 1997); it is exceedingly unlikely that this would have been sited in closed woodland. There are also persisting signs of the "lazy beds" characteristic of potato patches in the northwest of North Wood (Kelly 1975), indicating that part of the wood was cleared for cultivation at some point.

A number of derelict stone walls, apparently dating to the late eighteenth century (Mitchell 1990a), occur across the site, particularly in the North Wood (Fig. 3.8). Walls also appear on the Ordnance Survey maps of 1841 and 1896 (Figs. 3.10 and 3.11), although is difficult to determine if these are exactly the same structures as the contemporary remnants. At the point where the peninsula road heading west leaves North Wood and South Wood behind, there are ruined gate pillars on either side. It appears that North Wood at least was enclosed at some point prior to 1841, possibly to keep livestock off the limestone pavement. Whether this was to prevent livestock from accessing cultivated areas or to prevent them from feeding on yew foliage is unclear.

The late eighteenth century also saw industrial activities on the Muckross Peninsula, including copper mining, marble quarrying and in particular iron smelting. This is likely to have resulted in the felling of many trees, although the woodlands on the peninsula seem to have escaped the mass destruction typically of the Killarney woods (Watts 1984). An examination of twenty *Taxus* stumps by Watts (1984) found no trees older than 200 years. It is therefore likely that most of the present woodland developed following the cessation of industrial activities around 1800.

3.3.4 Distribution of vegetation types

Vegetation map

Reenadinna Wood is an area of complex topography and vegetation. To clearly visualise this variation, a contour map and a vegetation map were made of area. The contour map (Fig. 3.12) was derived from the orienteering map of the Muckross area by Costello & Cotter (1999). A comparison of this map and Fig 3.8 illustrates that the current extent of woodland cover is largely, though not exclusively, restricted to the higher ground where outcropping limestone is frequent. The maximum height is 30m above lake level. These areas of woodland are separated by tracts of seasonal marshland. Within the wooded areas there is considerable heterogeneity in the topography, with many gullies and hollows.

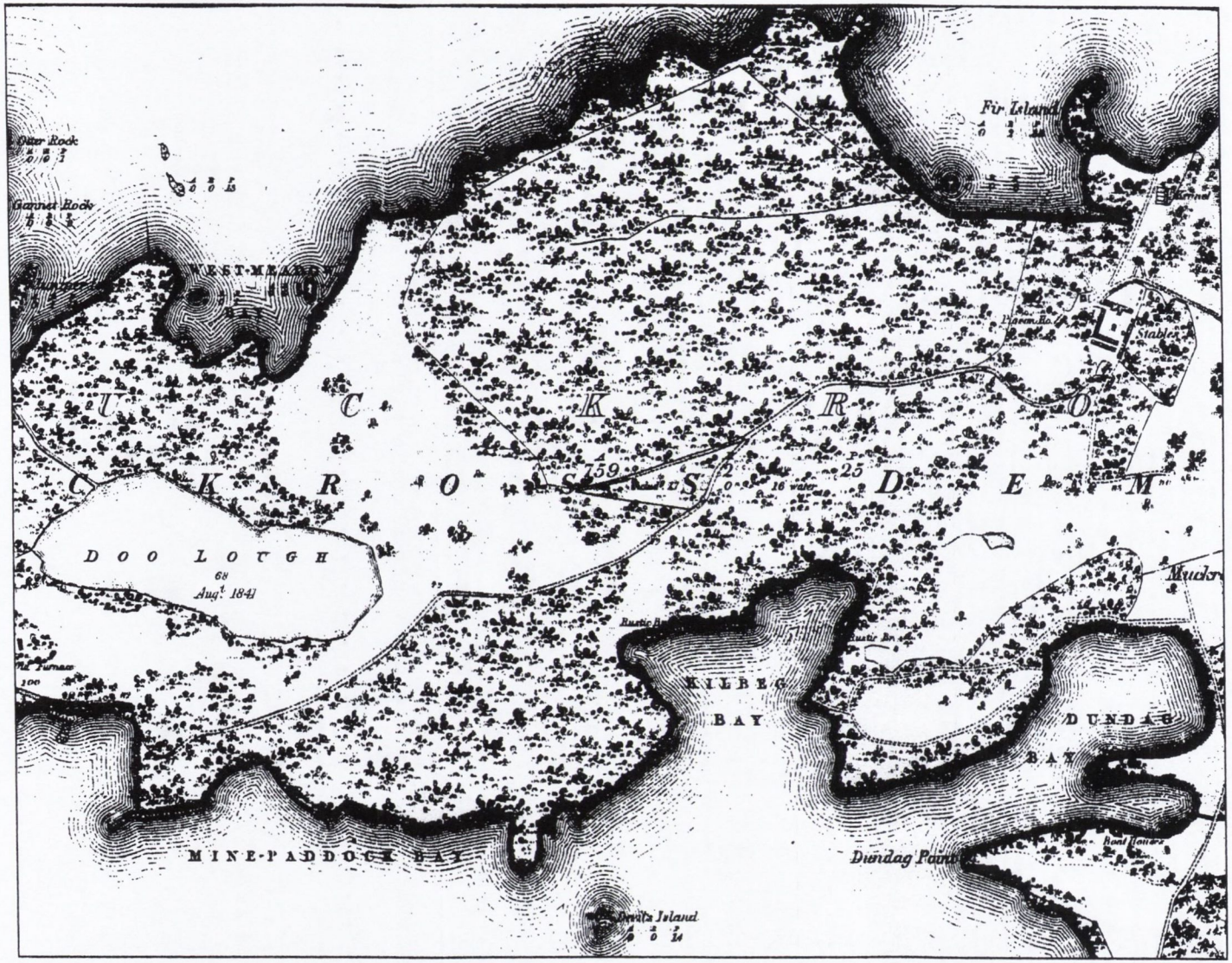


Figure 3.10 Reenadinna Wood and the eastern end of the Muckross Peninsula, from 1st Edition Ordnance Survey of 1841-1842. Scale 1: 8950. The North Wood appears to be enclosed at this time.

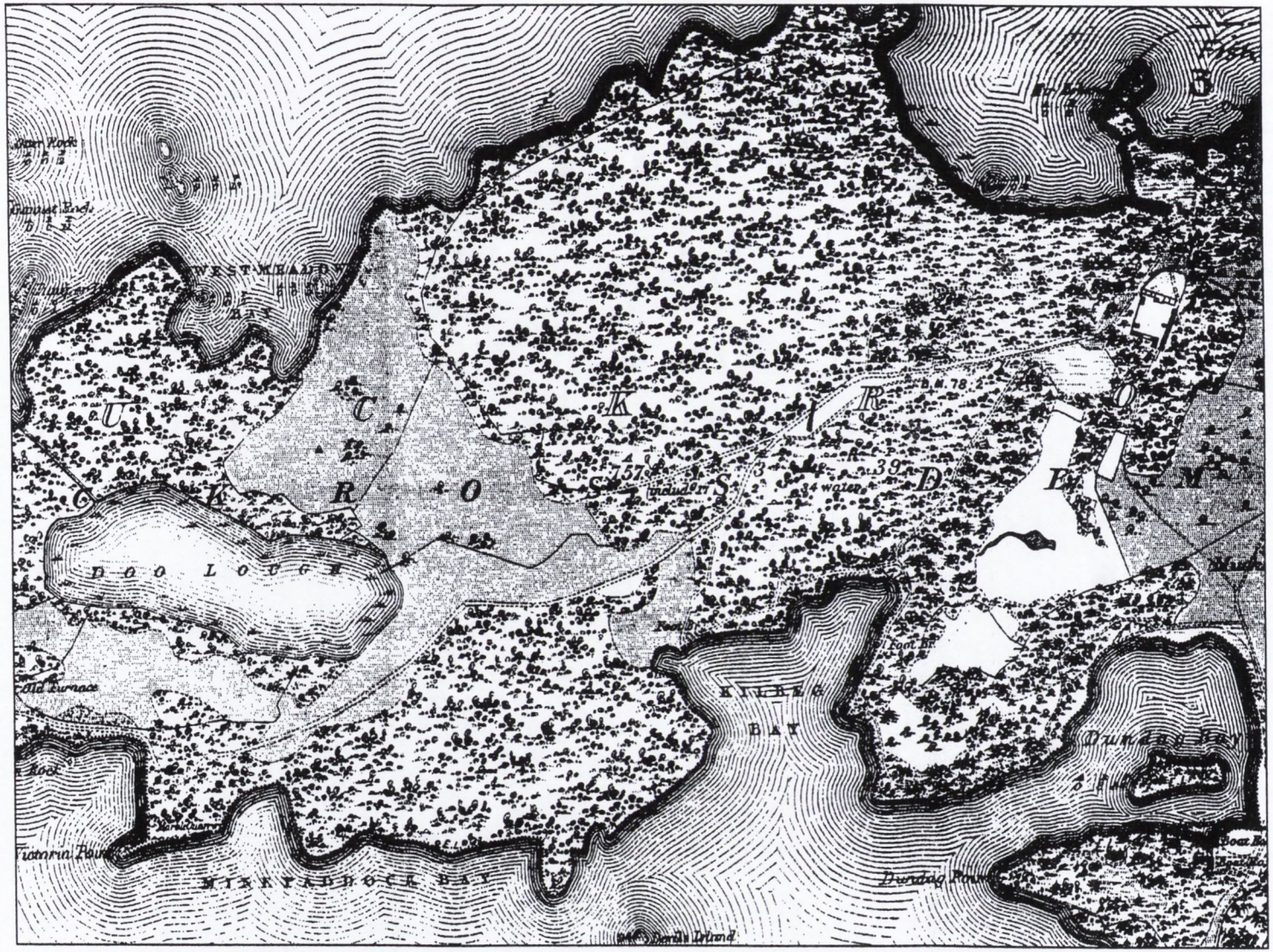


Figure 3.11 Reenadinna Wood and the eastern end of the Muckross Peninsula, from 2nd Edition Ordnance Survey of 1895. Scale 1:8950. Note that two areas (*) previously marked as woodland are now marked as scrub (presently wet woodland/marsh).

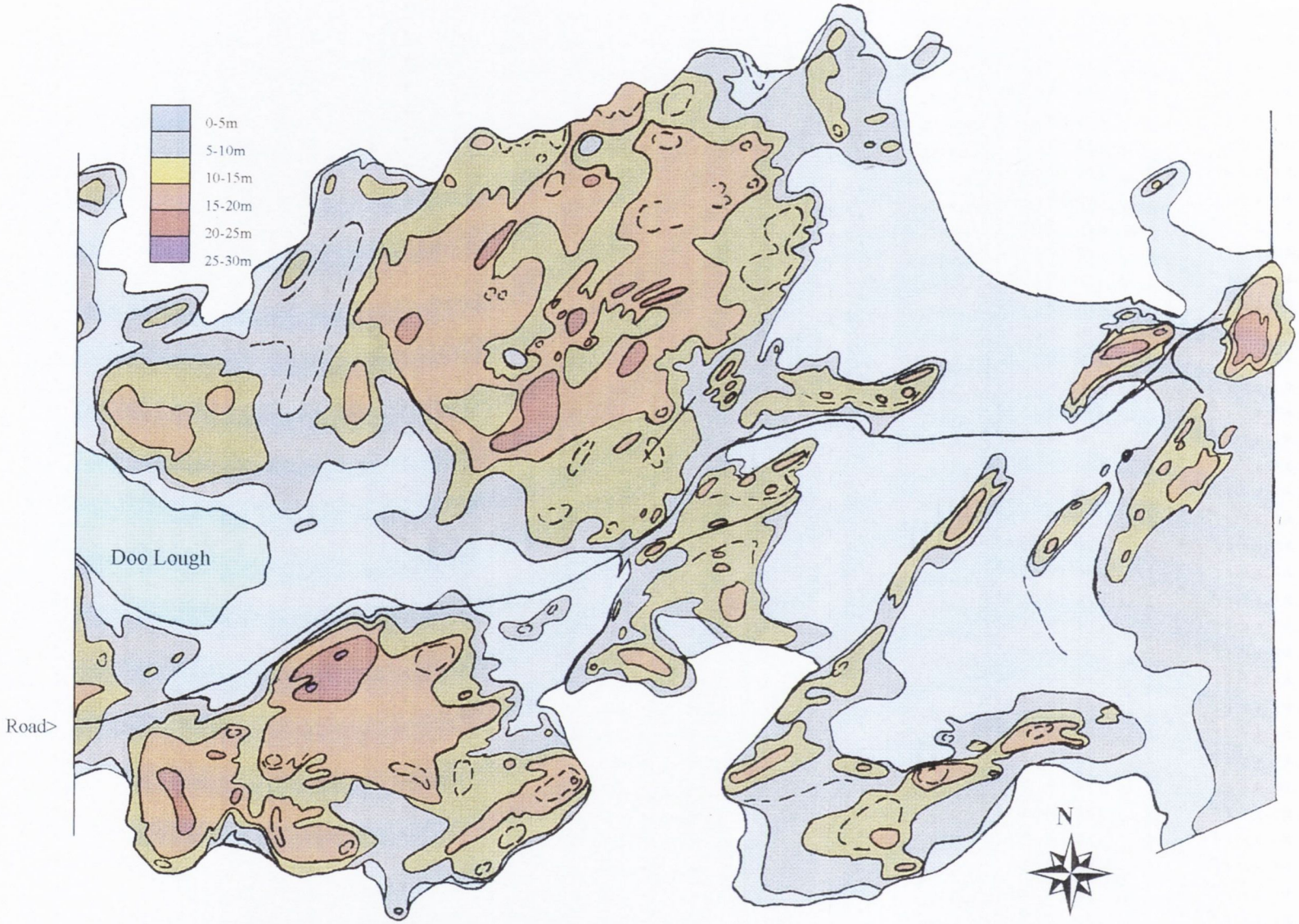


Figure 3.12 Contour map of the Reenadinna Wood area. Scale 1:8500

The vegetation map (Fig. 3.13) was constructed by walking the site. Yew community vegetation types defined in section 3.2 were identified, as were seven additional broad vegetation types in which yew was not present.

Seasonally flooded ***wet woodland***, which surrounds much of the limestone outcropping, typically consists of tangled, multistemmed willows (Plate 3.17), with birch and alder locally abundant (although an area of rare wet ash woodland occurs in a large hollow within North Wood; Plate 3.18). The field layer includes *Molinia caerulea*, *Carex remota*, *Filipendula ulmaria*, *Mentha aquatica* and *Galium palustre*. In drier areas this grades into ***birch scrub*** in which *Ulex* spp. and *Pteridium aquilinum* are abundant. Where seasonal flooding is more severe, woodland and scrub give way to extensive areas of ***marsh*** (Plate 3.19) dominated by *Molinia caerulea* with *Myrica gale* locally abundant, and in the deeper water *Phragmites australis*

To the west of North Wood is small ***conifer plantation*** of mature, non-native trees which form a very open canopy in comparison to the yew wood (Plate 3.20). The stand is composed chiefly of Norway spruce (*Picea abies*) and larch (*Larix decidua*), with two large (diameter > 1.5 m) individuals of Monterey cypress (*Cupressus macrocarpa*). The field layer here is dominated by large tangles of *Rubus fruticosus* agg. with *Pteridium aquilinum* abundant. A few hawthorn saplings are also present. In West Wood there are small ***Scots pine stands*** which have also been certainly planted. These contain a few holly trees and a field layer dominated by *Pteridium aquilinum*. The woodland of the ***earthy hollows*** and gullies in the outcroppings is largely dominated by oak with ash, hawthorn, holly and hazel common. Holly may be locally dominant forming small stands. Fallen birch trees are frequent and have created small canopy gaps. *Luzula sylvatica, Blechnum spicant, Vaccinium myrtillus* and *Agrostis canina* are common in the field layer. Some of the hollows are evidently seasonally flooded. Finally, there are narrow strips of ***cliff-top heath*** vegetation composed of *Ulex* spp. and *Calluna vulgaris*, which have yet to be invaded by *Cotoneaster* spp.

The map illustrates that Reenadinna Wood consists of a mosaic of vegetation types determined largely by topography and hydrology. *Taxus* woodland covers a sizeable proportion of the site, but *Taxus-Corlyus* woodland and *Taxus-Fraxinus* woodland are equally important stand types. A photograph of the Reenadinna Wood in early winter (Plate 4.21) further highlights the proportions and distribution of evergreen and deciduous canopy trees; the former are largely absent from the northwest of North Wood.

Fig. 3.13 Vegetation types of Reenadinna Wood with location of transects A and B. Scale 1: 9100

Plate 3.17. Wet woodland dominated by willow (*Salix cinerea),* fringing South Wood, Reenadinna (October 2001).

Plate 3.18. Wet ash (*Fraxinus excelsior*) woodland in large hollow in the centre of North Wood, Reenadinna (October 2001).

Plate 3.19. Marsh dominated by *Molinia caerulea* fringing South Wood, Reenadinna (December 2001). Note bare branches of deciduous trees amongst the yew foliage.

Plate 3.20 Conifer plantation with Norway spruce (*Picea abies*) and larch (*Larix decidua*), west edge of North Wood, Reenadinna (October 2001).

Plate 3.21 View of Reenadinna Wood and the eastern part of the Muckross Peninsula, looking north from the top of Torc Mountain (December 2001). Note distribution of evergreen canopy (predominantly yew).

Vegetation transects

The vegetation map presented in Fig. 3.12, as with most diagrams of this type, depicts the boundaries between blocks of adjacent vegetation types as sudden and precise, in a manner which is seldom seen on the ground. Environmental conditions between vegetation types tend to change along gradients, resulting in gradual shifts in the plant community composition due to the different sensitivity or tolerance of plant species to the changing conditions (Whittaker 1951). To illustrate these boundaries, or ecotones, between vegetation types in Reenadinna Wood and to investigate consequent patterns in species diversity, two 1 m wide belt transects (A and B) were established in the summer of 2001, as shown in Fig. 3.13. Transect A (85m) ran from an area of wet birch woodland, up through a steep earthy gully into an area of mature yew woodland on a limestone outcropping in North Wood. Transect B (40m) ran from the shore of Muckross Lake, up a small lough-side cliff and on into an area of low yew woodland in South Wood. A 1 x 1 m quadrat was taken every metre along each transect; the field layer cover of each vascular plant species and the total bryophyte cover were recorded according to the Domin scale (Table 3.1). In addition, the total canopy cover was estimated to the nearest 10% and the species present in the canopy at that point noted. Height relative to the base of the transect was estimated every 5 m. Patterns in species occurrence were interpreted with the aid of Rose (1981) and Webb *et al.* (1996).

The base of transect A (0-10 m; Figs. 3.14 and 3.15) was on wet, seasonally flooded ground beneath a fairly open canopy of birch and ash. The field layer was diverse with around 10-15 species per m^2, dominated by *Carex remota*, *Eupatorium cannibinum* and *Mentha aquatica*, with *Filipendula ulmaria, Ranunculus repens, Scutellaria galericulata* and *Galium palustre*. Several species typical of wet habitats were largely restricted to this zone, for example, *Molinia caerulea*, *Cirsium dissectum*, *Succisa pratensis* and *Juncus effusus*. Further along the transect (10-20 m), canopy cover increased and species of slightly more shady conditions started to occur, including *Circaea lutetiana*, *Glechoma hederacea*, *Hedera helix* and *Veronica chamaedrys*, although the dominant species listed above were still present. At around 25-30 m the ground started to slope upwards into the gully. Birch was lost from the canopy and replaced by the dense foliage of oak and yew; ash was still present. Holly and hazel started to occur in the understorey. With the exception of *Hedera helix*, the field layer species already listed disappeared, and species richness dropped to only 1-2 species per m^2. Bryophyte cover also declined, partly because the earth at this point was heavily poached by deer. At around 40-45 m there was a slight break in the canopy and a more diverse patch of species occurred, including holly seedlings, *Asplenium scolopendrium* and *Sanicula europaea*. From this point on, canopy cover was persistently high as the transect climbed out of the gully and on to the limestone outcropping. Oak was lost from the canopy which was

Figure 3.14 Abundance of selected species along transect A, from wet birch woodland (at 0 m) to yew dominated stands on limestone pavement (85m). Orange bars indicate limits of yew canopy.

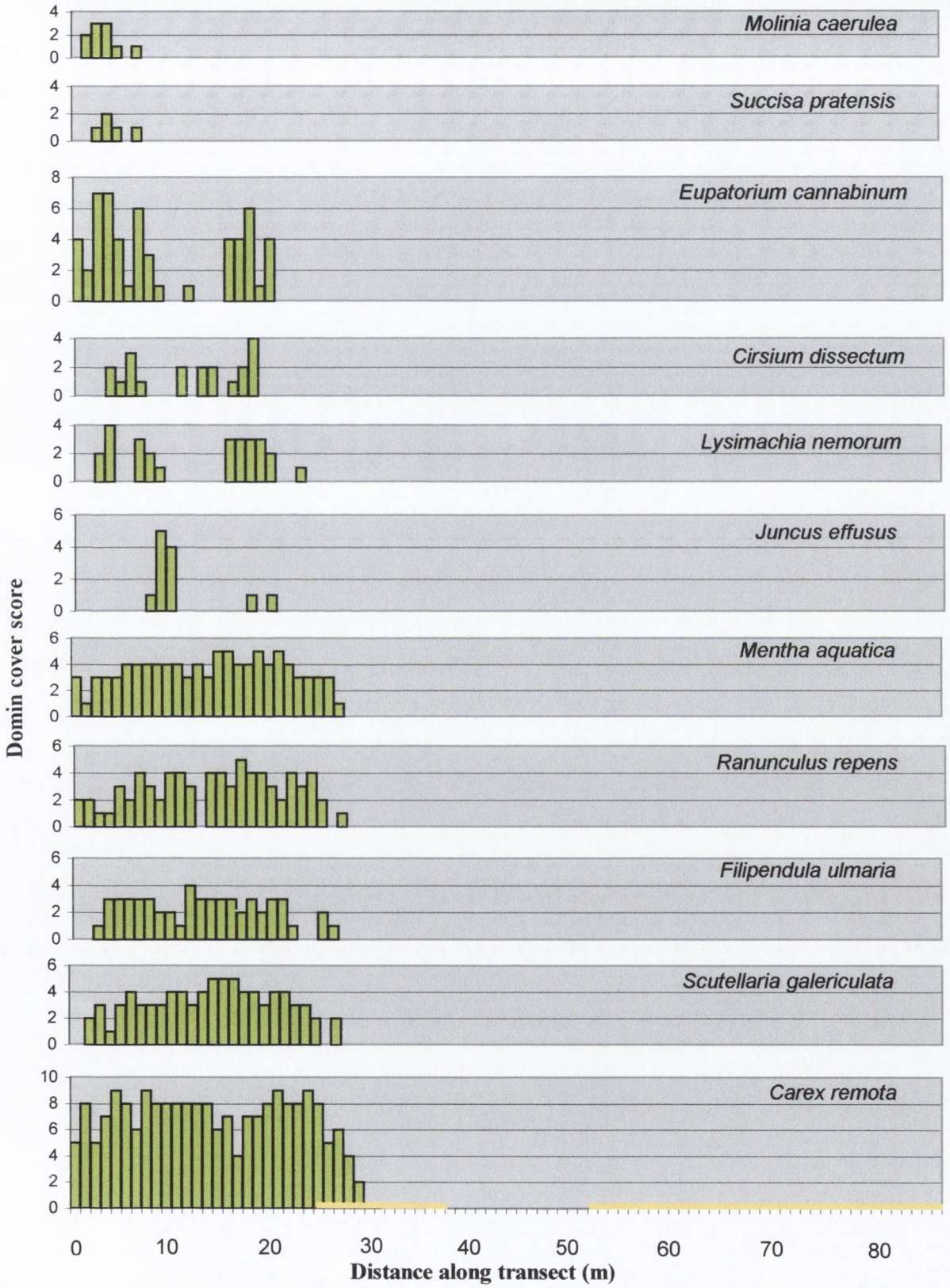


Figure 3.14 continued

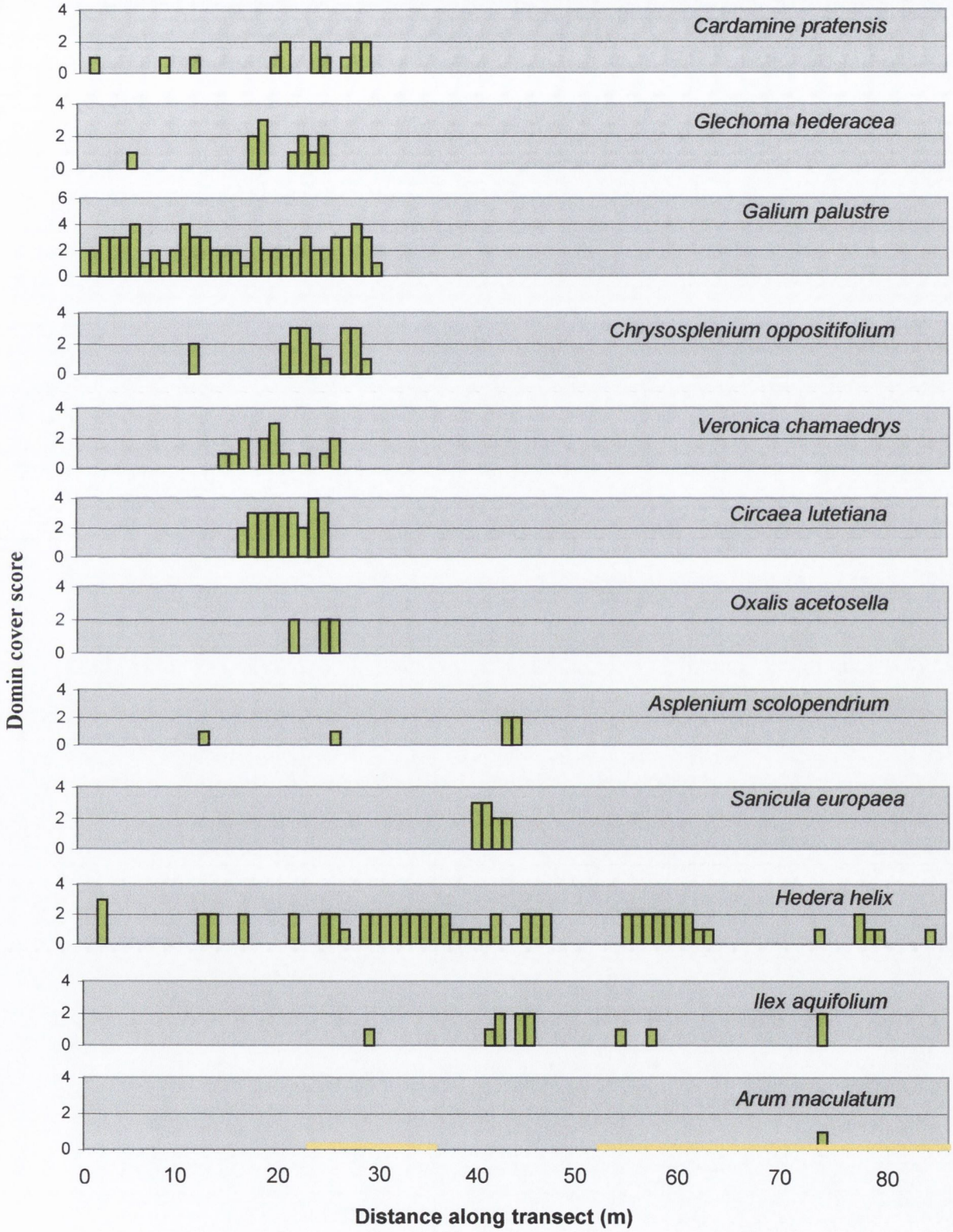
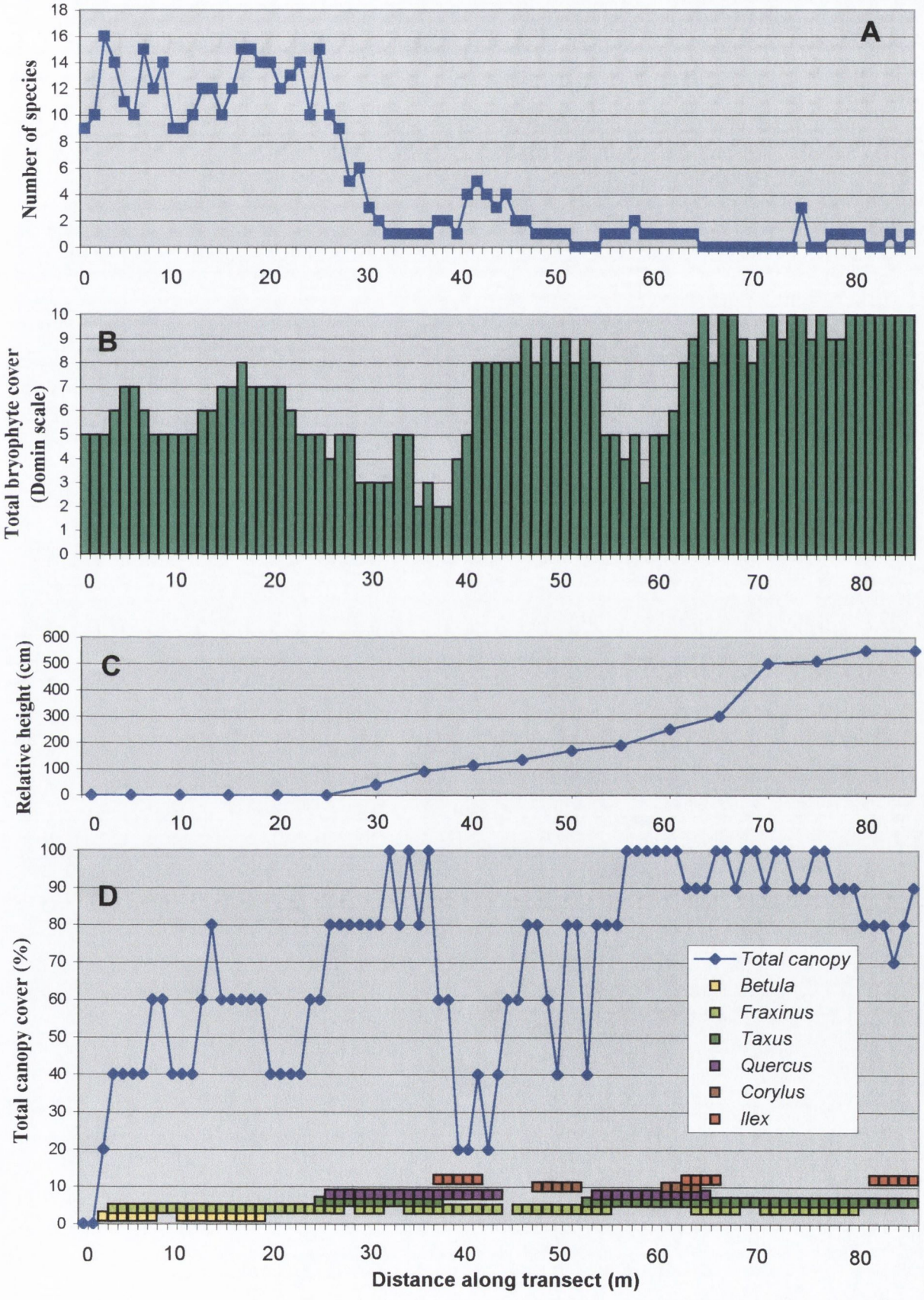


Figure 3.15 Comparison of trends along transect A in (a) vascular species richness, (b) total bryophyte cover, (c) height relative to base of transect, and (d) total canopy cover, with presence of species in canopy indicated by coloured boxes.



now composed of yew and ash. Field layer cover and field layer species richness were exceptionally low, with only holly seedlings, *Hedera helix* and a lone individual of *Arum maculatum* present. Bryophyte cover increased to nearly 100 % on the rocky substrate. Linear regression analysis showed that species richness was inversely proportional to total canopy cover ($r^2 = 0.371$, $P < 0.001$), total bryophyte cover ($r^2 = 0.098$, $P = 0.003$) and distance along transect ($r^2 = 0.657$, $P < 0.001$).

There was no field layer at the base of transect B (0-3 m; Figs. 3.16 and 3.17), the bottom of the cliff, due to regular inundation by the lake waters, but overhanging branches of yew and *Arbutus unedo* were present, as trees of these species were growing on the nearby cliff face. On the cliff face itself (3-10 m) was a straggly whitebeam, several species characteristic of limestone grassland habitat, including *Thymus praecox, Linum catharticum, Lotus corniculatus* and *Teucrium scorodonia,* and a sparse covering of bryophytes. At the top of the cliff this community graded into a narrow, species rich (12-14 species per m^2) scrub dominated by *Ulex europaeus*, *Pteridium aquilinum* and *Carex flacca* beneath a sparse *Arbutus unedo* canopy. Further back from the cliff top (20-30m), *Arbutus unedo* gave way to a denser canopy of yew which eliminated many of the forb species. A sparse sward of *Brachypodium sylvaticum*, *Carex pulicaris* and *Carex flacca* was formed and bryophyte cover gradually increased. Shade tolerant woodland species, such as *Fragaria vesca* and *Viola* spp. began to occur, but overall species richness dropped to around 4-5 species per m^2. From 30 m onwards, *Carex* spp. declined and were replaced by *Sanicula europaea*. Linear regression analysis showed that species richness was not significantly related to total bryophyte cover ($r^2 = 0.003$, $P = 0.724$), or distance along transect ($r^2 = 0.038$, $P = 0.229$). There was a nearly significant inversely propotional relationship between species richness and total canopy cover ($r^2 = 0.086$, $P = 0.066$).

These results highlight the species poor nature of the yew woodland in comparison with adjacent habitat types, a character which is largely due to the dense canopy that yew forms. Vegetation transects from Killarney woodlands have also been presented by Turner & Watt (1939). Although located on sandstone not limestone, the transect by these authors on Arbutus Island in the Upper Lake, makes an interesting comparison with transect B of the present study. The Arbutus Island transect proceeded from bare rock near the shore, through a rocky zone where *Molinia caerulea* was established in the fissures, to a heath zone dominated by *Calluna vulgaris* and *Ulex gallii*, to a scrub zone with holly and *Arbutus unedo,* and finally mature woodland dominated by sessile oak, in which yew and birch were occasional. Turner & Watt (1939) interpreted this transect as representing a successional sequence, but this appears to ignore the important factor of exposure which may also be responsible for the

Figure 3.16 Abundance of selected species along transect B, from base of loughside cliff (at 0 m) to a yew dominated stand on limestone pavement (40m). Orange bars indicate limits of yew canopy.

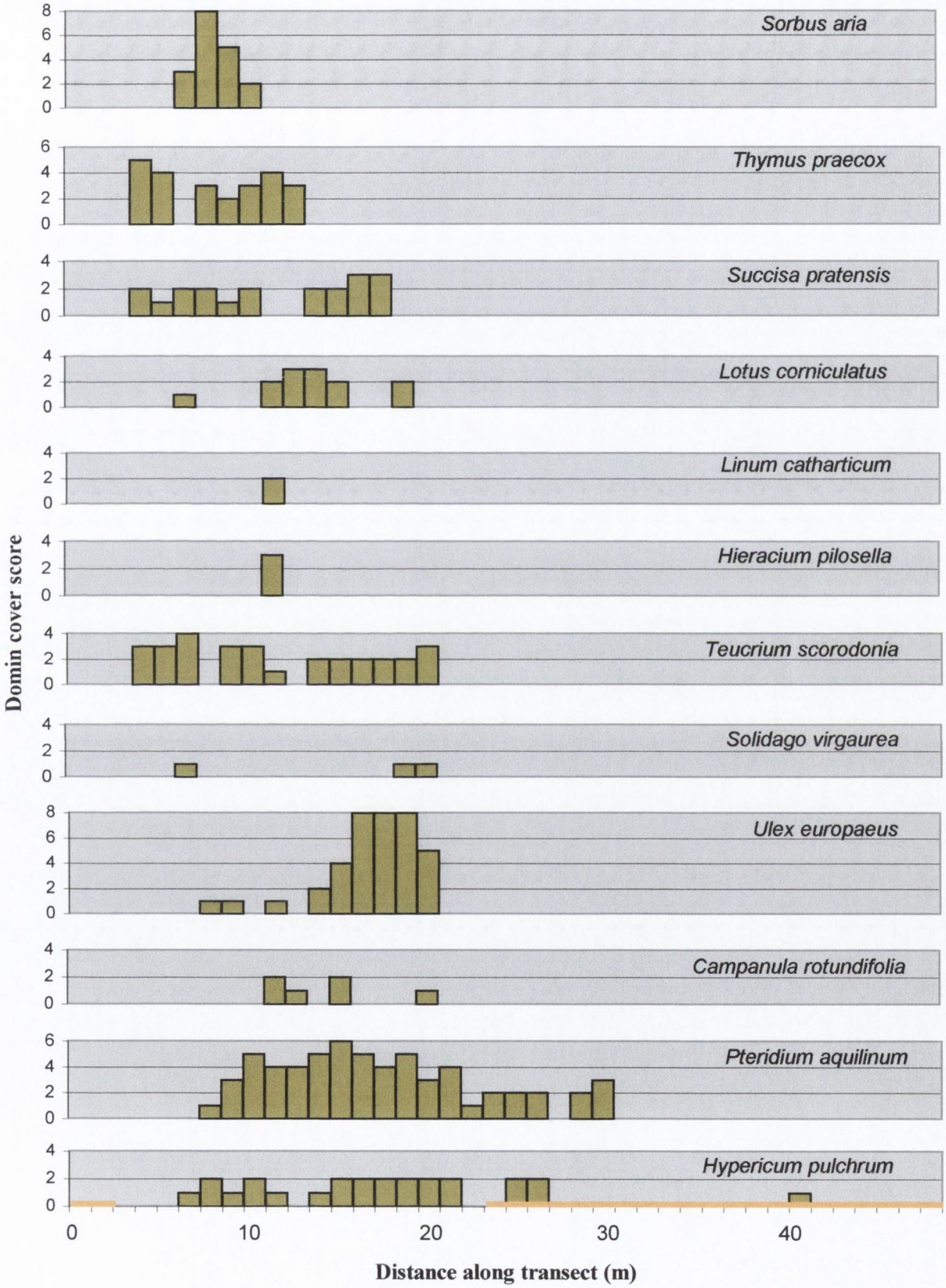


Figure 3.16 continued

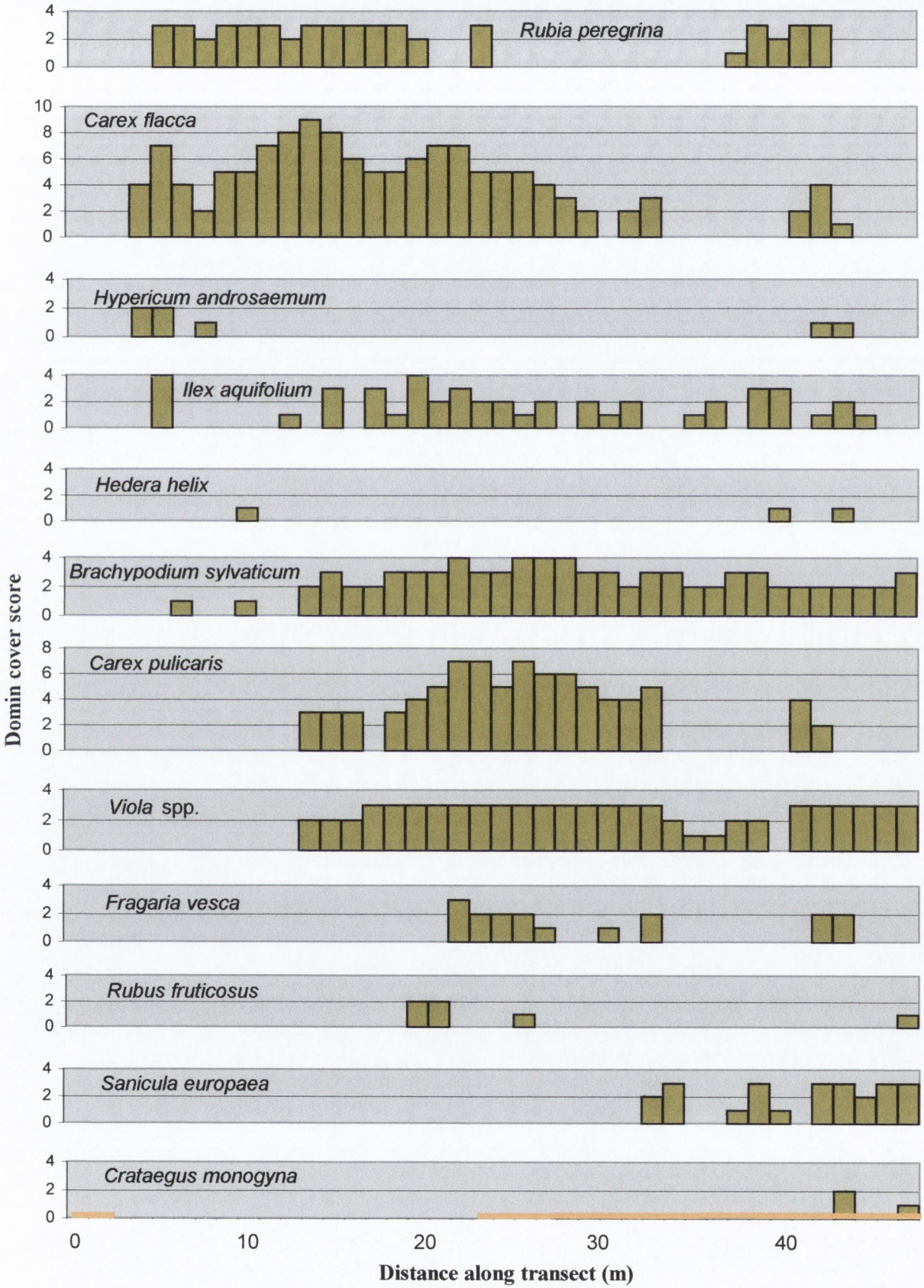
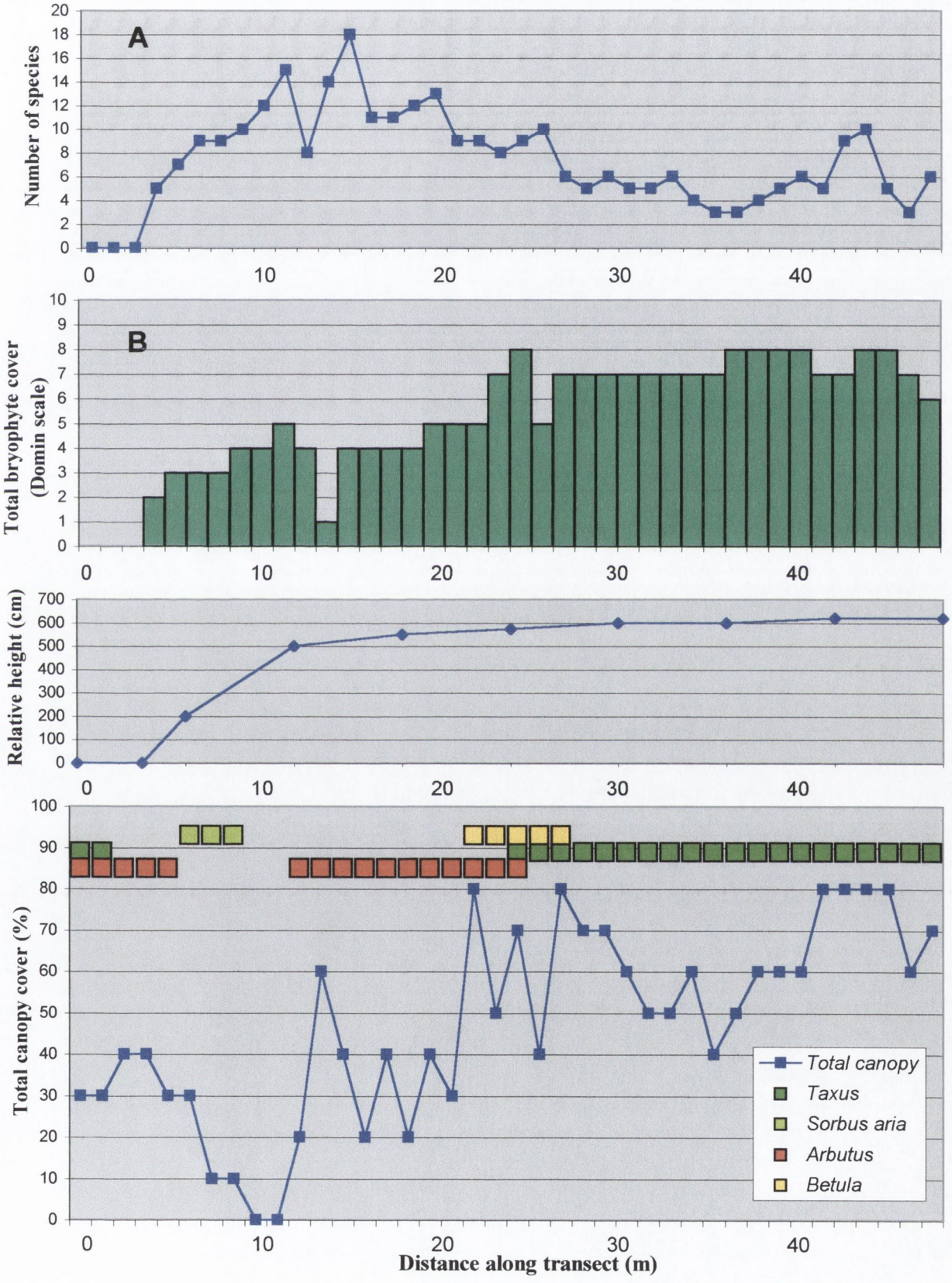


Figure 3.17 Comparison of trends along transect B in (a) vascular species richness, (b) total bryophyte cover, (c) height relative to base of transect, and (d) total canopy cover, with presence of species in canopy indicated by coloured boxes.



gradually increasing stature of the vegetation structure as one moves away from the lough-side.

3.3.5 Management issues

Non-native plants

The potential threats posed by beech and *Cotoneaster* spp. have already been highlighted in section 3.1. Mature beech trees are currently fairly rare in Reenadinna Wood although saplings and young trees are frequent on the deeper soils of the hollows. *Cotoneaster integrifolius* covers sizeable areas of the lough-side cliff-top in South Wood; although largely growing prostrate to a height of 50-70cm, there are high thickets of the species to 2m in height along the nature trail at this location (Plate 3.22). It has been suggested the species was originally deliberately planted at this location for aesthetic purposes (Larner 1973), but patches of *Cotoneaster* spp. are to found in small clearings throughout the woodland where their seeds have been disseminated by birds.

Rhododendron ponticum has infested almost all of the oak woodlands in the Killarney National Park; the problems posed by this highly invasive species have been well documented (e.g. Cross 1981, 1982; Colak *et al.* 1998). The yew-dominated areas of Reenadinna Wood have been less affected due to the rocky limestone terrain presenting fewer suitable sites for *Rhododendron*. However, the species has established at several locations throughout the site where deeper soils have accumulated, particularly in the wet woodlands fringing the outcrops (Plate 3.23), the cliff-top heath communities, and around the coves near the lough-side. Various methods have been used to clear affected areas and control its further spread, usually involving manual cutting and/or spraying with glyphosate herbicide (Plate 3.24).

A non-native species which has received less attention is *Clematis vitalba.* This plant is locally abundant on the southern cliff-tops but does not form dense swathes like *Cotoneaster* spp. It may have been planted here as early as the mid-eighteenth century (Kelly 1975). The species is also present at a few locations within the wood in small amounts, generally in more open areas. Along the western edge of North Wood, however, *Clematis vitalba* has become rampant, smothering a substantial area of woodland (Plate 3.25). Several of the ash and hawthorn trees are almost completely covered and there some are standing dead or fallen. *Clematis* is also abundant on the ground forming a dense layer in association with bramble. Several of the yew trees bordering this area are also becoming choked.

Plate 3.22. Cliff-top scrub along the nature trail, South Wood, Reenadinna. Note the large expanses of *Cotoneaster* spp. (October 2001).

Plate 3.23. Unsprayed *Rhododendron ponticum,* thriving and flowering, at bottom of outcrop, East Wood, Reenadinna (October 2001).

Plate 3.24. Area of birch scrub along east side of North Wood, heavily sprayed due to infestation with *Rhododendron ponticum* (October 2001).

Plate 3.25. Stand of ash choked by *Clematis vitalba*. Near western edge of North Wood, Reenadinna (October 2001).

Overgrazing

Although native red deer (*Cervus elaphus*) are to be found occasionally in Reenadinna Wood, the primary grazers are Japanese sika deer (*Cervus nippon*). This species was introduced into Killarney in 1865, when one stag and two hinds were brought from Powerscourt, Co. Wicklow. By 1935 the total herd was estimated at 3,000 – 5,000 animals, although this declined to around 1,000 animals by 1948 (Whitehead 1964 cited in O'Sullivan 1991). In the early 1970s, Larner (1977) estimated the population on the Muckross Peninsula to between 84 and 133. More recent estimates of grazing numbers in the area of Reenadinna Wood are presented in Table 3.6.

Table 3.6 Number of deer in the Muckross Management Block of the Killarney National Park in 1991 and 1996 (from Higgins *et al.* 1996).

	1991	1996
Red deer	6	6
Sika deer	143	179
Total no. grazers	149	185
Area (km^2)	8.3	8.3
Grazing density (grazers / km^2)	18.0	22.3

Larner (1977) found that sika deer were causing extensive bark damage to the yew trees in Reenadinna Wood by "horning" the trees with their antlers. Yew trees were selected over ash or holly trees and large yew trees were selected over smaller yew trees. Deer also appear to be responsible for a chronic absence of natural regeneration and the extreme sparseness of the field layer. A photograph of a yew-dominated stand is presented in Tansley (1939). The view is very similar to the present woodland, with a carpet of moss across the limestone pavement but no visible field layer or seedlings. The photograph is entitled "Yew wood (regenerating) in the Muckross demesne [with] ash saplings..."; presumably this mention of regeneration refers to the (rather mature) ash saplings, as no yew juveniles are visible. Kelly (1975) reported that recent yew regeneration was virtually absent, with only a few heavily browsed saplings observed in areas of open pavement. Recent surveys in Reenadinna Wood have found regeneration of all tree species to be negligible (Higgins *et al.* 1996; Higgins *et al.* 2001). Staines *et al.* (1995) suggested that to permit natural regeneration of Scots pine or birch in the uplands the maximum red deer density was about 7 animals / km^2, and that this density would need to be much lower for more favoured species, such as oak or rowan. If this figure is used a rough guideline, it is evident from the data available on deer numbers in the area of Reenadinna Wood (Table 3.6) that high grazing pressure is potentially having serious impacts on the vegetation and natural regeneration at this site.

3.4 Summary

1. Yew-dominated woodland in Ireland is restricted to sites of outcropping limestone. It appears to develop along a successional pathway from species rich open limestone pavement communities, through a seral scrub stage in which hazel is a characteristic component.

3. Yew also occurs as an occasional tree in sessile oak – holly woodland on sandstone, and ash woodland on calcareous soils over limestone.

2. Irish yew-woods have several features which distinguish them from English yew-woods on chalk, including the presence of hazel and an extensive bryophyte carpet, and the absence of whitebeam, *Mercurialis perennis* and *Buxus sempervirens*. Irish limestone pavement communities with yew appear to have some affinity with similar sites in Wales.

3. Irish vegetation communities in which yew occurs can contain several non-native species. The most significant threats are probably posed by beech and *Cotoneaster* spp.

4. Reenadinna Wood is mosaic of stand types largely determined by topography and hydrology, with yew woodland and yew-hazel woodland dominating the limestone outcroppings, whilst wet woodland and birch scrub occur on the lower lying ground. Vascular species richness in the yew woodland is poor in comparison with adjacent habitats.

CHAPTER 4

NATURAL REGENERATION AND VEGETATION CHANGE IN DEER EXCLOSURES.

4.1 Introduction

4.1.1 Overview

This chapter deals with the re-surveying of long-term deer exclosures on the Muckross Peninsula in the Killarney National Park. Field data collected in the course of this study are analysed in combination with those from previous surveys. The results are discussed in relation to natural regeneration processes and woodland management.

4.1.2 Long-term studies of woodlands

Natural processes in woodlands tend to occur on large timescales due to the longevity of the principal tree species. Peterken (1996) details six different approaches to investigating these changes: chronosequences; stand characteristics; pollen profiles; historical records; modelling; and permanent plots. Each approach has its strengths and weaknesses and hence the multidisciplinary approach to this thesis. However, it is only by the long-term monitoring of permanent plots that actual change in whole plant communities can be observed and the fate of individual trees followed. Such studies also have the advantage of detecting unforeseen developments and chance occurrences; they may be regarded as open-ended research programmes rather than finite ecological experiments (Peterken 1996). Consequently, baseline surveys need to be comprehensive if new questions which may arise during the course of the study are to be adequately addressed.

Inevitably, maintenance of long-term studies has its own particular difficulties. Monitoring episodes, if not regular, at least need to be relatively frequent if the time-course of processes is to be accurately followed and transient or subtle changes are not to be missed. Observer bias can adversely affect species data (Sykes *et al.* 1983; Kirby *et al.* 1986), hence studies ideally require a long-term commitment by the researcher establishing the plots. Mountford & Peterken (1998) highlight that many potential long-term studies fail early on due to loss of interest or financial support, or reformation of the institution responsible. More fundamentally, records of results and

methods employed must be safely stored, and plots need to be accurately marked so that they can be relocated over long time-periods (Peterken 1993).

Due to these difficulties, and also possibly the lack of suitable sites, there have been very few long-term woodland studies in Ireland. Notable exceptions are the Tomies Wood study (in sessile oak-holly woodland) established in 1972 (Kelly 2000, 2002) and the permanent plot network established throughout the Killarney National Park in 1991 (Hayes *et al.* 1991; Higgins *et al.* 1996; Higgins *et al.* 2001). In Britain, such studies are more numerous and cover a range of woodland types, e.g. pedunculate oak-birch woodland (Mountford *et al.* 2000), pedunculate oak-ash woodland (Kirby & Thomas 1995; Kirby *et al.* 1996a,b; Kirby & Thomas 1999; Hall & Kirby 2000), pedunculate oak-beech woodland (Putman *et al.* 1989), sessile oak-birch woodland (Pigott 1983), sessile oak-ash-beech woodland (Peterken & Jones 1987, 1989), ash-field maple woodland (Mountford & Peterken 1998), and pine woodland (Gong *et al.* 1991; Sykes 1992). There have been no previous reports on long-term studies in yew woodland except for Barkham's (1992) consideration of ground flora changes in a yew stand at Brigsteer Park Wood, Cumbria, over an eighteen year period.

4.1.3 Effects of large herbivores on woodland ecosystems

By erection of fences around permanent plots, many of these long-term studies have investigated natural regeneration of tree species and changes in vegetation composition and structure in the absence of grazing (e.g. Pigott 1983; Putman *et al.* 1989; Kelly 2000, 2002). This is partly because grazing or, as is too often the case, overgrazing is such an over-riding factor that it masks more subtle natural processes. Chiefly, however, grazing exclosures are used to investigate the impact that large herbivores are having on the potential vegetation.

Prolonged periods of heavy grazing can influence species composition by suppressing or eliminating sensitive species and permitting the competitive release of more tolerant species, such as those with spines, thorns or chemical defences (Putman *et al.* 1989; Kirby *et al.* 1994). Trampling and browsing of seedlings and saplings retards natural regeneration and heavily grazed woodlands have scanty understoreys as well as sparse field layers. This lack of recruitment will ultimately impact on the age structure of the woodland. Mature trees may also be damaged by deer browsing, bark stripping and fraying (Larner 1977; Gill 1992a). High grazing levels have also

been shown to reduce abundances of invertebrates (Baines *et al.* 1994), small mammals (Putman *et al.* 1989) and birds of prey (Putman 1986). However, light grazing levels suppress vigorous species which may otherwise dominate and competitively exclude less aggressive plants. Species diversity is also promoted by the increased heterogeneity in nutrient availability caused by dunging at particular sites in a woodland (Putman 1996). Ground disturbance caused by herbivores creates microsites suitable for seedling establishment (Mitchell & Kirby 1990). Grazing and browsing also create and maintain open gaps and glades where shade intolerant plants can persist; it is this kind of disturbance regime that coppicing mimics (Putman 1994).

4.1.4 Aims of this study

The woodlands of the Muckross peninsula are heavily browsed by introduced Japanese sika deer (*Cervus nippon*) and, to a lesser extent, by native red deer (*Cervus elaphus*). Regeneration in these woodlands in recent history has been very poor (Kelly 1975; Hayes *et al.* 1991; Higgins *et al.* 1996; Higgins *et al.* 2001). In particular there has been an almost total absence of yew saplings. The purpose of this study was to investigate the long-term effects of deer exclusion on: (i) natural regeneration; (ii) adult tree demography; (iii) field layer vegetation; and (iv) species richness in these woodlands, with particular attention to the dynamics of yew woodland.

4.2 Methods

4.2.1 Study sites

Four fenced exclosures were erected in the Muckross peninsula woodlands in the winter of 1969 / 70 under the direction of Dr. D.L. Kelly (R1, R2, R3 and C1 in Table 4.1). Three were located in Reenadinna yew-wood, on the limestone of the eastern part of the peninsula, with the fourth in Camillan oakwood on the sandstone to west. The Reenadinna exclosures were located so as to cover a representative range of yew-wood stand types.

Three further exclosures were erected in Camillan in 1974 / 1975 under the direction of Dr. A. Craig (C2, C4 and C5 in Table 4.1). Exclosures C2 and C4 were established in 1974 in areas which had been cleared of *Rhododendron ponticum* in 1972. Exclosure C5, known as the Mine Paddock exclosure, is a long, narrow exclosure approximately 50 m wide by 170 m long. It was

positioned so as to encompass the ecotone between mature oak-holly woodland at its western end and open grassland at its eastern end.

Two smaller exclosures were erected by the Killarney National Park rangers (C3 and W1 in Table 4.1). Exclosure C3 was established on the northern margin of Camillan, close the lough-shore, circa 1980. Exclosure W1 was constructed in 1991 near the Old Weir Bridge on Dinis Island to the west of Camillan.

Table 4.1 Location, canopy openness, vegetation type and area of exclosed and unexclosed plots on the Muckross Peninsula, with date of exclosed plot establishment. *a* indicates that this was a plot within a larger exclosure.

Site	Location	Canopy	Vegetation	Exclosed plot area (m^2)	Exclosed plot established	Unexclosed plot area (m^2)
R1	Reenadinna	Closed	*Taxus baccata* woodland	888	1969-70	600
R2	Reenadinna	Closed	*Taxus baccata - Corylus avellana - Quercus robur* woodland	764	1969-70	600
R3	Reenadinna	Semi-open	*Taxus baccata* scrub woodland	1036	1969-70	600
C1	Camillan	Semi-open	*Quercus petraea - Ilex aquifolium* woodland	1090	1969-70	600
C2	Camillan	Semi-open	*Quercus petraea - Ilex aquifolium* woodland	959	1974	600
C3	Camillan	Open	*Quercus petraea* woodland margin	169	*c.*1980	169
C4	Camillan	Semi-open	*Quercus petraea - Betula pubescens* woodland	260	1974	260
C5	Camillan	Closed	*Quercus petraea - Ilex aquifolium* woodland	225 [a]	1974-75	225
W1	Dinis	Open	*Quercus petraea – Pinus sylvestris* woodland clearing	200	1991	200

All exclosure fences are approximately 2 m high and composed of wire stock netting, typically topped with barbed wire. They have been maintained deer-proof throughout by the Killarney National Park rangers. Reenadinna exclosures have been unmanaged except for the removal of three large *Rhododendron* bushes from exclosure R1 sometime in the 1980s and the occasional removal of other exotic species, such as beech seedlings. In Camillan, *Rhododendron* clearance has been more extensive and most of the plots have probably been subject to periodic management to this end, although *Rhododendron* was left largely untouched inside exclosure C4. The location of all exclosures is shown in Fig. 4.1.

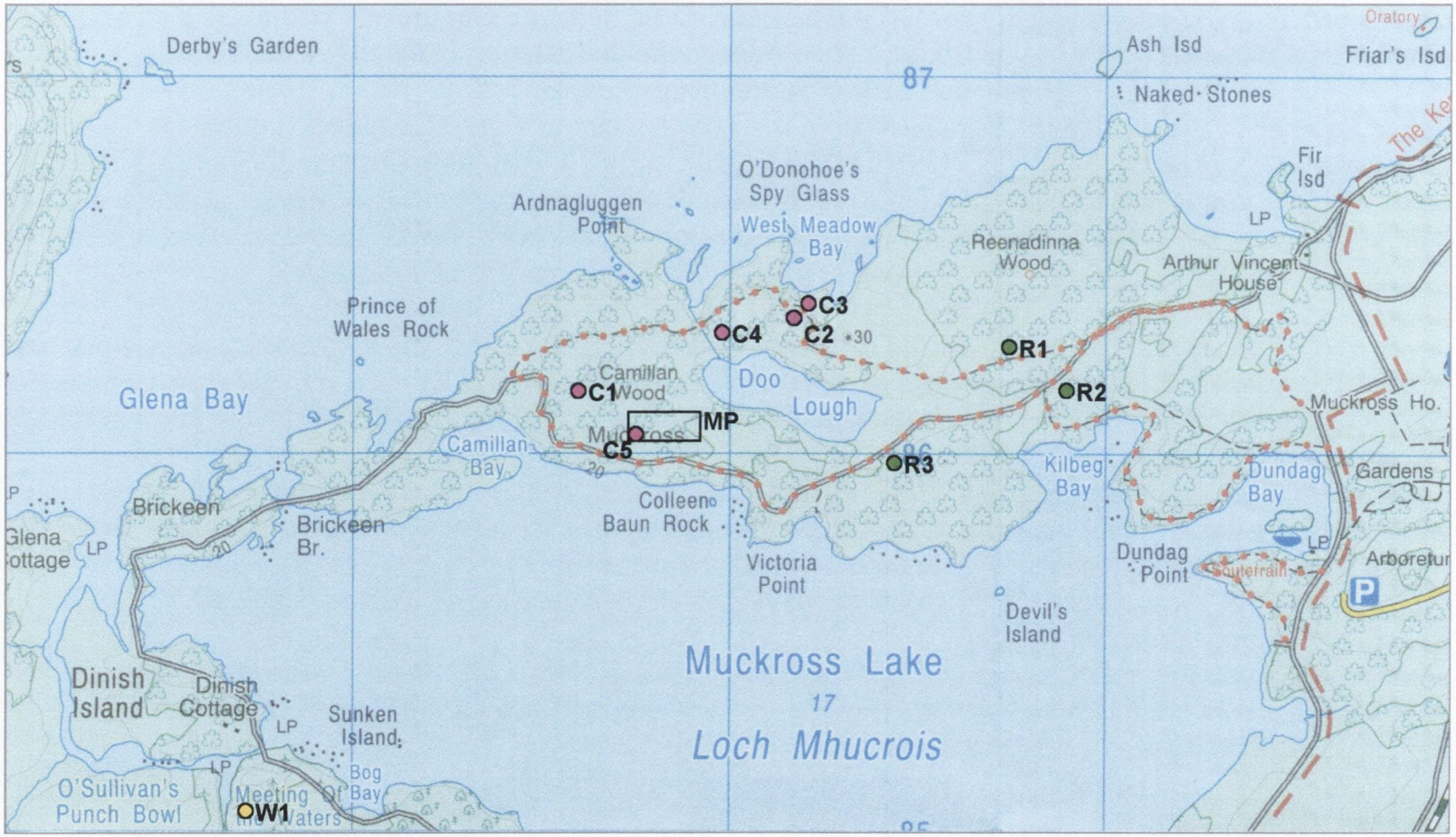


Figure 4.1 The Muckross Peninsula, Killarney National Park with location of long-term deer exclosures. Green dots indicate Reenadinna yew-wood exclosures, pink dots indicate Camillan oakwood exclosures, yellow dot indicates Dinis exclosure. Rectangle marked MP indicates position of the Mine Paddock exclosure. Scale 1: 17850

4.2.2 Data collection 1969-1997

A base-line field layer survey was conducted in exclosures R1, R2, R3 and C1 in 1969, prior to fencing, and these exclosures have been resurveyed several times since at irregular intervals (Tables 4.2 and 4.3; all surveys by Dr. D.L. Kelly, except 1997 survey of exclosure C1 by Dr. G.T. Higgins). Surveys consisted of a field layer species list for the entire exclosure and a quantitative quadrat survey. Quadrats, 1x1 m in size, were positioned at new random co-ordinates for each survey with the restriction that each quarter of an exclosure had approximately equal numbers of quadrats. Areas disturbed by *Rhododendron* removal in exclosure R1 were avoided. The number of quadrats used and the data recorded varied slightly between surveys, as shown in Tables 4.2 and 4.3. Note that before 1980 separate quadrats were used to assess bryophyte cover. The number of juvenile trees occurring within each quadrat was also counted in all years.

Table 4.2 Data collection for exclosures R1-3, 1969-1994. Asterisks (*) indicate data collected. *a* indicates 2x2m quadrats. *b* indicates bryophyte cover was estimated within 1x1m field layer quadrats

Year of survey	Exclosures surveyed	No. 1x1m quadrats	Species cover (%)	Total field cover (%)	Litter cover (%)	Total bryophyte cover (%)	Bryophyte quadrats
1969	R1	8					12x25cm (n=10)
	R2	12	*	*	-	*	12x25cm (n=10)
	R3	10					25x25cm (n=10)
1970	R1-2	5 [a]	*	*	-	*	12x25cm (n=10)
1974	R1-3	10	*	*	-	-	-
1980	R1-3	15	*	*	*	*	*b*
1985	R1-3	15	*	*	-	-	-
1992	R3	15	*	*	-	*	*b*
1994	R1-2	15	*	*	*	*	*b*

Table 4.3 Data collection for exclosure C1, 1969-1997. Asterisks (*) indicate data collected. *b* indicates bryophyte cover was estimated within 1x1m field layer quadrats.

Year of survey	No. 1x1m quadrats	Species cover (%)	Total field cover (%)	*Vaccinium* height (cm)	Litter cover (%)	Total bryophyte cover (%)	Bryophyte quadrats
1969	9	*	*	-	-	*	12x25cm (n=10)
1974	10	*	*	*	-	-	-
1980	15	*	*	*	*	*	*b*
1985	15	*	*	*	*	*	*b*
1993	15	*	*	-	*	*	*b*
1997	15	*	*	-	*	*	*b*

In addition, in November 1979, exclosure C1 and a nearby grazed area (approximately 27x27m) were surveyed by Dr. J. Cross using random 1x1m quadrats (n = 20 for both areas). Percentage estimates of each of the following variables were recorded: cover of each field layer species, total field layer cover, total bryophyte cover, litter cover, fallen wood, bare soil, bare rock. Seedling density for each tree species was recorded and the maximum height of tree seedlings, *Vaccinium myrtillus* and *Luzula sylvatica* in each quadrat was measured.

Exclosures C2 and C4 were surveyed annually by Dr. A. Craig from 1975 to 1982 and again in 1985. For each tree species present, the maximum height of juveniles within the exclosure was recorded. In exclosure C5, four 7x7 m subplots distributed along the length of the exclosure (Table 4.4) were surveyed annually (by Dr. A. Craig) from 1976 to 1982 and again in 1985. Within each plot the maximum height of juveniles for each tree species was again recorded. No baseline or subsequent recording was available for exclosures C3 and W1.

Table 4.4 Subplots within exclosure C5, the Mine Paddock exclosure.

Subplot	Location	Canopy type	Canopy species
A	Western end of exclosure	Closed	Oak and holly
B	Middle of exclosure	Semi-open	Birch and alder
C	Middle of exclosure	Closed	Oak with birch, holly and rowan
D	Eastern end of exclosure	Open	None

In 1981 the adult tree class in exclosures R1, R2, R3 and C1 was surveyed (by S. Kiang & A. Bloxham). Species, gbh and position co-ordinates were recorded. Where trees had two adult stems at breast height, the girth of each was recorded. Where three or more adult stems occurred at breast height, the average girth and the number of stems were recorded.

4.2.3 Data collection 2000-2001

In summer 2000, the field layer of exclosures R1, R2 and R3 was resurveyed (by Dr. D.L. Kelly and myself). The same methodology as the 1994 survey was employed: fifteen 1x1m quadrats were randomly located within each exclosure with three quarters having four quadrats and the fourth quarter (determined at random), three quadrats. Percentage estimates of the following variables were recorded: cover of each field layer species, total field layer cover, total bryophyte cover and litter cover. Seedling density of each tree species and field layer height were also recorded. An overall field layer species list for each exclosure was made.

In summer 2001, to permit a comparison of grazed and ungrazed woodland, an unexclosed plot was established adjacent to each exclosure, R1-3, C1-5 and W1 (Table 4.1). Each unexclosed plot were positioned so as to possess similar canopy and topography to that of the paired exclosure. Due to the close proximity of the peninsula road and an area of seasonally flooded woodland, unexclosed plot C1 had to be split into two sections, one of 300 m^2 and one of 150 m^2, on opposite sides of exclosure C1. To avoid edge effects and paths worn by deer around exclosures, unexclosed plots were position 2-3 m away from the fenceline. The exception to this was unexclosed plot R1 which had to be positioned on the other side of a small path due to the canopy composition of the exclosure.

A comprehensive survey inside exclosure C5 was not practical because of its size, so a 15 x 15 m "exclosed" plot was established at the western end of the exclosure. This was positioned so as to encompass the previously surveyed subplot A (which could not be accurately relocated). The area of subplot A was selected over that of the other subplots because it possessed an oak-holly canopy similar to that of the other Camillan exclosures and the nearby woodland outside the exclosure was suitable for an unexclosed plot.

The adult tree class in all exclosures and unexclosed plots was surveyed. Species, gbh and position co-ordinates were recorded. Where more than one adult stem occurred at breast height, the girth of each individual stem was recorded. This allowed comparison with the previous survey in exclosures R1-3 and C1, where maps drawn from the 1981 dataset were used to re-identify trees and note recruits and losses. However, if a tree had a fork between 20 cm and breast height, girth below the fork was also recorded as this permitted a more accurate calculation of basal area. In exclosure C2, due to an abundance of holly adults of 10 cm $\leq$ gbh $\leq$ 19 cm, this class was subsampled using the field layer quadrats. Birch was similarly subsampled in exclosure W1.

The field layer in all exclosed and unexclosed plots was surveyed using a stratified sampling method. Each plot was divided into four equal quarters, except at sites C4, C5 and W1 where the plots were divided into two "quarters" and C3 where each plot was counted as one "quarter". Within each quarter, five 1x1m quadrats were randomly located. This ensured an even distribution of sampling within each plot and a comparative intensity of sampling between sites. Percentage estimates of the following variables were recorded: cover of each field layer species, total field

layer cover, total bryophyte cover, litter cover, fallen wood, bare soil and bare rock. In the oakwood exclosures it was decided that survey of the dense thickets required further categorization so the field layer was defined as vegetation up to 2 m in height and understorey was defined as vegetation above 2 m in height excluding adult trees. The maximum height of *Rubus fruticosus* and *Lonicera periclymenum* was recorded for Reenadinna quadrats and the maximum height of *Vaccinium myrtillus* and *Luzula sylvatica* was recorded for Camillan quadrats. The heights of all juvenile trees within quadrats were measured. Additionally, an effort was made to locate and measure all juvenile yews within each plot area.

4.2.4 Data analysis

Field layer data 1969-2001

Inevitably, in a dataset collected over thirty years, there were a few inconsistencies in the data for exclosures R1-3 and C1, which needed to be resolved before analysis could be conducted. In some of the earlier surveys, 1969, 1970 and 1974, cover scores had not been recorded for seedlings when they were present in low numbers. Nominal scores were therefore assigned, on the basis of existing data, as follows: 1 seedling = 0.5%, 2-4 seedlings = 1%, 5-9 seedlings = 2%. Cover scores were also missing for a small number of saplings, to each of which a score of 3% was assigned after examination of values for other saplings at that time. Total field layer values were missing for the 1997 survey of exclosure C1. This variable was therefore estimated by summing the cover of individual species.

Both *Viola riviniana* and *Viola reichenbachiana* are present in the yew-wood, but were usually recorded as *Viola* spp. as surveys were conducted during the summer months when identification to species is difficult due to the lack of floral characters. Similarly, *Polypodium vulgare* and *Polypodium interjectum* are both present in the oak wood, but were frequently recorded as simply *Polypodium* sp. as identification to species is difficult when specimens are juvenile, lacking in sori, or heavily grazed. For the purposes of analysis therefore, data within each of these genera were pooled.

From the species lists, the total number of field layer species was calculated for each exclosure, for each survey, from 1969 to 2000. For the combined Reenadinna dataset (exclosures R1-3) and the Camillan dataset, (exclosure C1), changes over time in the proportion of species between five

broad vegetation categories were investigated with chi-squared tests: trees; low shrubs and climbers; grasses and sedges; forbs; and ferns. Data from the 2000 survey were similarly used to compare differences in proportions between Reenadinna and Camillan.

From the quadrat data, trends in species cover, general cover variables and seedling / sapling numbers in the combined Reenadinna dataset and the Camillan dataset were analyzed using linear regression analysis. To ensure that Reenadinna exclosures were equally represented at each time point, the 1970 data for exclosures R1 and R2 were excluded from the analysis. The 1992 data for exclosure R3 and the 1994 data for exclosures R1 and R2 were used combined as estimates for vegetation in 1993. Regression analysis was restricted to species occurring in 5% or more of the quadrats in a dataset as meaningful statistics could not be applied to rarer species.

Changes in the composition of vegetation quadrats as a whole were analyzed using non-metric multidimensional scaling ordination (NMS) using the same procedure detailed in Chapter 3. The field layer species cover data for Camillan (exclosure C1) were ordinated separately from the combined yew-wood data (exclosures R1-3). To reduce the influence of rare species, ordination analysis was restricted to species occurring three or more times in a dataset. In the yew-wood dataset, nineteen quadrats were omitted from the ordination because they contained no vascular vegetation. These were largely from the earlier surveys.

Data from the 1979 survey of site C1 were analysed using ANOVA for height measurements and Mann-Whitney U tests for percentage cover and densities. It was not possible to do meaningful statistical analysis on the maximum height data from exclosures C2, C4 and C5 for 1975-1985; these data were therefore visually inspected.

Adult tree data 1981-2001

Differences in mortality and recruitment between species (and sites for the Reenadinna data) during the period from 1981 to 2001 were investigated using chi square tests. In a few cases, the sites of former holly or hazel adults were now occupied by juvenile class trees which could possibly have been regrowth from the former tree. However, trees alive in 1981 were classified as "dead" in 2001 if they had been lost from the adult tree class. Differences in girth between trees which survived

this period and those which died were investigated by species using Mann-Whitney U tests. Density and basal area were calculated by species for each exclosure.

For the Reenadinna exclosures, differences in stem girth growth between species and sites were tested using a two-way ANOVA. Hazel was excluded from this analysis as specific stems could not be re-identified with confidence, and spindle and rowan were excluded due to insufficient data. A one-way ANOVA was used to test differences in girth growth between species in the Camillan exclosure. Rowan was again excluded due to insufficient data. Where forked trees had been measured above the fork in 1981, an estimate of below fork girth in 1981 was derived by deducting the observed growth of the above fork stems from the below fork girth in 2001. Basal area by species was subsequently calculated for each exclosure.

Adult trees were allocated to 30cm size classes; for multi-stemmed trees, the largest girth measurement was used. Differences in the resulting frequency distributions for 1981 and 2001 were tested by species using Kolgomorov-Smirnov tests. To investigate regeneration via basal sprouting, Mann-Whitney U tests were used to test differences in the number of stems per tree in 1981 and 2001. Kruskal-Wallis H tests were used to test differences in number of stems per yew between sites.

Exclosed and unexclosed plots 2001

Exclosed and unexclosed vegetation data was compared for the three locations, Reenadinna, Camillan and Dinis, using Mann-Whitney U tests. Separate NMS ordinations were used to investigate vegetation composition at the Reenadinna sites and the Camillan sites. Analysis was again restricted to species occurring three or more times in a dataset. For holly, rowan and *Rhododendron*, separate variables were included for the cover of each in the understorey in Camillan. Due to absence of vascular vegetation, four quadrats were excluded from the Reenadinna ordination and one quadrat was excluded from the Camillan ordination.

Mann-Whitney U tests were used to check for differences in the number of stems per tree. Analysis was restricted to species with sample sizes ten or greater. Adult tree data was again analysed using Kolgomorov-Smirnov tests to investigate differences in girth class frequency distributions between exclosed and unexclosed plots in each woodland.

Finally, differences in natural regeneration were investigated at site level. Due to the overwhelming effect of deer exclusion, only data from exclosed plots were utilised. An index of natural regeneration, NR, was calculated for each exclosure, where:

NR = (no. of saplings per ha) + 30 x (no. of 10-39cm girth class adults per ha)

The factor of 30 applied to adult trees here was approximately equal to the mean ratio in the exclosures of 10-39cm girth class adults to saplings. This meant that, overall, equal weighting was given to saplings and the young adult trees, and took into account the self-thinning process that occurs as saplings are recruited to the adult tree class.

SPSS (SPSS Inc 1999) was used for all univariate statistics. PC-Ord (McCune & Mefford 1999) was used for all ordinations.

4.3 Results:

4.3.1 Field layer vegetation 1969-2001

All four exclosures exhibited similar trends in overall species richness (Fig. 4.2a). After fencing in 1969 there was a rapid increase in the number of species present, reaching a maximum around 1980. This was followed by a slow and gradual decline, although only exclosure C1 had fewer species in 2000 than prior to fencing. There were clear differences in species richness between sites. Exclosure R3, scrub woodland which still has a fairly open canopy, consistently had the greatest number of species with a peak of 50 in 1980. Exclosure R2, in an area of yew-hazel woodland, had an intermediate number of species, whereas exclosure R1, in area of mature yew woodland with a dense, closed canopy, had the fewest species of the Reenadinna sites. The Camillan exclosure, C1, initially had more species than exclosure R1, but showed a gradual loss of species since 1974. These differences between the exclosures are underlined by the data for the mean number of species per survey quadrat (Fig. 4.2b), although the trends over time are not so evident.

There was no significant difference in the proportions of plant types (Fig. 4.3) within the total species inventory in 1969 and 2000, in either exclosures R1-3 ($P = 0.125$, chi-square) or exclosure

Figure 4.2 Changes in vascular species richness in the field layer of exclosures R1-3 (yew-wood) and C1 (oakwood): (a) total number of species present in each exclosure, 1969-2000; (b) mean number of species present in 1x1m survey quadrats, 1969-2001. Vertical bars indicate se.

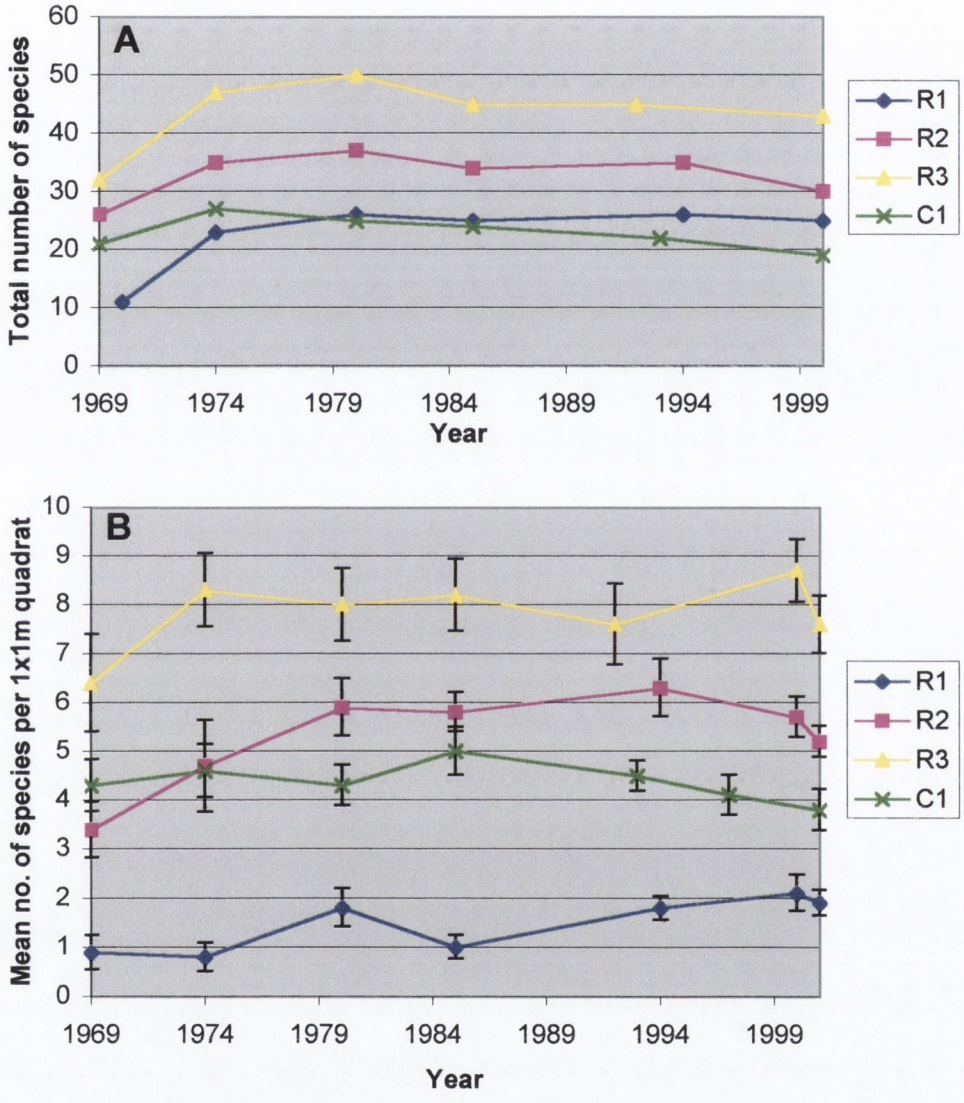
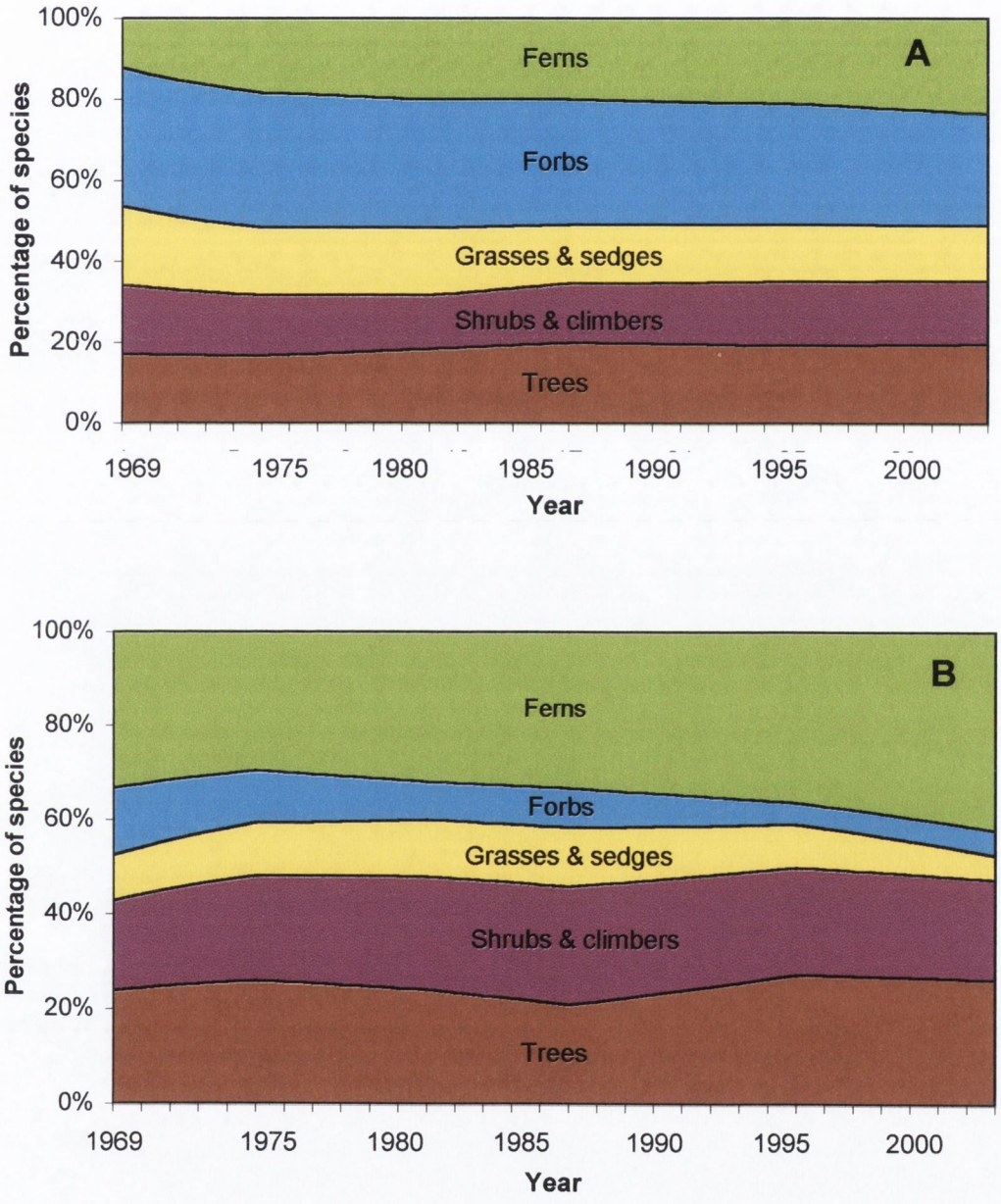


Figure 4.3 Proportion of plant types in the total field layer species inventory of (a) exclosures R1-3, and (b) exclosure C1, 1969- 2000.



C1 (P = 0.768, chi-square). There was however a difference in the proportions of plant types between exclosures R1-3 and C1 in 2000 (P < 0.001, chi-square). Forb species were the most numerous plant type in the Reenadinna exclosures whereas ferns were by far the largest species group in the Camillan exclosure, where they seem to have increased at the expense of forbs, grasses and sedges.

In the Reenadinna exclosures, total field cover, bryophyte cover and litter cover all increased significantly between 1969 and 2001, according to linear regression analysis (Table 4.5). The increase in field cover, from 3.8% to 48.4% was largely due to significant increases in *Hedera helix*, *Rubus fruticosus* and *Lonicera periclymenum*. *Brachypodium sylvaticum* and *Potentilla sterilis* decreased slightly during this period. Other species, which showed no clear trends, tended to be very sparse with mean cover <2%. Ash seedlings increased significantly in density between 1969 and 2001 (Table 4.6). Ash saplings appeared in 1985 and subsequently increased in density. Holly juveniles did not increase significantly between 1969 and 2001, but a linear regression analysis limited to data between 1969 and 1980 confirmed that numbers of holly saplings had increased early on (P < 0.001), with an ensuing period of fairly stable density. Rowan saplings appeared for the first time in 1980, but exhibited no significant subsequent increase.

In the Camillan exclosure, total field cover increased from 9.1% in 1969 to 67.0% in 2001 (Table 4.7). Bryophyte cover decreased slightly during this period. The increase in field cover can be attributed largely to expansion in the cover of *Hedera helix*, *Luzula sylvatica* and *Vaccinium myrtillus*. Two species, *Betula pubescens* and *Oxalis acetosella*, showed a significant decrease in cover. No tree species showed a trend of increasing density in seedlings or saplings, and holly and birch seedlings actually decreased in numbers (Table 4.8). This was possibly due to the competition presented by *Vaccinium myrtillus*, which increased in height as well as cover. Yew seedlings were found fairly frequently at low densities, from 1974, with the first sapling appearing in the data in 1993. Oak seedlings were consistently rare with the exception of the 1985 survey when a mean density of 18.6 seedlings per m^2 was recorded; this was the result of a mast year in 1984 (cf. Kelly 2002). Oak saplings were found in 1997 and 2001.

A three-dimensional solution (P = 0.048, Monte Carlo test) was found to be the most stable ordination for the Reenadinna dataset with a stress of 21.6%. The two dimensions which explained

Table 4.5 Mean percentage cover (± se) of vegetation in exclosures R1-3, 1969-2001. Analysis restricted to species occurring in 5% or more of quadrats. *n* values are number of quadrats. *P* values indicate significance of linear regression analysis. For significant changes ($P<0.05$), Inc indicates increase and Dec indicates decrease.

Species	1969 (*n*=30)	1974 (*n*=30)	1980 (*n*=45)	1985 (*n*=45)	1993 (*n*=45)	2000 (*n*=45)	2001 (*n*=60)	*P*	
Brachypodium sylvaticum	0.67 ± 0.16	0.57 ±0.13	0.92 ±0.15	0.93 ±0.15	0.60 ±0.13	0.73 ±0.13	0.33 ±0.07	**0.044**	Dec
Carex flacca	0.53 ±0.33	0.20 ±0.10	1.20 ±0.91	0.13 ±0.08	0.04 ±0.04	0.06 ±0.05	0.05 ±0.04	0.103	
Carex pulicaris	0.10 ±0.10	0.17 ±0.11	0.00	0.47 ±0.35	0.06 ±0.05	0.14 ±0.11	0.20 ±0.17	0.840	
Carex sylvatica	0.00	0.07 ±0.05	0.04 ±0.04	0.22 ±0.11	0.07 ±0.05	0.08 ±0.05	0.05 ±0.02	0.836	
Fragaria vesca	0.33 ±0.12	0.50 ±0.15	1.51 ±0.56	1.03 ±0.30	1.52 ±0.49	1.88 ±0.54	1.27 ±0.33	0.018	
Hedera helix	0.27 ±0.10	0.37 ±0.12	1.58 ±0.55	2.07 ±0.58	4.73 ±0.44	6.56 ±0.22	9.21 ±2.01	**<0.001**	Inc
Lonicera periclymenum	0.10 ±0.07	0.13 ±0.10	0.20 ±0.09	1.09 ±0.69	0.71 ±0.29	1.67 ±0.65	1.78 ±0.74	**0.004**	Inc
Potentilla sterilis	0.13 ±0.06	0.07 ±0.05	0.11 ±0.07	0.09 ±0.07	0.06 ±0.03	0.04 ±0.03	0.00	**0.038**	Dec
Rubia peregrina	0.27 ±0.11	0.37 ±0.14	0.96 ±0.30	1.67 ±0.73	0.56 ±0.20	0.98 ±0.38	1.10 ±0.34	0.265	
Rubus fruticosus	0.67 ±0.14	0.95 ±0.34	11.00 ±2.36	14.74 ±3.38	20.30 ±3.51	26.07 ±3.35	21.88 ±2.72	**<0.001**	Inc
Sanicula europaea	0.27 ±0.13	0.30 ±0.24	1.47 ±0.82	0.44 ±0.18	1.76 ±1.00	1.51 ±0.95	0.27 ±0.19	0.556	
Solidago virgaurea	0.13 ±0.06	0.13 ±0.06	0.22 ±0.12	0.29 ±0.11	0.14 ±0.08	0.20 ±0.09	0.18 ±0.09	0.876	
Teucrium scorodonia	0.13 ±0.08	0.13 ±0.08	0.44 ±0.15	0.36 ±0.23	0.44 ±0.18	0.98 ±0.43	0.72 ±0.32	**0.020**	Inc
Viola spp.	0.43 ±0.14	0.80 ±0.14	1.58 ±0.33	1.31 ±0.27	1.91 ±0.74	2.17 ±0.54	0.47 ±0.17	0.311	
Total field cover	3.81 ±0.66	14.53 ±3.58	22.81 ±3.16	29.58 ±4.43	39.59 ±4.02	50.64 ±3.97	46.38 ±3.21	**<0.001**	Inc
Total bryophyte cover	79.03 ±5.49	-	88.56 ±3.19	-	91.27 ±1.63	93.58 ±1.03	87.58 ±2.26	**0.013**	Inc
Litter	-	-	5.00 ±1.14		11.97 ±1.66	18.04 ±1.27	27.00 ±1.53	**<0.001**	Inc

Table 4.6 Mean seedling and sapling densities per m^2 (± se) in exclosures R1-3, 1969-2001. Data presented only for species occurring in 5% or more of quadrats. *n* values are number of quadrats. *P* values indicate significance of linear regression analysis. For significant changes ($P<0.05$), Inc indicates increase and Dec indicates decrease.

Species		1969 (*n*=30)	1974 (*n*=30)	1980 (*n*=45)	1985 (*n*=45)	1993 (*n*=45)	2000 (*n*=45)	2001 (*n*=60)	*P*	
Ilex aquifolium	seedlings	0.77 ±0.19	0.37 ±0.13	0.64 ±0.20	0.69 ±0.34	0.36 ±0.12	0.87 ±0.25	0.37 ±0.14	0.683	
	saplings	0.07 ±0.05	0.67 ±0.19	0.98 ±0.22	0.49 ±0.16	0.56 ±0.14	0.49 ±0.12	0.68 ±0.14	0.497	
Fraxinus excelsior	seedlings	0.10 ±0.06	0.27 ±0.18	0.80 ±0.40	0.71 ±0.22	1.78 ±0.55	2.67 ±1.16	0.87 ±0.39	**0.011**	Inc
	saplings	0.00	0.00	0.00	0.07 ±0.04	0.09 ±0.05	0.22 ±0.08	0.32 ±0.11	**<0.001**	Inc
Sorbus aucuparia	seedlings	0.40 ±0.14	0.30 ±0.14	0.22 ±0.09	0.36 ±0.25	0.09 ±0.04	0.11 ±0.06	0.15 ±0.06	0.061	
	saplings	0.00	0.00	0.13 ±0.06	0.82 ±0.48	0.38 ±0.15	0.27 ±0.12	±0.35 ±0.11	0.246	

Table 4.7 Changes in mean percentage cover (± se) of vegetation in exclosure C1, 1969-2001. Data presented only for species occurring in 5% or more of quadrats. *n* values are number of quadrats. *P* values indicate significance of linear regression analysis. For significant changes ($P<0.05$), Inc indicates increase and Dec indicates decrease.

Species	1969 (*n*=9)	1974 (*n*=10)	1980 (*n*=15)	1985 (*n*=15)	1993 (*n*=15)	1997 (*n*=15)	2001 (*n*=20)	*P*	
Betula pubsecens	0.33 ±0.17	0.05 ±0.05	0.00	0.00	0.00	0.07 ±0.07	0.00	**0.010**	Dec
Blechnum spicant	1.22 ±0.76	3.40 ±2.96	1.07 ±0.48	2.23 ±1.43	4.23 ±2.24	0.33 ±0.33	2.50 ±1.23	0.853	
Dryopteris aemula	0.11 ±0.11	0.00	0.07 ±0.07	0.40 ±0.27	1.00 ±1.00	0.00	0.00	0.851	
Hedera helix	0.06 ±0.06	0.30 ±0.21	0.40 ±0.19	1.10 ±0.36	2.73 ±1.62	2.17 ±1.02	6.53 ±2.60	**0.002**	Inc
Hymenophyllum tunbridgense	0.10 ±0.10	0.00	0.53 ±0.47	0.00	0.13 ±0.09	0.03 ±0.03	0.10 ±0.10	0.648	
Ilex aquifolium	0.50 ±0.24	0.70 ±0.26	0.70 ±0.15	0.80 ±0.16	2.33 ±1.77	1.27 ±0.99	0.30 ±0.25	0.705	
Lonicera periclymenum	0.00	0.50 ±0.50	0.40 ±0.27	0.33 ±0.33	0.23 ±0.20	0.73 ±0.45	3.93 ±2.50	0.069	
Luzula sylvatica	4.78 ±3.24	3.50 ±2.06	13.73 ±5.72	8.30 ±4.41	42.57 ±8.04	20.50 ±7.28	29.70 ±5.30	**<0.001**	Inc
Oxalis acetosella	0.78 ±0.40	0.10 ±0.10	0.33 ±0.33	0.33 ±0.23	0.07 ±0.07	0.13 ±0.13	0.05 ±0.05	**0.042**	Dec
Polypodium spp.	0.11 ±0.11	0.00	0.00	0.20 ±0.20	0.10 ±0.07	0	0.75 ±0.75	0.284	
Pteridium aquilinum	1.44 ±0.78	3.10 ±1.99	2.80 ±2.66	3.13 ±1.85	0.27 ±0.15	0.13 ±0.06	1.27 ±0.88	0.189	
Quercus petraea	0.06 ±0.06	1.20 ±0.35	0.37 ±0.16	6.93 ±3.52	0.00	2.10 ±1.03	0.10 ±0.10	0.734	
Rubus fruticosus	0.00	0.00	0.00	0.87 ±0.68	1.40 ±0.90	2.27 ±1.99	1.27 ±1.25	0.115	
Sorbus aucuparia	0.11 ±0.11	0.00	0.03 ±0.03	0.00	0.00	0.13 ±0.13	0.80 ±0.75	0.208	
Taxus baccata	0.00	0.10 ±0.07	0.03 ±0.03	0.07 ±0.05	0.20 ±0.20	0.00	0.03 ±0.03	0.782	
Vaccinium myrtillus	1.89 ±0.77	12.30 ±4.28	25.40 ±5.51	20.53 ±6.22	20.07 ±5.17	26.87 ±7.94	30.53 ±6.54	**0.005**	Inc
Total field cover	9.11 ±5.31	21.60 ±7.23	40.73 ±5.80	41.87 ±6.93	63.87 ±6.13	56.67 ±8.41	67.00 ±3.58	**<0.001**	Inc
Total bryophyte cover	32.44 ±9.59	-	35.80 ±5.73	33.33 ±6.93	18.93 ±6.11	14.93 ±2.73	23.75 ±5.40	**0.020**	Dec
Litter	-	-	60.67 ±4.60	60.33 ±6.73	83.00 ±3.80	43.00 ±5.81	71.75 ±4.46	0.517	

Table 4.8 Mean seedling and sapling densities per m^2 (± se) in exclosure C1, 1969-2001. Data presented only for species occurring in 5% or more of quadrats. Also shown is maximum height of *Vaccinium myrtillus* (cm). *n* values are number of quadrats. *P* values indicate significance of linear regression analysis. For significant changes ($P<0.05$), Inc indicates increase and Dec indicates decrease.

Species		1969 (*n*=9)	1974 (*n*=10)	1980 (*n*=15)	1985 (*n*=15)	1993 (*n*=15)	1997 (*n*=15)	2001 (*n*=20)	*P*	
Quercus petraea	seedlings	0.11 ±0.11	3.80 ±1.37	1.00 ±0.47	18.60 ±7.23	0.00	1.60 ±0.92	0.10 ±0.10	0.354	
	saplings	0.00	0.00	0.00	0.00	0.00	0.53 ±0.36	0.05 ±0.05	0.161	
Ilex aquifolium	seedlings	0.89 ±0.51	1.20 ±0.42	1.93 ±0.55	2.27 ±0.52	1.87 ±0.66	0.33 ±0.16	0.25 ±0.18	**0.040**	Dec
	saplings	0.00	0.00	0.00	0.00	0.13 ±0.13	0.00	0.10 ±0.10	0.229	
Taxus baccata	seedlings	0.00	0.20 ±0.13	0.07 ±0.07	0.13 ±0.09	0.00	0.13 ±0.09	0.05 ±0.05	0.720	
	saplings	0.00	0.00	0.00	0.00	0.07 ±0.07	0.13 ±0.09	0.00	0.207	
Sorbus aucuparia	seedlings	0.22 ±0.22	0.00	0.07 ±0.07	0.00	0.00	0.00	0.15 ±0.11	0.843	
	saplings	0.00	0.00	0.00	0.00	0.00	0.13 ±0.13	0.00	0.399	
Betula pubsecens	seedlings	0.78 ±0.40	0.10 ±0.10	0.00	0.00	0.00	0.07 ±0.07	0.00	**0.002**	Dec
Maximum height of *Vaccinium* (cm)		-	28.13 ±3.26	48.00 ±2.60	53.50 ±3.08	-	-	61.76 ±6.27	**<0.001**	Inc

most variation are shown in Fig. 4.4a. The trends apparent in the regression analyses are strongly reflected in the ordination graphs. Exclosure communities in 1969 were centred near herbaceous species such as *Viola riviniana / reichenbachiana, Oxalis acetosella, Potentilla sterilis, Hypericum pulchrum* and *Brachypodium sylvaticum* (Fig. 4.4b). By 2001 there had been a transition to communities centred on woody plants, particularly *Rubus fruticosus, Rubia peregrina, Hedera helix, Lonicera periclymenum,* holly and rowan. All three exclosures have progressed in the same direction, although exclosure R3 initially had a species composition differing slightly to the other two sites.

For the Camillan dataset a two-dimensional solution was proposed by the ordination ($P = 0.048$, Monte Carlo test), with a stress level of 20.7% (Fig. 4.5a). There was a change from a sparse 1969 community characterised by oak, birch and *Oxalis acetosella*, towards a 2001 community characterised by *Luzula sylvatica, Vaccinium myrtillus* and *Rubus fruticosus* (Fig. 4.5b). The vegetation has also become more homogeneous, as indicated by the tighter clustering of points for 1997 and 2001.

Ten years after the fence at site C1 was erected there were surprisingly few differences between the vegetation inside and outside the exclosure (Tables 4.9 and 4.10). The cover of *Vaccinium myrtillus* and total herb cover were significantly higher inside the exclosure, whilst litter cover was significantly higher in the unfenced quadrats. There were no significant differences in seedling densities or maximum seedling heights, although the maximum heights of *Vaccinium myrtillus* and *Luzula sylvatica* were markedly higher inside the exclosure.

In exclosures C2 and C4, oakwood sites with semi-open canopies, species exhibited differential response to the cessation of deer browsing (Figs. 4.6 and 4.7). The maximum height of holly and rowan juveniles increased markedly during the first ten years of fencing in both exclosures with both species reaching 150-250 cm. Birch exhibited a similar response in exclosure C4 but failed to grow higher than 55 cm in exclosure C2, possibly due to suppression by the faster growing holly; in 1980 when the birch curve flattens out there is a marked increase in the maximum height of holly. Yew showed a slow but steady increase in maximum height in both exclosures reaching 100 cm in exclosure C4 and 55 cm in exclosure C2. Oak exhibited the slowest response in both exclosures. The maximum height of *Arbutus* dropped dramatically in exclosure C4 between 1979

Figure 4.4 (a) NMS ordination of vegetation quadrats in exclosures R1-3, 1969-2001. Dashed inset indicates position of (b) species box. Red lines connect centroids for 1969 and 2001 for each exclosure which are indicated by black numbers. See Appendix 1 for key to species abbreviations.

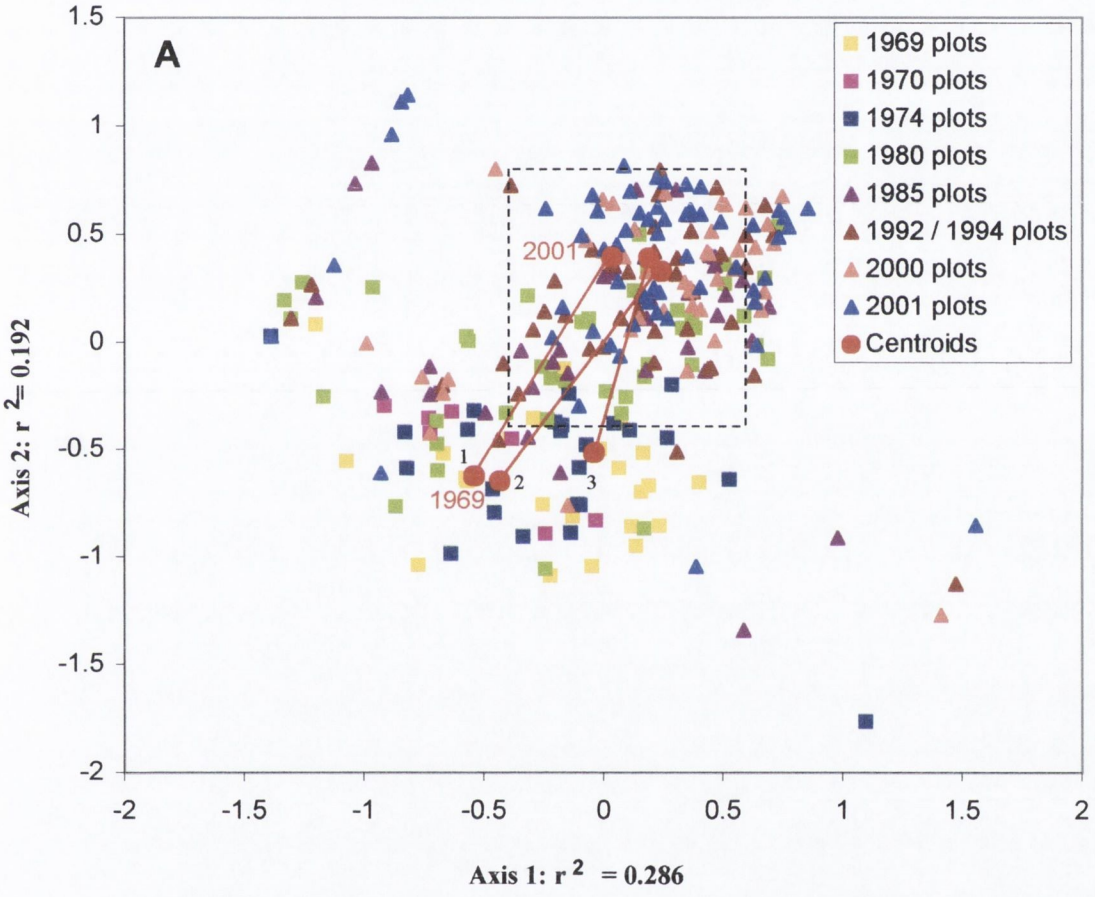


Figure 4.4 continued

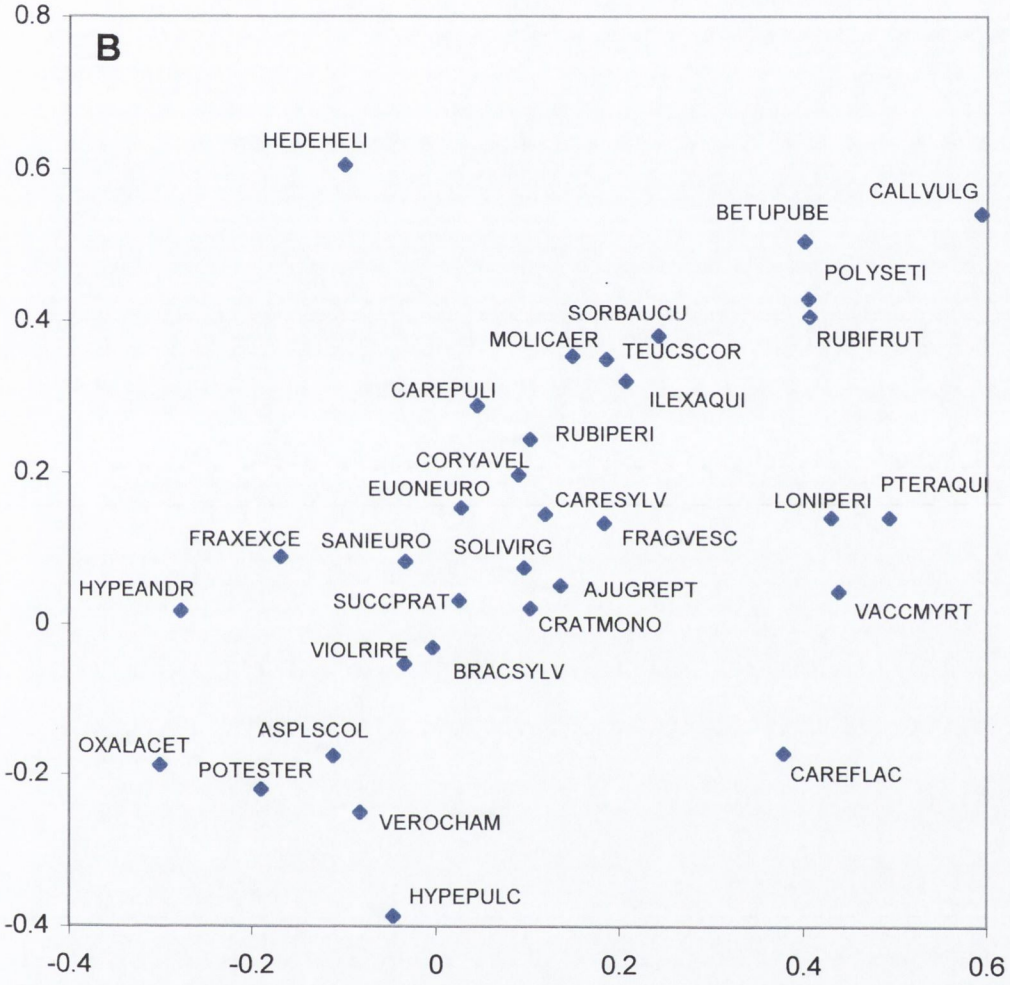


Figure 4.5 NMS ordination of (a) vegetation quadrats and (b) species in exclosure C1, 1969-2001; red lines connect centroids for 1969 and 2001. See Appendix 1 for key to species abbreviations.

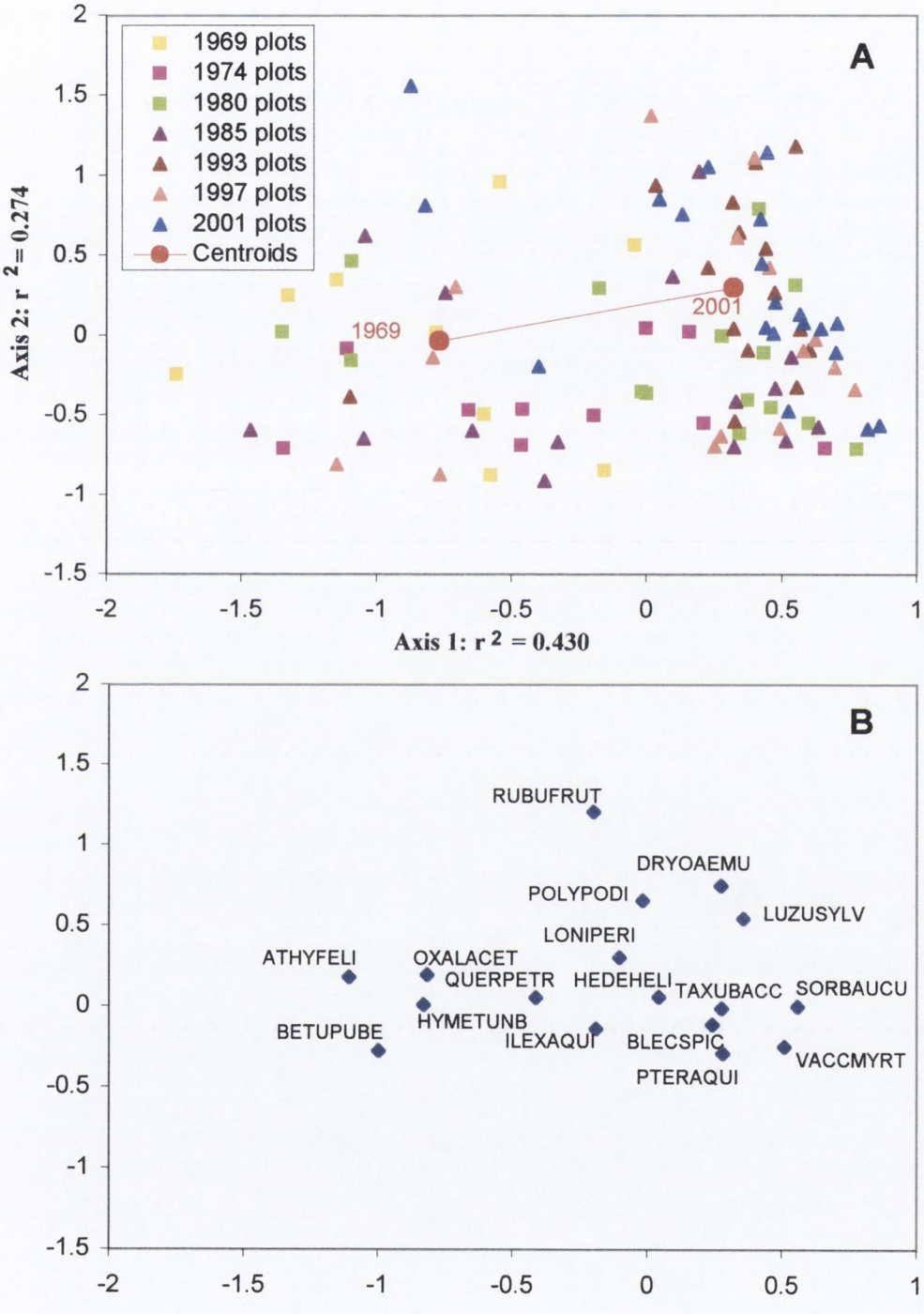


Table 4.9 Comparisons between exclosed and unexclosed vegetation, site C1. $n = 20$. Unpublished data from survey by Dr. J. Cross, 1979. Data analyzed using Mann-Whitney U test. Mean percentage cover (± se) shown as medians tend to zero.

	Percentage cover		Frequency (*x*/20)		*P* (% cover)
	Exclosed	Unexclosed	Exclosed	Unexclosed	
Athyrium filix-femina	0.25 ±0.25	0.00	1	0	1.000
Blechnum spicant	1.50 ±1.01	1.27 ±0.41	5	8	0.334
Dryopteris spp.	0.90 ±0.68	0.05 ±0.05	2	1	0.487
Hedera helix	0.18 ±0.05	0.10 ±0.05	7	4	0.480
Lonicera periclymenum	0.25 ±0.25	0.00	1	0	1.000
Luzula sylvatica	23.15 ±5.85	12.20 ±3.09	13	16	0.412
Oxalis acetosella	0.23 ±0.20	0.13 ±0.07	2	3	0.802
Polypodium spp.	0.05 ±0.05	0.00	1	0	1.000
Pteridium aquilinum	3.75 ±1.92	0.75 ±0.53	5	3	0.276
Vaccinium myrtillus	22.25 ±4.89	5.60 ±1.90	17	15	**0.002**
Viola spp.	0.03 ±0.03	0.00	1	0	1.000
Total herb cover	44.75 ±6.22	18.10 ±4.11	20	20	**0.001**
Total bryophyte cover	39.25 ±5.81	41.00 ±4.35	19	20	0.711
Litter	39.75 ±4.25	55.20 ±4.04	20	20	**0.015**
Fallen wood	0.25 ±0.25	0.35 ±0.26	1	2	1.000
Bare soil	0.05 ±0.05	0.90 ±0.53	1	4	0.106
Bare rock	0.25 ±0.25	0.05 ±0.05	1	1	1.000

Table 4.10 Comparisons of seedling density, maximum seedling height and maximum height of *Vaccinium* and *Luzula* between exclosed and unexclosed woodland, site C1. $n = 20$. Unpublished data from survey by Dr. J. Cross 1979. ANOVA used to compare mean heights. Mann-Whitney U test used to compare densities. Means are shown as medians tend to zero.

Species	Density (m^{-2})		*P*	Maximum height (cm)		*P*
	Exclosed	Unexclosed		Exclosed	Unexclosed	
Quercus petraea	0.85 ±0.46	0.20 ±0.12	0.235	20.50 ±2.85	11.00 ±2.52	0.060
Ilex aquifolium	4.10 ±1.14	2.40 ±0.57	0.501	5.40 ±0.64	4.40 ±0.34	0.253
Betula pubescens	0.05 ±0.05	0.00	1.000	3.00 ± 3.00	-	-
Taxus baccata	0.05 ±0.05	0.00	1.000	6.00 ± 6.00	-	-
Rhododendron ponticum	0.20 ±0.12	0.15 ±0.11	0.934	-	-	-
Vaccinium myrtillus				30.65 ±2.61	11.21 ±0.81	**<0.001**
Luzula sylvatica				16.92 ±1.51	8.19 ±0.74	**<0.001**

Figure 4.6 Maximum height of juvenile trees in exclosure C4, 1976-1985. Unpublished data of Dr.A. Craig.

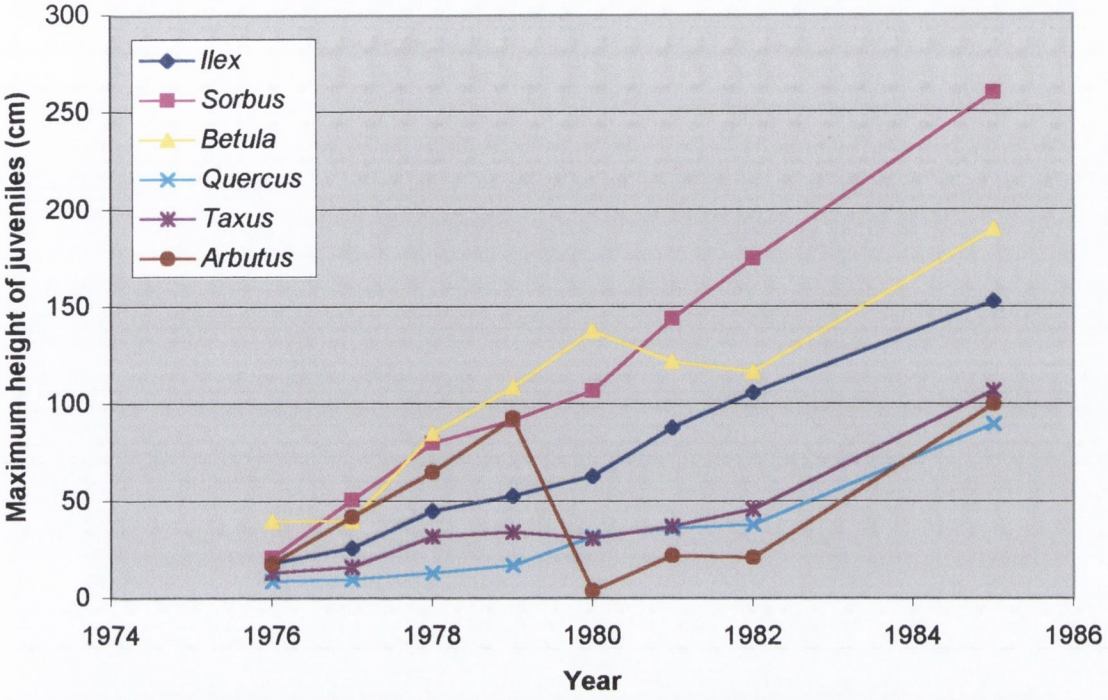
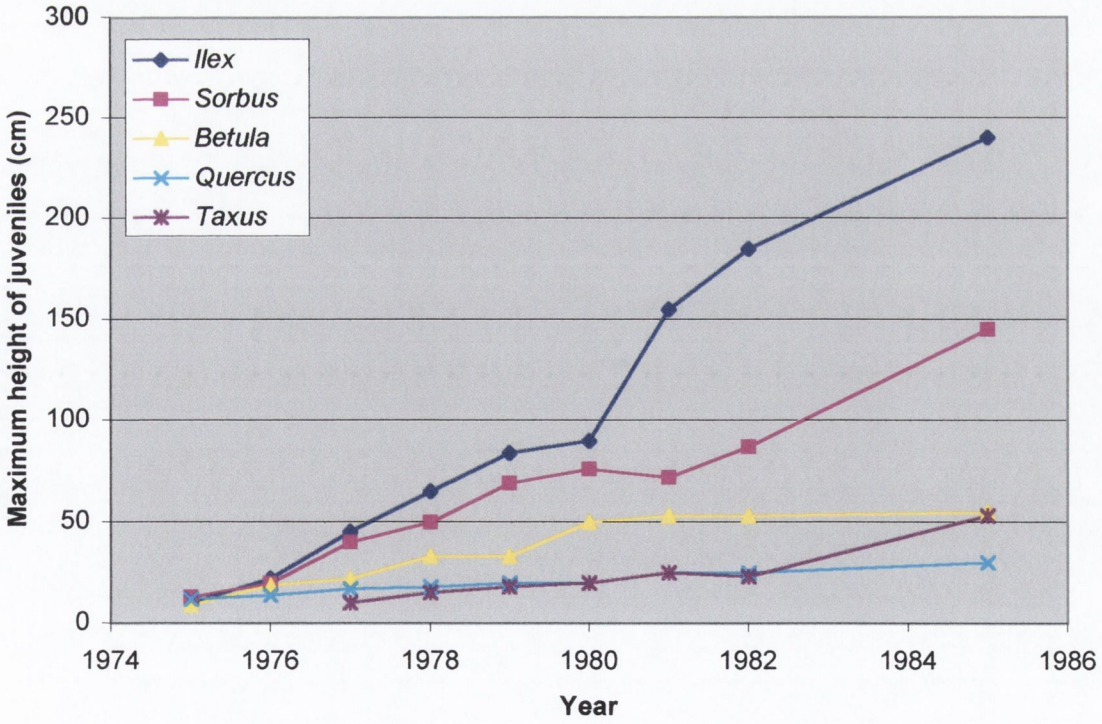


Figure 4.7 Maximum height of juvenile trees in exclosure C2, 1975-1985. Unpublished data of Dr. A. Craig.



and 1980, but gradually recovered over the next five years. This possibly indicates that a single individual was present and was felled by some natural event, such as a falling bough, with subsequent regrowth from the base.

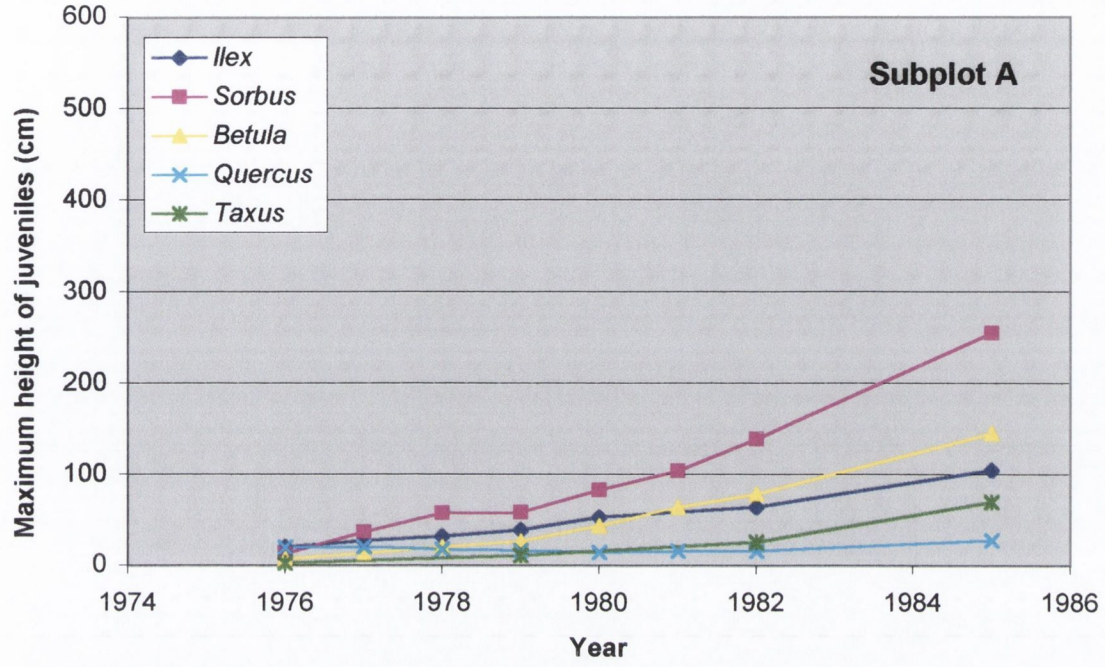
In exclosure C5, the Mine Paddock, canopy cover seems to have dictated the response of species to the exclusion of deer (Fig. 4.8a-d). Under a closed canopy in subplots A and C, holly, birch and rowan showed the greatest increase in maximum height, reaching 100-250 cm by 1985. Oak exhibited almost no increase in maximum height during this period, whereas yew, which was present in subplot A only, showed an intermediate response, reaching a maximum height of 70 cm in 1985. Under the partial canopy in subplot B, birch and rowan increased in maximum height at a faster rate reaching 300 cm by 1985. With more light available, oak also increased substantially in maximum height, reaching 175 cm by 1985. Holly appears to have been suffering from competition under these conditions, but the data for 1985 are missing. Yew was absent from this subplot. Beyond the woodland edge, in subplot D where there was no canopy cover, the overall increase in maximum height was at its greatest. By 1985, birch had reached 600 cm, oak had reached 170 cm and hazel, which was absent from the other subplots, had reached 300 cm. Holly, rowan and yew were all absent from this subplot.

4.3.2 Adult tree class 1981-2001

The spatial distribution of all adult trees in 1981 and 2001, and an indication of their girths, are shown in Figs. 4.9 to 4.12. Analyses showed no differences in rates of girth growth between sites in Reenadinna (Table 4.11), but there were some significant differences between species (Fig. 4.13). Birch was the fastest growing tree although ash also displayed a high growth rate. Yew had a comparable growth rate to holly and oak, whilst hawthorn was the slowest growing tree. This is unsurprising as most of the hawthorns present are suppressed, spindly trees. There was no difference between the girth growth of oak and holly in the Camillan exclosure (P = 0.230, ANOVA), where trees grew at a similar rate to those in the yew-wood.

There were significant differences in mortality in the Reenadinna exclosures between species (P<0.001, Pearson chi-square), but not between sites (P = 0.555, Pearson chi-square). Overall mortality between 1981 and 2001 was 15.7% (Fig. 4.14), but was markedly higher for birch (85.7%) and rowan (100%) and slightly lower for yew (9.1%). There were no differences in

Figure 4.8 Maximum height of juvenile trees in four subplots in exclosure C5, the Mine Paddock exclosure, 1976-1985. Unpublished data of Dr. A.Craig.



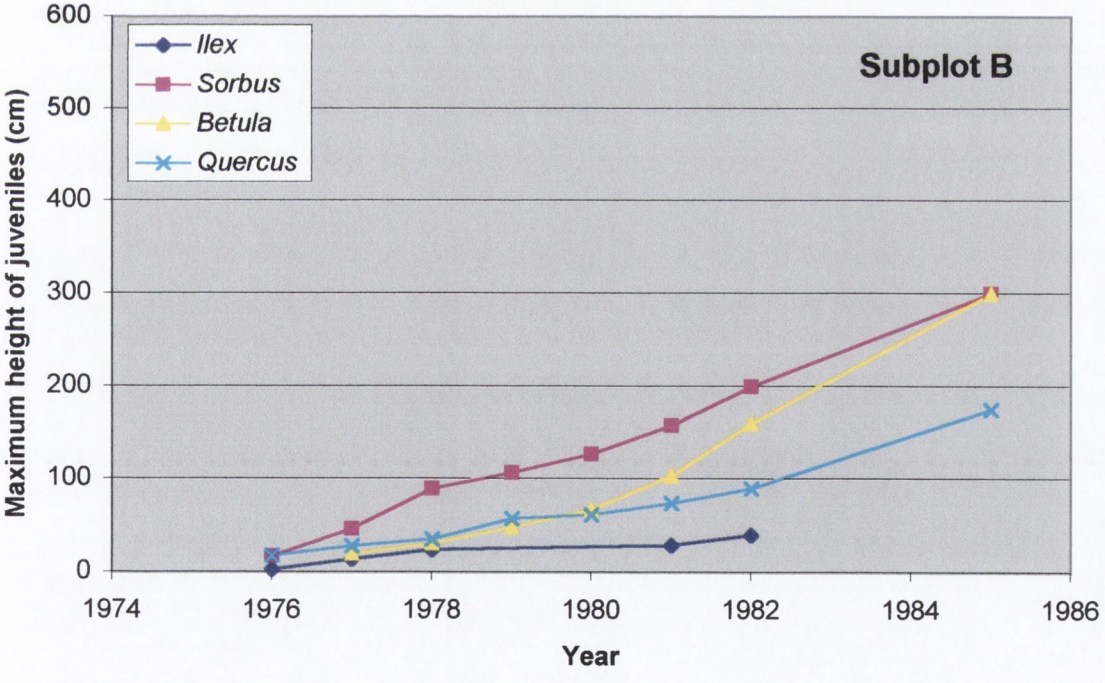
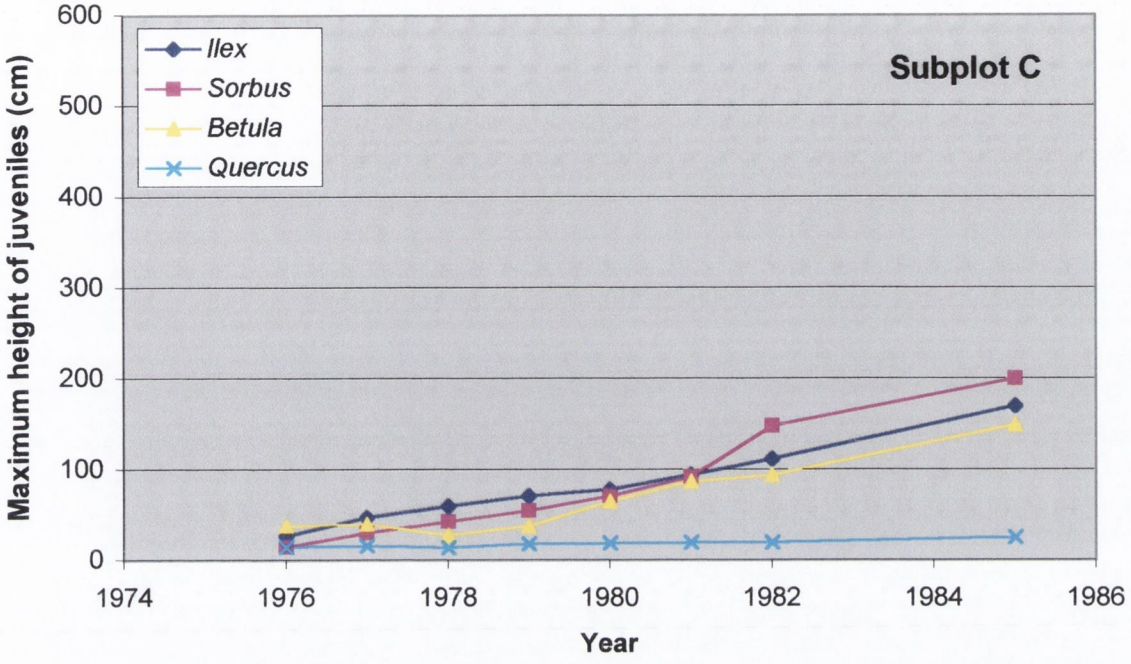


Figure 4.8 continued



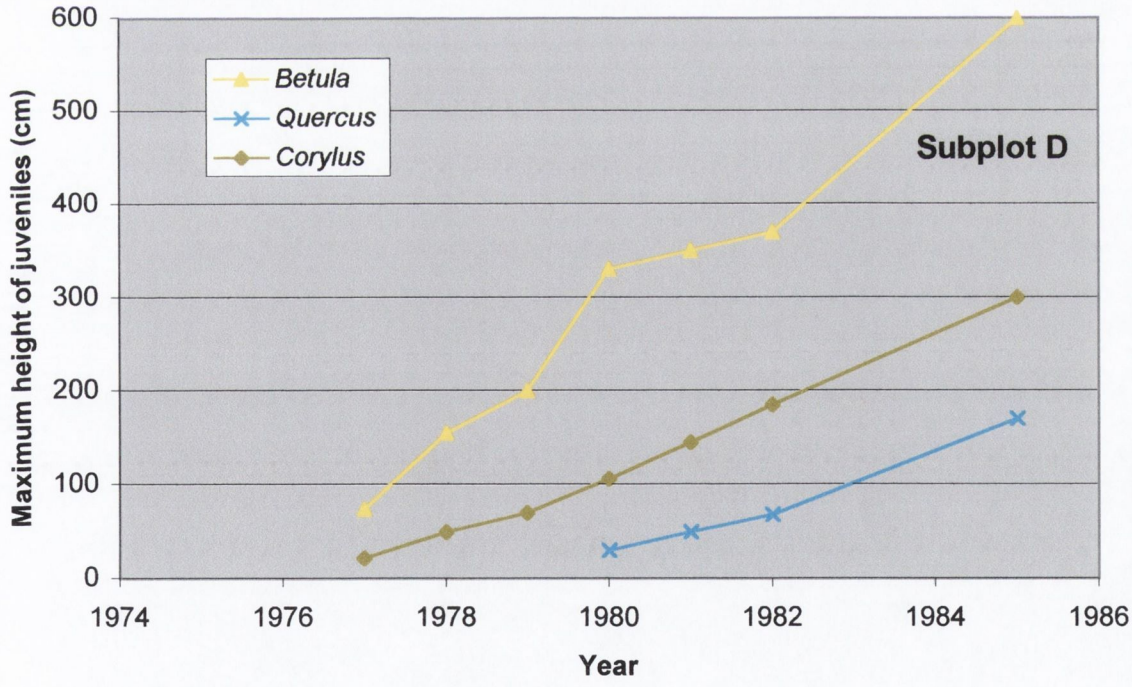


Figure 4.9 Map of adult class trees in exclosure R1 in 1981 and 2001. Size of circles is proportionate to basal area. Concentric circles indicate multistemmed trees. For small trees, I = *Ilex*, C = *Crataegus*, E = *Euonymus*, H = *Corylus*, F = *Fraxinus*. Continuous line indicates fence.

Figure 4.10 Map of adult class trees in exclosure R2 in 1981 and 2001. Size of circles is proportionate to basal area. Concentric circles indicate multistemmed trees. For small trees, I = *Ilex* , C = *Crataegus,* H = *Corylus,* T = *Taxus.* Continuous line indicates fence.

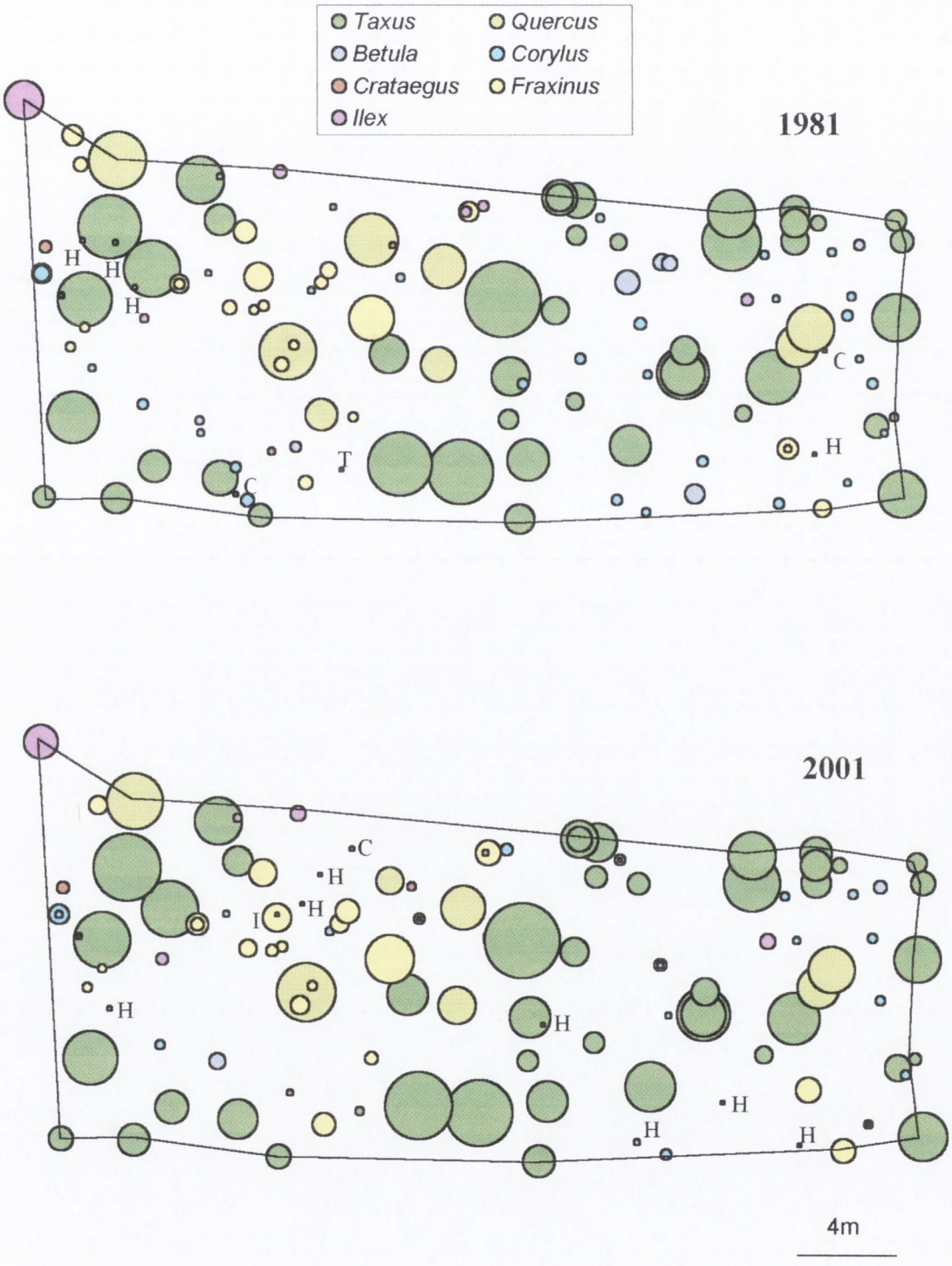


Figure 4.11 Map of adult class trees in exclosure R3 in 1981 and 2001. Size of circles is proportionate to basal area. Concentric circles indicate multistemmed trees. For small trees, I = *Ilex* , C = *Crataegus*, S = *Sorbus*. Continuous line indicates fence

Figure 4.12 Map of adult class trees in exclosure C1 in 1981 and 2001. Size of circles is proportionate to basal area. Concentric circles indicate multistemmed trees. For small trees, I = *Ilex*. Continuous line indicates fence.

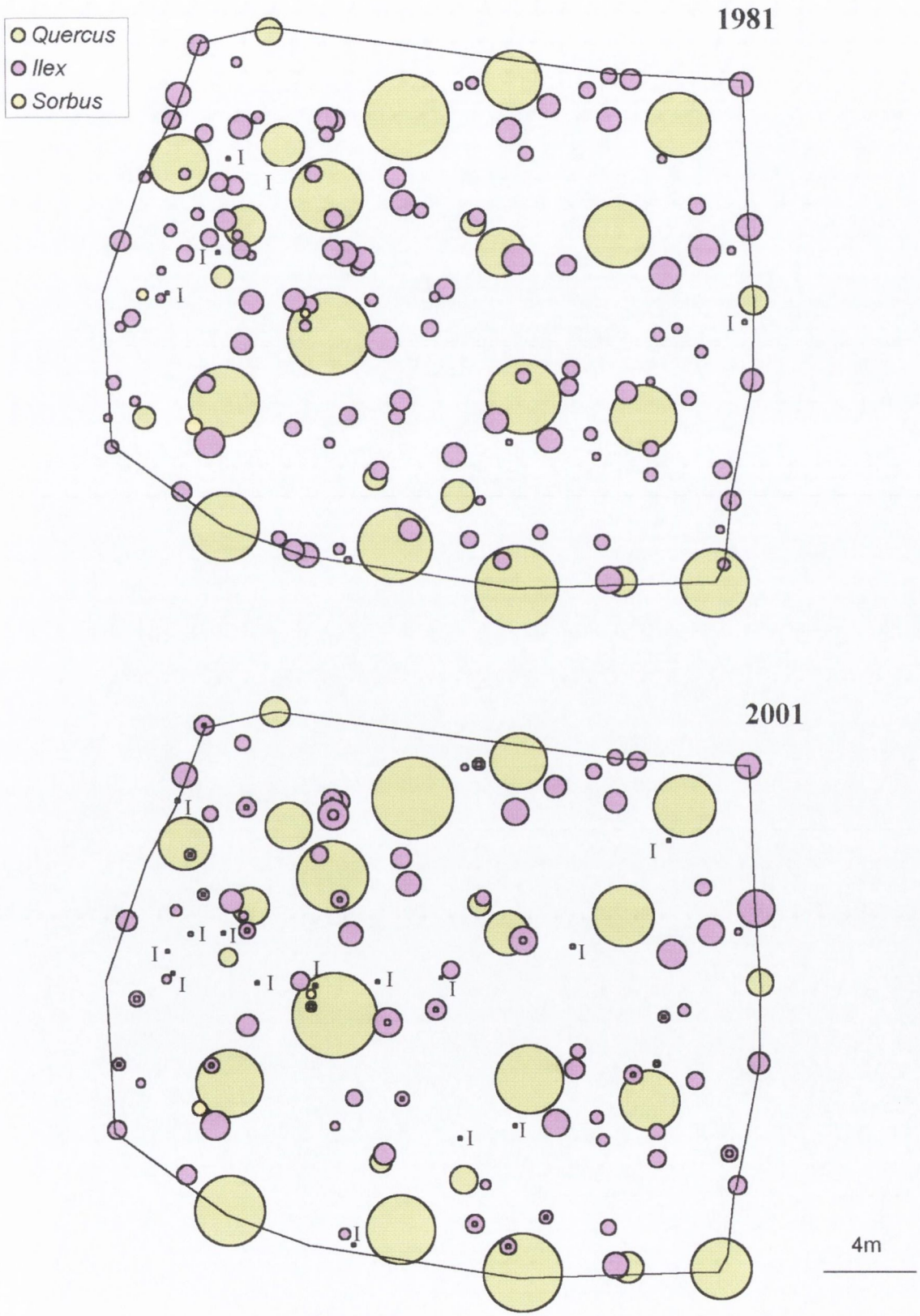


Table 4.11 Two-way ANOVA of the effects of species and site on mean girth increase of adult trees in exclosures R1-3 between 1981 and 2001.

Source	df	Mean Square	F	*P*
Intercept	1	0.103	41.597	0.000
SPECIES	5	0.006	2.473	**0.033**
SITE	2	0.002	0.802	0.449
SPECIES * SITE	7	0.001	0.351	0.930
Error	293	0.002		

Table 4.12 Effect of tree girth in 1981 on mortality of adult trees in exclosures R1-3 between 1981 and 2001. Figures are means (±se) with median values in parentheses. Data analyzed with Mann-Whitney U tests.

	Girth 1981 (m)		*P*
	Survived	Died	
Reenadinna			
Taxus baccata	0.78±0.03 (0.72)	0.26±0.02 (0.23)	**<0.001**
Ilex aquifolium	0.21±0.03 (0.18)	0.19±0.04 (0.21)	0.863
Fraxinus excelsior	0.34±0.03 (0.31)	0.28±0.18 (0.28)	0.688
Corylus avellana	0.22±0.02 (0.20)	0.19±0.02 (0.20)	0.571
Crataegus monogyna	0.19±0.04 (0.15)	0.14±0.04 (0.12)	0.433
Betula pubescens	0.55±0.37 (0.23)	0.40±0.03 (0.38)	0.454
Quercus robur	0.91±0.09 (0.92)	0.68 (0.68)	0.500
Camillan			
Quercus petraea	1.33±1.05 (1.50)	0.57 (0.57)	0.160
Ilex aquifolium	0.43±0.02 (0.43)	0.38±0.03 (0.37)	0.201

Figure 4.13 Mean increase in girth of adult trees in exclosures R1-3 (blue) and C1 (red) from 1981 to 2001. For each woodland letters denote homogeneous subsets according to Tukey's HSD test Note that *Quercus* denotes *Q. petraea* for the C1 data and *Q. robur* for the R1-3 data. Vertical lines indicate se.

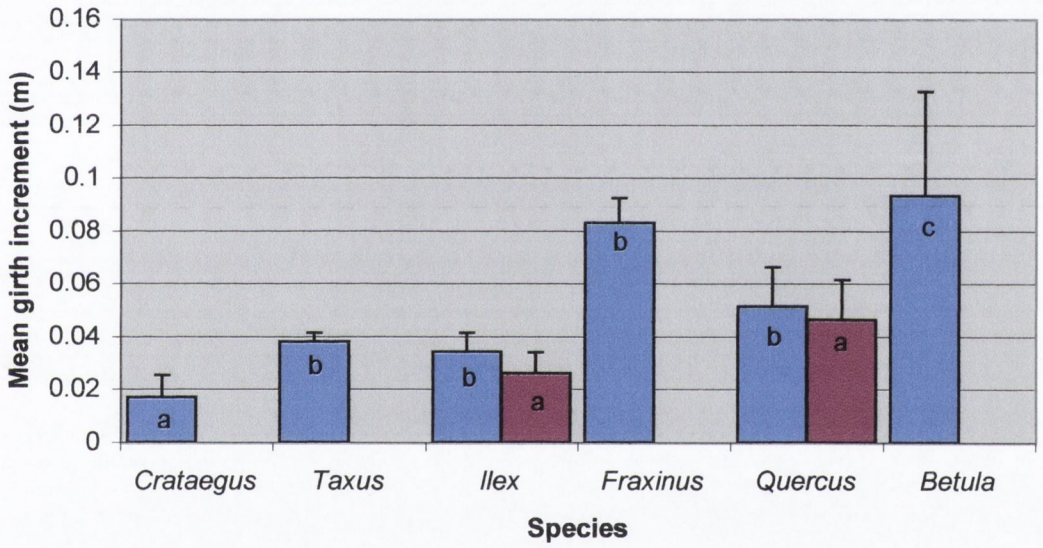


Figure 4.14 Percentage mortality of adult trees between 1981 and 2001 in exclosures R1-3 (blue) and C1 (red). Figures indicate number of adult trees in 1981.

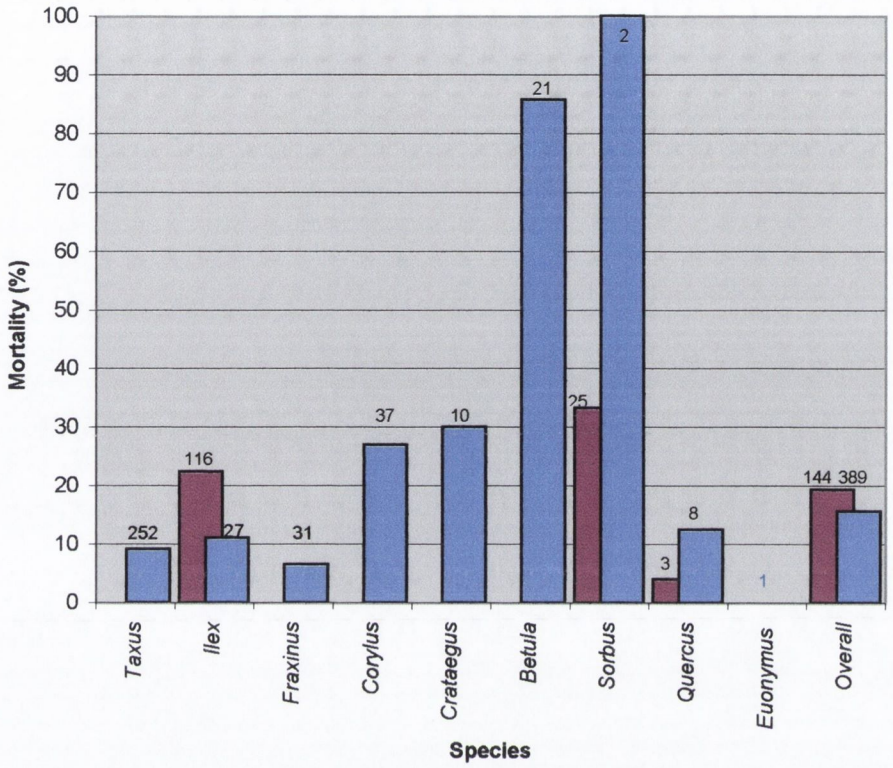
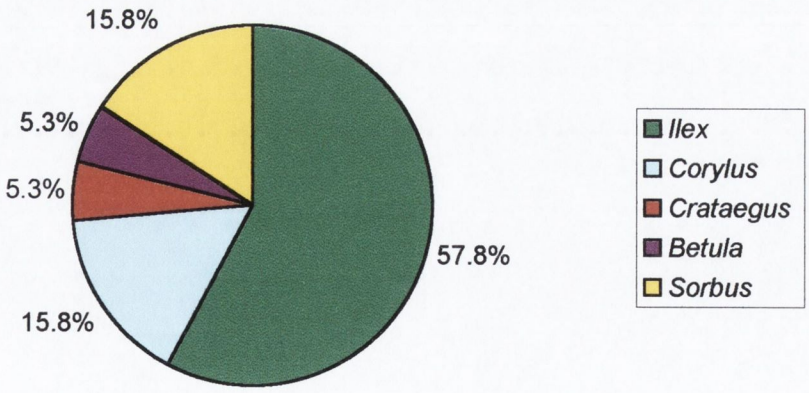


Figure 4.15 Percentages of new recruits to the adult tree class in exclosure R1-3 in 2001.



mortality between the species in the Camillan exclosure ($P = 0.101$, Pearson chi-square) where overall mortality was 19.4%. The yew trees which died between 1981 and 2001 were significantly smaller in girth in 1981 than those that survived (Table 4.12). Yew was the only species which showed this trend.

There was no recruitment to the adult tree class in the Camillan exclosure, but there were significant differences in recruitment in the Reenadinna exclosures between both species ($P < 0.001$, Pearson chi-square) and sites ($P = 0.025$, Pearson chi-square). Of all adult trees present in 2001, 5.5% were new recruits. The majority of new recruits were in exclosure R3 (73.7%) where a small group of birch trees had fallen, creating a canopy gap (Fig. 4.11), with less recruits in exclosures R1 (5.3%) and R2 (21.1%). New recruits consisted largely of holly, rowan and hazel (Fig. 4.15).

Density of trees decreased in all four exclosures (Table 4.13), reflecting the relatively high mortality and low recruitment rates. Basal area, however, increased in all four exclosures (although only slightly in exclosure C1), as reductions due to mortality were offset by the growth of the remaining trees.

Girth class frequency distributions did not change significantly between 1981 and 2001 for any species in either woodland (Table 4.14). In the Reenadinna exclosures it is clear, however, from Fig. 4.16 that a number of yew trees were lost from the lowest, 10-39cm, girth class. This was largely due to lack of recruitment and mortality (Figs. 4.11 and 4.12, and Table 4.14) rather than progression to the larger girth classes. The loss of most of the birch trees is also apparent, as is the progression of many of the ash trees to the 40-69cm girth class. There is little difference in the Camillan distributions (Fig. 4.17), although the loss of several of the hollies and the progression of oak towards the larger girth classes can be seen; the thinning of the hollies is particularly noticeable in Fig. 4.12.

The number of stems per holly tree increased significantly in the Camillan exclosure as a result of increased growth of basal sprouts, and there was a nearly significant increase in the number of stems per hazel stool at the Reenadinna sites (Table 4.15). None of the other species showed significant differences, although yew, ash and holly had fewer stems in 2001. There were no

Table 4.13 Changes in density and basal area of adult trees in exclosure R1-3 and C1, between 1981 and 2001

	Exclosure R1		Exclosure R2		Exclosure R3		Exclosure C1	
	1981	2001	1981	2001	1981	2001	1981	2001
Density (trees/ha)								
Taxus baccata	698.2	596.8	602.1	602.1	1390.0	1264.8	-	-
Ilex aquifolium	123.9	135.1	91.6	91.6	86.9	154.4	1070.1	830.3
Fraxinus excelsior	101.4	90.1	261.8	248.7	19.3	19.3	-	-
Corylus avellana	45.0	45.0	418.9	327.2	9.7	9.7	-	-
Crataegus monogyna	33.8	22.5	78.5	52.4	9.7	19.3	-	-
Euonymus europaeus	11.3	11.3	-	-	-	-	-	-
Betula pubescens	-	-	91.6	26.2	135.1	19.3	-	-
Quercus robur	-	-	104.8	91.6	-	-	-	-
Quercus petraea	-	-	-	-	-	-	230.6	221.4
Sorbus aucuparia	-	-	-	-	19.3	29.0	27.7	18.5
All species	1013.5	900.9	1649.2	1439.8	1669.9	1515.4	1328.4	1070.1
Basal area (m^2/ha)								
Taxus baccata	70.43	72.63	32.67	36.90	54.32	59.20	-	-
Ilex aquifolium	0.27	0.40	1.15	1.07	0.36	0.50	18.46	16.34
Fraxinus excelsior	1.01	1.52	3.49	4.77	0.09	0.17	-	-
Corylus avellana	1.40	0.82	3.71	2.43	0.15	0.45	-	-
Crataegus monogyna	0.19	0.17	0.17	0.17	0.01	0.02	-	-
Euonymus europaeus	0.02	0.02	-	-	-	-	-	-
Betula pubescens	-	-	0.86	0.23	2.92	1.23	-	-
Quercus robur	-	-	7.92	7.08	-	-	-	-
Quercus petraea	-	-	-	-	-	-	36.84	39.35
Sorbus aucuparia	-	-	-	-	0.09	0.04	0.22	0.16
All species	73.30	75.57	49.98	52.65	57.94	61.61	55.52	55.85

Table 4.14 Results of Kolmogorov-Smirnov tests comparing frequency distribution of adult girth classes in 1981 and 2001

	P Exclosures R1-3	*P* Exclosure C1
Taxus baccata	0.084	-
Ilex aquifolium	1.000	0.451
Fraxinus excelsior	0.066	-
Corylus avellana	1.000	-
Betula pubescens	0.480	-
Quercus robur	1.000	-
Quercus petraea	-	0.980

Figure 4.16 Girth class frequency distributions for adult trees in exclosures R1-3, (a) 1981 and (b) 2001.

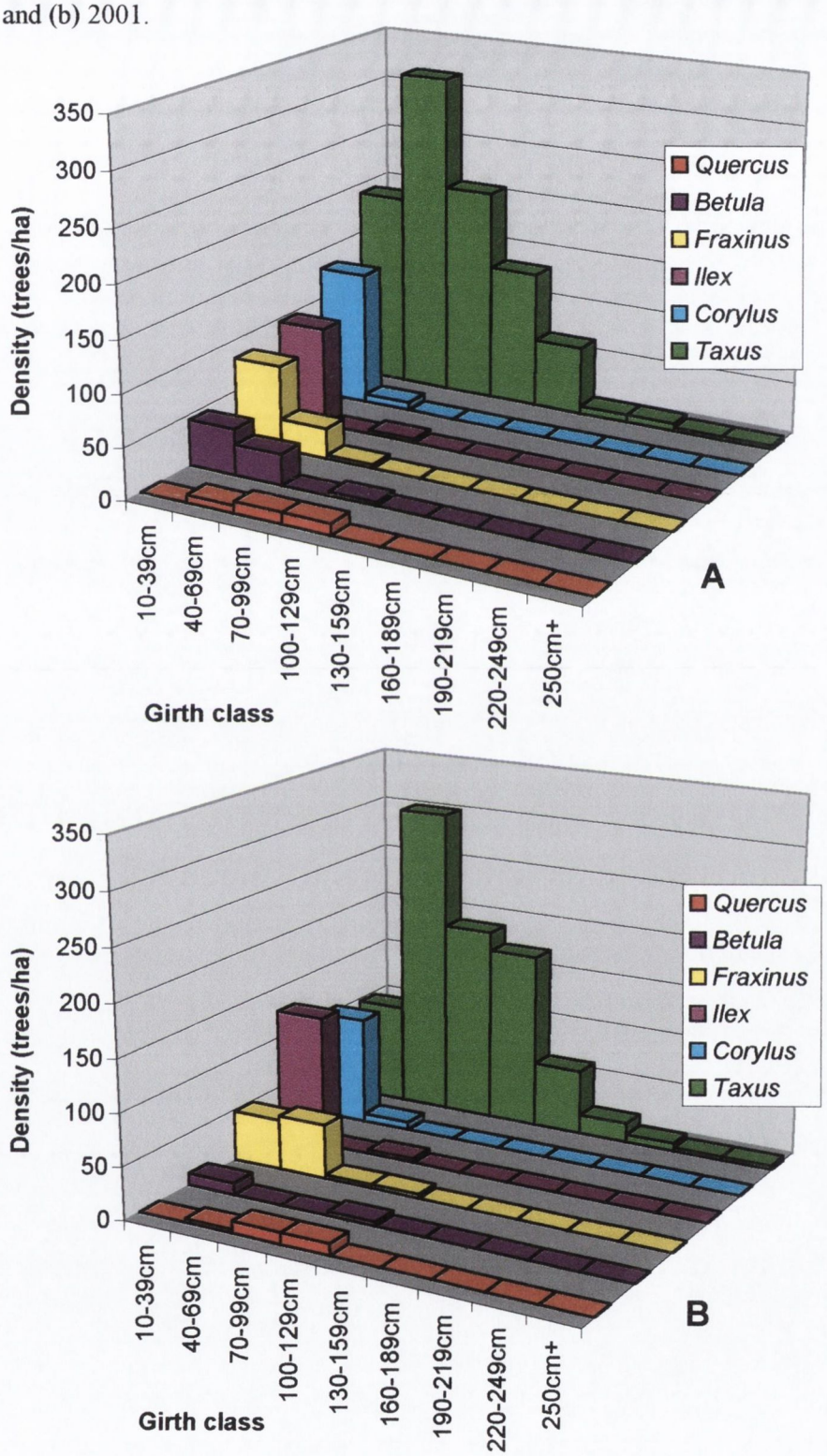


Figure 4.17 Girth class frequency distributions for adult trees in exclosure C1, (a) 1981 and (b) 2001.

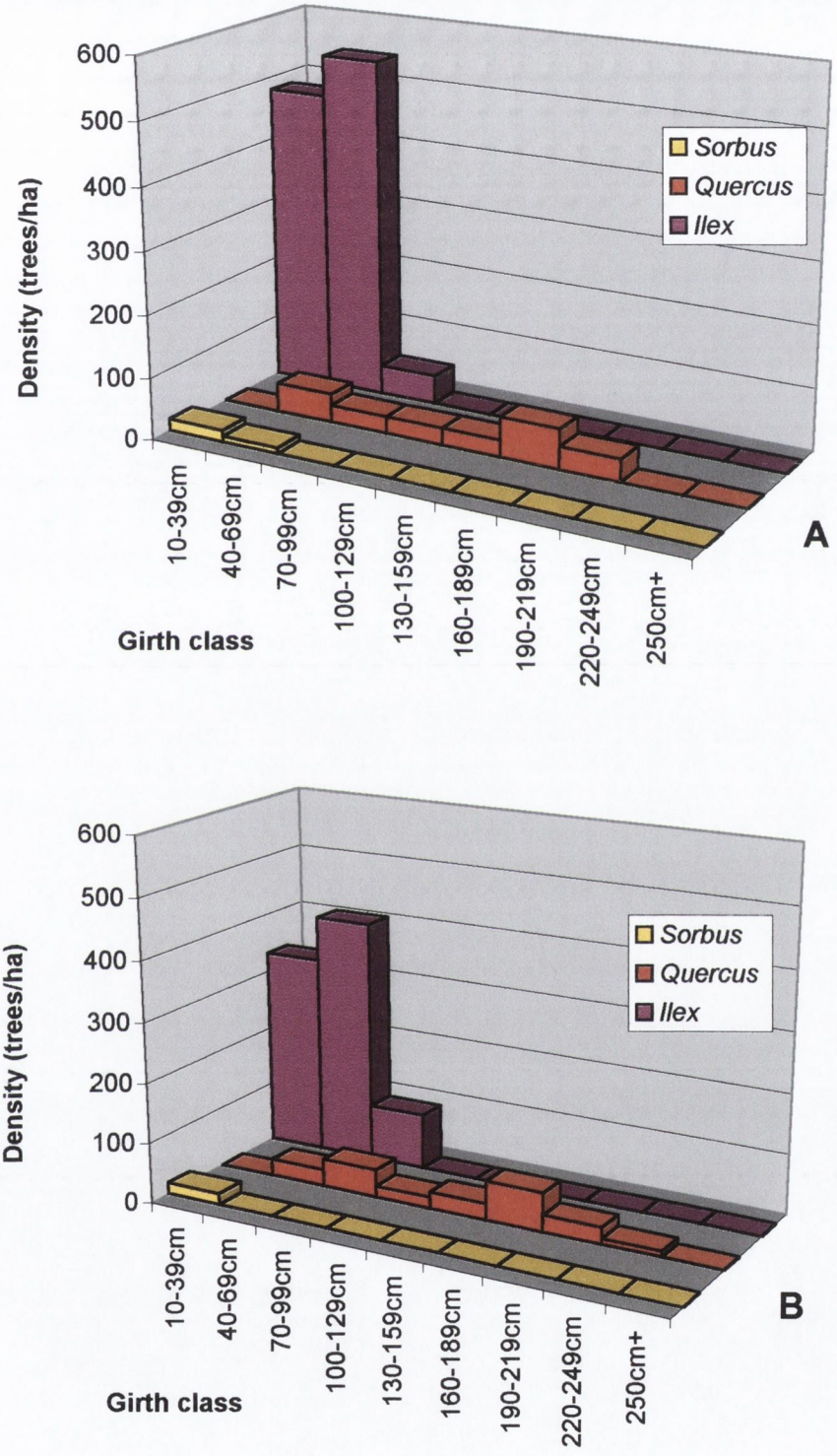


Table 4.15 Changes in mean number of stems per tree in exclosures R1-3 and exclosure C1 between 1981 and 2001. Figures in parentheses are medians. Data analyzed with Mann-Whitney U-tests.

	Exclosures R1-3		*P*	Exclosure C1		*P*
	1981	2001		1981	2001	
Taxus baccata	1.07 (1)	1.03 (1)	0.134	-	-	-
Ilex aquifolium	1.22 (1)	1.11 (1)	0.308	1.12 (1)	1.60 (1)	**<0.001**
Fraxinus excelsior	1.10 (1)	1.03 (1)	0.613	-	-	-
Corylus avellana	2.65 (2)	3.23 (3)	0.095	-	-	-
Crataegus monogyna	1.00 (1)	1.00 (1)	1.00	-	-	-
Euonymus europaeus	1.00 (1)	1.00 (1)	1.00	-	-	-
Betula pubescens	1.00 (1)	1.00 (1)	1.00	-	-	-
Quercus robur	1.50 (1)	1.00 (1)	1.00	-	-	-
Quercus petraea	-	-	-	1.04 (1)	1.04 (1)	1.00
Sorbus aucuparia	1.00 (1)	1.00 (1)	1.00	1.00 (1)	1.00 (1)	1.00

significant differences in the number of stems per yew between sites in either 1981 ($P = 0.790$, Kruskal-Wallis H test) or 2001 ($P = 0.710$, Kruskal-Wallis H test).

4.3.3 Field layer vegetation in exclosed and unexclosed plots 2001

As expected, differences in exclosed and unexclosed vegetation at the Reenadinna sites (Table 4.16) were similar to those between the vegetation in 1969 and 2001. Total field layer cover was higher inside the exclosures due to the greater amount of *Rubus fruticosus*, *Hedera helix* and *Lonicera periclymenum* (Plates 4.1 and 4.2). Bryophyte and litter cover were also higher within the fences. Several herb species, however, were more abundant in the unexclosed plots, for example, *Oxalis acetosella, Potentilla sterilis, Veronica chamaedrys*, *Viola* spp. and *Sanicula europaea*. This differentiation in the vegetation is also shown by the results of the ordination analysis, which yielded a three-dimensional solution ($P = 0.048$, Monte Carlo test). The two axes which explained the most variation are shown in Fig. 4.18. Exclosed quadrats are associated with woody species, including climbers and juvenile trees, whilst unexclosed quadrats are associated with forbs, grasses and sedges. The segregation of these two vegetation types was confirmed by a multi-response permutation procedure (MRPP) test ($P < 0.001$). Variation between sites was low, particularly within the exclosures.

Saplings of holly, ash and rowan were more abundant in exclosed plots (Table 4.17), whilst holly and ash seedlings were more abundant outside the fences. It follows that, holly, ash and rowan juveniles were taller inside the exclosures, as was *Rubus fruticosus*. Yew was present only at very low densities.

At the Camillan sites (Table 4.18), total field layer cover was again higher in the exclosed plots, due mainly to greater amounts of *Rubus fruticosus, Hedera helix* and *Rhododendron*. The higher levels of *Rhododendron* inside the exclosures, however, were due to more effective removal of this weed species in the more accessible unfenced plots, rather than a result of grazing exclusion. Species more abundant in the unfenced plots were *Oxalis acetosella, Brachypodium sylvaticum,* oak and birch. *Vaccinium myrtillus* and *Luzula sylvatica* were not significantly more abundant inside exclosures, but these species had grown markedly taller (Table 4.19). One of the most important differences, however, was the presence of an understorey layer in some of the oakwood exclosures. This was chiefly comprised of holly with smaller areas of *Rhododendron* thicket.

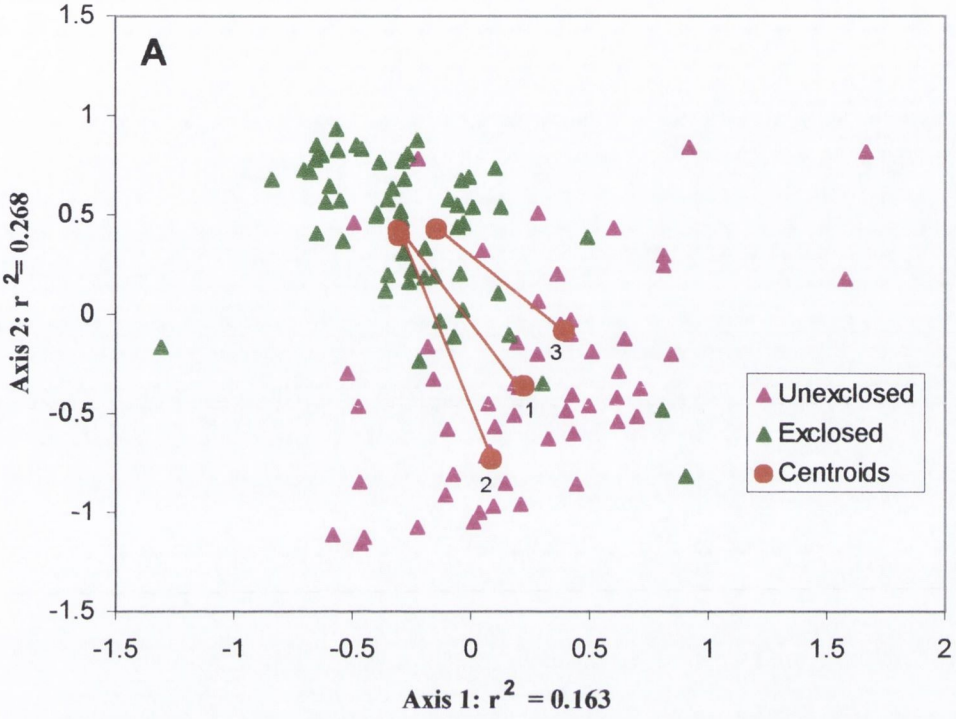
Table 4.16 Comparisons between exclosed and unexclosed vegetation, sites R1-3, 2001. $n = 60$. Analysis restricted to species occurring in 5% or more of total quadrats plus *Taxus baccata*. Data analyzed using Mann-Whitney U test. Mean percentage cover (± se) shown as medians tend to zero.

	Percentage cover		Frequency (%)		*P* (% cover)
	Exclosed	Unexclosed	Exclosed	Unexclosed	
Brachypodium sylvaticum	0.33 ±0.07	1.06 ±0.34	38.3	48.3	0.151
Carex flacca	0.05 ±0.04	1.09 ±0.50	3.3	11.7	0.050
Carex pulicaris	0.20 ±0.17	2.63 ±1.62	6.7	11.7	0.228
Carex sylvatica	0.05 ±0.02	0.08 ±0.08	8.3	1.7	0.207
Fragaria vesca	1.27 ±0.33	0.37 ±0.12	31.7	21.7	0.108
Fraxinus excelsior	1.50 ±0.62	0.30 ±0.05	31.7	46.7	0.522
Hedera helix	9.21 ±2.01	0.14 ±0.06	68.3	18.3	**<0.001**
Ilex aquifolium	8.85 ±1.99	1.43 ±0.76	51.7	65.0	0.189
Lonicera periclymenum	1.78 ±0.74	0.05 ±0.03	23.3	5.0	**0.001**
Oxalis acetosella	0.00	0.18 ±0.10	0.00	10.0	**0.027**
Potentilla sterilis	0.00	0.13 ±0.05	0.00	15.0	**0.003**
Rubia peregrina	1.10 ±0.34	0.08 ±0.04	26.7	10.0	**0.008**
Rubus fruticosus	21.88 ±2.72	0.56 ±0.14	78.3	40.0	**<0.001**
Sanicula europaea	0.27 ±0.19	1.48 ±0.53	6.7	21.7	**0.012**
Solidago virgaurea	0.18 ±0.09	0.01 ±0.01	15.0	1.7	**0.012**
Sorbus aucuparia	3.92 ±1.41	0.07 ±0.02	20.0	11.7	0.128
Taxus baccata	0.01±0.01	0.03 ±0.01	1.7	5.0	0.619
Teucrium scorodonia	0.72 ±0.32	0.37 ±0.24	15.0	5.0	0.109
Veronica chamaedrys	0.00	0.07 ±0.03	0.00	10.0	**0.027**
Viola spp.	0.47 ±0.17	1.98 ±0.38	38.3	61.7	**<0.001**
Total field cover	46.38 ±3.21	11.73 ±2.44	96.7	96.7	**<0.001**
Total bryophyte cover	87.58 ±2.26	82.13 ±2.02	100.0	100.0	**<0.001**
Litter	27.00 ±1.53	20.42 ±1.38	100.0	93.3	**0.001**
Bare earth	0.00	1.04 ±0.39	0.0	30.0	**<0.001**
Bare rock	2.48 ±1.39	2.29 ±0.37	26.7	83.3	**<0.001**
Fallen wood	1.28 ±0.67	4.59 ±1.00	48.3	93.3	**<0.001**

Plate 4.1 Fenceline of exclosure R3, Reenadinna Wood (September 2001). Note abundance of holly saplings and *Hedera helix* inside exclosure, and sparseness of field layer outside

Plate 4.2 Interior of exclosure R3, Reenadinna Wood (September 2001).

Figure 4.18 NMS ordination of (a) vegetation quadrats and (b) species in exclosed and unexclosed plots, sites R1-3, 2001. Red lines connect centroids for exclosed and unexclosed plots for each site which are indicated by black numbers. Stress on this ordination solution = 18.5%. See Appendix 1 for key to species abbreviations.



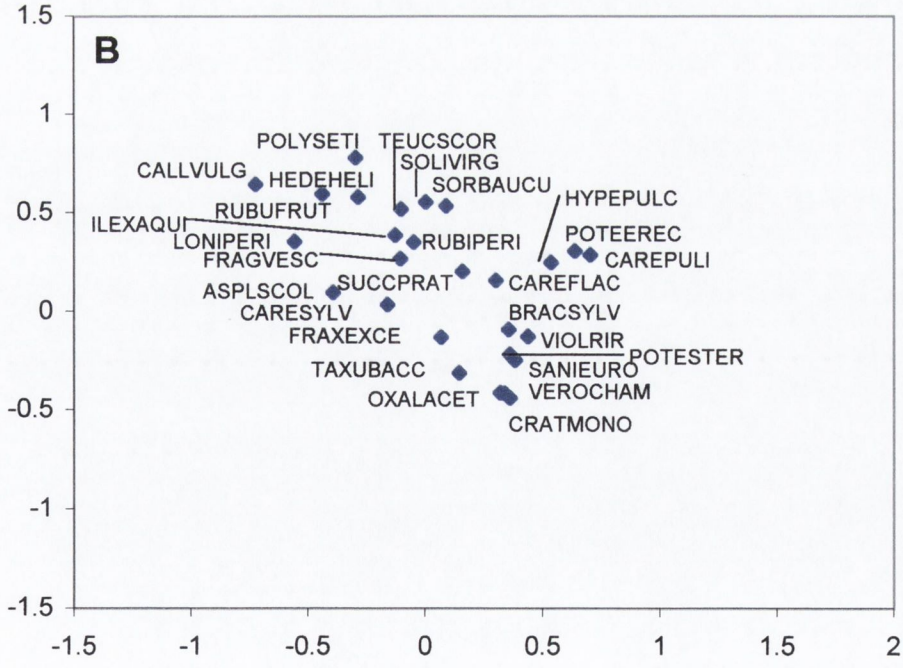


Table 4.17 Comparisons of seedling / sapling densities, juvenile heights and maximum vegetation heights for exclosed and unexclosed plots, sites R1-3, 2001. Data analyzed with Mann-Whitney U tests. Data presented are means (± se) as medians tend to zero. Analysis restricted to species occurring in 5% or more of total quadrats plus *Taxus baccata*. For density, $n = 60$.

Species		Density (m^{-2})		*P*	Height (cm)		*P*
		Exclosed	Unexclosed		Exclosed	Unexclosed	
Ilex aquifolium	seedlings	0.37 ±0.14	2.13 ±0.57	**<0.001**	44.40 ±5.59	8.22 ±0.71	**<0.001**
	saplings	0.68 ±0.14	0.03 ±0.02	**<0.001**			
Fraxinus excelsior	seedlings	0.87 ±0.39	1.18 ±0.33	**0.002**	22.07 ±2.02	7.44 ±0.30	**<0.001**
	saplings	0.32 ±0.11	0.00	**0.001**			
Sorbus aucuparia	seedlings	0.15 ±0.06	0.13 ±0.05	0.991	67.53 ±8.98	9.63 ±1.53	**<0.001**
	saplings	0.35 ±0.11	0.00	**0.001**			
Taxus baccata	seedlings	0.02 ±0.02	0.07 ±0.04	0.494	7.00±7.00*	5.50 ±0.50	0.400
	saplings	0.00*	0.00	1.000			
Maximum height of *Lonicera periclymenum* (cm)		-	-		21.36 ±4.61	-	-
Maximum height of *Rubus fruticosus* (cm)		-	-		36.98 ±3.39	9.96 ±2.39	**<0.001**

*additionally one *Taxus* sapling present outside quadrats, 50cm in height.

Table 4.18 Comparisons between exclosed and unexclosed vegetation, sites C1-5, 2001. n = 65. Analysis restricted to species occurring in 5% or more of total quadrats. Data analyzed using Mann-Whitney U test. Mean percentage cover (± se) shown as medians tend to zero.

	Percentage cover		Frequency (%)		P (% cover)
	Exclosed	Unexclosed	Exclosed	Unexclosed	
Field layer					
Betula pubescens	0.08 ±0.08	0.20 ±0.05	3.1	23.1	**0.001**
Blechnum spicant	1.57 ±0.56	0.80 ±0.42	15.4	16.9	0.998
Brachypodium sylvaticum	0.00	0.34 ±0.18	0.0	10.8	**0.013**
Fraxinus excelsior	0.07 ±0.07	0.09 ±0.05	1.7	9.2	0.115
Hedera helix	15.18 ±2.70	0.97 ±0.14	83.1	67.7	**<0.001**
Ilex aquifolium	10.55 ±1.99	6.38 ±1.26	55.4	76.9	0.845
Lonicera periclymenum	2.22 ±1.05	0.10 ±0.07	13.8	4.6	0.050
Luzula sylvatica	9.91 ±2.37	7.79 ±2.10	30.8	30.8	0.795
Oxalis acetosella	0.08 ±0.03	0.31 ±0.09	9.2	18.5	0.081
Pteridium aquilinum	3.88 ±1.64	6.92 ±2.18	15.4	20.0	0.408
Quercus petraea	0.10 ±0.04	0.74 ±0.11	10.8	58.5	**<0.001**
Rhododendron ponticum	11.86 ±3.43	0.01 ±0.01	20.0	1.5	**<0.001**
Rubus fruticosus	6.25 ±1.71	0.01 ±0.01	30.8	1.5	**<0.001**
Sorbus aucuparia	0.62 ±0.29	0.23 ±0.05	15.4	26.2	0.196
Taxus baccata	1.16 ±0.74	0.02 ±0.01	7.7	3.1	0.161
Vaccinium myrtillus	9.47 ±2.65	5.05 ±1.48	29.2	30.8	0.931
Understorey					
Ilex aquifolium	17.62 ±3.77	0.00	33.8	0.0	**<0.001**
Rhododendron ponticum	2.46 ±1.03	0.00	12.3	0.0	**0.006**
Total field cover	58.03 ±3.38	29.88 ±3.04	98.3	100.0	**<0.001**
Total understorey cover	21.85 ±3.99	0.00	41.2	0.0	**<0.001**
Total bryophyte cover	9.28 ±2.15	29.70 ±2.77	60.0	100.0	**<0.001**
Litter	84.63 ±1.97	64.40 ±2.76	100.0	100.0	**<0.001**
Bare earth	2.13 ±0.80	0.31 ±0.12	23.1	13.8	0.127
Bare rock	0.06 ±0.05	0.23 ±0.06	3.1	21.5	**0.002**
Fallen wood	5.89 ±1.20	6.12 ±1.53	69.2	84.6	0.219

Table 4.19 Comparisons of seedling / sapling densities, juvenile heights and maximum vegetation heights for exclosed and unexclosed plots, sites C1-5, 2001. Data analyzed with Mann-Whitney U tests. Data presented are means (± se) as medians tend to zero. Analysis restricted to species occurring in 5% or more of total quadrats. For density $n = 65$.

Species		Density (m^{-2})		*P*	Height (cm)		*P*
		Exclosed	Unexclosed		Exclosed	Unexclosed	
Betula pubescens	seedlings	0.00	0.63 ±0.21	**<0.001**	255.0 ±145.0	9.00 ±0.83	**0.001**
	saplings	0.03 ±0.02	0.00	0.496			
Ilex aquifolium	seedlings	0.48 ±0.13	20.35 ±3.52	**<0.001**	127.15 ±7.54	11.19 ±0.19	**<0.001**
	saplings	2.82 ±0.64	0.58 ±0.15	**0.006**			
Fraxinus excelsior	seedlings	0.00	0.29 ±0.17	**0.028**	103.67 ±40.22	9.47±0.79	**0.001**
	saplings	0.05 ±0.03	0.00	0.496			
Quercus petraea	seedlings	0.23 ±0.10	2.71 ±0.57	**<0.001**	17.35 ±1.77	12.29 ±0.42	**0.003**
	saplings	0.03 ±0.02	0.06 ±0.05	1.000			
Rhododendron ponticum	seedlings	0.08 ±0.06	0.02 ±0.02	0.369	123.92 ±15.43	2.00 ±2.00	**0.038**
	saplings	0.31 ±0.12	0.00	**0.003**			
Sorbus aucuparia	seedlings	0.02 ±0.02	0.71 ±0.21	**<0.001**	223.52 ±32.01	10.57 ±0.84	**<0.001**
	saplings	0.31 ±0.15	0.02 ±0.02	**0.023**			
Taxus baccata	seedlings	0.02 ±0.02*	0.05 ±0.03	0.748	96.96 ±6.40*	5.33 ±0.33	**<0.001**
	saplings	0.03 ±0.02*	0.00	0.496			
Maximum height of *Luzula sylvatica*		-	-	-	41.55 ±3.84	29.61 ±3.94	**0.023**
Maximum height of *Vaccinium myrtillus*		-	-	-	48.00 ±7.48	22.95 ±2.98	**0.010**

outside quadrats, 100 *Taxus* saplings and 13 *Taxus* seedlings were found – mean height calculated using all data.

The results of the ordination analysis ($P = 0.048$, Monte Carlo test), which again produced a three-dimensional solution, (Fig. 4.19) show that there was considerable variation between the oakwood sites. Site C1, at which *Vaccinium myrtillus* and *Luzula sylvatica* were abundant (Plate 4.3), showed the smallest differences in vegetation between treatments. Sites C2 and C4 were those where a dense understorey of holly saplings and young trees developed in the exclosures, with *Rhododendron* also present at site C4 (Plates 4.4 and 4.5). Holly was extremely prevalent in the field layer of the unexclosed plots at these sites, forming a carpet of stunted juveniles. The exclosures at sites C3 and C5 were characterised by dense patches of *Rubus fruticosus*, whilst the unexclosed plots had a sparse covering of *Pteridium aquilinum*. An MRPP test again confirmed overall differences between exclosed and unexclosed vegetation ($P < 0.001$).

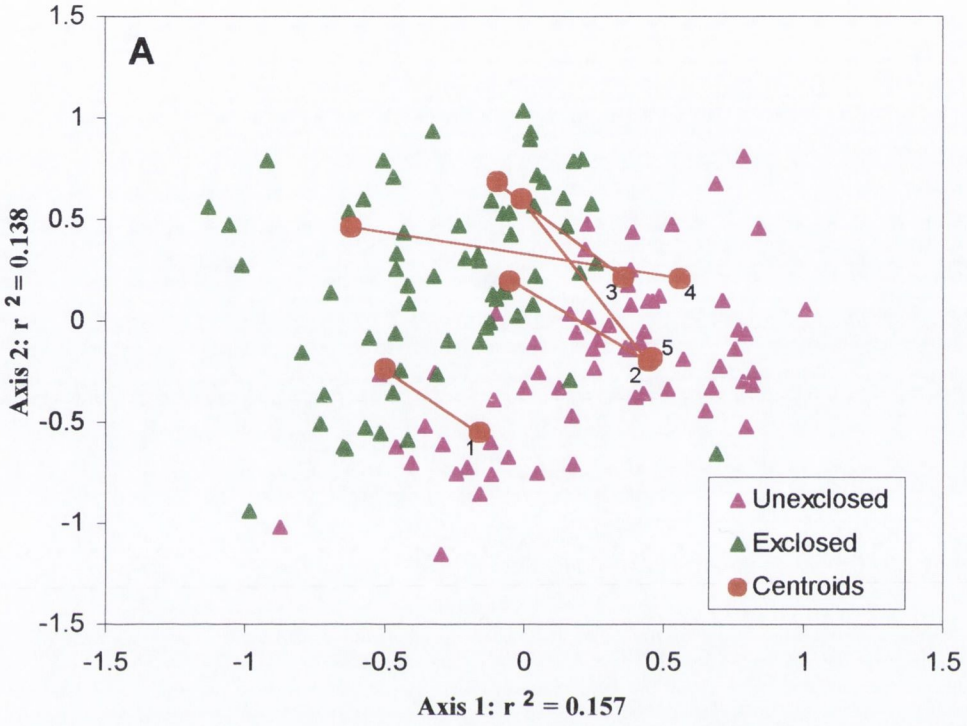
Seedlings of several species (birch, holly, ash, oak and rowan) were present in higher densities in the unexclosed plots (Table 4.19), whilst saplings of holly, rowan and *Rhododendron* were significantly more abundant inside the fences. Yew was again present at low densities, but, importantly, juveniles were significantly taller inside the exclosures, reaching almost 1 m on average (Plate 4.6). Significantly taller juveniles of the other trees species were also found inside the exclosures.

At site W1, the clearing at Dinis, a dense thicket of birch had formed in the exclosed plot, with significantly more Scots pine (*Pinus sylvestris*), oak and *Rubus fruticosus* than in the unexclosed area (Table 4.20). Seedlings of birch, holly and *Rhododendron* were present at higher densities outside the fences (Table 4.21), whilst oak seedlings, and oak and birch saplings were more abundant inside. Birch, holly, oak and Scots pine juveniles, were all significantly taller inside the exclosure. Natural regeneration of *Arbutus* in this exclosure was also noteworthy, but there was no regeneration of yew.

4.3.4 Adult tree structure in exclosed and unexclosed plots 2001

At the Reenadinna sites there were only minor differences in the frequency distribution of adult tree girth class between exclosed and unexclosed plots (Fig. 4.20 and Table 4.22). The higher number of smaller birch trees in the exclosed plots may be a genuine result of the recruitment shown in Fig. 4.16, but the higher number of smaller ash trees cannot be explained in this fashion. Ash recruitment in the exclosures may have occurred prior to the tree survey in 1981, or it may be an

Figure 4.19 NMS ordination of (a) vegetation quadrats and (b) species in exclosed and unexclosed plots, sites C1-5, 2001. Red lines connect centroids for exclosed and unexclosed plots for each site which are indicated by black numbers. Stress on this ordination solution = 17.9%. See Appendix 1 for key to species abbreviations.



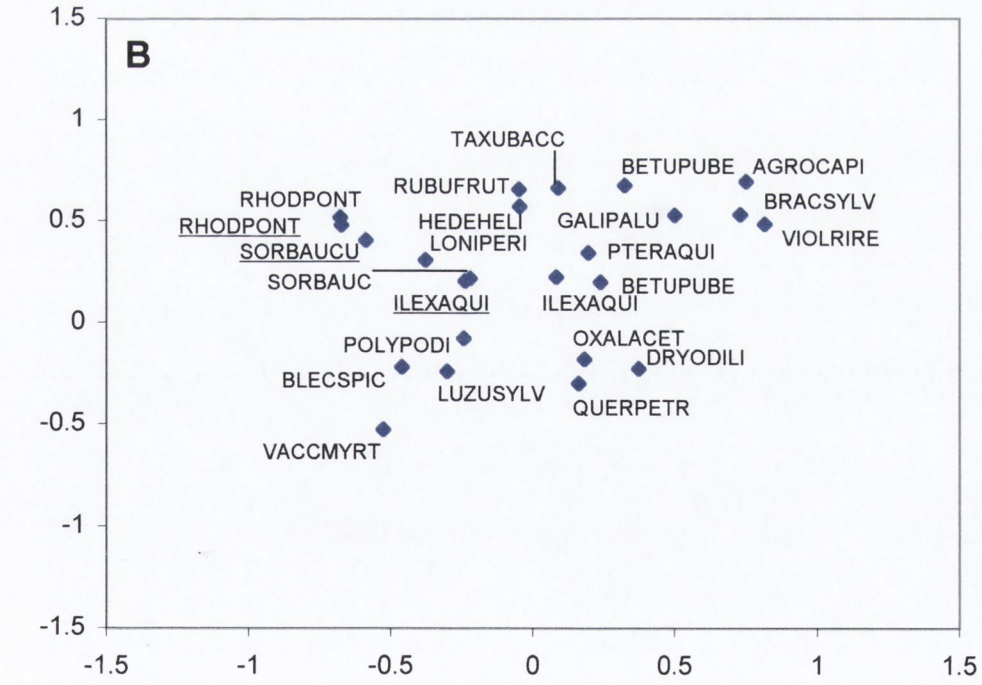


Plate 4.3 Interior of exclosure C1, Camillan Wood (November 2001). Note dense field layer of *Vaccinium myrtillus* with *Pteridium aquilinum* and *Luzula sylvatica.*

Plate 4.4 Fenceline of exclosure C2, Camillan Wood (November 2001). A dense holly thicket has formed inside the exclosure, whilst outside is a bank of heavily grazed holly seedlings

Plate 4.5 Fenceline of exclosure C4, Camillan Wood (November 2001). Interior of exclosure is a dense thicket of holly and *Rhododendron.*

Plate 4.6 Yew sapling (approximately 2 m) in exclosure C1, Camillan Wood (November 2001).

Table 4.20 Comparisons between exclosed and unexclosed vegetation, site W1, Dinis, 2001. $n = 10$. Data analyzed with Mann-Whitney U tests. Data presented are means (± se) as medians tend to zero.

	Percentage cover		Frequency (%)		*P* (% cover)
	Exclosed	Unexclosed	Exclosed	Unexclosed	
Field layer					
Abies alba	5.60 ±5.49	0.00	20.0	0.0	0.474
Agrostis capillaris	0.00	0.10 ±0.07	0.0	20.0	0.474
Arbutus unedo	14.50 ±8.58	0.00	30.0	0.0	0.211
Betula pubescens	33.50 ±5.58	2.80 ±1.01	100.0	70.0	**<0.001**
Calluna vulgaris	5.45 ±2.49	5.70 ±3.42	90.0	60.0	0.618
Erica cinerea	0.00	0.05 ±0.05	0.0	10.0	1.000
Erica tetralix	0.00	0.15 ±0.11	0.0	20.0	0.474
Fraxinus excelsior	0.00	0.05±0.05	0.0	10.0	1.000
Ilex aquifolium	8.30 ±6.92	0.85 ±0.17	60.0	90.0	0.517
Molinia caerulea	0.05 ±0.05	0.40 ±0.27	10.0	20.0	0.474
Pinus sylvestris	3.20 ±1.66	0.05 ±0.05	60.0	10.0	**0.026**
Polypody spp.	0.00	0.05 ±0.05	0.0	10.0	1.000
Quercus petraea	17.85 ±5.82	1.65 ±0.32	100.0	90.0	**0.001**
Rhododendron ponticum	0.00	1.10 ±0.31	0.0	80.0	**0.001**
Rubus fruticosus	23.00 ±6.02	0.80 ±0.51	90.0	40.0	**<0.001**
Sorbus aucuparia	2.50 ±1.71	0.15 ±0.11	20.0	20.0	0.721
Understorey					
Abies alba	0.10 ±0.10	0.00	10.0	0.0	1.000
Betula pubescens	36.30 ±9.71	0.00	90.0	0.0	**<0.001**
Total field cover	76.50 ±6.15	13.20 ±3.96	100.0	100.0	**<0.001**
Total understorey cover	36.40 ±9.66	0.00	100.0	100.0	**<0.001**
Total bryophyte cover	0.50 ±0.31	42.35 ±11.68	30.0	0.0	**<0.001**
Litter	94.60 ±0.52	59.90 ±10.65	100.0	100.0	0.134
Bare earth	0.00	0.80 ±0.51	0.0	30.0	0.211
Bare rock	0.05 ±0.05	1.15 ±0.47	10.0	70.0	**0.005**
Fallen wood	1.50 ±0.98	2.45 ±0.47	40.0	100.0	**0.016**

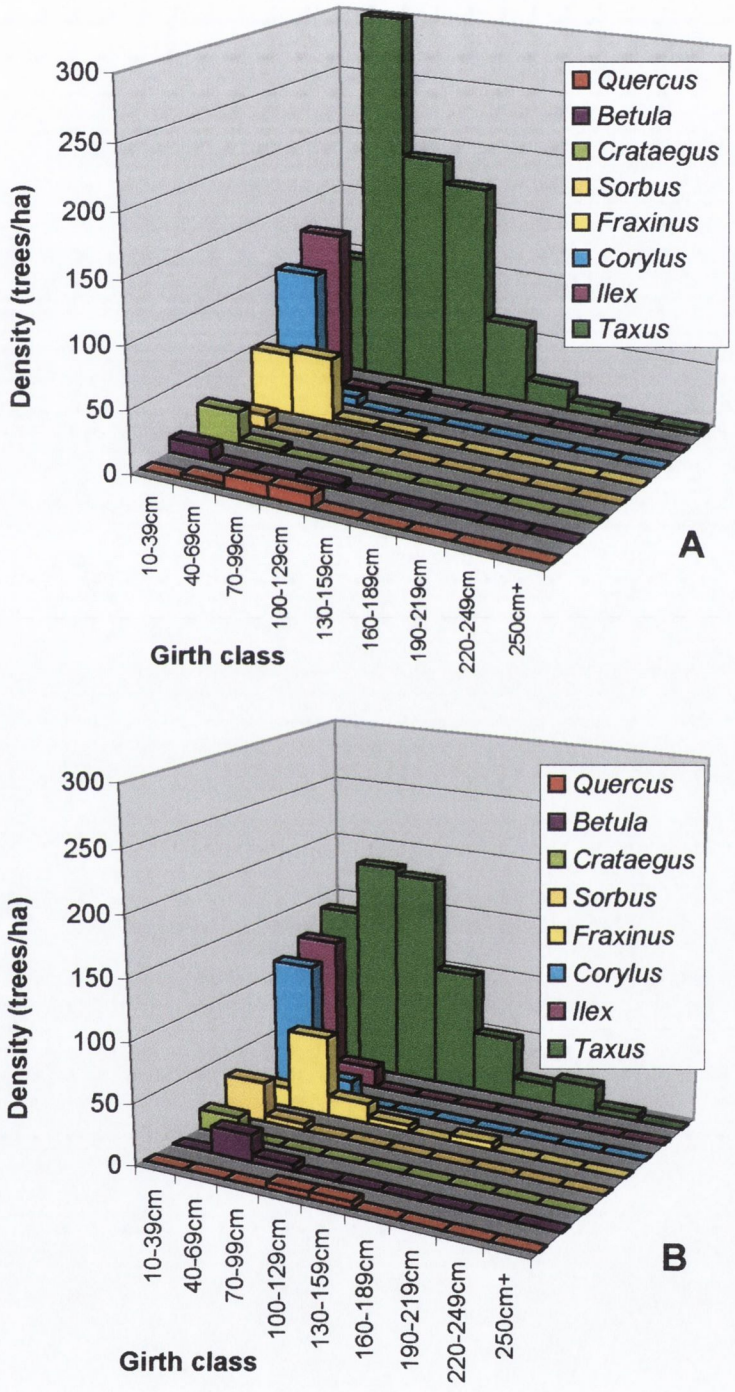
Table 4.21 Comparisons of seedling / sapling densities and juvenile heights for exclosed and unexclosed plots, sites W1, 2001. Data analyzed with Mann-Whitney U tests. Data presented are means (± se) as medians tend to zero. For density $n = 10$

Species		Density (m^{-2})		*P*	Height (cm)		*P*
		Exclosed	Unexclosed		Exclosed	Unexclosed	
Abies alba	saplings	0.10 ±0.10	0.00	1.000	225.00 ±225.00	0.00	-
Arbutus unedo	saplings	0.20 ±0.13	0.00	0.474	165.00 ±40.00	0.00	-
Betula pubescens	seedlings	0.10 ±0.10	9.70 ±3.23	**0.003**	203.50 ±19.33	8.37 ±0.63	**<0.001**
	saplings	3.90 ±1.35	0.10 ±0.10	**0.002**			
Fraxinus excelsior	seedlings	0.00	0.10 ±0.10	1.000	0.00	4.00 ±4.00	-
Ilex aquifolium	seedlings	0.30 ±0.21	3.00 ±0.93	**0.005**	46.50 ±16.92	6.39 ±1.10	**0.008**
	saplings	0.30 ±0.21	0.10 ±0.10	0.737			
Quercus petraea	seedlings	19.70 ± 6.22	5.20 ± 1.40	**0.010**	25.82 ±1.26	7.62 ±0.41	**<0.001**
	saplings	11.60 ±2.91	0.00	**<0.001**			
Pinus sylvestris	seedlings	0.00	0.20 ±0.13	0.474	96.75±12.55	4.50 ±2.50	**0.022**
	saplings	0.80 ±0.42	0.00	0.087			
Rhododendron ponticum	seedlings	0.00	8.90 ±3.79	**0.001**	0.00	1.52 ±0.08	-
Sorbus aucuparia	seedlings	0.00	0.30 ±0.21	0.474	150.00 ±20.00	12.00 ±5.29	0.100
	saplings	0.20 ±0.13	0.00	0.474			

Table 4.22. Results of Kolmogorov-Smirnov tests comparing frequency distribution of adult girth classes between exclosed and unexclosed plots, 2001

	P Sites R1-3	*P* Sites C1-5
Taxus baccata	0.203	-
Ilex aquifolium	0.298	<0.001
Fraxinus excelsior	0.036	-
Corylus avellana	0.644	-
Betula pubescens	0.048	0.145
Quercus robur	0.444	-
Quercus petraea	-	0.870
Sorbus aucuparia	1.000	-
Crataegus monogyna	1.000	-

Figure 4.20 Girth class frequency distributions for adult trees at sites R1-3 in (a) exclosed and (b) unexclosed plots, 2001



artefact of plot positioning. The higher densities of yew in the 40-69 cm girth class in exclosed plots are certainly attributable to this second explanation: at site R3 the uncommonly high densities of yew in the exclosure were difficult to replicate in the unexclosed plot. This resulted in a slightly lower overall density of trees and total basal area in the Reenadinna unexclosed plots compared to the exclosures (Table 4.23). Importantly, however, both frequency distributions for yew are unimodal, with little difference in the number of 10-39 cm girth class trees. There were no significant differences in the distributions for hazel, holly, hawthorn or rowan, despite the observed recruitment in the exclosures (Fig. 4.15), but there were significantly more stems per hazel tree inside the exclosures (Table 4.24).

At the Camillan sites, there were some major differences in the adult tree class structure (Fig. 4.21 and Table 4.22). In the exclosed plots, there had been very considerable recruitment of holly to the lowest girth class. Small numbers of young trees of alder, rowan, willow and, importantly, yew, were also present in the exclosures, but were absent or nearly absent from the unexclosed plots. There appears to have been a low level of birch recruitment in the exclosures, but both of the frequency distributions for oak were unimodal with no recent recruitment. Single young trees of *Arbutus* and alder buckthorn (*Frangula alnus*) were present in exclosure C4, as was a large juniper bush (Table 4.23). The large number of holly recruits meant that overall tree density was much higher within the exclosures, although there was little difference in total basal area (Table 4.23). Despite most of these recruits being single stemmed, there was still a significantly higher number of stems per holly tree in the exclosures due to sprouting from the base of mature trees (Table 4.24).

At the Dinis site, which had originally contained no adult trees in either plot, adult birches were present within the exclosure at a density of 3000 per ha. In combination with the high densities of oak and birch saplings, this meant that exclosure W1 had the highest NR out of the nine exclosures (Fig. 4.22). Exclosure C2, which had high levels of holly regeneration, and exclosure C4, which had a wide variety of regenerating species, also scored highly. Regeneration in exclosure C5 was chiefly holly. Exclosures C1 and C3 scored poorly, although here, as in all the Camillan exclosures, yew was actively regenerating. At the Reenadinna sites there was again little regeneration, with exclosure R3 exhibiting the highest score.

Table 4.23 Differences in density and basal area of adult trees in exclosed and unexclosed plots at sites R1-3 and C1-5, 2001.

	Density (trees/ha)				Basal area (m^2/ha)			
	Sites R1-3		Sites C1-5		Sites R1-3		Sites C1-5	
	Excl.	Unexcl.	Excl.	Unexcl.	Excl.	Unexcl.	Excl.	Unexcl.
Taxus baccata	855.65	694.44	22.25	-	57.30	47.04	0.09	-
Ilex aquifolium	130.21	138.89	2325.24	469.26	0.63	0.80	14.62	12.24
Fraxinus excelsior	107.89	111.11	-	5.39	1.92	4.61	-	0.09
Corylus avellana	111.61	127.78	-	-	1.14	1.15	-	-
Crataegus monogyna	29.77	16.67	-	-	0.11	0.17	-	-
Euonymus europaeus	3.72	-	-	-	0.01	-	-	-
Betula pubescens	14.88	27.78	48.21	59.33	0.54	0.85	4.41	2.69
Quercus robur	26.04	11.11	-	-	2.01	1.25	-	-
Quercus petraea	-	-	122.38	151.02	-	-	32.22	37.72
Sorbus aucuparia	11.16	38.89	55.63	5.39	0.01	0.27	0.20	0.05
Arbutus unedo	-	-	3.71	-	-	-	0.01	-
Alnus glutinosa	-	-	18.54	-	-	-	0.10	-
Frangula alnus	-	-	3.71	-	-	-	0.01	-
Juniperus communis	-	-	3.71	-	-	-	0.03	-
Rhododendron ponticum	-	-	7.42	-	-	-	0.01	-
Salix cinerea	-	5.56	14.83	-	-	0.85	0.02	-
Prunus avium	-	5.56	-	-	-	0.05	-	-
Malus sylvestris	-	-	-	5.39	-	-	-	0.09
All species	1290.92	1177.78	2625.63	695.79	63.67	57.04	51.72	52.88

Table 4.24 Differences in mean number of stems per tree between exclosed and unexclosed plots in 2001, at sites R1-3 and C1-5. Figures in brackets are medians. Data analyzed with Mann-Whitney U-tests.

	Sites R1-3			Sites C1-5		
	Exclosed	Unexclosed	*P*	Exclosed	Unexclosed	*P*
Taxus baccata	1.03 (1)	1.02 (1)	0.708	-	-	-
Ilex aquifolium	1.11 (1)	1.08 (1)	1.000	1.20 (1)	1.05 (1)	**0.049**
Fraxinus excelsior	1.03 (1)	1.15 (1)	0.460	-	-	-
Corylus avellana	3.23 (3)	1.78 (1)	**0.003**	-	-	-
Crataegus monogyna	1.00 (1)	1.00 (1)	1.000	-	-	-
Betula pubescens	1.00 (1)	1.00 (1)	1.000	1.62 (1)	1.18 (1)	0.522
Quercus petraea	-	-	-	1.03 (1)	1.04 (1)	1.000
Sorbus aucuparia	1.00 (1)	1.00 (1)	1.000	1.13 (1)	1.00 (1)	1.000

Figure 4.21 Girth class frequency distributions for adult trees at sites C1-5 in (a) exclosed and (b) unexclosed plots, 2001

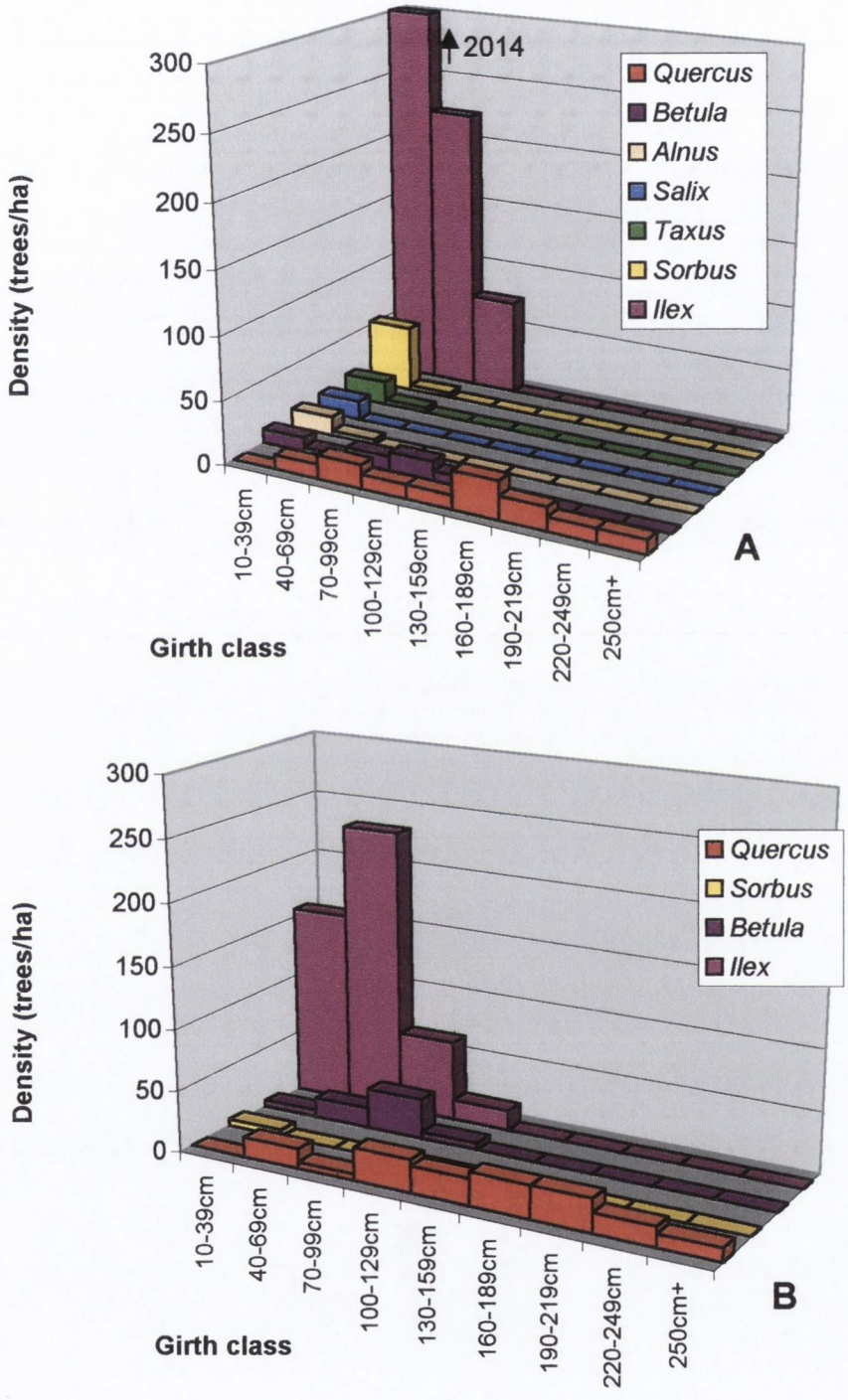
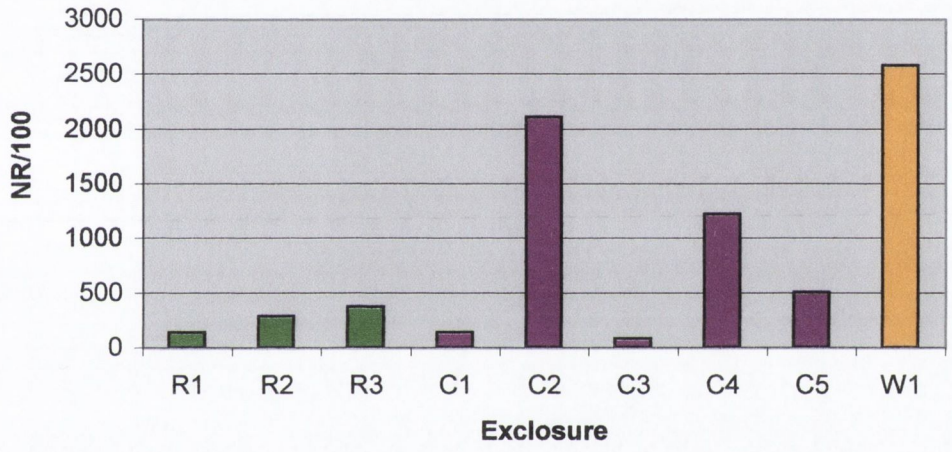


Figure 4.22 Comparison of natural regeneration index (NR) between exclosures.



4.4 Discussion

4.4.1 Natural regeneration

A number of factors can limit natural regeneration at each stage of the process, from seed production and dispersal, to germination, establishment and recruitment (Harmer 1994, 1995). However, as mentioned in the introduction to this chapter, heavy grazing has such an overwhelming effect on all but the most unpalatable or well-protected species, that these other effects can be difficult to detect when large numbers of herbivores are present. The exclusion of deer from fenced plots on the Muckross Peninsula over the last thirty years has permitted several tree species to regenerate successfully, but has also highlighted considerable variation in success between species, sites and woodland types. A discussion of these variations at a species level follows, with due consideration of what other factors may be involved.

Yew

Despite being highly toxic to some animals, particularly cattle and horses, yew foliage is freely eaten by deer, goats, hares, rabbits and sheep (Watts 1926; Edlin 1965; Rodwell 1991). Deer browsing is clearly limiting yew regeneration in Camillan; in the exclosures several large yew saplings are present and recruitment to the adult tree class has occurred. Similarly, young yew trees, approximately 2.5-3.0 m in height, are to be found in old exclosures in Derrycunihy Wood in the southern part of the Killarney National Park (pers. obs.) and on some of the small, ungrazed lake islands. Ferguson & Westhoff (1987) found a low density of yew saplings in Derryclare Wood, Co. Galway, and estimated that they dated from the time that wood was fenced off from sheep and goats.

However, in Reenadinna Wood, deer browsing alone is not responsible for the paucity of yew regeneration which was negligible even within the exclosures. Several potentially important factors not investigated by this exclosure study are discussed further below, but an explanation suggested from the present data is a lack of suitable germination microsites. The scarce yew seedlings that do occur in Reenadinna are typically found in small soil-filled hollows with a sparse bryophyte cover rather than on moss-covered rocks or in grykes (pers. obs). Bryophyte and litter cover inside the Reenadinna exclosures increased during the course of the study with an apparent elimination of bare earth, already a scarce commodity in a woodland on limestone pavement. In Camillan,

however, bare earth has become more abundant in the exclosures due to a significant decrease in bryophyte cover. This appears to have declined in response to increased shade from the developing holly understorey and the expansion of *Vaccinium myrtillus* and *Luzula sylvatica* in the field layer. Could this continued availability of bare earth be responsible for the successful regeneration of yew in Camillan? Small-seeded trees (e.g. birch, Scots pine) typically require bare ground for seedlings to establish as they produce relatively weak radicles which cannot penetrate deep layers of moss or litter (Miles & Kinnaird 1979a). Experiments with Scots pine (e.g. Edwards 1980; Gong *et al.* 1991) have shown that removal of the ground layer vegetation can greatly enhance seedling establishment, particularly when the upper layer of the soil is also disturbed. Large-seeded trees, such as oak, produce more robust radicles and seedlings are less dependent on bare or disturbed ground in order to establish (Pigott 1983). The germination microsite requirements for yew seeds, which are of intermediate size, are unknown and it is uncertain whether they are more stringent than those of ash, holly and rowan, all of which have established saplings in the Reenadinna exclosures.

No yew regeneration was found in the Dinis exclosure. This was possibly due to the peatier, less well-draining soil, although the distance from available seed sources may also be a key factor, as mature yew trees are less abundant at Dinis than even in Camillan.

Oak and birch

The different responses of oak and birch to deer exclusion at Camillan and at Dinis appear to be partly due to canopy shade, as the Camillan sites are predominantly semi-open / closed, and Dinis is predominantly open. Regeneration outside exclosures was negligible at both sites. In Camillan, deer exclusion caused a reduction in seedling densities of both species, probably due to competition from the increased field layer or shade from the holly understorey. Persisting juveniles increased in height, markedly so in the case of birch, but there was no significant change in sapling density. Both oak and birch are shade intolerant species as demonstrated by their strikingly better growth in the less shaded subplots (B and D) in the Mine Paddock, compared with the more shaded subplots (A and C). Likewise, restriction of oak and birch regeneration to unshaded or lightly shaded sites was found in Tomies Wood by Kelly (2002) and the intolerance of oak seedlings to shade has been experimentally demonstrated by several authors (e.g. Jarvis 1964; Ziegenhagen & Kausch 1995). Failure of fencing to promote oak regeneration within woodland was similarly found by Linhart &

Whelan (1980) at Coed Gorswen, North Wales, where increased shade from *Rubus fruticosus* and lack of disturbed ground microsites were thought to be responsible.

At Dinis, a birch thicket has very rapidly formed from existing birch seedlings released by fencing or new birch seedlings establishing soon after deer exclusion. Birch is a fast growing pioneer species with annual height increments up to 60 cm reported in Ireland (Nieuwenhuis & Barrett 2002). It can compete effectively with other species in open conditions (Atkinson 1982). Increased shade and the accumulation of a dense litter layer, however, appear to have subsequently prevented new cohorts of birch seedlings from establishing. Soil disturbance, typically by large herbivores, is known to be important for birch regeneration (Kinnaird 1974; Miles & Kinnaird 1979a; Pigott 1983; Hester *et al.* 1996; Henderson *et al.* 1997). A dense layer of oak saplings has also formed in this exclosure, but they are very much shorter on average than the faster growing birches, and appear to have been suppressed by the birch and the development of a thick bramble layer (cf. Linhart & Whelan 1980). Hence, it is unclear whether these established at the time that the fence was erected or subsequently. Kelly (2002), found that in the exclosed clearing in Tomies oakwood, where a birch stand also formed, only the initial cohort of oaks survived; additional cohorts were unable to establish under dense birch. However, Pigott (1983) found that oak seedlings continued to establish beneath birch in the exclosure at Yarncliff Wood; the considerable nutrient reserves present within acorns enabled radicles and plumules to penetrate the thick layers of leaf litter that had accumulated.

Holly

Despite its spiny leaves, holly is palatable to many species (Peterken & Lloyd 1967; Pigott 1983) and deer browsing has clearly prohibited its regeneration outside the exclosures in recent decades. It has been suggested that selective browsing of holly by sheep and deer is responsible for its scarcity in the shrub layer of many western oakwoods in Britain (Mitchell & Kirby 1990; Mitchell *et al.* 1996). Even small holly seedlings are remarkably tolerant to browsing, however, and Peterken & Lloyd (1967) comment that in the New Forest: "The height growth of young individuals may be checked indefinitely by heavy browsing to form a low scrub less than 50cm high". This certainly describes several of the unexclosed Camillan plots where very high densities of small (<30 cm) gnarled holly plants are almost the sole components of the field layer. Deer exclusion has released this high density bed of established plants with the result that impenetrable

holly thickets have formed in many of the exclosures. Holly is a shade tolerant species (Peterken & Lloyd 1967) and evidently able to establish saplings under a fairly closed oak canopy. The failure to produce holly saplings in exclosure C1 may therefore be a result of increased competition in the field layer from *Vaccinium myrtillus* and *Luzula sylvatica*; regeneration here was almost entirely restricted to basal sprouting from mature holly trees. Kirby *et al.* (1994) reported that a dense holly understorey formed in several English woods following the cessation of grazing. In Tomies Wood, Kelly (2000) also found that a holly thicket developed in the wooded area of the exclosure, through a combination of the release of pre-established juveniles and the establishment of seedlings post fencing. Holly is also pre-eminent in the understorey of exclosed plots established in the oak woodlands of Glendalough, Co. Wicklow in 1970-71 (pers. obs.).

In the Reenadinna exclosures, holly regeneration was markedly less than in those in Camillan, but it was still the most successful species, forming a sparse, low shrub layer in some areas. Holly is evidently able to endure the considerable shade of the yew-wood canopy. Saplings increased in number fairly rapidly following fencing, but despite no significant trend in seedling data since 1969, seedlings are now scarcer inside the exclosures than outside. This is a puzzling, but may again reflect germination microsite availability.

Rowan

Rowan seedling density did not decline significantly following exclosure in Reenadinna. There was some recruitment to the sapling class, which is now taller on average than holly, though less dense. Rowan has larger seed reserves than birch and hence is less dependent on bare earth and light for establishment (Hester 1995 in Hester *et al.* 1996). Thus Pigott (1983) found that, like oak, rowan was able to continue regenerating inside the Yarncliff Wood exclosure. Pigott (1983) also noted that established rowan seedlings are more shade-tolerant than either birch or oak. Rowan grew well under the shaded conditions of subplots A and C in the Mine Paddock. The greater height of rowan over holly suggests that it is etiolating, however, and is evidently not as shade tolerant as holly.

Conversely, in Camillan rowan seedling density was lower inside the exclosures. Hester *et al.* (1996) found a similar result following a reduction in grazing pressure. In exclosure C1, rowan regeneration has been poor throughout the period of exclosure. Presumably, germination microsites become limiting for rowan regeneration under certain circumstances. As with yew, rowan seedlings

and saplings occurred even when mature rowan trees were absent from canopy. This is evidence of the effectiveness of bird dispersal.

Ash

Ash juveniles increased in density in the Reenadinna exclosures, but increased little in height. Although often regarded as light-demanding, ash seedlings are tolerant of canopy shade and may persist for many years, but do not effectively increase in height until the occurrence of a canopy gap (Wardle 1961). For example, Gardner (1975) found ash saplings 15-28 years old beneath an ashwood canopy in Derbyshire. Outside the Reenadinna exclosures ash saplings were absent. Ash is a highly palatable species, but very resilient to browsing and able to repeatedly compensate for lost growth (Mitchell *et al.* 1996; Hester *et al.* 1996). Marked increases in ash regeneration in the event of stock exclusion have been reported by Linhart & Whelan (1980) and Latham & Blackstock (1998). That ash seedlings appeared more abundant outside the exclosures (Table 4.17) is difficult to explain in view of the observed increases within the fences (Table 4.6); it seems unlikely that there was any real increase in seedling density in the unexclosed plots.

Hazel

Hazel juveniles not growing from old stumps were exceedingly scarce, even within yew-wood exclosure R2 where adult hazels were abundant, and regeneration was largely limited to basal sprouting from existing stools. Cooper (1984) found similar results in a survey of hazel scrub in the northeast of Ireland. Peterken & Jones (1989) reported low numbers of hazel seedlings in the young-growth stands at Lady Park Wood in south-west England, despite an abundance of regenerating coppice stools. After a review of the literature, Vera (2000) concluded that hazel was fairly shade intolerant and unable to regenerate within closed woodland. In Britain, lack of regeneration from seed has been attributed to predation of hazelnuts prior to ripening by grey squirrels (*Sciurus carolinensis*) and is a serious problem (White 1995; Rackham 1986). Grey squirrels are absent from the Killarney region, but the native red squirrel (*Sciurus vulgaris*) is present, and was observed during the present study feeding in hazel trees in the vicinity of exclosure R2

4.4.2 Adult tree demography

Tree size-distributions within stands can be used as an indication of past and present regeneration patterns (e.g. Cooper 1984; Ågren & Zackrisson 1990), but should not be used as proxies for age distributions without caution. Due to differences in growth rates, different species may display almost identical size-distributions, and yet have widely disparate age structures (Knowles & Grant 1983). Differences in growth rates occur even between individuals of the same species in a single cohort due to the heterogeneous distribution of substrate and nutrients in woodlands. The size-distributions of species in even-aged stands are also strongly influenced by shade tolerance (Lorimer & Krug 1983). The idea that the present Reenadinna Wood may have arisen following the cessation of industrial activities on the Muckross Peninsula in the late eighteenth century, and therefore be essentially even-aged, is thus not discounted by the fairly broad range of yew girth sizes recorded in this study. Indeed, the evidence that self-thinning of smaller stems and individuals is still occurring within this population, is indicative of relatively recent origins; this is the aggradation phase of the model for forest development following major disturbance proposed by Bormann & Likens (1979). A rough comparison between the total tree density for Reenadinna Wood sites (1100-1300 trees ha^{-1}) and the densities Hulme (1996) recorded for woodlands in the northeast of England with sizeable yew populations (159-329 trees ha^{-1}), serves to highlight the developing nature of the Reenadinna Wood. The data also suggest that different areas of the wood are at different stages of the aggradation phase; although the stands in all three Reenadinna exclosures thinned between 1981 and 2001, exclosure R1 has a substantially lower density of trees and a higher total basal area than either exclosures R2 or R3.

The occurrence of self thinning and the associated variation in growth rates precludes the derivation of an age-distribution curve from the whole of the size-distribution curve. However, growth of the larger yew trees (130-250 cm gbh, n = 26) has probably been relatively unsuppressed by competition. Hulme (1996) employed a mean growth rate of 0.1cm year-1 to calibrate trees size measurements; similar growth rates had been reported by a number of studies. If a similar constant growth rate is assumed for yew trees in Killarney, this would make the larger yew trees 207-398 years old; again this is not inconsistent with the theory that most of woodland developed between 200-250 years ago. The observed radial growth rate of these trees over a 20 year period, however, was 0.05 cm $year^{-1}$. This suggests that either these larger trees predate the

industrial period of the late eighteenth century (being 414-796 years old), or that growth rates have not been constant throughout their lifespan; i.e. growth rates have declined with time.

A reasonably sized canopy gap (approximately 8-10 m in diameter) was created in the corner of exclosure R3 by the fall of several birch trees between 1981 and 2001 (Fig. 4.11). This gap is currently being filled by several young rowan and holly trees; yew has been unable to take advantage of this gap opportunity. This contrasts with the findings of Mitchell (1990b) who showed from pollen evidence that yew was able to respond to the fall of an oak tree more rapidly than birch or holly, and dominate the understorey in the absence of grazing. Hannon & Bradshaw (1989) found that following woodland clearance episodes on Connemara lake islands, yew was an early dominant in the absence of grazing. The different response in the present study is possibly due to the smaller size of the gap, although the data suggest that the gap was filled by rowan and holly because saplings of these species were already available when the gap was created, whilst yew saplings were not.

Natural regeneration within the Camillan exclosures, stimulated by the exclusion of deer, has begun to impact on the adult tree class, as demonstrated by the girth distribution curves (Fig. 4.21). Several tree species have been recruited to the adult tree class. The size distribution for holly has an inverse-J curve (or negatively exponential relationship) indicating an actively regenerating population with a balance of recruitment and gradual mortality, whereas outside the exclosures holly has a declining curve (*sensu* Whipple & Dix 1979). The size-distribution curves for yew in Reenadinna are also of this type, which is indicative of a recent lack in recruitment.

4.4.3 Field layer vegetation

In broad terms, the absence of grazing resulted in the development of a field layer dominated by tall growing, palatable species. The main species to benefit in Reenadinna, holly aside, were *Rubus fruticosus*, *Hedera helix* and *Lonicera periclymenum*. Higher abundance of these species in exclosed plots was also found by Latham & Blackstock (1998) in the alder woodland at Coedydd Aber, North Wales and by Putman *et al.* (1989) in the New Forest. Kirby (1998) reported that *Rubus fruticosus* spread rapidly in fenced areas in a wide range of woodland types in England. The decline in *Rubus fruticosus* in various unexclosed stand types at Brigsteer Wood, Cumbria,

including a yew dominated stand, was attributed to the increase in roe deer (*Capreolus capreolus*) abundance (Barkham 1992). *Rubus fruticosus* is clearly susceptible to browsing despite its thorns.

Increases in these woody species are generally accompanied by decreases and losses of broadleaved herbs and grasses (Putman 1994). This is not particularly striking in the Reenadinna data, because of the extreme paucity of the field layer in the presence of grazing, although the virtual restriction of the unpalatable *Oxalis acetosella* to grazed plots is interesting. Indeed, perhaps the most noteworthy feature of the current field layer in the yew-wood exclosures, is its total abundance: 46%, compared with 12% in the contemporaneous grazed plots, and only 4% in the exclosure plots prior to fencing. An extreme sparseness of the field layer is reported as a characteristic of yew-woods in Britain (Rodwell 1991). In Reenadinna, however, it is grazing pressure and not shade which is primarily responsible for the scarcity of field layer plants.

The development of the field layer in Camillan was more site-dependent. Beneath the holly thickets it was largely eliminated, but outside these *Rubus fruticosus* again benefited at several sites. In exclosure C1 there was a marked increase in cover of *Vaccinium myrtillus* and *Luzula sylvatica*. Spread of *Vaccinium myrtillus* was also noticeable at Yarncliff Wood, Yorkshire (Pigott 1983). Baines *et al.* (1994) observed that *Vaccinium myrtillus* cover did not differ between grazed and ungrazed woodland, but that grazed plants were only half as tall due to removal of leading shoots by deer. *Luzula sylvatica* is also reported as being sensitive to grazing. Barkham (1978) reported that there was considerable regrowth of this species in the exclosure in Wistman's Wood, Dartmoor, established in 1965, whilst at Black Tor Copse, also on Dartmoor, it was restricted to areas of steeply sloping, unstable clitter, which were inaccessible to animals.

The impact of the expansion of these vigorous oakwood plants on less competitive vascular species is again not apparent from available data. The loss of *Hymenophyllum tunbridgense* and several angiosperm herbs from the exclosure in Tomies oakwood was ascribed by Kelly (2000) to increased competition from *Luzula sylvatica* and *Ilex* saplings. Bryophytes, however, have clearly suffered beneath the shade of the taller vegetation in Camillan. Kirby *et al.* (1994) commented that in two woodland nature reserves in Wales, Coed y Rhygen and Coed Ganllywyd, initial plans to eliminate sheep grazing, had to be later modified to allow a controlled level of grazing, in order to conserve rare Atlantic bryophytes.

4.4.4 Species richness

Excluding deer caused a rapid rise in the number of vascular plant species, although a gradual decline is now occurring. Kelly (2000) found similar results in Tomies Wood, where there were less vascular species in his wooded exclosure after 26 years than prior to fencing. Removal of large herbivores enables a number of species to colonise exclosures, but these species appear to be soon out-competed by a few vigorous plants previously controlled by grazing. In Reenadinna, transient species included the grasses *Danthonia decumbens*, *Deschampsia flexuosa* and *Festuca rubra* and the fern *Athyrium felix-femina*. In Camillan, *Calluna vulgaris*, *Viola riviniana / reichenbachiana* and *Euphorbia hyberna* were all recorded by the baseline survey in 1969, but had disappeared by 1993 due to the spread of holly, *Vaccinium myrtillus* and *Luzula sylvatica*.

Two of the three Reenadinna exclosures had a greater number of species than the Camillan exclosure throughout the period of monitoring, and the other Reenadinna exclosure (R1) had a greater number of species from 1980 onwards (Fig. 4.2). In the absence of grazing, shade would appear to have partially limited the spread of the more vigorous yew-wood species, holly, *Hedera helix* and *Rubus fruticosus*, and thus the decline in species richness has been slower. The overall greater species richness in the yew-wood, however, is partly attributable to the broader range of ecological niches available, particularly the presence of lime-free pockets of soil (Kelly 1981). Nelson & Walsh (1991) describe how $CaCO_3$ can be leached from hummocks of soil on the surface of the limestone in the Burren. In addition, Grime (1963) found that although surface-leaching may be absent, calcifuge invasion can be facilitated if certain nutrient deficiencies are offset by conditions related to reduced soil aeration. By these mechanisms niches suitable for calcifuge species can form in an area dominated by calcareous substrate. Hence, a number of plants more associated with acidic habitats were recorded in the Reenadinna exclosures, including: *Calluna vulgaris*, *Erica cinerea*, *Vaccinium myrtillus*, *Danthonia decumbens*, *Deschampsia flexuosa*, *Luzula sylvatica*, *Luzula pilosa*, *Hypericum pulchrum*, *Potentilla erecta* and *Blechnum spicant*.

The long history of deer grazing on the peninsula has not only reduced field layer diversity and regeneration, but has also limited tree species diversity. Fencing in Camillan resulted in a number of tree species being recruited to the adult class which were wholly absent from the grazed plots: yew, juniper, *Arbutus*, Scots pine, alder, alder buckthorn and willow.

4.4.5 Rhododendron *management*

Acidified pockets of soil have permitted the invasion of *Rhododendron* on the limestone outcropping of Reenadinna as noted already by Kelly (1981). *Rhododendron* has serious impacts on native plant communities in Ireland, reducing species diversity by shading out the ground flora and preventing regeneration of trees and shrubs (Cross 1982). Potential allelopathic effects of *Rhododendron* spp. in the field have also been investigated (e.g. Nilsen *et al.* 1999).

Rhododendron management in Reenadinna has not impacted on this study as the species was rare in the area of the exclosures and our samples avoided the small area from which it was cleared in exclosure R1. Exclosures R2 and R3 never had *Rhododendron* present. In Camillan and at Dinis, however, where acidic conditions are widespread, the results must be interpreted in view of widespread *Rhododendron* clearance that has taken place over the last twenty years. This clearance work did not systematically include the Camillan exclosures. Therefore, although this shrub was significantly more abundant inside the exclosures, this is obviously a result of management being more intense in the unexclosed plots, rather than any grazing effect; *Rhododendron* is unpalatable to deer due to foliar chemicals (Cross 1982). *Rhododendron* infestation was limited largely to exclosure C4 where it may have substantially reduced holly regeneration. Field layer vegetation beneath this *Rhododendron* was negligible, but cover is also low beneath holly thicket, and the differential effect was probably minor. Outside the exclosures, plots were positioned to avoid areas obviously sprayed or mechanically cleared in the recent past, but it is almost inevitable that *Rhododendron* management has impacted on these plots at some time subsequent to fencing. Field layer recovery is slow after *Rhododendron* clearance, although it is slower still if grazed. *Rhododendron* management may therefore have exaggerated the apparent effects of grazing in the unexclosed plots, but the response to deer exclusion has been so striking that this unlikely to have altered the general pattern of results.

4.4.6 Methodological considerations

The importance of surveying a wide variety of sites is highlighted by the site-dependent nature of vegetation in Camillan. Exclosure C1, which was monitored since 1969, was fairly unrepresentative of change in the other exclosures. However, the continuous dataset for this exclosure enabled changes in species richness over time to be detected. A comparable picture is lacking for the other sites. Importantly, it is not clear whether the extant holly thickets were

preceded by *Vaccinium – Luzula* or *Rubus* dominated field layers. If so, the observed variation between the Camillan exclosures may actually indicate different points along a successional pathway. The importance of monitoring both control and treatment plots throughout the course of a long-term monitoring project is also highlighted. The baseline survey in Reenadinna in 1969 recorded a field layer cover of 4%, whereas the field layer cover of the adjacent grazed plots in 2001 was 12%. Similarly, the baseline survey of exclosure C1 in 1969 recorded a field layer cover of 9%, but the survey of 1979 recorded the field layer cover of the unexclosed plots as 18%. This seems to indicate that grazing pressure on the peninsula was reduced somewhat between 1969 and 2001. This does not tally with available data (Table 3.6). Whatever changes may have occurred, grazing pressure evidently remains far too high to permit natural regeneration.

In order to be consistent with the previous surveys, quadrats 1x1 m in size were used throughout the course of this study. Whilst this has been appropriate to investigate changes in vegetation cover, it appears to have rendered presence-absence data susceptible to spatial heterogeneity in species distributions. Hence, the mean number of species per quadrat (Fig. 4.2b) was a relatively poor indication of the total species richness in the exclosures (Fig. 4.2a). In comparison, the study of diversity in Tomies Wood (Kelly 2000) which used 8x8m quadrats found a high degree of correlation between these two measures of diversity. Estimation of species cover and counting of juvenile trees is more difficult and time intensive in larger quadrats, however; possibly 2 x 2 m quadrats, as used in the exclosure study of Latham & Blackstock (1998), are a reasonable compromise.

4.5 Conclusions

Chronic overgrazing on the Muckross peninsula has evidently had major impacts on vegetation composition and structure in both Reenadinna yew-wood and Camillan oakwood. In the short term, deer exclusion promoted an increase in natural regeneration and species richness. However, in the longer term, lack of large herbivore disturbance resulted in reduced seedling establishment and a fall in species richness as the vegetation becomes dominated by a small number of aggressive species. This is a clear example of the intermediate disturbance hypotheses of Connell (1978) who proposed both large or frequent disturbances and small or infrequent disturbances would result in decreased diversity, and concluded that high diversity is only maintained in a non-equilibrium state.

Long-term management of the woodlands on the Muckross Peninsula requires some level of grazing, intermediate between high to very high (the general situation throughout the period of this study) and zero (inside the exclosures). In deciding upon the optimal level of grazing and the means to the achieve it, it is imperative to consider the ultimate objectives of management. If the aim of nature conservation is to achieve naturalness in addition to diversity, management needs to emulate natural woodland dynamics in some fashion. Historically these were principally driven by vegetation-herbivore-carnivore interactions. Our knowledge of the role that large herbivores played in the prehistoric woodlands of Ireland is poor, however, and new research approaches are required (Bradshaw & Mitchell 1999). Much can also be learned by further study of existing Irish woodlands that do combine light grazing regimes with successful natural regeneration (cf. Kelly 2000).

In Camillan Wood, deer grazing is limiting natural regeneration of yew, but in Reenadinna Wood some factor in addition to deer browsing must be involved as regeneration was negligible even inside the exclosures. An obvious candidate is light; the dense yew-wood canopy casts considerably more shade than that of the oakwood, and as major components are evergreen (yew and holly) it is present throughout the year. However, yew is reported as being extremely shade tolerant and able to persist in its own considerable shade (e.g. Brzeziecki & Kienast 1994; Rodwell 1991). This shade tolerance is demonstrated by the presence of juveniles under closed oak canopy and amongst dense holly thickets in the Camillan exclosures. The absence of yew saplings and the rarity of yew seedlings in Reenadinna is therefore puzzling when saplings of less shade tolerant species such as ash and rowan are present. Furthermore, yew appears to have been unable to take advantage of the increased light conditions that ensued when the canopy gap event occurred in exclosure R3. Another potential factor is post-dispersal seed predation. Exceptionally high densities of woodmice (*Apodemus sylvaticus*) have been recorded in Reenadinna (Smal & Fairley 1982), where yew seeds and arils form the major component of the diet (Smal & Fairley 1980a). High rates of yew seed predation have been reported from yew-woods in north-east England (Hulme 1996) and southern England (Williamson 1978). The bank vole (*Clethrionomys glareolus*), a species introduced to Ireland in the 1950s, is also present in these woodlands and can, by damaging tree seedlings, be an important factor in regeneration failure (Pigott 1985). Low germination rates for yew have also been reported by some authors (Schopmeyer 1974; Melzack & Watts 1982b), but total yew seed production in Reenadinna appears to be copious; Smal & Fairley (1980b) estimated crops of

$9.4x10^5$ seeds per ha in 1975-1976 and $3.9x10^6$ seeds per ha in 1976-1977. Lack of viable seeds is unlikely to account for the differential regeneration of yew in two woods in such close proximity.

Investigations into these factors and their potential influence on the regeneration of yew will form the basis of the following two chapters.

The research conducted in the woodlands of the Muckross Peninsula over the last thirty years and presented in this chapter has made several important new findings. In particular, this work has proved for the first time that whilst extremely sparse field layers are viewed as an inherent feature of yew-woods in England (Rodwell 1991), appreciable field layers (*c.*50% cover) can develop in Irish yew-woods in the absence of heavy grazing. Striking floristic paucity is also a feature of English yew-woods (Rodwell 1991), but this study has shown that in the short-term absence of grazing and therefore potentially under long-term intermediate grazing regimes, vascular plant species richness at Irish sites increases and can reach 8-9 species per m^2. Finally, it has long been suspected that browsing by the introduced sika deer are responsible for the dearth of yew regeneration in Reenadinna Wood – this study has clearly shown that other factors besides browsing are limiting the regeneration process.

4.6 Summary

1. Natural regeneration of yew is being limited by deer grazing in Camillan; at reduced levels of grazing it has the potential to increase significantly in abundance. In Reenadinna, deer grazing alone is not limiting regeneration. Lack of suitable germination microsites may be responsible.

2. Natural regeneration of oak is also being limited by deer grazing in Camillan and at Dinis, but growth of seedlings into established saplings is also dependent on light conditions associated with woodland margins and large clearings.

3. Cessation of grazing in Reenadinna would result in a field layer dominated by *Rubus fruticosus* and *Hedera helix* with a sparse holly understorey.

4. Vegetation changes following cessation of grazing in the acid woodlands of Camillan and Dinis appear to be highly site dependent. Formation of a dense holly understorey would occur beneath the oak canopy. Birch thickets would be favoured in more open conditions. *Vaccinium myrtillus*, *Luzula sylvatica* and *Rubus fruticosus* would expand in the field layer.

5. Mortality amongst the yew population in Reenadinna Wood is predominantly amongst the smaller individuals; a self-thinning process is occurring indicating relatively recent origins to the stand structure, although the largest trees may be considerably older.

6. High grazing pressure and the absence of grazing both result in fairly uniform vegetation with a lack of seedling establishment. An undetermined intermediate level of grazing is required to maximise species richness and promote continual natural regeneration.

CHAPTER 5

THE EFFECTS OF SMALL MAMMALS ON NATURAL REGENERATION OF YEW

5.1 Overview

This chapter deals with investigations into the potential effects on yew regeneration of post-dispersal seed predation and seedling damage by small mammals. These investigations consisted of: (i) a live-trapping programme which compared densities of woodmice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) in Reenadinna Wood with those in the neighbouring oakwood of Camillan, (ii) an exclusion experiment which examined the establishment of yew seedlings in the absence of small mammals, and (iii) seed removal experiments which compared differences in seed predation between Reenadinna and Camillan.

5.2 Introduction

High percentages of viable seed fall in European woodlands can be lost through post-dispersal seed predation (Shaw 1968a,b; Gardner 1977; Castro *et al.* 1999). Variation in rates of this predation is influenced by a range of factors including location, seed species, burial and density (Hulme & Borelli 1999; Hulme & Hunt 1999). Several recent field studies have shown that rodents are responsible for the majority of this seed predation (e.g. Hulme 1997; Kollman *et al.* 1998; Castro *et al.* 1999; Schreiner *et al.* 2000), with the chief species involved being the woodmouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*). Woodmice are native and ubiquitous in Ireland (Fairley 1984), but the bank vole is a recent introduction which appears to have arrived in the Limerick area *c.*1955, since when it has spread across the south-east of Ireland, including the Killarney valley (Claassens & O'Gorman 1965; Smal & Fairley 1984; Ryan *et al.* 1996). These two species may also affect natural regeneration through damage to young tree seedlings (Ashby 1959; Kelly 2002). For example, Pigott (1985) concluded that bank voles were an important factor in the failure of small-leaved lime (*Tilia cordata*) to regenerate in English woodlands, due to the low densities of the palatable seedlings and infrequency of high density crops.

An extensive study on small mammals has previously been conducted in the Killarney National Park by Smal & Fairley (1982). A comparison was made between population levels of woodmice and bank voles in a range of woodland habitats (Table 5.1). Reenadinna yew-

wood was found to support unusually high densities of small mammals, much higher than in Tomies Wood where the oakwood trapping had been conducted. The previous record peak density for woodmice in Ireland was 46 ha^{-1} in hazel scrub near Carran in the Burren (Gallagher & Fairley 1979). The high densities in Reenadinna were thought to be due to the three-dimensional terrain provided by the karst limestone pavement, which effectively reduced home range areas, coupled with an abundant food source. Smal & Fairley (1980a) showed that yew seed and fruit were the staple diet of woodmice in Reenadinna, comprising 86-100% of stomach contents in the autumn months.

Table 5.1 Maximum and minimum population densities for small mammals in numbers/ha in a range of woodland habitats in the Killarney National Park, June 1975 – February 1977 (from Smal & Fairley 1982).

	Yew-wood	Oakwood	Beechwood	Pinewood	*Rhododendron*-infested oakwood
Woodmice	23-92	10-40	6-45	0-20	4-50
Bank voles	4-22	1-7	0-3	0-11	0-23

In the previous chapter it was clearly demonstrated that deer browsing was not the limiting factor in the failure of natural regeneration of yew in Reenadinna yew-wood, but that deer were preventing yew regeneration in Camillan oakwood. In view of the extremely high densities of small mammals recorded in Reenadinna compared with oakwood habitat by Smal & Fairley (1982), and the predominance of yew seeds in the diet of woodmice in Reenadinna (Smal & Fairley 1980a), it was speculated that post-dispersal seed predation by small mammals might be responsible for the observed difference in natural regeneration. It was also desired to investigate the effects that dense ground vegetation, such as developed inside some of the Muckross Peninsula deer exclosures over the last thirty years, might have on small mammal populations and rates of seed predation, as this has proved an important factor in other studies (Schreiner *et al.* 2000). The experiments in this study were therefore designed to test the following hypotheses:

i) populations of small mammals are higher in Reenadinna Wood exclosures than in Camillan Wood exclosures;

ii) yew seedling establishment in Reenadinna Wood will be greater where small mammals are excluded than where small mammals have access;

iii) rates of post-dispersal yew-seed predation are higher beneath dense ground vegetation than in open sites;

iv) rates of post-dispersal yew-seed predation are higher in Reenadinna Wood than in Camillan Wood.

5.3 Methods

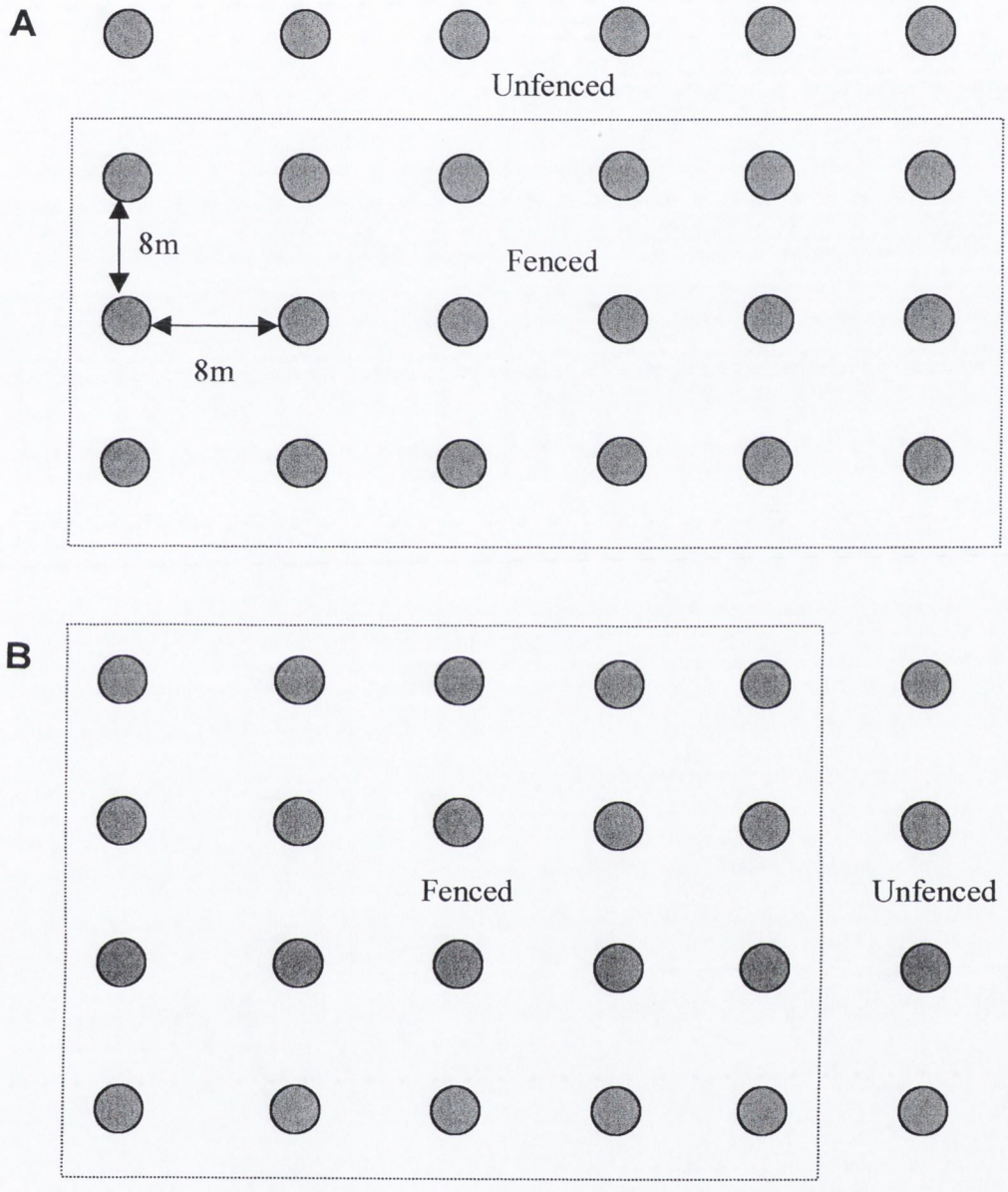
5.3.1 Small mammal population survey

A small mammal trapping programme was conducted in summer / autumn 2001, in exclosure R2 in Reenadinna Wood and exclosure C1 in Camillan Wood (see Fig. 4.1 for location). These sites were primarily selected because of the significantly different levels of yew regeneration; exclosure R2 contained no yew saplings, whilst exclosure R3 contained more than 40 yew saplings, and several yew seedlings. Another consideration was that both sites had a well-developed field layer (49.3% and 67.0% cover in exclosures R2 and C1, respectively), but were still easily accessible for working in. Three trapping sessions were conducted, approximately four weeks apart, in July, August and late September / early October. Each session consisted of four days at the yew-wood site, followed immediately by four days at the oakwood site. At each site, one day was spent pre-baiting followed by three days trapping.

Methodology largely followed the recommendations of Gurnell (1976). Trapping in each woodland was conducted over a 4 x 6 grid of trap points with a spacing of 8m. Due to the different size and shape of the exclosures, this unfortunately resulted in a difference in the layout of the grids, with six trap points in the yew-wood compared with four trap points in the oakwood being outside the exclosure fences (Fig. 5.1). However, this also permitted the effects of fencing on mammal activity to be examined. Three Longworth traps (Penlon, Abingdon, UK) were initially set within 1m of each trap point. The nest box of each trap was filled with organically-grown hay and supplied with a mixture of sunflower seeds and peanuts. Traps were positioned so as to maximise the chance of encounter with woodmice or bank voles. Hence, they were placed alongside natural linear features (e.g. logs, tree roots, or in grykes) which animals were likely to use as habitual pathways.

For the 24 h pre-baiting period, which was used to allow animals to become accustomed to the traps, trap tunnel doors were locked open. Traps were placed on the grid in early evening and sunflower seeds were cast outside the tunnel entrances to encourage animals to enter. The following evening, trap doors were set in the catch position. Traps were now checked in early morning and late afternoon for the next three days. This was necessary to ensure that animals did not remain trapped for long periods, as woodmice are predominantly nocturnal, whilst bank voles are predominantly crepuscular (Fairley 1984). The species and trap location of each animal caught was noted, as was whether they had been previously captured. Identification of previously caught animals was facilitated by a six-point fur clipping system. Once it had been recorded, each animal was immediately released at is point of capture.

Figure 5.1 Trapping grids at (a) Reenadinna exclosure R2 and (b) Camillan exclosure C1, showing distribution of the trapping points (green dots) in relation to the exclosure fence (dotted line).



Activated traps were refilled with fresh hay and replaced on the grid. Where all traps at any given trap point had caught during one day or night period, an additional trap was placed at that trap point for the remainder of that trapping session to ensure that empty traps were available for potential captives.

5.3.2 Small mammal exclosure experiment

The experiment was conducted at five sites distributed across Reenadinna Wood (Fig. 5.2) and largely followed the procedure of Hulme (1994). The sites were small (< 5 m across) soil-filled patches in the limestone pavement, located beneath a mature yew canopy. At each site, three experimental plots were established in September 2000, each 0.9 x 0.9 m in area and within 2 m of at least one of the other plots. Existing vegetation was uprooted and litter material was removed from all of plots. One of three different exclosure treatments was applied to each plot, such that each site had one plot of each treatment. For the "open" treatment, plots were simply marked at the corners with four wooden stakes. For the "small mammal" treatment, a cage 0.6 m high was constructed over the plot from wooden stakes and a 5.0 cm wire mesh. This permitted access to small mammals, but prevented access to large animals, including browsing deer. For the "closed" treatment, a cage 0.6 m high was constructed using two layers of 1.2 cm wire mesh, with the second layer displaced relative to the first to create smaller apertures (Fig. 5.3). For both cage treatments, the wire mesh was buried to prevent burrowing animals from gaining access; due to the shallowness of the soil at several of the sites the depth to which the mesh was buried ranged from 5-10 cm.

Yew seeds, which had been collected from Reenadinna that autumn and from which arils had been removed, were surface-sown into each of the fifteen experimental plots in October 2000 at the density of 100 seeds per plot. A further 100 seeds per plot were sown in mid-December 2001. In July 2002, each plot was revisited and all vascular plants present were recorded.

5.3.3 Seed removal experiments

An experiment was conducted in October 2000 and largely followed the procedure of Hulme (1994, 1996). Within each woodland habitat, Camillan oakwood and Reenadinna yew-wood, 25 seed dishes were placed at dispersed locations. Each consisted of a 9 cm petri dish, recessed flush with the soil and containing ten cleaned yew seeds which had been collected on the Muckross Peninsula that autumn. In each habitat, five dishes were located in each of five different subhabitats: beneath an oak tree, beneath a yew tree, beneath a low holly tree, amongst tall ground vegetation, and in an open site with no immediate cover. Small coloured flags were placed nearby to aid relocation. After three days, the dishes were revisited and the

Figure 5.2 Location of small mammal exclosure sites in Reenadinna Wood..

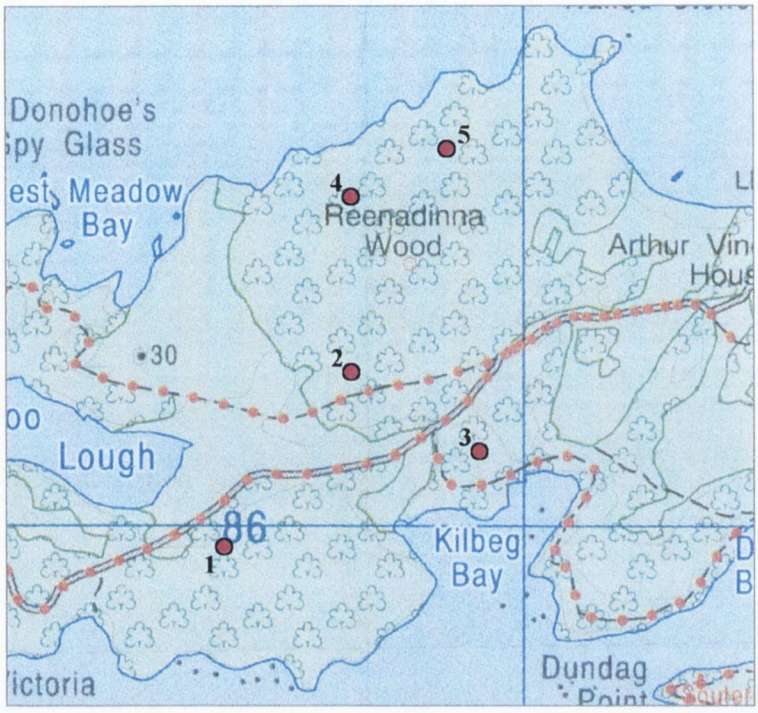


Figure 5.3 Small mammal exclosure plots at site 2, Reenadinna Wood. Closed treatment on the left, small mammal treatment on the right, and open treatment in between.

number of yew seeds remaining recorded. Any seed fragments found in the dishes were collected for examination.

A second experiment was conducted in exclosures C1 and R2 using the trapping grids described above, in late October 2001. Seed dishes were placed singly at each trapping point and revisited after two days.

5.4 Results

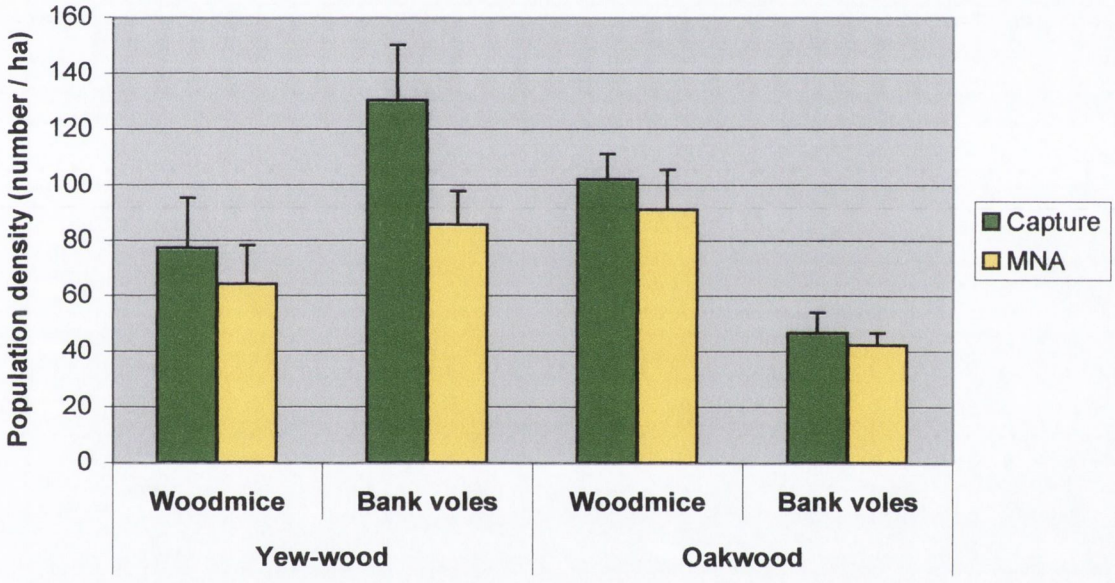
5.4.1 Small mammal population survey

In total, the survey comprised 2,645 trap-periods, where a trap-period was the occasion of one trap being on a trapping grid for one day or night period. This resulted in 548 successful captures of woodmice or bank voles, with 257 captures in Reenadinna yew-wood and 291 captures in Camillan oakwood. A few pygmy shrews (*Sorex minutus*) were also caught, but as this species is strictly insectivorous (Fairley 1984) and numbers were low (<10) these data were omitted from the analysis.

Population estimates for woodmice and bank voles were calculated for each trapping session in each habitat type by Lynch (2002). Two types of population estimates were made: MNA (Minimum Number Alive) and an estimate derived by the computer programme CAPTURE (White *et al.* 1982). MNA is a conservative estimate simply based on the number of different individuals recorded. CAPTURE runs trap data through a series of nine different population models, known as estimators, before selecting the one which statistically fits the data best. Population estimates are made on the basis of capture and recapture rates.

Woodmice populations display annual cycles, whereas bank vole populations are thought to be more erratic in nature. However, due to the relatively short period over which trapping was conducted in this study, no attempt was made to examine temporal patterns. Mean population densities for the three trapping sessions are shown in Fig. 5.4. These were calculated on the basis of a 3,072 m^2 sampling area; each trapping point was assumed to be at the centre of square with 8 m sides, and an 8 m wide boundary strip was added to each grid area to reduce edge effects (Lynch 2002). Factorial analyses for both estimation methods (Tables 5.2 and 5.3) showed that there were no overall significant differences in population size between habitats or species, but there was a significant interaction between habitat and species. Further analysis of the CAPTURE estimates (which are probably more accurate than MNA) indicated that bank voles had significantly higher population estimates in Reenadinna than in Camillan

Figure 5.4 Population estimates (±se) for small mammals in Reenadinna yew-wood site and Camillan oakwood site during July to September-October 2001.



($P = 0.017$, T test) and that woodmice had significantly higher population estimates than bank voles in Camillan ($P = 0.010$, T test).

Table 5.2 Two-way ANOVA examining differences in habitat (yew-wood or oakwood) and species (woodmouse or bank vole) with regards to CAPTURE population estimates.

Source	df	Mean square	F	*P*
Intercept	1	8965.333	148.187	0.000
HABITAT	1	243.000	4.017	0.080
SPECIES	1	0.333	0.006	0.943
HABITAT * SPECIES	1	833.333	13.774	0.006
Error	8	60.500		

Table 5.3 Two-way ANOVA examining differences in habitat (yew-wood or oakwood) and species (woodmouse or bank vole) with regards to MNP population estimates

Source	df	Mean square	F	*P*
Intercept	1	5720.333	144.819	0.000
HABITAT	1	16.333	.414	0.538
SPECIES	1	48.000	1.215	0.302
HABITAT * SPECIES	1	341.333	8.641	0.019
Error	8	39.500		

To investigate the effect of location of trapping points at a species level, a series of chi-square tests were run to examine the proportions of successful captures that occurred at fenced and unfenced trapping points (Table 5.4). For both species combined, a significantly greater than expected proportion of captures occurred at fenced trapping points, due to a highly significant effect of fencing in the oakwood. For woodmice, a significantly greater than expected proportion of captures occurred at fenced trapping points in the oakwood, but a significantly lower than expected proportion of captures occurred at fenced trapping points in the yew-wood. For bank voles, there was no significant effect of fencing in the yew-wood, but in the oakwood all of the captures occurred within the exclosure.

Table 5.4 The observed percentage of small mammals captured at trap points in the fenced and unfenced areas of the trapping grids. *P* values indicate significance of deviation from expected values (in parentheses) according to chi-square tests.

		Fenced	Unfenced	*P*
Both species	Both habitats	83.2 % (79.2 %)	16.8 % (20.8 %)	0.015
	Yew-wood	72.0 % (75.0 %)	28.0 % (25.0 %)	0.264
	Oakwood	93.1 % (83.3 %)	6.9 % (16.7 %)	<0.001
Woodmice	Both habitats	79.5 % (79.2 %)	10.5 % (20.8 %)	0.830
	Yew-wood	61.0 % (75.0 %)	39.0 % (25.0 %)	0.001
	Oakwood	89.4 % (83.3 %)	10.6 % (16.7 %)	0.020
Bank voles	Both habitats	87.3 % (79.2 %)	12.7 % (20.8 %)	0.001
	Yew-wood	79.0 % (75.0 %)	21.0 % (25.0 %)	0.249
	Oakwood	100 % (83.3 %)	0.0 % (16.7 %)	<0.001

To examine the effect of fenced and unfenced location of trapping points on overall trapping success, odds ratio analysis (*sensu* Sokal & Rohlf 1995) was used; this type of analysis compares the risk of a dichotomous event occurring under two different treatments. Trapping success was calculated as the proportion of trap-periods that yielded a capture of either species. Location relative to the exclosure had no significant effect on trapping success in Reenadinna yew-wood, but in Camillan oakwood unfenced traps were approximately a third as likely as fenced traps to successfully capture an animal (Table 5.5).

Table 5.5 Odds ratios (and 95% confidence intervals) expressing the likelihood of successful capture at unfenced trapping points relative to fenced trapping points, controlled for habitat type. The odds of successful capture are significantly different at unfenced and fenced trapping points if the 95% confidence interval does not include 1.

Yew-wood		Oakwood	
Odds ratio	95 % CI	Odds ratio	95% CI
1.216	(0.895-1.651)	0.306	(0.189-0.494)

A second analysis (Table 5.6) showed that unfenced traps in Reenadinna were nearly three times as likely as unfenced plots in Camillan to capture an animal, but fenced plots in Reenadinna were roughly two-thirds as likely as fenced plots in Camillan to achieve a successful capture.

Table 5.6 Odds ratios (and 95% confidence intervals) expressing the likelihood of successful capture in yew-wood habitat relative to oakwood habitat, controlled for fenced or unfenced nature of trapping points. The odds of successful capture are significantly different in yew-wood and habitats if the 95% confidence interval does not include 1.

Fenced		Unfenced	
Odds ratio	95 % CI	Odds ratio	95% CI
0.700	(0.567-0.863)	2.780	(1.638-4.717)

5.4.2 Small mammal exclosure experiment

As the data yielded by this experiment were too sparse to permit statistical analysis, the results are presented in full in Table 5.7. In total, 3,000 yew seeds were sown into the experimental plots, with an unknown number of additional yew seeds falling or being dispersed into them. After 22 months, however, only three yew seedlings had established. This represents an establishment rate of <0.001%. Notably, however, all three yew seedlings were within the closed plots, whilst holly seedlings, of which there were ten in total, were present in plots of all three treatments. Ash seedlings, numbering five in total, were present in open and closed plots.

Table 5.7 Vascular plants present in exclosure plots, 22 months after plot establishment. For tree species, the number of seedlings present is indicated. For other plants the percentage of the plot that they covered is indicated.

Site	Open plots	Small mammal plots	Closed plots
1	2 x *Fraxinus* seedlings 3 x *Ilex* seedlings	*Viola* sp. (1%)	1 x *Taxus* seedling 2 x *Fraxinus* seedlings
2	*Sanicula europaea* (1%)	-	1 x *Ilex* seedling *Polystichum setiferum* (5%)
3	*Viola* sp. (1%)	1 x *Ilex* seedling	-
4	2 x *Ilex* seedlings	1 x *Ilex* seedling	1 x *Fraxinus* seedling 2 x *Ilex* seedlings 2 x *Taxus* seedlings *Viola* sp. (1%)
5	*Brachypodium sylvaticum* (1%)	2 x *Ilex* seedlings	-

5.4.3 Seed removal experiment

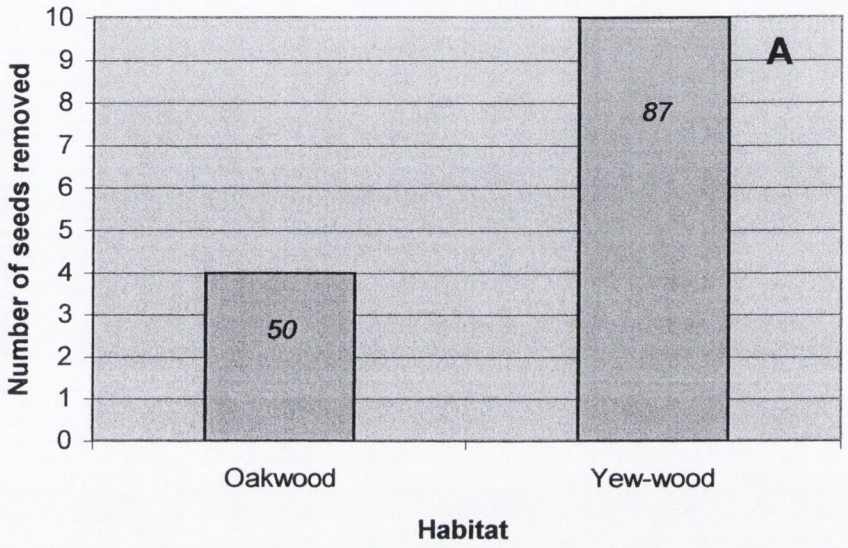
In the first experiment, at the dispersed sites, there were significant differences in the number of seeds removed after three days between different habitat types ($P = 0.002$, Mann-Whitney U test; Fig. 5.5a) and subhabitats ($P = 0.009$, Kruskal-Wallis H test; Fig. 5.5b). Seed removal was roughly twice as high in Reenadinna yew-wood as in Camillan oakwood. Seed removal in open subhabitats was markedly lower than under trees, or amongst ground vegetation which showed the highest mean percentage of seed removal. Fragments of seed shell recovered from the petri dishes were consistent with rodent predation.

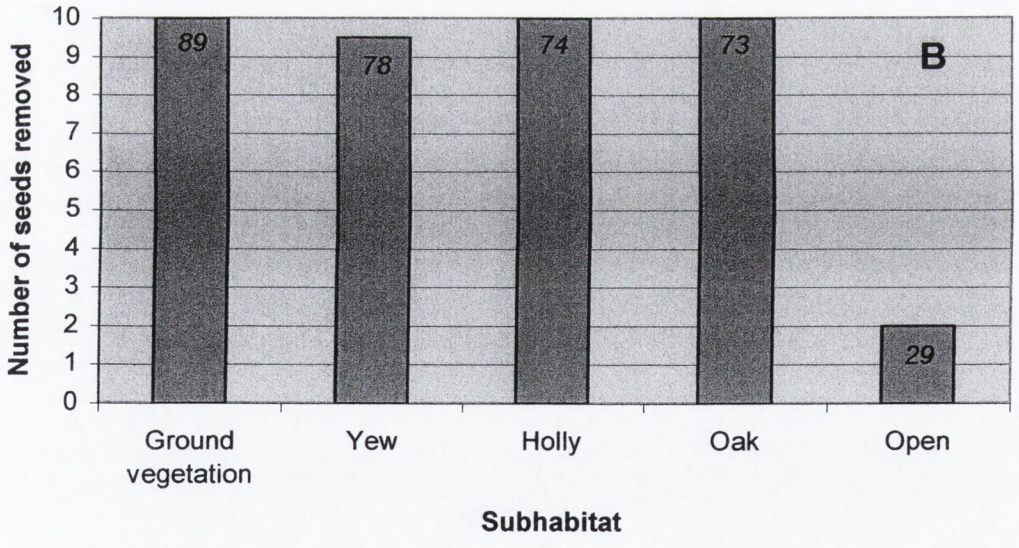
In the second experiment, on the trapping grids, seed removal was exceptionally high in Camillan with all but one of the 240 seeds being removed (99% removal), this being at one of the unfenced trap points. In Reenadinna, total seed removal was lower than in Camillan (71%). There was an apparent difference in seed removal rates between fenced (77%) and unfenced (55%) trap points, but this was not significant ($P = 0.290$, Mann-Whitney U test).

5.5 Discussion

Due to the relatively short period over which trapping occurred and the slight difference in the number of fenced and unfenced trapping points in the yew-wood grid and the oakwood grid, the results of the population density analyses must be accepted with a degree of caution. Nevertheless, there is no *prima facie* indication from these results that total small mammal densities in the Reenadinna exclosure are significantly higher than in the Camillan exclosure, and certainly not sufficiently different to explain the observed patterns in yew regeneration. The higher densities of bank voles in Reenadinna were offset by lower densities of woodmice.

Figure 5.5 Rates of postdispersal yew seed predation as described by (a) different habitats and (b) different subhabitats. Bars indicate median number of seeds removed. Figures in italics indicate mean percentages removed.





Making direct comparisons with the study of 1975-1977 (Smal & Fairley 1982) is difficult, as their oakwood grid was in Tomies Wood not Camillan, and their yew-wood grid was in a different part of Reenadinna. However, three important points are apparent. Firstly, the 1975-1977 study found a clear difference in small mammal densities between yew-wood and oakwood habitats, whereas the present study found no clear differences. Secondly, the 1975-1977 study found much lower densities of bank voles than of woodmice in both habitats, whereas the present study found a difference only in the oakwood, and this was not as pronounced as previously. Thirdly, densities in the present study are substantially higher than those from the previous survey. In unfenced areas of woodland throughout the Killarney National park, ground vegetation cover for small mammals is low due to heavy deer browsing, but in Reenadinna, grykes provide an alternative type of cover. Ground cover is important to small mammals as it reduces chances of predation. It appears from the present study that the increased cover provided by ground vegetation in *both* exclosures not only increased absolute abundance, but has had an equalising effect on differences between sites and species. This is supported by the odds ratio results which showed that fencing greatly increased the chances of trapping success in Camillan, but not in Reenadinna, and that the chances of trapping success at unfenced points were much greater in Reenadinna.

Vegetative ground cover in the oakwood appears to be more important to bank voles than to woodmice as vole capture were completely restricted to the fenced trap points. Their lower overall density in the oakwood is probably a reflection of this. Vole density is usually positively correlated with ground vegetation cover, and depletion in cover by grazing has been shown to reduce vole numbers (Gill 1992b). Schreiner *et al.* (2000), for example, only caught bank voles under bramble thickets and not in experimental clear-cut plots, whereas woodmice were caught in almost equal numbers. This strong requirement for cover is possibly because bank voles are active during the daytime as well as at night (Fairley 1984). In the yew-wood, bank vole capture was only slightly higher at fenced trap points, indicating that outside the exclosure here they were able to make use of cover provided by the grykes. The higher frequency of woodmouse capture at the unfenced trap points is curious, but possibly reflects competitive displacement by the high densities of bank voles present. It may also indicate that woodmice are more inclined to make use of "gryke-only" cover.

The results of the first seed removal experiment, that rates of seed removal were lowest in open sites and highest in dense ground vegetation, parallel those of several other studies. Alcántara *et al.* (2000) found that losses of wild olive (*Olea europaea* var. *sylvestris*) seeds due to woodmouse predation were higher in dense scrub patches (67%) than in sparse ones (33%). Schreiner *et al.* (2000) observed higher losses of conifer seeds from experimental

dishes under brambles than in cleared plots. Hulme (1996), investigating removal of yew seeds in yew-woods in north-east England, differentiated between seed encounter (the probability of at least one seed being removed) and seed exploitation (the proportion of seeds removed once a seed depot has been encountered). It was found that seed depots in open sites had the least chance of encounter, and depots in tall herb vegetation had the highest rates of exploitation. Broadly similar results were found for elm (*Ulmus glabra*) seed by Hulme & Hunt (1999). Even when total post-dispersal seed predation rates are low (<10%), this pattern of results has been observed (García 2001). The results of the second seed removal experiment also support the theory that rates of seed predation are high amongst dense ground cover. The apparent reversal of results with regards to woodland type between these two experiments is almost certainly due to strong winds during the course of the second experiment, which brought down an exceptionally heavy fall of yew-seeds in Reenadinna. This provided an abundant alternative food source which was not available in Camillan. Smal & Fairley (1982) conducted seed-removal experiments in the Killarney woodlands throughout a two year period, during which they also measured fruit and seed fall (Smal & Fairley 1980b), and showed that the mean rate of seed removal was inversely correlated with the availability of natural seeds.

The small mammal exclusion experiment yielded similar results to those of Williamson (1978), who recorded that only about 2% of 600 yew seeds that he had sown into mouse-proof cages in Kingley Vale germinated. The occurrence of yew seedlings only within the closed cages, tentatively supports the second hypothesis outlined above, that yew seedling establishment will be higher where small mammals are excluded, but evidently the low rates of establishment suggest that there is some other factor involved. Poor levels of yew-seed viability have been suggested by casual experiments by staff of the Killarney National Park (G.T. Higgins pers. comm.): an assessment of seed viability will be reported in the next chapter. It is possible that invertebrate predators, which would have had access to all three plot types, may have been responsible for the poor germination / establishment rates observed. Nystrand & Granström (2000), for example, showed that carabids and not rodents were the principal Scots pine seed predators in Swedish boreal forests, and that slugs were important predators of juvenile Scots pine seedlings. Hulme (1997) and Hulme & Borelli (1999), however, found that invertebrates had negligible impact on yew seed removal. A more plausible explanation is offered by observations regarding the effect of the wire mesh on litter cover. Although not frequent in the areas where the cages were sited, broadleaved trees appeared to contribute a large proportion of the leaf litter. Windblown and falling leaves were not substantially obstructed from entering the open or small mammal plots, but the dense mesh of the closed plots excluded this litter, which was observed to accumulate outside the

cages. When sown, the yew seeds were cast on the surface of the plots to simulate natural dispersal. Possibly seeds failed to germinate as they were neither incorporated into the top layer of soil by animal disturbance, or cover by a layer of litter. The latter has proved to be beneficial to the chances of germination for other trees species (Ovington & McRae 1960; Shaw 1968b).

A final point is that equal weighting with regards to potential seed predation has been given in this study to woodmice and bank voles. However, whilst woodmice are generally deemed granivorous, bank voles are intermediate between pronounced granivores and folivores (Hansson 1985). Bank vole diet is related to availability though, rather than optimal preferences, and whilst green material (including seedlings) is important in the summer, seeds are consumed during the autumn (Hansson 1985). Smal & Fairley (1980a) demonstrated that bank voles consumed yew seeds in Reenadinna. In practice, both woodmice and bank voles are likely to impact on yew regeneration at the seed and seedling stages.

5.6 Summary

1. Differences in small mammal population densities between deer exclosures in Reenadinna yew-wood and Camillan oakwood were insufficient to explain differences in yew regeneration through post-dispersal seed predation. Increasing ground vegetation by deer exclusion appears to reduce differences in small mammal population densities between these woods.

2. In Camillan oakwood, a significantly higher proportion of woodmice and bank voles were caught amongst dense ground vegetation inside exclosures than amongst sparse ground vegetation outside exclosures.

3. In Reenadinna yew-wood, proportions of woodmice and bank voles caught inside exclosures were not significantly higher than those caught outside exclosures, probably due to grykes providing alternative cover.

4. The chances of a successful capture were higher in fenced plots than in unfenced plots in Camillan oakwood, but not in Reenadinna yew-wood. Chances of a successful capture in unfenced plots were higher in Reenadinna yew-wood than in Camillan oakwood.

5. Rates of seed removal were lower in open sites than in sites with dense ground vegetation, such as inside deer exclosures.

6. Exclusion of small mammals from open sites resulted in an increase in yew seedling abundance, but field germination / establishment rates were still extremely low.

CHAPTER 6

EX SITU EXPERIMENTS INVESTIGATING THE REGENERATION ECOLOGY OF YEW

6.1 Overview

This chapter deals with a series of *ex situ* experiments investigating a range of factors potentially influential to yew regeneration: shade, germination, allelopathy and browsing. These experiments were designed to address hypotheses generated by the field surveys. It was desired to investigate a broad range of potentially important factors in order to highlight which may be of particular significance and worthy of further investigation. Hence some experiments are only preliminary in nature. All experiments were conducted at Trinity College Botanical Gardens, Dublin (Lat. 53° 20', Long. 6° 15').

6.2 Shade experiments

6.2.1 Introduction

Yew-woods are characterized by dense canopies which cast exceptionally heavy shade (Rodwell 1991, Kelly 1981). Yew is repeatedly reported as a highly shade tolerant species (e.g. Packham & Harding 1982; Rodwell 1991; Brzeziecki & Kienast 1994), yet beneath these canopies natural regeneration of yew is poor as has been demonstrated in Chapter 4. It has been suggested that these habitats regenerate primarily from the edges where light conditions are more favourable (Watt 1926, Smith 1980). There have, however, been few studies on the growth performance of the species under different light levels (the notable exception being Mitchell 1998).

Field experiments based on variations in shading intensity invariably have several inherent problems as discussed by Grime & Jeffrey (1965) and Ziegenhagen & Kausch (1995). These are due to the difficulty of controlling light intensity (photosynthetic active radiation, hereafter PAR) without altering the light quality (in terms of the red / far-red ratio) or the nature of light (the proportions of direct and diffuse light). Furthermore, the shading frames usually utilised may significantly alter microclimate conditions around experimental plants; affecting temperature,

humidity and exposure. Plants themselves may begin to influence conditions differentially between treatments during the course of an experiment. These factors complicate the interpretation of results with regards to light conditions but possibly reflect a more realistic simulation of conditions beneath a woodland canopy (Ovington & McRae 1960). Variations in such factors, however, have been found to be small in comparison to the differences in light intensity (Phares 1970).

General conclusions on the effects of shade on plant growth and morphology were drawn by Grime (1979) from experiments on a wide range of species. These are that increased shade causes a reduction in overall plant dry weight, a shift in the root / shoot ratio in favour of above ground growth, development of longer internodes and petioles, and the production of larger, thinner leaves. The magnitude of these responses varies considerably between species and can be diagnostic of the shade strategy of a species: either shade tolerance or shade avoidance (shade intolerance). Shade avoiders tend to show a marked response to low light conditions with etiolation being particularly pronounced. These are generally species of grassland or disturbed habitats where rapid height growth causes a seedling's photosynthetic systems to emerge from the shaded stratum (Grime & Jeffrey 1965). Under woodland conditions where rapid initial height growth does not result in increased light interception, shade avoiders suffer high mortality due a lack in net carbohydrate gain and increased susceptibility to fungal pathogens (Grime & Jeffrey 1965). Shade tolerant species conversely show a limited height response to low light intensities due to the futility of competing for light on the forest floor (Grime 1966). These species achieve a net carbohydrate gain by maximising their photosynthetic rates via foliar and physiological adaptations, and by exhibiting markedly lower respiration rates than shade intolerant species (Loach 1967, 1970). Shade tolerant tree seedlings are thus available to survive under dense shade until such a time as improved light conditions, such as those associated with the creation of a canopy gap, permit an increase in growth rate. Some species, however, being obligate shade species, lack this phenotypical plasticity and suffer severe photoinhibition on exposure to bright light resulting in decreased productivity (Hart 1988).

The experiments reported in this section sought to examine the effects of different shade treatments on the growth and leaf morphology of two sizes of juvenile yew plants. The hypotheses being tested were: (i) as artificial shade increases, yew plants will display growth characteristics indicative of shade tolerance, and (ii) as artificial shade increases, yew mortality will not increase.

6.2.2 Methods

Experiment 1: The effects of shade on yew saplings

The experiment was conducted on an open plot of ground at Trinity College Botanical Gardens. Young, bare-rooted yew trees (approximately 35cm in height) were obtained from a nursery. Suitable Irish plants could not be sourced, therefore those used were of Belgian provenance. These were planted in 23 cm plastic pots in a general purpose peat-based compost (Shamrock, Bord na Móna) and randomly allocated to one of five shade treatments (Table 6.1, n=24 per treatment):

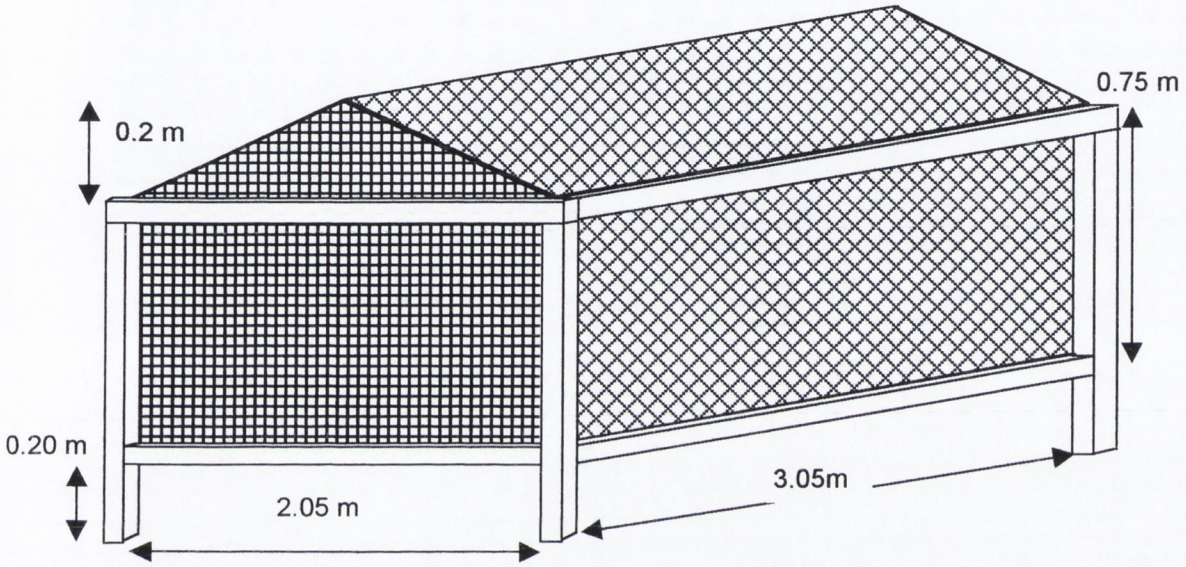
Table 6.1. Percentage of daylight PAR available to plants in each shade treatment.

Treatment	Shading	% daylight PAR
A	Control	100
B	Low	27
C	Medium	7
D	Heavy	3
E	Heavy	3

Shading was achieved by placing plants in a 4 x 6 formation beneath wooden frames covered in layers of green, plastic, commercial shade netting (Gardman) (Plate 6.1; see Fig. 6.1 for construction and spacing). The level of PAR available beneath each frame was measured on a uniformly overcast day using a photometer (model LI-189, LI-COR Biosciences), and expressed relative to the PAR available for the control treatment, i.e. PAR of daylight. An uncovered gap at the bottom of the frames permitted air circulation. Plants were watered as required throughout the year and during the growing season plants were fed regularly with a liquid NPK plant feed.

The experiment was initiated in February 2000 at which time the height of each plant (from level of root collar to highest living bud) and stem diameter 2 cm above the root collar were measured. In December 2000 the height of all plants was remeasured and eight plants were randomly selected for harvest. From each harvested plant twenty leaves were removed, five from the midpoint of each of the top four lateral shoots of current year growth. These sampled leaves were scanned using a flat-bed scanner (ScanMaker X12 USL, Microtek). The resulting digitised leaf images were then analysed using the Scion Image computer application (Scion Corporation) to obtain the mean area, length and width of leaves from each plant. The weight of these leaf samples, other new shoots, the remaining above-ground material and the roots of each harvested plant was measured after drying

Figure 6.1 Above, dimensions of shade tents used in experiments into effects of artificial shade on *Taxus*. Cross-hatching represents shade netting. Frame constructed from 2x2 inch timber throughout. Below, plan view showing arrangement of shade treatments and spacing: green dots represent individual plants, rectangles indicate shade tents, letters indicate treatments.



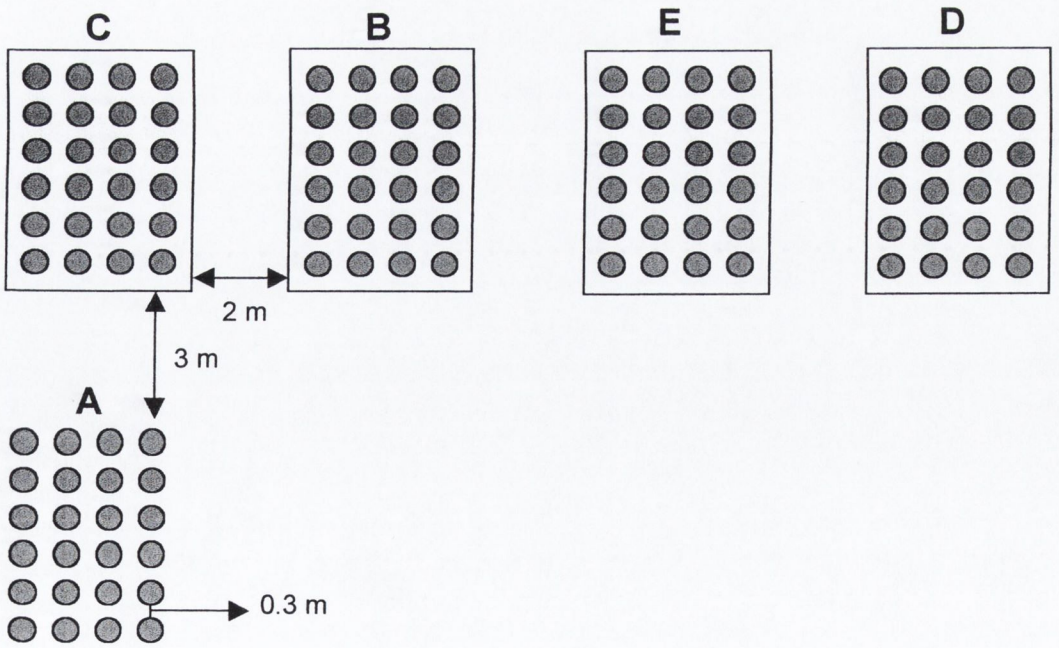


Plate 6.1 Shading frames used for treatments B-E in shade experiments at Trinity College Botanical Gardens. Plant pots visible beneath.

Plate 6.2. Windshorn yew trees on clifftop, Lough Leane, Killarney National Park

material in an oven for 72 h at 75°C. The plants remaining in each treatment, were repositioned in a 4 x 4 formation to maintain plant density.

In January 2002, the height and basal diameter of all plants was remeasured. Eight plants were again randomly selected from each treatment and harvested as detailed above. In addition, chlorophyll content was measured from bulked leaf samples from three plants randomly selected from each of treatments A, B, C and E (approximately fifteen leaves per treatment). Following determination of fresh weight, chlorophyll was extracted with 80% acetone from ground samples and extracts were centrifuged at x500 gravity. Replicated measurements (n = 5) of the light absorbance of these samples at a wavelength of 652 nm were made using a spectrophotometer. Chlorophyll content was then deduced using the known relationship between chlorophyll concentration and absorbance at this wavelength: 1 mg cm^{-3} has an absorbance of 34.5 (Hall and Rao 1994). The remaining plants were again repositioned to maintain density and were topped up with a small amount of compost, containing approximately 5g of Osmacote Plus (Scotts) per pot. This is a slow-release fertiliser, containing 15% N, 9% P, 11% K, 2% MgO, 0.4 % Fe, 0.06% Mn, 0.05% Cu, 0.02% Mb, 0.02% B and 0.015% Zn.

Shortly after bud burst in May 2002, plants in treatment E were exposed to 100% daylight PAR conditions by removing the shading frame completely. This was an attempt to simulate the opening of a large canopy gap. The height and basal diameter of all the remaining plants was remeasured for a last time in November 2002.

The effect of shade treatment on the following variables was investigated using ANOVA with Tukey's HSD post hoc test: height, basal diameter, new shoot dry weight, total shoot dry weight, root dry weight, total dry weight, root / shoot dry weight ratio, mean leaf area, mean leaf length, mean leaf width, mean leaf dry weight, mean specific leaf area and chlorophyll content. To achieve normality prior to analysis, mean leaf dry weight, mean leaf length and root / shoot dry weight ratio were log transformed. Some of the other variables varied slightly from normality but ANOVA is robust to such deviations (Sokal & Rohlf 1995).

Experiment 2: The effects of shade on one-year old yew cuttings

Shoot material was collected from mature yew trees in Reenadinna Wood, Killarney, in November 1999. Heel cuttings of one-year growth, 5-10 cm long, were obtained from this material, dipped in growth rooting hormone (active ingredients indolebutyric acid (IBA) plus captan fungicide), and planted in seed trays in a 1:1 sand / soil mixture. The trays were covered with propagator hoods and placed on a bottom-heated shelf in a greenhouse. In May 2000, successfully rooted cuttings were planted in 9.5 cm plastic pots in a 1:1:2 sand / compost / loam mixture with a small amount Osmacote Plus. The plants were placed in a shady greenhouse for one month to harden before transfer to a sunnier greenhouse where they were grown on for one year. In April 2001, healthy plants were allocated randomly between the five shade treatments detailed above (n = 12). Plants were placed in groups of six at either end of each shading frame, on a stone block which raised them above the ventilation gap. Plants were watered regularly.

In January 2002, the height and basal diameter of all surviving plants was measured. Five leaves were removed from the midpoint of the leading shoot on each plant. Area, length and width of each leaf was measured by analysing scanned images as detailed above. The weight of these leaf samples, the remaining shoot material, and the roots was then recorded after drying for 72 h at 75°C.

The effect of shade treatment on the following variables was tested, again using ANOVA with Tukey's HSD post hoc test: height, diameter, shoot dry weight, root dry weight, total dry weight, root / shoot dry weight ratio, mean leaf area, mean leaf length, mean leaf width, mean leaf dry weight, and mean specific leaf area. Height, shoot dry weight and mean specific leaf area were log transformed to achieve normality prior to analysis.

6.2.3 Results

Experiment 1: The effects of shade on yew saplings

Only one plant died during the duration of the experiment, in treatment D in the second growing season. However, this was possibly due to insufficient watering. One plant harvested from treatment E in December 2000 was found to have damage to the main root stock which pre-dated the experiment. Both these plants were therefore excluded from analysis.

At the start of the experiment there were no significant differences in height (Fig. 6.2a; $P = 0.183$) or basal diameter (Fig. 6.3a; $P = 0.388$) between the treatments. After the first growing season plants in treatment B, light shade, were significantly taller than plants in the heavier shade treatments (Fig. 6.2b; $P = 0.002$). By the end of the second year this difference had disappeared (Fig. 6.2c; $P = 0.147$), but treatment had clearly had an effect on basal diameter which became significantly smaller as shade increased (Fig. 6.3b; $P < 0.001$). Exposure of plants in treatment E to full light resulted in a rapid bleaching effect of the foliage. However, subsequent growth of these plants during the third growing season does not appear to have been adversely affected; by the end of the experiment there was no significant difference in height between treatments D and E, although plants under light and medium shade (treatments B and C) were significantly taller than those under full light (treatment A) (Fig. 6.2d; $P = 0.008$). Indeed, the plants in treatment E, exhibited a positive response to the increased light conditions with a rapid increase in basal diameter in the third year. This did not quite result in a significant difference with treatment D, but basal diameters were now comparable with those under full light (treatment A) and medium shade (treatment C) (Fig. 6.3c; $P < 0.001$).

Mean total dry weight of plants harvested after the first growing season differed significantly between treatments (Fig. 6.4a; $P < 0.001$), with plants under the heavy shading being less than half the weight of the unshaded controls. This pattern was also reflected in the dry weight means for old shoots, new shoots and roots (all $P < 0.001$). In autumn and winter 2000, frost and high winds appeared to cause severe scorching of the leaves in the control treatment (A). Damage to buds resulted in lower new shoot production in these plants in the second year, and a reduction in height increment in both the second and third year. Possibly as a consequence of this there was no significant difference in new shoot dry weight for the second growing season (Fig. 6.4b; $P = 0.117$), although total dry weight, old shoot dry weight and root dry weight were again significantly lower under the heavy shade treatments ($P < 0.001$). Root / shoot dry weight ratio differed significantly between treatments (Fig. 6.5; both years $P < 0.001$), with roots comprising a greater proportion of total dry weight in the unshaded or lowly shaded treatments. This difference became more pronounced in the second year when roots of plants from treatments D and E constituted only 29% of total dry weight compared to 54% in plants from treatment A.

Figure 6.2 Mean height (cm) of yew saplings grown under different shade treatments: (a) at start of experiment; (b) after one year; (c) after two years; (d) after three years. Vertical bars indicate se. Lower-case letters indicate homogeneous subsets according to Tukey's HSD post hoc tests.

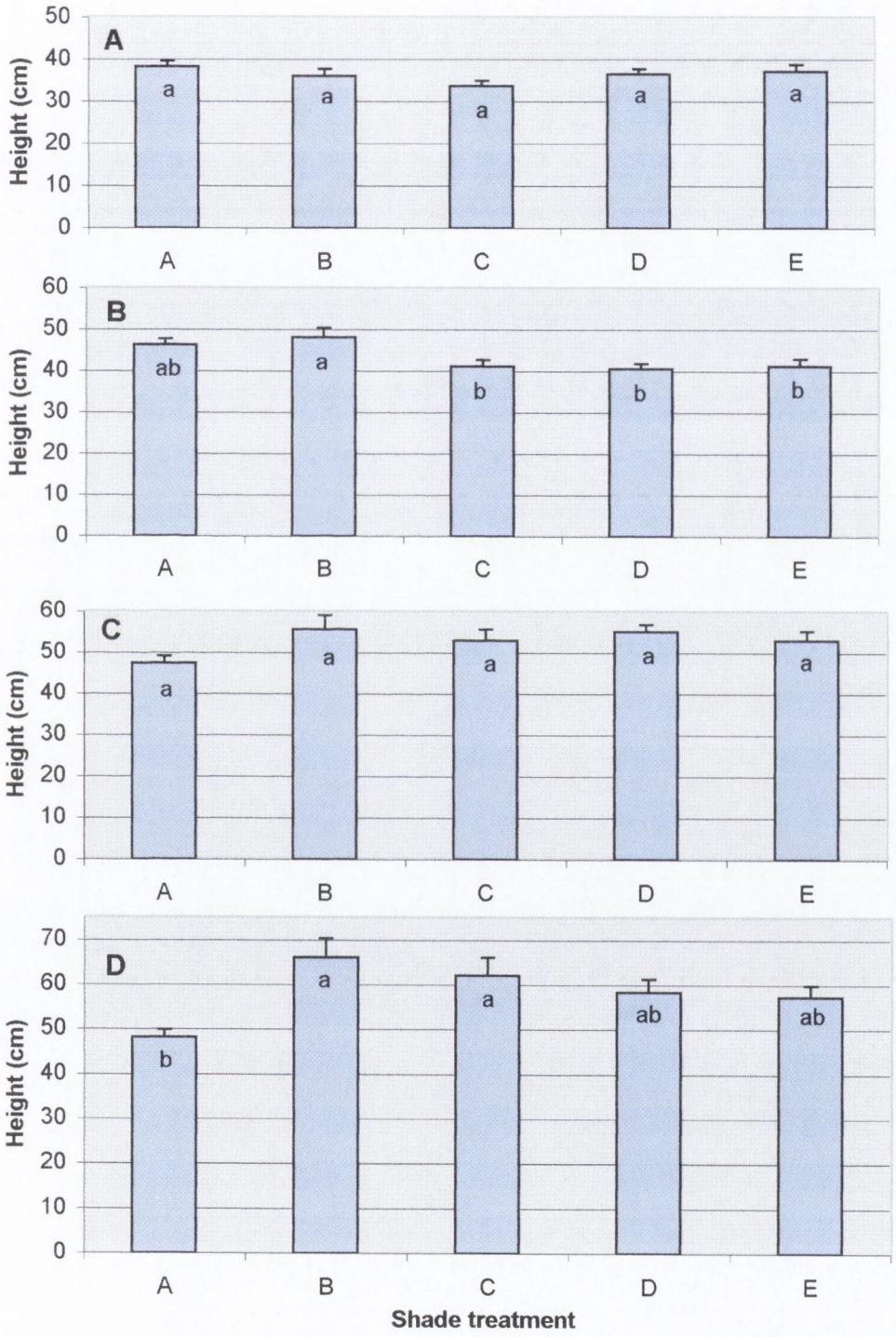


Figure 6.3 Mean basal diameter (mm) of yew saplings grown under different shade treatments: (a) at start of experiment; (b) after two years; (c) after three years. Vertical bars indicate se. Lower-case letters indicate homogeneous subsets according to Tukey's HSD post hoc tests.

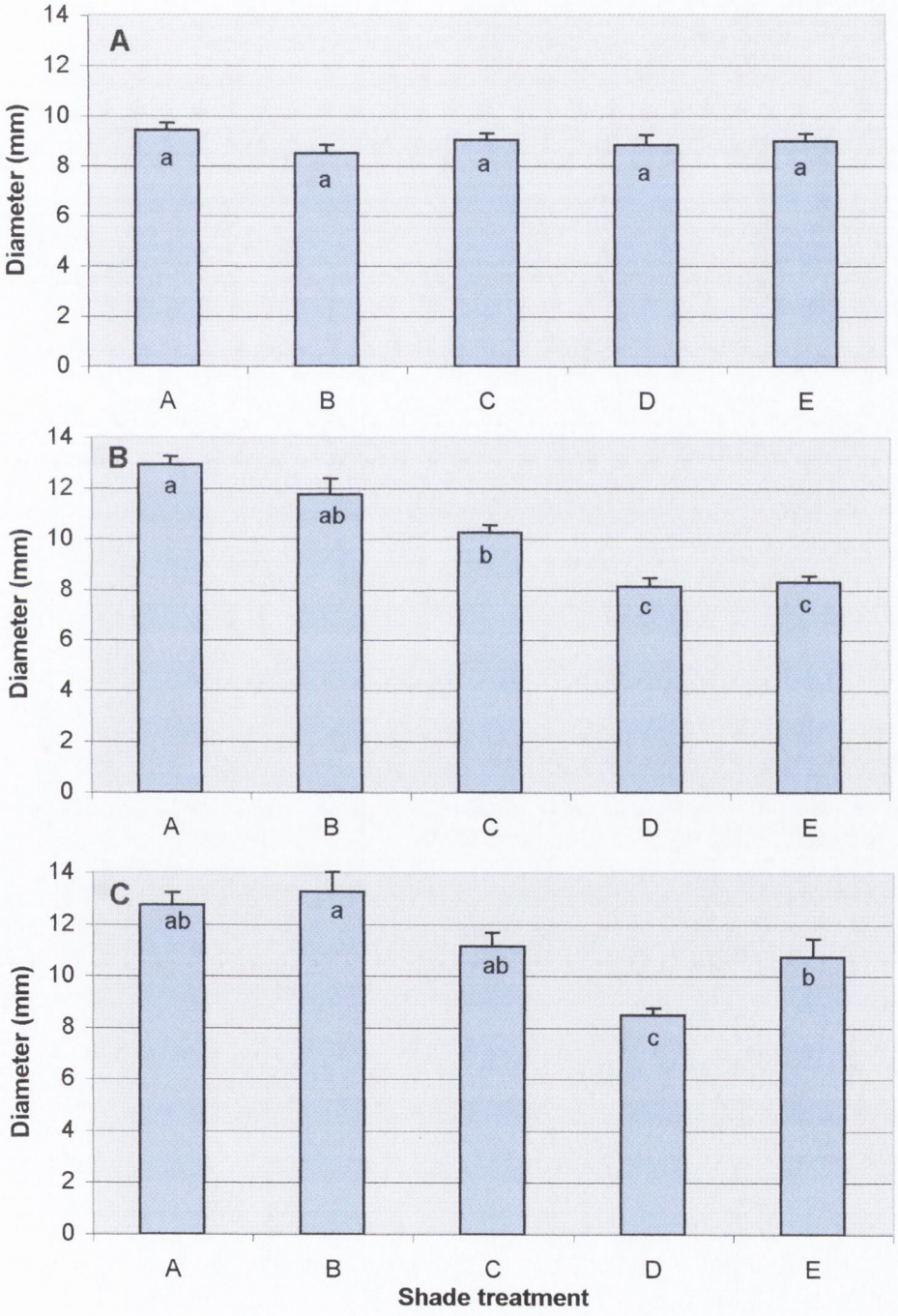


Figure 6.4 Dry weight (g) of yew saplings grown under different shade treatments: (a) after one year; (b) after two years. Vertical bars indicate se. Lower-case letters indicate homogeneous subsets of weight partitions according to Tukey's HSD post hoc tests.

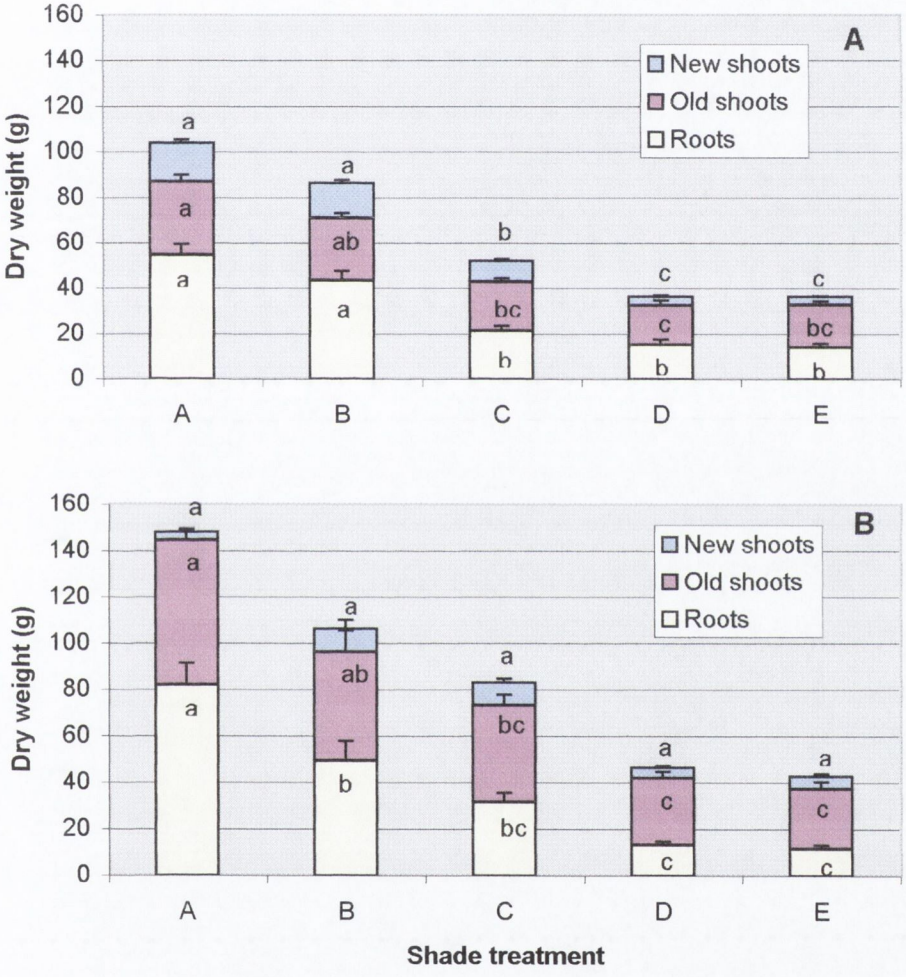
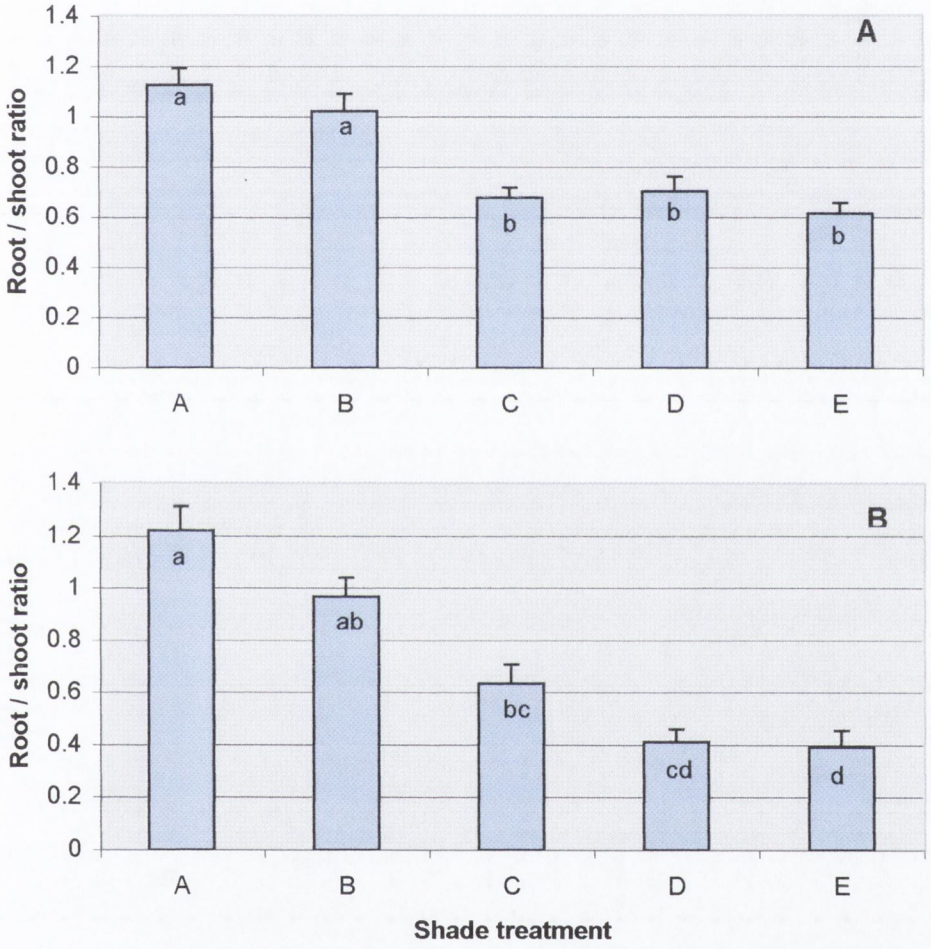


Figure 6.5 Root / shoot dry weight ratio of yew saplings grown under different shade treatments: (a) after one year; (b) after two years. Vertical bars indicate se. Lower-case letters indicate homogeneous subsets according to Tukey's HSD post hoc tests.



Increased levels of shade resulted in a higher specific leaf area index in both of the first two years (Table 6.2). This was due primarily to larger leaf area; leaves under heavier shade were both longer and wider than leaves under low shade or no shade. In the second year there were significant differences in leaf dry weight but this was due to the much smaller leaves produced by the control plants. Chlorophyll content of foliage grown in the second year differed significantly between treatments (Fig. 6.6; $P < 0.001$) with higher levels of chlorophyll in the plants under medium and heavy shade.

Table 6.2 Mean (±se) leaf length (mm), width (mm), area (cm^2), dry weight (g) and specific leaf area (SLA; $cm^2\ g^{-1}$) of current-year foliage from *Taxus* saplings grown for two years under five shade treatments. P values indicate results of ANOVA. Within columns and for each year's data letters signify homogeneous subsets according to Tukey's HSD post hoc test.

	Treatment	Length	Width	Area	Dry weight	SLA
First year	A	19.48 a ±0.47	2.59 a ±0.04	0.43 a ±0.02	0.0042 a ±0.0002	103.0 a ±3.4
	B	21.03 a ± 1.27	2.75 ab ±0.09	0.49 a ±0.05	0.0043 a ±0.0005	116.3 a ±6.2
	C	21.06 a ±1.26	2.92 abc ±0.10	0.51 a ±0.05	0.0031 a ±0.0004	172.8 b ±8.5
	D	24.08 ab ±1.14	3.09 bc ±0.17	0.59 ab ±0.04	0.0029 a ±0.0003	209.2 c ±11.7
	E	26.35 b ±1.64	3.32 c ±0.16	0.74 b ±0.07	0.0037 a ±0.0004	196.2 bc ±7.8
	P	0.003	0.001	0.001	0.037	<0.001
Second year	A	9.82 a ±0.97	2.23 a ±0.12	0.17 a ±0.03	0.0017 a ±0.0004	115.2 a ±6.0
	B	16.95 b ±2.48	2.69 a ±0.14	0.41 b ±0.08	0.0035 b ±0.0008	122.5 ab ±5.1
	C	19.52 bc ±0.58	3.35 b ±0.08	0.55 bc ±0.02	0.0037 b ±0.0002	149.6 b ±4.6
	D	24.02 cd ±0.81	3.45 b ±0.12	0.71 cd ±0.03	0.0035 b ±0.0003	208.2 c ±10.2
	E	28.44 d ±1.66	3.69 b ±0.12	0.87 d ±0.05	0.0043 b ±0.0004	205.9 d ±9.4
	P	<0.001	<0.001	<0.001	<0.001	<0.001

Experiment 2: The effects of shade on one-year old yew cuttings

Ten plants under heavy shade (treatments D and E) and one plant under low shade (treatment B) were dead or moribund at the time of harvesting (n per treatment = 12). It was not possible to attribute this conclusively to effect of the treatment – again insufficient watering was a possible

Figure 6.6 Chlorophyll content (mg / g fresh weight) of current year leaves of yew saplings grown for two years under different shade treatments. Vertical bars indicate se. Lower-case letters indicate homogeneous subsets according to Tukey's HSD post hoc tests.

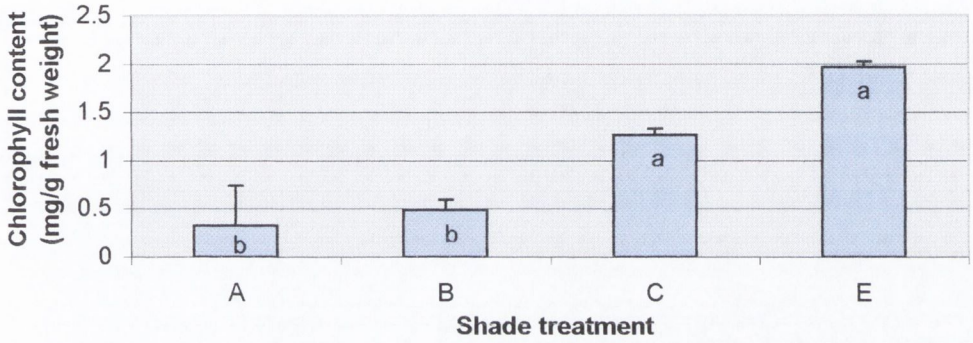
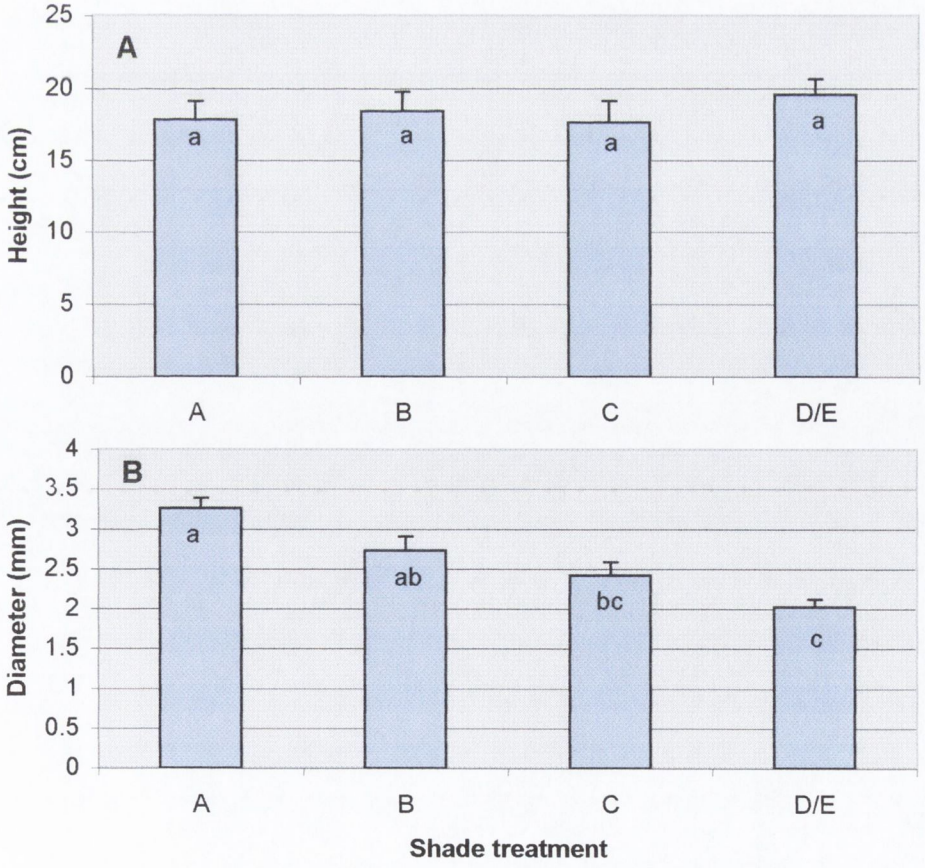


Figure 6.7. Growth parameters of yew cuttings grown for one year under different shade treatments: (a) mean height (cm); (b) mean basal diameter (mm). Vertical bars indicate se. Lower-case letters indicate homogeneous subsets according to Tukey's HSD post hoc tests.



explanation. These plants were therefore excluded from the analysis and data for the two heavy shade treatments were combined (thus for treatment D/E, $n = 14$, for treatment B, $n=11$).

There was no significant effect of shade on plant height (Fig. 6.7; $P = 0.626$), but basal diameter was lower under the higher levels of shading ($P < 0.001$). Shoot dry weight was also not significantly affected by shade (Fig. 6.8; $P = 0.167$), but root dry weight was higher in the unshaded plants than under any of the shade treatments ($P < 0.001$). This resulted in a significant difference in both total dry weight ($P = 0.011$) and root / shoot dry weight ratio (Fig. 6.9; $P < 0.001$) with shading producing smaller plants with a greater proportion of their dry weight above ground.

There were no significant differences in mean leaf area, mean leaf width or mean leaf length, but mean leaf dry weight was lower under the heavier shade treatments resulting in a significant difference in specific leaf area (Table 6.3).

Table 6.3 Mean (±se) leaf length (mm), width (mm), area (cm^2), dry weight (g) and specific leaf area (SLA; $cm^2\ g^{-1}$) of current-year foliage from one year old yew cuttings grown for one year under five shade treatments. *P* values indicate results of ANOVA. Within columns letters signify homogenous subsets according to Tukey's HSD post hoc tests.

Treatment	Length	Width	Area	Dry weight	SLA
A	20.23 a	2.35 a	0.43 a	0.0064 a	73.0 a
	±1.51	±0.10	±0.05	±0.0009	±3.6
B	24.43 a	2.67 a	0.57 a	0.0072 a	81.0 a
	±1.97	±0.07	±0.06	±0.0009	±2.5
C	22.79 a	2.45 a	0.50 a	0.0048 ab	111.6 b
	±1.89	±0.11	±0.06	±0.0007	±4.5
D/E	23.70 a	2.49 a	0.49 a	0.0030 b	168.7 c
	±1.07	±0.06	±0.03	±0.0002	±8.1
P	0.294	0.102	0.324	0.001	<0.001

6.2.4 Discussion

It is evident from these results that yew is a very shade tolerant species. Plants were able to survive and grow for three years under a heavy shade treatment that admitted only 3% of daylight PAR. Both saplings and cuttings exhibited foliar and growth form adaptations characteristic of shade tolerant plants.

Figure 6.8 Dry weight (g) of yew cuttings grown for one year under different shade treatments. Vertical bars indicate se. Lower-case letters indicate homogeneous subsets of weight partitions according to Tukey's HSD post hoc tests.

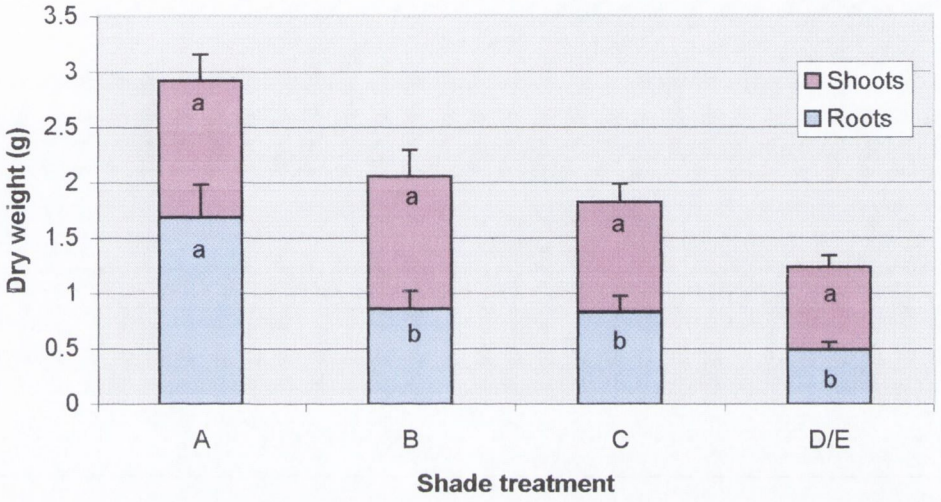
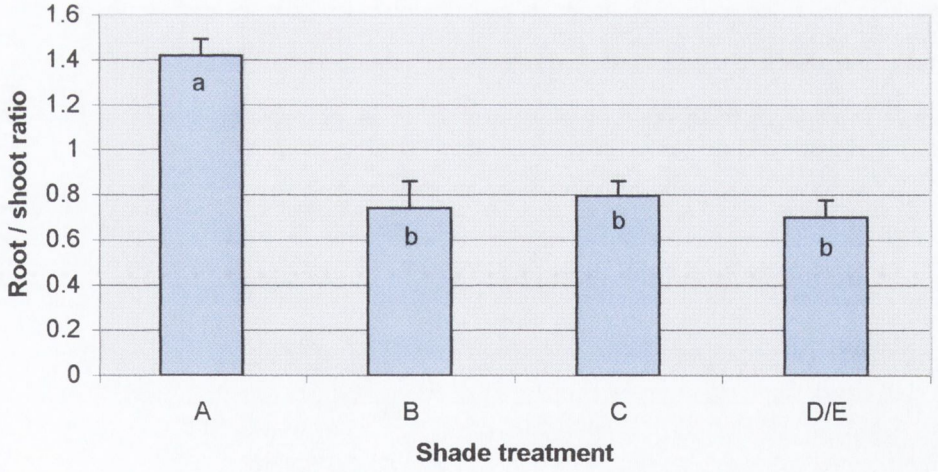


Figure 6.9 Root / shoot dry weight ratio of yew cuttings grown for one year under different shade treatments. Vertical bars indicate se. Lower-case letters indicate homogeneous subsets according to Tukey's HSD post hoc tests.



Responses to shade in yew

Specific leaf area increased with shading in both yew saplings (Table 6.2) and cuttings (Table 6.3). Similar findings have been found in other tree species, including pedunculate oak (Ziegenhagen & Kausch 1995), Pacific yew (*Taxus brevifolia*) (Mitchell 1998), red oak (*Quercus rubra*) and American beech (*Fagus grandifolia*) (Loach 1970). This increase usually reflects not only larger but thinner leaves as increased shade results in a reduction in the number of palisade parenchyma layers (Ziegenhagen & Kausch 1995). In combination with increases in chlorophyll content, as were found in this study, maximum harvesting of the available light is achieved. Other biochemical adaptations can lead to low levels of respiration and consequently a low light-compensation point (Hart 1988).

Increased shade resulted in less total biomass accumulation in both yew saplings (Fig. 6.4) and cuttings (Fig. 6.8). Growth which did occur was concentrated in the shoots maximizing the available photosynthetic systems. Again, this is consistent with reports for other species including beech (*Fagus sylvatica*) (Welander & Ottosson 1998), sessile oak (Ovington & McRae 1960) and pedunculate oak (Ziegenhagen & Kausch 1995). Yew stems were narrower under denser shade but there was little differentiation in height. As discussed above, this is consistent with a shade tolerance strategy. Conversely, significant increases in height under low light conditions have been found in shade intolerant species such as sessile oak (Ovington & McRae 1960) and pedunculate oak (Welander & Ottosson 1998). Under very low light levels, however, shoot extension drops dramatically in these intolerant species as they are unable to maintain growth (Phares 1970; Igboanugo 1990).

The exposure of the plants in treatment E, which had been growing for two years under 3% daylight PAR, to 100% daylight PAR produced particularly interesting results. Leaves which had been produced in the last two years, and were therefore adapted to the low light conditions, were damaged by the increase in light levels. This was probably due to a reduction in the waxy cuticle which protects the photosynthetic structures for harmful wavelengths of radiation. Nevertheless, new foliage was produced and these plants markedly increased in girth. Transposal of pedunculate oak seedlings from low light to higher light conditions been shown to result in an increase in productivity (Ziegenhagen & Kausch 1995; Welander & Ottosson 1998). Although dry weight

analysis was not conducted in the final year of the experiment, the results suggest that yew can also respond positively to increased light levels.

The paucity of new shoot production in the unshaded saplings (treatment A) in the second year was attributed above to poor weather the previous winter. Plants in the other treatments would have been afforded some degree of protection from cold winds by the shading frames. Yew is certainly susceptible to strong winds with windshorn trees common on the shores of Lough Leane, Killarney (Plate 6.2). Watt (1926) identified wind as significant factor in the distribution of yew-woods in southern England where they occur in sheltered valleys or on leeward slopes. The unshaded plants may also have been more exposed to frost; Melzack & Watts (1982) demonstrated that cold hardiness in yew populations from across England reached a maximum in January but declined rapidly in early spring and were susceptible to unexpected frosts. The use of saplings of Belgian provenance is unlikely to be a factor as winters in Ireland are not as severe as those in continental Europe. Leaching of nutrients from the soil due to exposure to heavy rains is possible, but again unlikely as bronzing of leaves was conspicuously confined to the upper, more exposed foliage. The addition of extra fertiliser in January 2002 was attempted to remedy this potential problem.

Strong light conditions themselves appear to be an unlikely explanation for the poor growth of the control plants in the second and third growing seasons, considering the vigorous growth displayed in the first year. Mitchell (1998), investigating photoinhibition in yew, concluded that both *Taxus baccata* and *Taxus brevifolia* were tolerant of high light conditions such as might be found in a nursery. As has been discussed, damage to the leaves of plants in treatment E was due to their prior adaptation to exceedingly low light levels, not an intolerance of 100% daylight conditions *per se*. Smith (1980), however, reports that whilst yew seedlings growing in the shade of their parent trees produce dark green leaves, those in the open grow little and have leaves that turn orangey-brown in colour. It is possible that sun tolerance is in some way age-dependent.

The results of these experiments support the first hypothesis stated above, that as artificial shade increases yew plants will display growth characteristics indicative of shade tolerance. Although several of the yew cuttings under heavy shade died during the experiment, mortality could not be unequivocally attributed to shade. Mortality amongst the saplings was very low (< 1 %). The second hypothesis is therefore also supported, but with some caution.

Implications for natural regeneration of yew

These shade tolerance adaptations should permit yew to persist for long periods in the woodland understorey awaiting the enhanced light conditions associated with a canopy gap. This theory is supported by the field observations reported in Chapter 4; the yew saplings in the Camillan exclosures are growing beneath oak canopies and holly thickets casting considerable shade and are remarkably similar morphologically to the plants grown under shade in experiment 1 - large leaved and spindly individuals with long internode lengths. This would suggest an advance regeneration strategy for yew in oak woodland, that is the occurrence of a seedling bank which provides a competitive advantage in the event of a canopy gap (Morin & Laprise 1997). Mitchell (1990a) found that yew responded positively the creation of an oak canopy gap on Rough Island, Killarney. Yew has also been recorded as a persistent juvenile beneath the dense shade cast by beech canopy (Edlin 1970; Rodwell 1991) although mortality beneath beech canopy was noted by Król (1978) and Czartoryksi (1978). The ability of seedlings to tolerate the shade of juniper and hawthorn bushes is crucial to the "nurse plant" theory proposed by Watt (1926) for the development of yew-woods in southern England.

Relating the artificial shade treatments used in this experiment to woodland conditions is difficult without extensive field measurements. Tentative comparisons could probably be made, however, between the medium and heavy shade treatments (C, D and E) and the dense canopy of yew-wood stands, whilst the lowly shaded treatment (B) is probably closer to the more open canopy of yew-hazel stands.

The question that re-emerges from these observations is that if yew is so shade tolerant why is there an almost complete lack of regeneration beneath yew canopy in the Reenadinna exclosures when seedlings and saplings of less shade tolerant species, such as ash and rowan, are relatively abundant? One explanation may be that the germinal seedlings of yew are far less shade tolerant than the mature plants that have been used in this experiment. For example, conifer seedlings have been shown to be especially susceptible to damping-off under low light conditions (Taher & Cooke 1975a, b). Further experiments are thus required which examine the growth response of yew seedlings under low light conditions from the point of germination. The effect of different red to far red ratios has also been shown to be important for woodland plants (Mitchell & Woodward 1988).

6.3 Germination experiments

6.3.1 Introduction

In Reenadinna Wood, Killarney, production of yew seedlings is low (see Chapter 4) despite an abundance of seed (Smal & Fairley 1980b). Low rates of germination have been reported by staff of the Killarney National Park from casual experiments (G.T. Higgins, pers. comm.), whilst the field experiment reported in Chapter 5 found that rates of yew seedling establishment were low even in absence of small seed predators. There have been few studies of yew seed viability due to complications of delayed germination, and incompletely developed and deeply dormant seeds (Melzack & Watts 1982b; Suszka 1985; Lewandowski 1999). This means that under field conditions, yew seeds do not germinate until at least the second spring after they fall, which is a period of about 18 months. By using a stratification method that markedly shortens the germination period this experiment sought to investigate the size and viability of yew seed from Irish populations in comparison with other European provenances. The hypothesis being tested was: poor yew seed viability is responsible for lack of regeneration in Reenadinna Wood.

6.3.2 Methods

Seeds were collected from seven Irish populations and one English population in September-November 2000 (Table 6.4). Seeds were collected from at least five different trees as germination rates have been shown to vary significantly between individuals (Lewandowski 1999). Seeds were selected which had bright red, fully developed arils. In addition, seeds which had been excreted (probably by mammals) or regurgitated (probably by birds) were collected from two of these sites, Cottagehill Wood and Reenadinna Wood. Arils were removed by hand in the laboratory after soaking in water and the seeds dried at room temperature. Seeds produced in the autumn of 2000, which had been collected in a similar manner were also obtained from a Danish population and a Czech population (Table 6.4). In total this gave 13 different sets of seeds.

Subsamples of thirty seeds were selected randomly from each seed set and individually weighed. All seeds were then surface sterilised by agitating vigorously in 10% hypochlorite solution for 1 minute, rinsed thoroughly and placed 1 cm apart in Petri dishes lined with sterile cotton wool, with 32 seeds per dish. The number of replicate dishes per seed set varied as indicated in Table 6.4. The cotton wool was moistened with distilled water and the lidded dishes were covered in

aluminium foil to exclude light. A stratification procedure similar to that used by Suszka (1985) and Lewandowski (1999) was then followed. The dishes were placed in a growth room for stratification (15-25 °C, 12 /12 h cycle) for 6 months and checked regularly - the cotton wool was remoistened with distilled water as required. Due to considerable mould growth in many of the petri dishes the cotton wool was replaced and all of the seeds were resterilized after 3 months and again after 6 months. Seeds were then moved to a cold room for chilling at 3-5 °C for a further 3 months, before being returned to the growth room. Seeds were then checked for germination after 2, 3, 4, 8, 9, 10, 14, 16, 23, 30, 36 and 51 days, after which point there was no further germination. Germination was deemed to have occurred when the radical had equaled or exceeded the length of the seed. Once germinated, seeds were carefully transferred to seed trays containing a 1 : 1 sand / compost mixture and planted to a depth of 0.5 cm. These were placed under propagator hoods and remained in the growth room, being spray misted with water twice a day. After 112 days, the number of established seedlings from each seed set was counted.

Table 6.4. Location of populations from which seeds were obtained for the germination experiment. Treatment indicates if seeds were uneaten (U), regurgitated (R) or excreted (X). No. of dishes indicates number of replicate petri dishes, each containing 32 seeds.

Country	Site	Latitude / Longtitude	Treatment	No. of dishes
Ireland	Reenadinna Wood, Co. Kerry	52° 03 / 9° 30	U	6
			R	5
			X	3
	Garryland Wood, Co. Galway	53° 06/ 8° 52	U	8
	Rosturra Wood, Co. Galway	52° 03/ 8° 23	U	4
	Cornalack, Co. Tipperary	53° 02/ 8° 16	U	4
	Cottagehill Wood, Co. Tipperary	52° 26/ 7° 56	U	4
			X	2
	Clorhane, Co. Offaly	53° 13/ 8° 01	U	4
	St. John's Wood, Co. Roscommon	53° 34/ 8° 01	U	4
England	Chee Dale, Derbyshire	53° 10/ 1° 30	U	4
Denmark	Munkebjerg Strandskov	55° 41/ 9° 37	U	3
Czech Rep.	Krivoklatsko Biosphere Reserve	50° 00/ 13° 86	U	4

6.3.3 Results

There was a significant difference in dry seed weight of uneaten seeds collected in autumn 2000 (Fig. 6.10; $P < 0.001$, ANOVA) with seeds from Irish populations being heavier than those from England, Denmark and the Czech Republic. Amongst the Irish seeds, those from the two most westerly sites, Reenadinna and Garryland were significantly heavier than those from the five midland sites. Combining the data from all seven Irish sites gives a mean dry seed weight for *Taxus*

Figure 6.10 Mean dry weight of uneaten *Taxus* seeds from ten different populations across Ireland and Europe, collected in autumn 2000. Letters signify homogeneous subsets according to Tukey's HSD post-hoc test. Colours indicate different countries. n = 30 in each case.

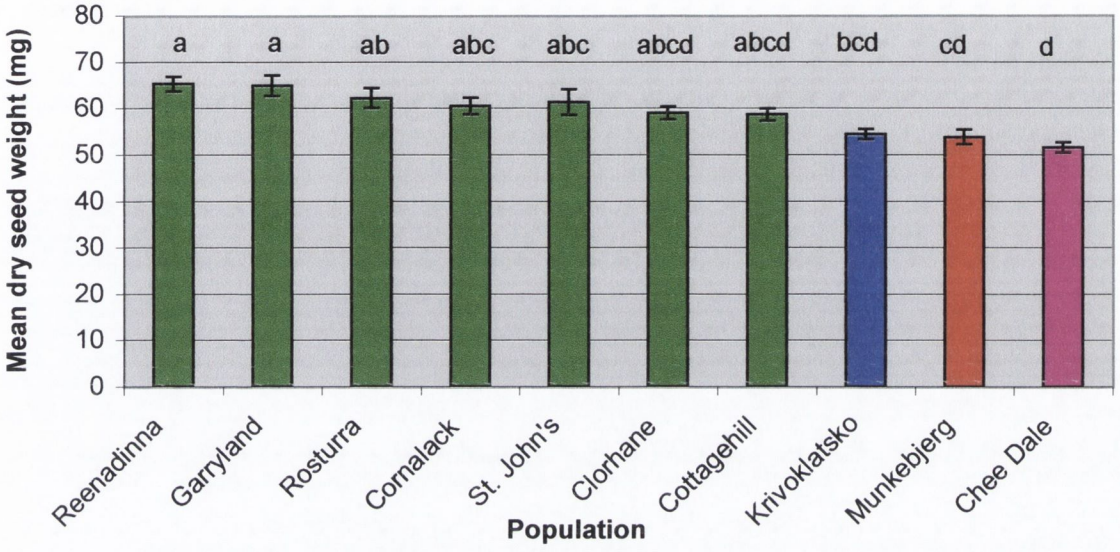


Figure 6.11 Differences between treatments on mean dry weight (mg) of *Taxus* seeds (n = 30). U denotes uneaten seeds, X denotes excreted seeds, R denotes regurgitated seeds. Asterisk (*) indicates a significant difference between treatments ($P < 0.05$). N.S. indicates non-significance. Data analyzed with ANOVA and T-tests as appropriate.

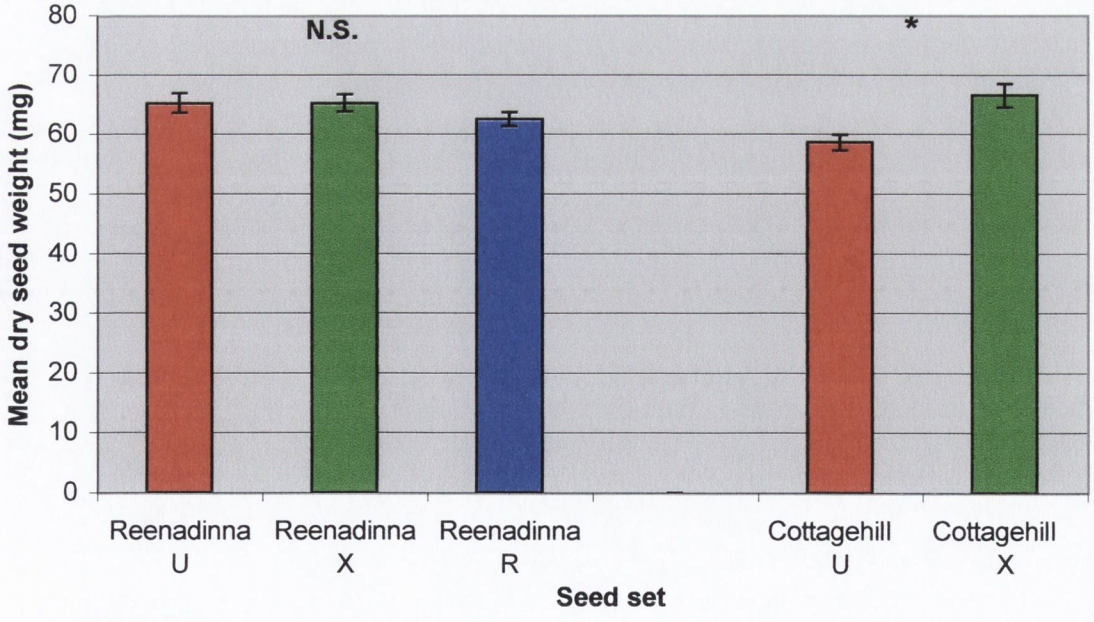


Figure 6.12 Course of germination of uneaten *Taxus* seeds after 9 months of stratification.

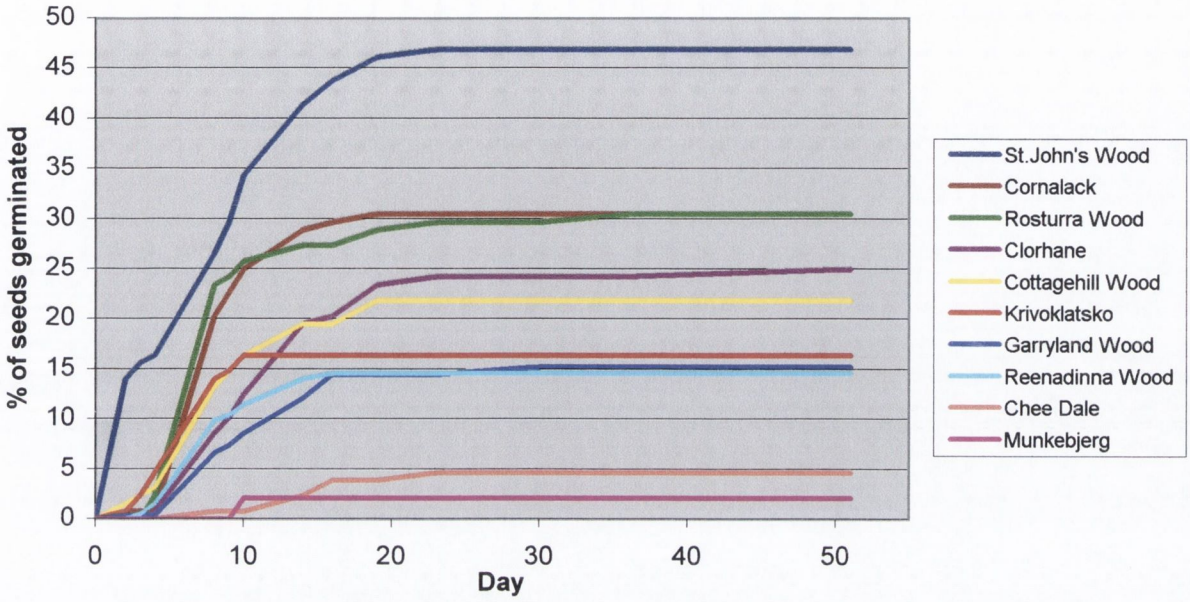
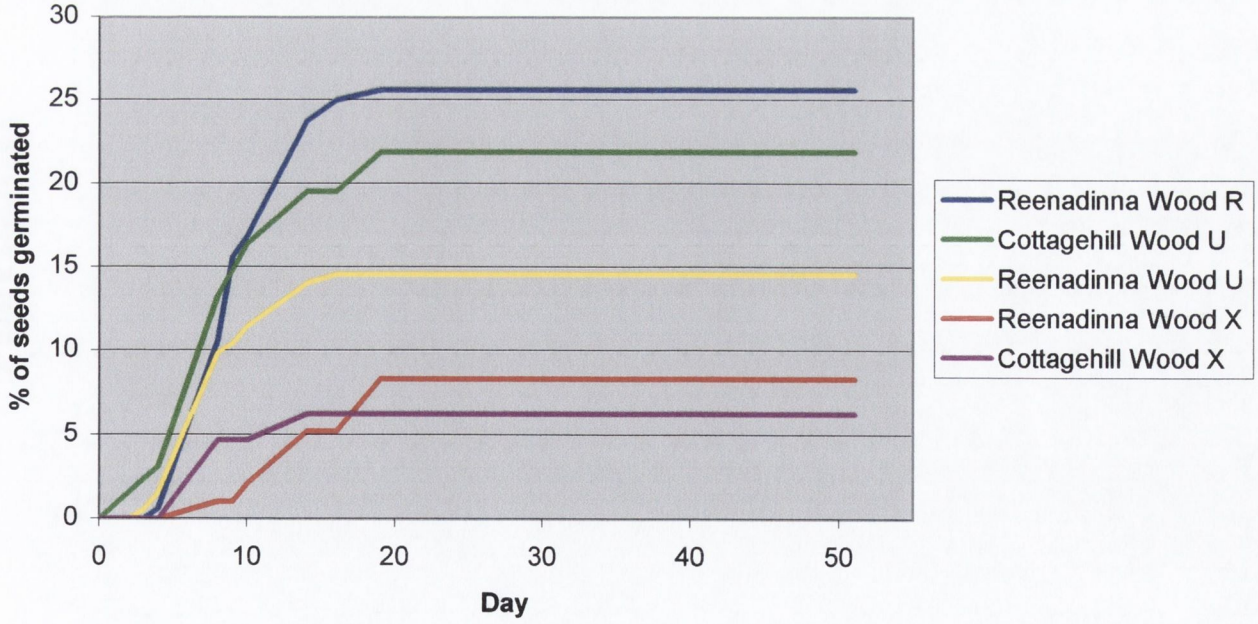


Figure 6.13 Course of germination of uneaten (U), excreted (X) and regurgitated (R) *Taxus* seeds following 9 months of stratification.



in Ireland of 61.6 mg. There was no significant difference in dry seed weight between uneaten, regurgitated and excreted seeds from Reenadinna (Fig. 6.11; $P = 0.312$, ANOVA), but excreted seeds collected from Cottagehill Woods were significantly heavier than uneaten seeds (Fig. 6.11; $P = 0.001$, T-test).

There was a significant variation in the germination success of uneaten seeds between populations (Fig. 6.12 and Table 6.5; $P < 0.001$, ANOVA) ranging from only 2.1% for Munkebjerg to 46.9% for St. John's Wood. There was also significant variation in the t/50 for germination (Table 6.5; $P = 0.028$, Kruskal-Wallis H test) which varied from 7.5 to 13.3 days. Mean dry seed weight was not significantly correlated with either mean germination success ($P = 0.147$, linear regression analysis) or establishment success ($P = 0.633$, linear regression analysis). Establishment success ranged from 34.4 % for Clorhane, to 79.5% for Rosturra Wood.

Table 6.5 Percentage germination of uneaten *Taxus* seeds 51 days after end of cold stratification. Letters indicate homogeneous subsets according to Tukey's HSD post hoc test. t/50 indicates that mean length of time taken to reach 50% of maximum germination for each population.

Population	Mean % of seeds germinated	t/50 (days)	% of germinated seeds establishing
St. John's Wood	46.9 a	7.5	53.3
Rosturra Wood	30.5ab	8.0	79.5
Cornalack	30.5ab	8.5	66.7
Clorhane	25.0 bc	13.0	34.4
Cottagehill Wood	20.9 bc	8.5	46.4
Krivoklatsko	16.4 bc	5.8	66.7
Garryland Wood	15.2 bc	11.3	66.7
Reenadinna Wood	14.6 bc	9.0	46.4
Chee Dale	4.7 c	13.3	50.0
Munkebjerg	2.1 c	-	-

Treatment had a significant effect on germination success amongst the seeds from Reenadinna (Fig. 6.13 and Table 6.6; $P = 0.003$, ANOVA), with significantly more regurgitated seeds germinating than either uneaten or excreted seeds. There was also a slightly significant variation in the t/50 for germination with excreted seeds being slower to germinate ($P = 0.041$, Kruskal Wallis H test). There were insufficient replicates to statistically test the data for Cottagehill Wood, but germination of excreted seeds was again lower than for uneaten seeds.

Table 6.6 Percentage germination of uneaten (U), excreted (X) and regurgitated (R) *Taxus* seeds from Reenadinna and Cottagehill Woods 51 days after cold stratification. Letters indicate homogeneous subsets according to Tukey's HSD post-hoc test. t/50 indicates that mean length of time taken to reach 50% of maximum germination for each population.

Seed set	Mean % of seeds germinated	t/50 (days)	% of germinated seeds establishing
Reenadinna Wood U	14.6 a	9.0	46.4
Reenadinna Wood X	8.3 a	12.7	87.5
Reenadinna Wood R	25.6 b	8.8	43.9
Cottagehill Wood U	20.9	8.5	46.4
Cottagehill Wood X	6.25	8.0	0.0

6.3.4 Discussion

Germination success of the uneaten Irish seeds after approximately 11 months of stratification was low, ranging between 14.6% and 46.9%. A similar figure resulted for the Czech population (16.4%). Relatively low values have also been reported from England (10.57% to 32.09%, Melzack & Watts 1982b), and from Poland (39%, Lewandowski 1999). The percentage germination scores for Chee Dale and Munkebjerg Strandskov were suspiciously low and there may have been a problem with stratification of these seeds. However, Lewandowski (1999) demonstrated that if ungerminated seeds were stratified again, overall germination success was much higher (93% in the Polish experiment). Thus, the values for germination success obtained in this experiment are probably a poor indication of actual seed viability. Unfortunately, attempts to stratify the ungerminated seeds in this experiment a second time were precluded by an equipment failure. Nevertheless, although germination success of uneaten seeds from Reenadinna Wood was the lowest for any Irish provenance, a minimum seed viability of 14.6% in combination with the heavy crops of seed reported by Smal & Fairley (1980b) makes it very unlikely that poor seed viability is responsible for the lack of observed regeneration in Reenadinna Wood, and therefore the hypothesis is rejected.

Lewandowski (1999) found that germination ceased 22 days after seeds were returned to the growth room but that most germination occurred within the first 10 days. This pattern is supported by the results of this study. The mean t/50 for the Irish populations varied between 7.5 and 11.3 days and although germination continued until day 51, the vast majority of germination had occurred by day 20. In the procedure used by Melzack & Watts (1982b), seeds were not returned

to growth room conditions after cold stratification, even when germination had begun. Under these conditions, germination continued to occur over a period of at least 6 months. Hence, the stratification protocol used in this study is recommended where the aim is to achieve germination in the shortest possible period.

The seeds used in this experiment were collected over a period of three months, which raises the question of a possible effect of seed maturity on germination; although uneaten seeds were selected on the basis of a mature aril, a proportion of these seeds were green and not dark brown at time of collection. However, Lewandowski (1999) investigated this possibility and found that seed colour had no significant effect on germination success. This is probably due to the long period (6 months) of after-ripening involved in the stratification process.

Melzack & Watts (1982b) suggested a clinal pattern of variation in yew seed size in England, with a decrease from the warmer south to the cooler north, and with smaller seeds in the east than the west of the country. The average seed weight for England was 56.5 mg. The data presented here tentatively support the idea of a west-east gradient in seed size as the average weight of Irish seeds was 61.6 mg and the largest seeds were again from more westerly sites. Melzack & Watts (1982b) also suggested that this trend extended across Europe. For example, Herrara (1987) reported a mean seed weight of 69.9 mg on the Iberian peninsula, whereas Suszka (1978) found that seeds in Poland were in the range of 43-59 mg and this study found an average weight for Czech seeds of 54.4 mg. These differences could be the result of climatic conditions, with oceanic conditions producing larger seeds than continental conditions. However, an unusually high seed weight has been reported from the Netherlands of 77 mg (Detz & Kemperman 1968). There is also evidence of year to year variation in seed weight: in this study the average seed weight of Danish seed from 2000 was 53.7 mg, but seeds at the same site in collected in autumn 1993 averaged 56.0 mg. A systematic study of seed weights from across Europe would be required before firm conclusions could be drawn. From a practical regard, however, the present results do not indicate a significant relationship between seed weight and subsequent germination success. Melzack & Watts (1982b) also found no such relationship, and in addition found no relationship between seed weight and seedling weight two months after germination.

Consumption and regurgitation of seeds appeared to improve germination success whilst consumption and excretion did not, and may even have reduced the chance of seeds germinating. However, Suszka (1978) examined the claim that germination was improved after passage through a bird's digestive tract and found that treatments of hot water or sulphuric acid to mimic this process did not increase germination rates. Heit (1969) suggested that it was simply the removal of the aril and not the action of digestive juices that was important as this reduced the chance of the seed rotting. This statement does not tally with the results of the present study, where germination success was higher in regurgitated seeds despite the arils being removed from all treatments.

A final point is that even after three months of cold stratification at 3-5°C, dormancy was not broken in the majority of yew seeds collected. This raises the question of whether in Ireland, where winters are typically mild and especially so in the southwest, temperatures fall low enough to break the dormancy of yew seeds on a regular basis. The longer that seeds remain in the soil ungerminated, the greater the chances that they will be eaten, become unviable, or rot. Harmer (1995) proposed that the figures for percentage germination obtained from artificial testing in the laboratory may bear little relationship to field performance, which is highly dependent on the environment of the germination site. This idea is supported by a comparison of the present results with those of the small mammal exclosure experiment, presented in Chapter 5.

In conclusion, this experiment shows that germination rates of Irish yew seeds after stratification for one year are comparable to those from elsewhere in Europe, but stratification for two years is probably recommended to achieve maximize germination success. Poor seed viability is unlikely to be the critical cause of the lack of yew regeneration in Reenadinna Wood. Experiments investigating germination rates in the field, however, are required to determine whether germination and establishment success may be limiting natural regeneration of yew.

6.4 Allelopathy experiments

6.4.1 Introduction

Allelopathy is a natural process by which a plant species inhibits the growth of other plants by the release of toxic compounds (allelopathic chemicals). It has been widely studied in forest ecosystems and particularly in conifer forests, and it has been claimed that allelopathy could be a common cause of natural regeneration failure (Pellissier & Souto 1999). In several studies, the

interaction has been one of understorey species inhibiting the germination and seedling development of tree species. For example, chemicals produced by crowberry (*Empetrum hermaphroditum*) have been shown to have strong negative effects on Scots pine (*Pinus sylvestris*) regeneration (Nilsson & Zackrisson 1992; Zackrisson & Nilsson 1992; Nilsson *et al.* 1993). Bilberry (*Vaccinium myrtillus*) and sheep laurel (*Kalmia angustifolia*) have been implicated in regeneration failure of Norway spruce (*Picea abies*) and black spruce (*Picea mariana*) (Jaderlund *et al.* 1996; Mallik & Pellissier 2000; Mallik 2001; Inderjit & Mallik 2002). However, autotoxicity has also been suggested as a potential factor affecting conifer regeneration (Pellissier 1993; Gallet 1994). Autotoxicity is a type of intraspecific allelopathy where a species inhibits growth of plants of its own kind, and has been reported from a wide variety of ecosystems (Singh *et al.* 1999).

Chemical extracts from yew have been studied in tremendous depth with regards to anti-cancer drugs (see Chapter 1) but the potential for ecological effects via the mechanisms of allelopathy and autotoxicity have received little attention. Nevertheless, yew woodlands are characterized by both poor regeneration rates and extremely sparse field layers and it has been suggested that allelopathic effects may be partially responsible (Smith 1980; Milner 1992). Hence, this brief study sought to investigate the allelopathic potential of yew through a bioassay using aqueous leaf extract. The hypotheses being tested were: (i) yew has the potential to inhibit the growth of other species through allelopathic chemicals, and (ii) yew trees have the potential to inhibit the growth of other yew plants through autotoxic effects.

6.4.2 Methods

A 5% w/v aqueous extract was made from leaves collected from mature yew trees at Trinity Botanic Gardens, Dublin in April 2001, following the method of Nilsson & Zackrisson (1992). After air-drying at 20°C, 50g of foliage was added to 1 l of distilled water. This was incubated in a growth room (15-25°C on a 12/12 h cycle) for 48 h and was vigorously shaken at irregular intervals. The mixture was filtered through Whatman No.1 filter paper and the resulting orange-yellow extract was stored at 5°C until use.

Experiment 1: Effect of aqueous extract on seed germination

Seeds of three bioassay species, lettuce (*Lactuca sativa*, Sutton Seeds), cress (*Lapidum sativum*, Sutton Seeds) and birch (*Betula pubescens*, identity no. BC-IECORK A62, Coillte Seed Centre,

Ballintemple, County Carlow) were used to investigate potential inhibition of seed germination by the leaf extract. *Lactuca* and *Lapidum* were selected as they germinate rapidly and have been widely used in previous bioassay experiments (e.g. Nilsen *et al.* 1999; Robles *et al.* 1999). Birch was selected to investigate a more realisitic effect on a woody species. To a petri-dish containing two layers of Whatman No.1 filter paper 3 ml of the 5% extract was added. Thirty seeds of either *Lactuca, Lapidum* or birch were evenly spaced on the paper and the dish was sealed with Parafilm. For *Lactuca* and *Lapidum* the experiment was replicated six times, for birch the experiment was replicated five times. For each species an equal number of controls were employed, using 3ml of distilled water instead of extract. All petri dishes were placed in a growth room (15-25°C on a 12/12 h cycle). The number of seeds that had germinated was counted daily at the same time, until further germination had ceased. Seeds were deemed to have germinated when the length of the radical had equaled or exceeded that of the seed.

Experiment 2: Effect of aqueous extract on growth of yew cuttings

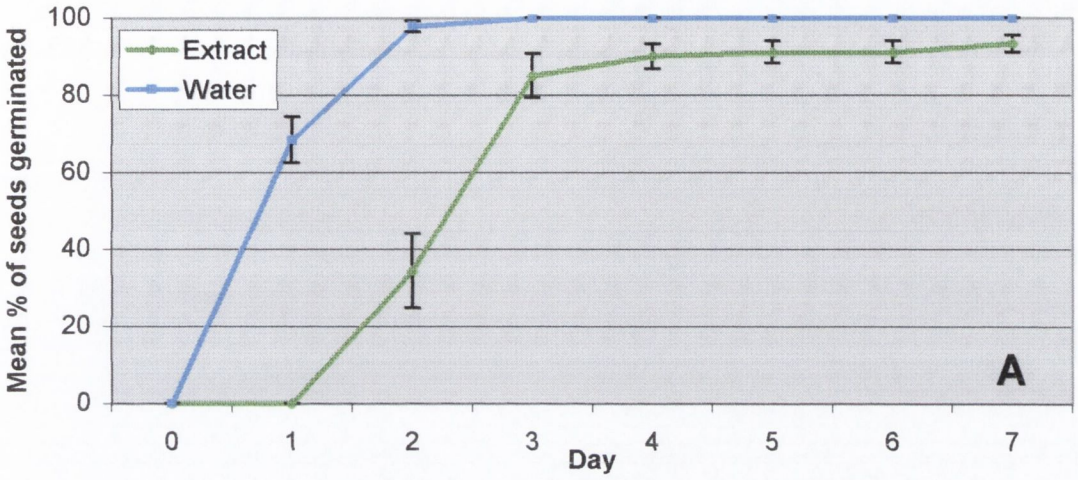
Cuttings were raised as described above for shade experiment 2. In April 2001, twenty-four of these plants were planted in 12.5cm plastic pots in general purpose peat-based compost (Shamrock, Bord na Móna) and placed on a table in a sunny greenhouse in a Latin square formation. Every 7 days 10ml of 5% aqueous extract was added to twelve of these plants whilst 10ml of distilled water was added to the other twelve. Plants were also watered with tap water as required. At the end of the growing season, in October 2001, the height and basal diameter of all the plants was measured. The plants were harvested and above and below ground dry weights were recorded after drying material for 72 h at 75°C. Mann-Whitney U tests were used to test the effects of treatment on final germination success and t/50 (i.e. the time taken to achieve 50% of maximum germination).

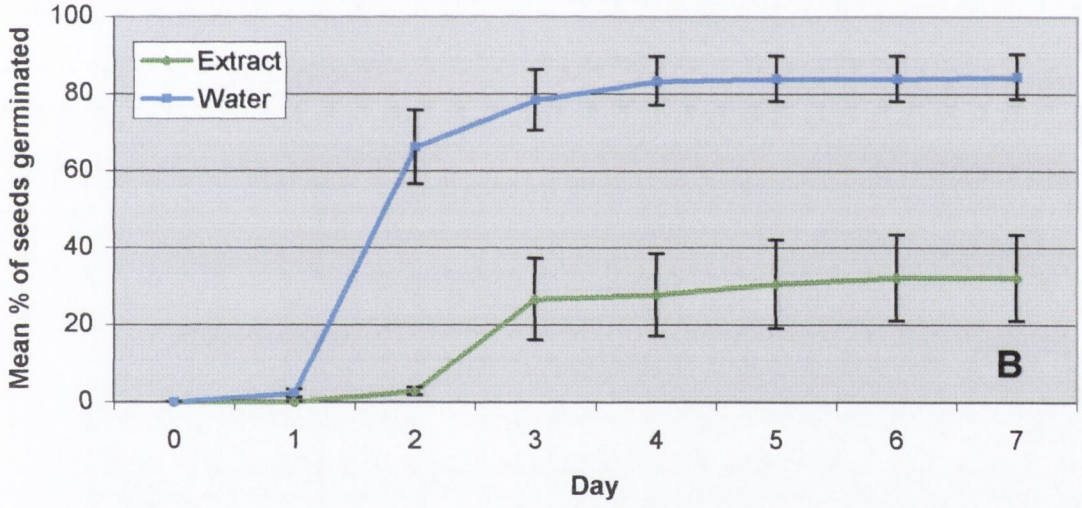
6.4.3 Results

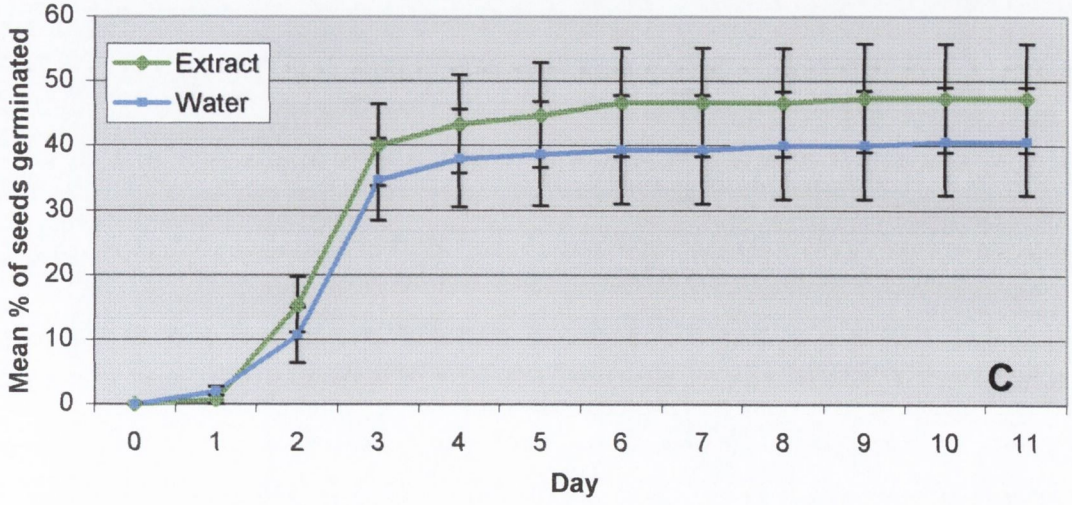
Experiment 1: Effect of aqueous extract on seed germination

Germination of *Lactuca* and *Lapidum* ceased after 7 days. The leaf extract clearly had an effect on the germination of both species. The effect on *Lapidum* was largely to slow the rate of germination rather than to preclude it as there was a highly significant difference in the t/50 scores ($P = 0.006$), although there was also a significant difference in the mean number of germinated seeds by day 7 (Fig. 6.14a; $P = 0.015$). However, the effect of the extract on the *Lactuca* seeds appears to have

Figure 6.14 Effect of 5% yew leaf extract on germination of (a) *Lapidum* seeds, (b) *Lactuca* seeds, and (c) *Betula* seeds. Error bars indicate ± se.







been a complete prevention of germination in a large proportion of the cases; by day 7 only 32% of the seeds treated with the extract had germinated, compared with 84% of those treated with distilled water (Fig. 6.14b; $P = 0.009$). Again there was a significant difference in the t/50 scores ($P = 0.015$). There was no significant effect of treatment on birch seeds (Fig. 6.14c), on either germination success ($P = 0.651$), which was less than 50% in both instances, or the t/50 ($P = 1.000$)

Experiment 2: Effect of aqueous extract on growth of yew cuttings

The leaf extract had no significant effect on the growth of the cuttings (Table 6.7), although those treated with the extract were slightly larger on average.

Table 6.7. Mean growth variables (± se) for *Taxus* cuttings treated weekly with either 5% *Taxus* leaf extract or distilled water. Data analyzed with Mann-Whitney U test, (n=12).

	Extract	Distilled water	P
Height (cm)	18.5 ± 1.5	18.3 ± 2.4	0.297
Basal diameter (mm)	3.3 ± 0.2	3.3 ± 0.3	0.898
Shoot dry weight (g)	2.1 ± 0.3	1.5 ± 0.3	0.081
Root dry weight (g)	2.8 ±0.4	2.1 ± 0.4	0.086

6.4.4 Discussion

These results indicate that there is a potential for allelopathic effects of yew on germination and radicle extension in other species and therefore support the first hypothesis. It appears that a water-soluble chemical is involved. Alcoholic extracts of *Taxus* shoots have previously been shown to interfere with mitotic division in meristematic cells (Majewska *et al.* 2000). Further experiments are needed to elucidate the chemicals and the mechanisms that might operate in an ecological context. In particular, it is important to ascertain whether phytotoxic substances from yew are able to accumulate in the soil of yew woodlands; as these are invariably on limestone pavement in Ireland, leaching of substances from the thin soil is likely to be high. With regards to the second hypothesis, there is no indication from these results of autotoxicity, but the plants used were rather large in proportion to the dosage applied; further experiments investigating the effects of foliage or humus leachate on seeds and germinal seedlings are required.

6.5 Simulated browsing experiments

6.5.1 Introduction

Tree seedlings and small saplings are particularly susceptible to damage or death as a result of browsing as the entire plant, including the leading shoots, are exposed to potential herbivory. Seedlings may also lack the reserves of plant materials needed to recover from severe cropping (Crouch 1966). Young trees thus remain particularly vulnerable to browsing by large herbivores until they have grown sufficiently tall to remove their apical meristems from the browsing zone of the animals present. Furthermore, browsing may reduce subsequent growth rates and keep trees within the browsing zone for many years (Gill 1992), although some species have been shown to have the ability to compensate for browsing losses (Hjältén *et al.* 1993; Lehtilä *et al.* 2000).

Experiments which simulate browsing, usually by manual clipping of shoots or leaves, have been used to investigate a range of factors effecting the response of trees to browsing events. Harmer (1999) examined interactions between shade and simulated browsing for a range of British tree species. The effect of intraspecific competition on browse response has been studied using *Betula pubescens* (Hjältén *et al.* 1993) and *Pinus sylvestris* (Edenius *et al.* 1993), whilst the influence of canopy cover was tested by McClaren (1996) and Saunders & Puettman (1999). A particular emphasis, however, has been placed on studying the effects of the nature of the browsing regime itself and the frequency, seasonality and intensity of the clipping have proved to be important factors (Canham *et al.* 1994; Bergström & Danell 1995; Saunders & Puettman 1999). The ability of trees to survive browsing events and to compensate for lost growth tends to decline with increased frequency and intensity. Deciduous trees transfer nutrients and carbohydrates to stems and roots for winter storage, whereas evergreen trees retain these reserves in their foliage, therefore winter browsing is relatively more serious for evergreen species than deciduous species (Gill 1992).

Despite its toxic properties, yew is browsed by a range of animals including rabbits, deer, goats and sheep (Watt 1926; Kelly 1981; Mitchell 1988, 1990). Welch & Haddow (1993) claimed that yew had an almost total inability to replace leading stems once they had been damaged, although the ability of yew to respond positively to damage of lateral shoots is demonstrated by its widespread use to form dense garden hedges. However, as has been discussed in Chapter 3, heavily

browsed, sprawling yew plants growing on the limestone pavement in the Burren are able to produce new leading (vertical) shoots once released from browsing pressure.

The aim of this study was to investigate the response of yew to the seasonality, frequency an intensity of simulated browsing in terms of height and basal diameter. The hypotheses being tested were: (i) compensatory growth in yew is affected by the seasonality of browsing, (ii) compensatory growth will decline with increased frequency of simulated browsing and (iii) compensatory growth will decline with increased intensity of simulated browsing.

6.5.2 Methods

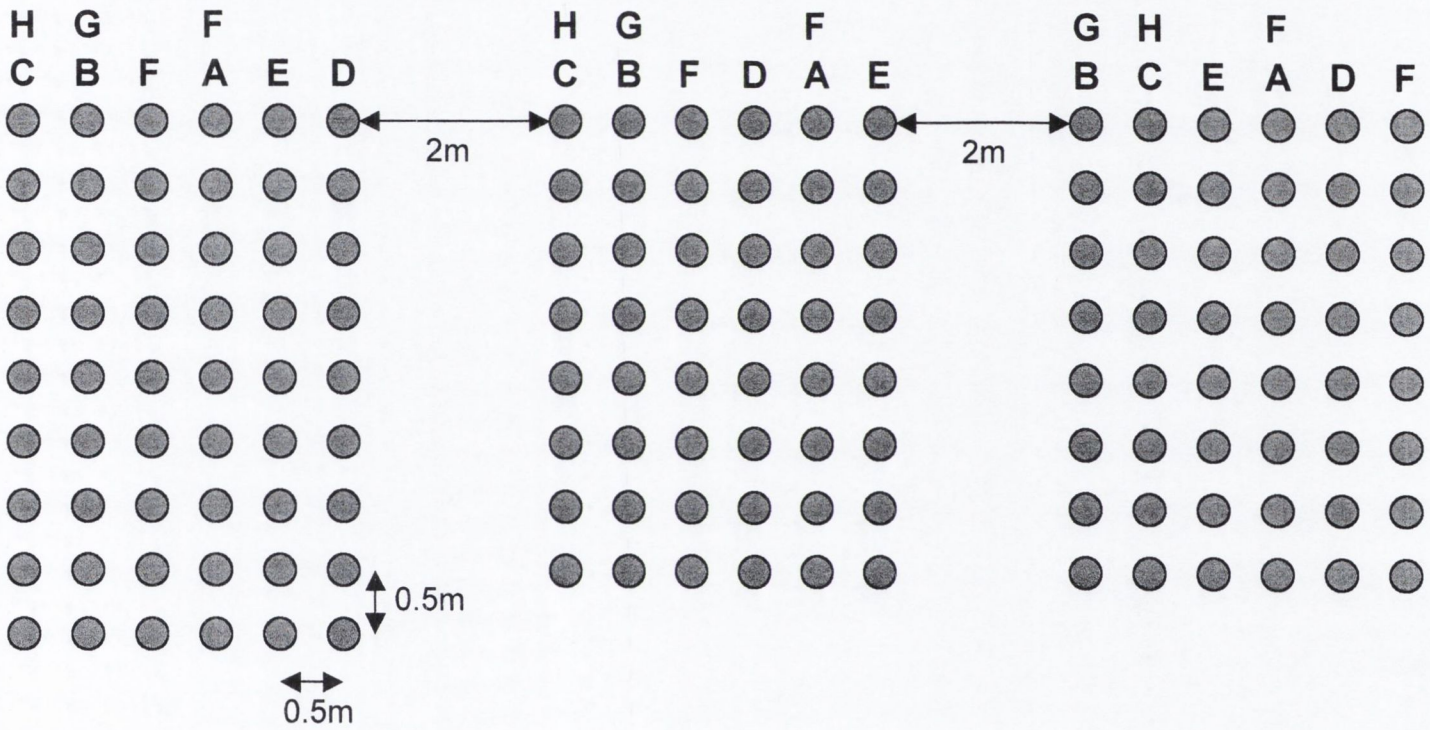
The experiment was conducted on an open plot of ground at the Trinity College Botanic Garden. Young, bare-rooted yew trees (approximately 40-45 cm in height) were obtained from a nursery. Suitable Irish plants could not be sourced, therefore those used were of Belgian provenance. These were planted in 23 cm plastic pots in a general purpose peat-based compost (Shamrock, Bord na Móna) and randomly allocated between eight browsing treatments (Table 6.8). Plants were divided between three pseudo-replicate blocks (Fig 6.15) and watered as required.

Table 6.8 Intensity, seasonality and frequency of simulated browsing on young yew trees.

Treatment	Intensity	Season	Frequency	Sample size
A	100%	Summer	2nd year	12
B	100%	Summer	1st year	12
C	60%	Summer	1st year	12
D	100%	Winter	1st year	25
E	60&	Winter	1st year	25
F	0%	-	-	37
G	100%	Summer	1st and 2nd year	13
H	60%	Summer	1st and 2nd year	13

The experiment was initiated in February 2000 at which time the height of each plant, from root collar to highest living bud, was measured. It continued over three growing seasons and concluded in November 2002, during which time the plants were regularly watered and fed with a liquid NPK fertiliser. At the end of the first growing season, in late August / early September 2000, the height of each plant was remeasured. Plants in treatments B and G were then clipped with secateurs to remove all of the new shoots (simulating "heavy browsing"). Plants in treatments C and H were clipped so as to remove approximately 60% of new shoot material by weight (simulating "medium browsing") – clipping started at the top of each plant and proceeded downwards until it was

Figure 6.15 Arrangement of potted yew saplings (green dots) for simukated browsing experiment. Letters indicate treatment of plants in that column. Where two letters are indicated, treatments alternate between adjacent plants.



estimated that required proportion of shoots had been removed. Hence, the new shoot material that remained was that which would be least accessible to animals browsing from above. Leading shoots were removed at both browsing intensities. All clipped shoot material was dried in an oven at 75 °C for 72 h and weighed. During the winter, late January / early February 2001, plants in treatments D and E were similarly treated with 100% clipping and 60% clipping respectively.

In late August / early September 2001, treatments G and H were clipped a second time and the plants in treatment A were clipped for the first time (100% new shoot removal). Growth of the plants during this year had been poor, however, as discussed in section 6.2.4. Plants in other treatments were left unclipped. In February 2002, each pot was topped up with a small amount of compost, containing approximately 1g of Osmocote Plus. At the end of the experiment the height and basal diameter 2 cm above the root collar of each plant was recorded. The net increase in height for each plant during the course of the experiment was calculated. Data were inspected for normality and log transformed as required prior to analysis with ANOVA.

6.5.3 Results

There were no significant differences in height between the treatments at the start of the experiment in February 2000 ($P = 0.124$), or after the first growing season in late August / early September 2000 ($P = 0.211$), i.e. before the plants had been subjected to simulated herbivory. For the plants from which an estimated 60% of new shoot material was removed after the first growing season (treatments C, E and H), an estimate of total new shoot dry weight was calculated by multiplying the dry weights of harvested clippings by a factor of 5/3. A comparison of these estimates and the dry weight values for the plants from which 100% of new shoot material had been clipped (treatments B, D and G), found no significant differences ($P = 0.736$). Hence, it was concluded that the method of estimating the amount material that needed to be clipped had been sufficiently accurate.

There were overall significant differences between the treatments in mean net height increment (Fig 6.16; $P < 0.001$) but not in basal diameter (Fig. 6.17; $P = 0.364$). However, few statistically distinct subsets were defined by Tukey's post hoc test. This was probably due to poor growth in summer 2001, reducing potential differences between the treatments - results are thus tentatively described in general terms. Timing of clipping appears to have had some effect on subsequent

Figure 6.16 Effect of simulated browsing treatments on net height increment of young *Taxus* trees over three years. Letters denote homogeneous subsets according to Tukey's HSD post hoc test.

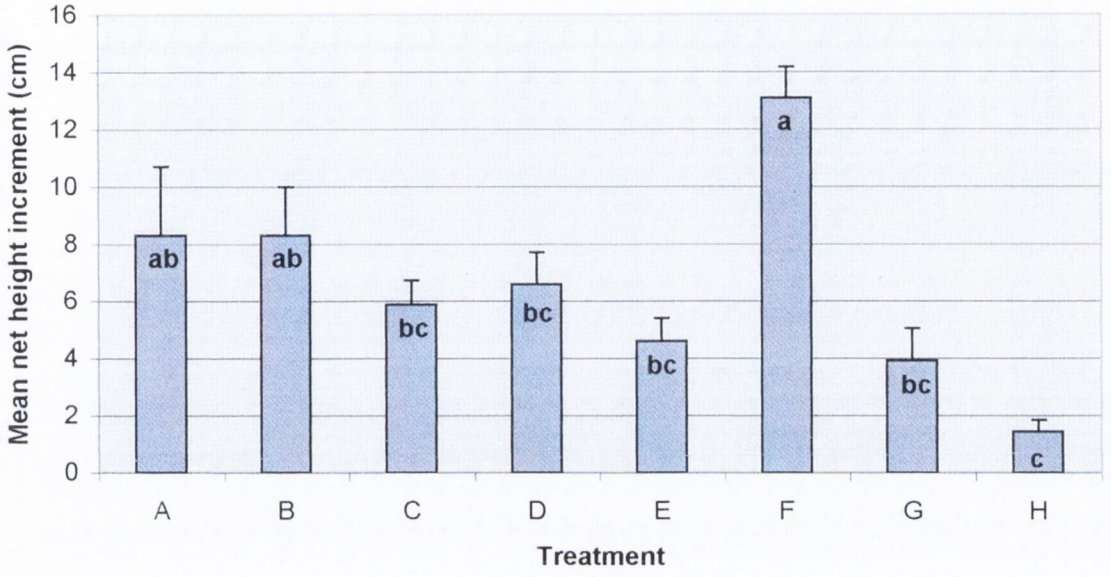
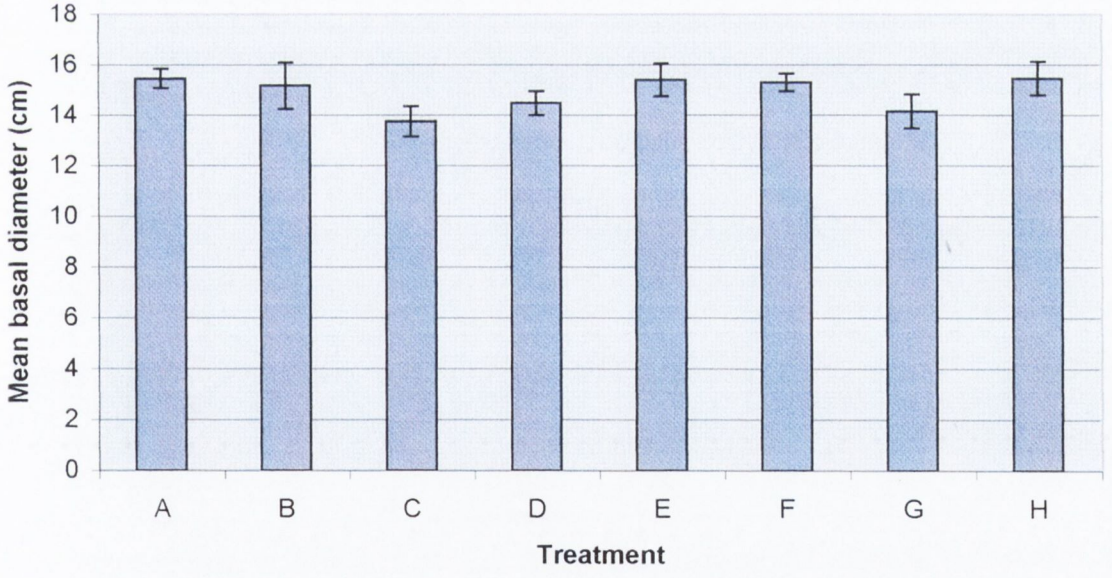


Figure 6.17 Effect of simulated browsing treatments on basal diameter of young *Taxus* trees after three years.



growth with treatments B and C (summer clipping) growing taller than their respective counterpart treatments D and E (winter clipping). As one would expect, frequency of clipping also had an effect, with those plants clipped once (treatments B and C) growing taller than those clipped twice (treatments G and H). The year in which clipping occurred however, appears to have had no effect with treatments A and B yielding similar results. The control plants (treatment F) displayed the greatest increase in height by some margin. Interestingly though, plants under the 100% clipping regime (treatments B, D and G) appear to have grown slightly taller than those in the corresponding treatments under the 60% clipping regime (treatments C, E and H).

6.5.4 Discussion

Overall, compensatory height growth of the clipped yews was poor. The only plants which did not grow significantly less than the controls were those in treatments A and B and these still grew much less on average. Edenius *et al.* (1993) suggested that compensatory growth in conifers is possibly limited by the fairly unflexible growth patterns and single bursts of annual growth. However, although 125 plants were clipped during the experiment, with some being clipped severely for two consecutive years, there were no mortalities. Furthermore, despite significant differences in height growth, basal diameter was unaffected. This suggests that browsing tolerance of yew plants of the size used in this experiment is high.

All treatments which were clipped after the first growing season produced a mean net increase in height by the end of the experiment. Often this was due to clipped leading shoots being replaced by multiple new shoots from buds just below the damaged tip. In many cases, however, vertical shoots were not replaced and height increment was due to the upwards growth of the top lateral shoots. Such responses to the loss of apical dominance have been reported for several species according to Gill (1992a).

The literature reviewed above reports that winter browsing is relatively more damaging for evergreens than for deciduous trees as translocation is far less pronounced. Similarly, summer browsing is more serious for deciduous species than winter browsing as defoliation can result in the loss of a large proportion of reserves; Canham *et al.* (1994) demonstrated this for a number of broadleaved tree species in eastern North America. However, it does not immediately follow from this that winter browsing should be more serious for evergreens than summer browsing. Possibly,

the suggested effect of seasonality in the present study, with winter-clipped plants growing less well than summer-clipped plants, may be due to an inability of plants clipped in January /February to replace buds before the onset of the growing season in April / May. An increased susceptibility to winter browsing in evergreen species, is compounded by the increased dependence of herbivores on evergreen species at this time due to the absence of deciduous browse material (Gill 1992a,b,c).

Finally, the apparent effect of clipping intensity may be the result of resource allocation and physiological sinks. Haukioja *et al.* (1990 cited in Lehtilä *et al.* 2000) showed that destruction of apical meristems, which are strong physiological sinks, resulted in increases in leaf size and the quality of the rest of the foliage in birches. A similar sink-shift in resources may have occurred in the 60% clipping intensity yew plants: following the loss of the leading shoot and the apical meristems, nutrient reserves in the following growth season were drawn to the intact buds and shoots in the lower part of the plant. Hence, these plants invested less resources in replacing the leading shoots than the 100% clipping intensity plants in which all buds (and potential physiological sinks) had been removed. This mechanism of lateral growth as result of vertical truncation is tentatively supported by the form prostrate yew plants in the Burren.

Firm conclusions with regards to hypotheses cannot be drawn from this experiment, due to the lack of significant results. Nevertheless yew plants of the size used in this experiment appear to combine a high browse tolerance with a poor compensatory ability in the short term. The first and second hypotheses are weakly supported by the available data. The third hypothesis, that compensatory growth will decline with intensity of grazing is rejected by the available data with regards to height, but a more extensive experiment investigating dry weight of growth material is required.

6.6 Summary

1. Yew is a highly shade tolerant plant; saplings and cuttings grown under heavy artificial shade displayed foliar and growth form adaptations for growing at low light levels. There are indications that growth performance maybe adversely effected in unshaded / unsheltered situations, although dark adapted yew saplings appear to be able to respond positively to increased light conditions; yew may have seedling bank regeneration strategy.

2. Germination success of Irish yew seeds after 11 months of stratification was low (14.6% to 46.9%) but poor seed viability is unlikely to be the critical cause of regeneration failure in Reenadinna Wood. A geographical cline in the weight of yew seeds is suggested, with heavier seeds occurring in the oceanic west of Europe.

3. Aqueous extract from yew foliage has the potential for allelopathic effects on germination and radicle extension in other species. Autotoxic effects on juvenile yew plants remained unconfirmed.

4. Established yew saplings appear to be highly tolerant of browsing but exhibit poor compensatory ability.

CHAPTER 7

GENERAL CONCLUSIONS

7.1 Ecological considerations

The primary aims of this research were to investigate the past distribution of yew in Ireland, to survey the plant communities in which yew currently occurs, to examine the effects of deer grazing on natural regeneration and vegetation in yew-woods and to investigate other potential factors which may influence natural regeneration of yew. With regards to these aims the research presented in this thesis propounds the following conclusions:

a) ***Palaeoecology and history***: Yew was probably present in Ireland as far back as 9,800 BP as a scattered understorey tree. Following the elm decline, *c.*5100 BP, localised and usually brief expansions of yew occurred as the canopy of the woodland opened up. According to the available data, these expansions were most prominent in the west and south-west and suggest that grazing pressure in these areas at this time was low. Yew populations declined as a part of general woodland clearance for agriculture, selective felling for its attractive timber and probably due to the threat of livestock poisoning. Yew populations expanded again during the Late Iron Age Lull, *c.*1900 BP and similar opportunistic colonisations of abandoned farmland have been recorded in south-east England. By the Early Christian Period, yew woods were scattered across the central limestone lowlands, with further sites in the drumlin area which still remained heavily wooded. As agricultural intensification increased, yew populations in Ireland declined dramatically. In recent times it has been widely planted as an ornamental, but is now rare in semi-natural habitats, generally occurring on cliffs or other rugged terrain. Its prominence in past natural Irish woodland has been previously underestimated.

b) ***Plant communities and succession***: Yew-dominated woodland in Ireland is rare and restricted to sites of outcropping limestone. This habitat appears to develop along a successional pathway, from species-rich open limestone pavement communities, such as are found in the Burren, through a seral scrub stage in which hazel is a characteristic component. The role of a protective thorny scrub stage remains unclear, although hawthorn, blackthorn, gorse and juniper may all be involved. Alternatively yew-wood development may be

restricted to situations where browsing animals are absent, such as marsh islands, lake islands and enclosed land. Yew also occurs as an occasional tree in sessile oak- holly woodland on sandstone, and ash woodland on calcareous soils over limestone. Irish yew-woods have several features which can distinguish them from English yew-woods on chalk, including the presence of hazel and an extensive bryophyte carpet, and the absence of whitebeam, Mercurialis perennis and Buxus sempervirens. Irish limestone pavement communities with yew appear to have some affinity with similar sites in Wales. Irish vegetation communities in which yew occurs can contain several non-native species; the most significant threats are probably posed by beech and *Cotoneaster* spp.

Reenadinna Wood contains the most extensive areas of yew-wood remaining in Ireland. It is a mosaic of stand types largely determined by topography and hydrology, with yew woodland and yew-hazel woodland dominating the limestone outcroppings, whilst wet woodland and birch scrub occur on the lower lying ground. Vascular plant species richness in the yew woodland is poor in comparison with adjacent habitats. The vegetation composition of the yew-dominated stands is similar to that in nearby Monk's Wood and in Garryland Wood, Co. Galway. Mortality amongst the yew population in Reenadinna Wood is predominantly amongst the smaller individuals; a self-thinning process is occurring suggesting relatively recent origins to the stand structure, although the largest trees may be considerably older.

c) ***Natural regeneration***: Chronic heavy browsing on the Muckross Peninsula, chiefly by introduced sika deer has had major impacts on field layer vegetation and natural regeneration in Reenadinna yew-wood and neighbouring oak woodlands on sandstone. Natural regeneration of yew is being limited by deer grazing in Camillan Wood: at reduced levels of grazing yew has the potential to increase significantly in abundance even beneath a closed oak canopy. Saplings of yew display foliar and growth form adaptations characteristic of shade tolerant species, and appear to form seedling banks in oak woodland, awaiting the opportunity presented by canopy gap development. Natural regeneration of oak is also being limited by deer grazing; regeneration in exclosures is restricted to less shaded sites. General vegetation changes following cessation of grazing in the acid woodlands of Camillan and Dinis appears to be highly site dependent. Formation of a dense holly understorey occurs beneath oak canopy whilst birch thickets are favoured in more open conditions. Adult tree species diversity increases and *Vaccinium myrtillus*, *Luzula sylvatica* and *Rubus fruticosus* expand in the field layer. If left unmanaged, however, *Rhododendron ponticum* can form dense thickets. In Camillan, increases in field layer vegetation associated with deer exclusion result in higher levels of small mammal activity. Rates of yew seed removal also appear to be higher under dense field layer vegetation than in heavily grazed areas. Therefore, whilst

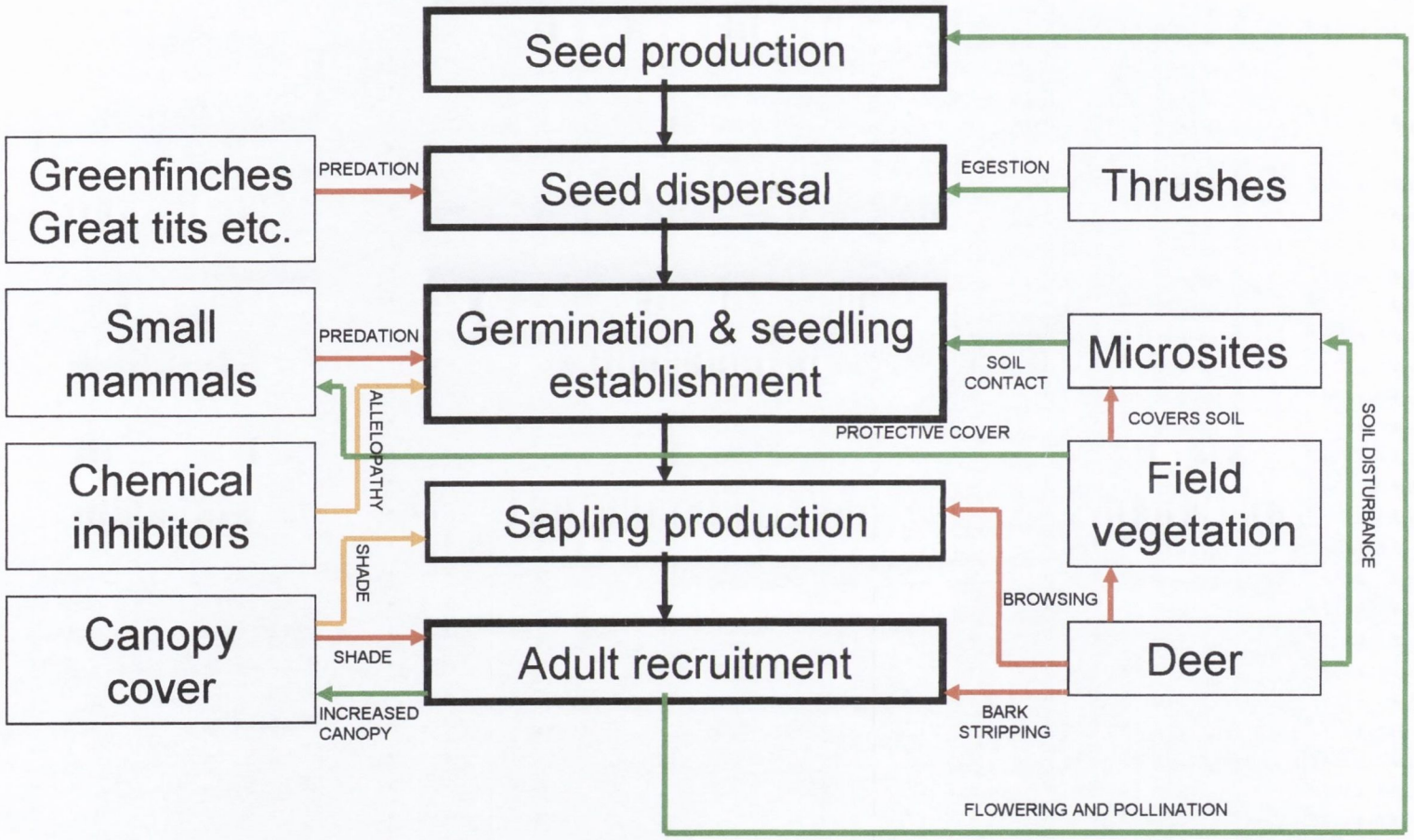


Figure 7.1 Stages in the natural regeneration of yew and influencing factors. Green lines indicated positive interactions, red lines indicate negative interactions and orange lines indicate uncertain interactions.

fencing prevents deer from browsing yew seedlings and saplings, it increases the effects of post-dispersal seed predation by woodmice and bank voles.

The sparseness of the field layer in Reenadinna Wood is not due alone to the heavy shade cast by the yew canopy. Cessation of grazing in Reenadinna results in an open field layer dominated by *Rubus fruticosus* and *Hedera helix* with a sparse holly understorey. Species diversity in ungrazed plots is higher than in Camillan, due to the additional ecological niches presented by decalcified patches of soil amongst the limestone pavement. In Reenadinna, deer grazing alone is not limiting regeneration. Intolerance of the heavy shade appears unlikely in view of the experimental results and the occurrence of less shade tolerant saplings, including ash and rowan. Differences in small mammal population densities between deer exclosures in Reenadinna and Camillan were insufficient to explain differences in yew regeneration regeneration through post-dispersal seed predation as increasing ground vegetation by deer exclusion appears to reduce differences in small mammal population densities between these woods. In Reenadinna yew-wood, proportions of woodmice and bank voles caught inside exclosures were not significantly higher than those caught outside exclosures, probably due to grykes providing alternative cover. Exclusion of small mammals from open sites resulted in an increase in yew seedling abundance, but field germination / establishment rates were still extremely low. Germination trials in the laboratory, however, prove that poor seed viability is unlikely to be the critical cause of regeneration failure in Reenadinna Wood. A geographical cline in the weight in yew seeds is suggested, with heavier seeds occurring in the oceanic west of Europe. Aqueous extract from yew foliage has the potential for allelopathic effects on germination and radicle extension in other species. Autotoxic effect on juvenile yew plants remain unconfirmed. A summary of the various factors influencing the natural regeneration of yew is presented in Fig. 7.1.

High grazing pressure and the absence of grazing both result in fairly uniform vegetation with a lack of seedling establishment. Intermediate levels of grazing maximise species richness and promote continual natural regeneration. In addition, complete exclusion of grazing animals results in large areas of dense vegetation with associated increases in post-dispersal seed predation.

7.2 Management recommendations

From these conclusions the following recommendations can be made regarding the management of existing yew communities in Ireland, and the place of this species in woodland creation schemes:

a) Some ***intermediate level of grazing*** is required to maintain species richness and natural regeneration in Irish yew-woods, and indeed oakwoods, as concluded for British woodland by Mitchell & Kirby (1990) and Kirby *et al.* (1994). Where livestock are the primary grazers, stocking densities and seasonality of grazing can be manipulated (Hester *et al.* 1996; Mitchell *et al.* 1996), but where deer are the main grazers, as in the Killarney National Park, the principal management techniques are fencing and culling. The advantages and disadvantages of these tools were discussed by Putman (1996) and are briefly outlined here.

Temporary fencing can be used to protect saplings until terminal buds are high enough to avoid deer browsing, but it is expensive and can still involve a fairly long-term maintenance commitment. Sykes (1992) projected that fencing at Coille Coire Chuilc, Perthshire, would be required for 25-30 years to enable sufficient Scots pines to reach the critical height. Another major problem of fences is that, once breached, they may be just as effective, if not more so, at trapping animals inside and thus exacerbating browsing damage. Indeed, where large areas or difficult terrain are fenced, it can be problematic ensuring that animals are not trapped inside when the fence is first erected. Fencing can also have the effect of concentrating deer impact on neighbouring habitats. Once fences are removed the problems of overgrazing return. Due to the long-lived nature of most dominant woodland tree species, even brief, periodic pulses of regeneration can ensure the long-term survival of a woodland, as Peterken & Tubbs (1965) found in the New Forest, but the age structure produced is distinctly uneven. In the context of Reenadinna Wood, fencing would result in the displacement of deer and grazing pressure into adjacent woodlands (wet woodland and oakwoods) which are already heavily utilised.

For culling to be effective it needs to be co-ordinated over the entire population range but, as deer have little regard for property boundaries, this is difficult to achieve. Culling may also be politically sensitive; despite scientific support, it can be difficult to justify to the public the killing of animals in an area designated as a nature reserve. Furthermore, population dynamics dictate that a continued effort is required to maintain animal populations below the carrying capacity of the environment, as a reduction in population density tends to be followed by an increase in reproductive productivity. A long-term commitment of finances and manpower is therefore entailed. However, culling can be successful in mimicking the natural limitation of herbivore populations by carnivores. In Ireland this role would have been principally fulfilled by the wolf (*Canis lupus*) which became extinct as recently as the eighteenth century (Fairley 1984), although winter mortality is also a significant factor in controlling herbivore numbers.

b) Increased ***monitoring of non-native species*** in Irish yew-communities is needed and potentially ***subsequent clearance work*** may be required. *Rhododendron ponticum* is the high profile invader of Irish vegetation, but several other species including beech, *Cotoneaster* spp., and *Clematis vitalba* have shown the ability to be invasive and locally dominant at Irish sites on calcareous substrate; it is recommended that these species are removed. Beech invasion is probably best tackled by uprooting plants at the small sapling stage (0.5-1.0 m in height). Uprooting of *Cotoneaster* and *Clematis* shrubs on areas of bare limestone is probably not feasible without causing serious damage to the surface of the pavement: plants should be lopped manually back as far as possible and the stumps treated with herbicide. Where *Clematis* occurs in the canopy it easily dealt with by sawing through the main stems at chest height as they twine up the supporting trees. An ongoing programme of work tackling *Rhododendron* infestation in the Killarney National Park has demonstrated that after clearance of persistent species, follow-up monitoring is an essential requirement (G.T. Higgins, pers. comm.).

c) ***Maintenance of a mosaic of woodland edge yew scrub*** is a management objective of yew-woodlands in England as it increases habitat diversity (Anon 1985; C. Barron pers. comm.). This is difficult to achieve at Reenadinna as the current woodland has almost filled the suitable ground available; the wood is restricted by marshland, loughs and meadows. However, clearance of *Cotoneaster* spp. from along cliff-tops in South Wood, would restore to a more native state a sizeable area of species-rich limestone pavement with calcareous heath and yew scrub elements. ***Felling of the small conifer plantation*** on the western borders of North Wood would also create an area for native scrub development and into which yew might expand, although the ground here is falling away off the limestone outcropping.

d) The yew-wood stands in ***Garryland Wood*** and ***Monk's Wood*** should be afforded conservation value on a par with that of Reenadinna Wood. Topographically and floristically these three wooded areas are very similar, although the occurrence of non-native species is more prominent at the first two sites. The limestone outcropping on which Monk's Wood is located is in reality part of the same series of outcroppings on which Reenadinna Wood is situated. However, because it is slightly removed from the other areas and possibly because of its different name and traditional association with Muckross Abbey, it has not received such a high profile.

e) Yew should be included as a ***component of native woodland planting schemes*** across the country, but particularly so in the west. The creation of yew-dominated stands is probably unrealistic except in areas of bare limestone, such as in the Burren, but yew should be considered as an occasional to frequent component in new woodland on calcareous soils, and a rare to occasional component on new woodland on acidic soils in both the lowlands and the uplands where the terrain is rocky.

7.3 Further research

This research has highlighted a number of areas towards which futures studies regarding yew and its ecology in Ireland should be directed. Recent palynological research has been concentrated predominantly in the west of the country; future pollen work is needed from the midlands and east of Ireland, and particularly from the east of Ulster. Combined with the completion of a systematic countrywide toponymical survey, this would greatly elucidate the past distribution of not only yew, but also other native tree species. The addition of more relevés to the yew community dataset, particularly from lake islands where grazing is absent, from areas of siliceous geology, and from dense thorny scrub would serve to improve our understanding of the relationship between yew communities and how they develop.

An aspect which particularly demands attention is the influence of environmental factors on the germination and establishment phases of yew regeneration. These include the effects of heavy shade, variations in the red : far red ratio, and germination microsites, for example rock, litter, humus or moss. Experiments should be conducted both in the laboratory and in the field. Further work in the area of allelopathy should focus on the potential for chemical inhibition in the field, by producing leachate for samples of foliage, humus and litter, and testing the effect on the germination of yew seeds and seeds of other yew community species.

There are two major areas of research which have not been investigated in depth in this study as they were deemed beyond the scope of a single project, and these are bryophytes and soil conditions. Bryophytes have not been reported at the species level, and measures of species richness have taken into account only vascular species. Kelly (2000), however, demonstrated that bryophyte and lichen diversity was an important component of biodiversity in Irish woodlands, especially given (i) the relative poverty of the Irish vascular plant flora, and (ii) the luxuriance of bryophyte growth in the hyper-oceanic climate of the south-west. Soil conditions in areas of limestone pavement can display high levels of spatial heterogeneity, being either completely absent, calcareous, decalcified by leaching or even waterlogged. Both of these topics are worthy of further investigation.

7.4 Concluding remarks

Studies of processes in Irish woodlands are greatly hampered by the relative scarcity of remaining sites, which are typically highly modified. This study has used a multidisciplinary approach which has enabled a range of results and ideas to be combined to reconstruct the

place of yew in Irish woodland ecology. It has highlighted the importance of yew in the past natural Irish landscape and investigated several aspects of yew's complex regeneration requirements. Although yew trees are renowned for their slow growth and extreme longevity, the strategy of yew in Irish native woodlands appears to be one of an opportunist or even a pioneer. Populations expand post-disturbance in the absence of grazing, and once established in the canopy, yew is a supreme competitor. Lack of current regeneration in natural populations is a cause for concern, but must viewed in the context of the long-life span of these stands. The yew has been an important part of Irish heritage and is worthy of a place in the new woodlands of the future.

POSTSCRIPT :

During the final year of this thesis study, in summer 2002, a deer-proof fence was erected around large areas of the North and South Wood of Reenadinna. This operation was funded by the Peoples' Millenium Forests project. The decision to erect this fenceline and the positioning of it predated the completion of this thesis. The analysis, discussion and conclusions presented here were therefore not part of the decision-making process.

" The great bow bent and sprang, in a salute to all that had been."

Robin May

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Appendix I

Accounts of yew in Irish floras (1864-1950)

A flora of Ulster and botanist's guide to the north of Ireland. Dickie (1864)

"Upland woods. Rare in the wild state. Rocks in Glenarrife, County Antrim, north-side, halfway up the glen; formerly plentiful being used as timber. It is now (August 1795) reduced to a few stunted plants growing in the crevices of the rocks, only accessible to a man lowered by ropes from above". *Mr Templeton MSS.*

"On Ben Evenagh, County Derry, in crevices of rocks at 1,200 feet, where is assumes the appearance of a low shrub; large trunks and roots of it are dug up on the Magilligan flat". *Dr. Moore*

Contributions towards a fauna and flora of the County of Cork. Power (1845)
The flowering plants and ferns of County Cork. Allin (1883)

"On hills, in woods - rare in the wild state, often planted".

"In Blarney woods, and growing out of a rock over Hellhole above Carrigohane on the Lee". *Dr. Power.*

"In mountainous woods". *Mr. J. Drummond*

"Woods near Castletown, Berehaven". *Rev. Dr. Hincks*

Cymbele Hibernica (Colgan & Scully 1898)

"...still abundant at Muckross and the Upper Lake, Killarney, with many old dead trees". *R.W. Scully*

"Grows spontaneously in several parts of Carbery. There is one growing on the side of a rocky hill a mile north of Dunmanway where there is scarce any earth to support it, yet it is 17feet in circumference". *Smith's Cork 1750*

"Mountain near Adrigole, 1894; mountain at Lough Hyne, 1896; islands in the river Lee at Geragh, Macroom, 1897". *Philips*

"Many fine old trees are to be seen in the mountainous woods of Glanquin, Burren". *Wade Rar.*

"Some dwarf trees here [in the Burren,] in 1879". *Corry 1880*

"Abundant on steep cliffs in Burren". *Foot 1864*

"Bilberry Island, Lough Corrib." *Ir.Flor.*

"Islets in Craigga More Lake, Connemara". (Praeger) *Ir. Nat. 1896*

"Cliffs at Glencar, Sligo, rare". *B & V 1885*

"Sparingly on limestone cliffs at Carrick and Knockmore mountains, Fermanagh". *Stewart 1882*

"Rocks in the little Deer Park, Glenarm, and on the Cave Hill, 1836". *Herb. Moore*

"Extremely rare in the north-east and not seen recently". *Flor. N. E.*

Flora of County Donegal. Hart (1898)

"Wooded glens and mountainous situations. Very rare. East side of Glenveagh; formerly abundant here. Thick logs are often dug out of the peat. On an island in a lake in the Rosses, to which it gives its name, Lough-an-Ure, the lake of the yew."

Flora of the County Dublin. Colgan (1904)

"There can be little doubt that the yew was in ancient times native in Co. Dublin and possibly some of the older trees which still flourish there are relics of indigenous. In more modern times, however, it has been so frequently planted that it is hardly possible at present to determine the standing of the species in Co. Dublin. Instances of its natural reproduction in the county are very rare."

Irish Topographical Botany. Prager (1901)

"Kerry South	Cloonee '98. rather rare – *Scully*
Kerry North	Ardfert '99: chiefly in the south – *Scully*
Cork West	Near Macroom '97: rare – *Phillips*
Cork East	Castletownroche '00: rare in a wild state – *Phillips*
Clare.	Rocks at Doonass '97, Bentley – *Hb.L.F.C. Burren f.*
Galway SE	Garryland '00 – P. Kilmacduagh '97 – *Mrs Joyce!*
Galway W	L. Inagh '98 – Colgan. Craigga More and L. Corrib
Galway. NE.	Wild ground by the Suck at Donamon '97
King's	Clonad Wood among Rhamnus &c
Wicklow	Rough wood on Avondale '99
Longford	Inchcleraun, one old tree, '85. *B. & V. 113*
Mayo E.	By Lough Mask below Ballinrobe '94 – *Mrs Persse!*
Mayo W.	Rocks on SW. shore of Lough Conn '00
Sligo	Cliffs of Seefin '96 – Colgan
Leitrim	Lough Gill on rocks '99. Glencar – *B.&V. 112"*

"Rocks, cliffs, old woods and lake shores, now almost confined to the west: formerly more abundant. The Wicklow, Longford, and E. Mayo records very possibly represent the last remnants of aboriginal stock, but it is impossible now to say, and introduced trees grow around."

Flora of County Kerry. Scully (1916)

"Native. Rocky places, woods and thickets, &c. Rather rare. A small tree"

" In several places about Kenmare and some fine trees in Ardtully demesne, 1904; about Cloonee Lakes, especially fine on an island in the Middle Lake, 1900-12."

" Sparingly about Kenmare, Blackwater bridge, Darrynane, 1904, and more frequently in the Owenreagh valley south of the Upper Killarney Lake, 1909."

" Sparingly in the Lickeen woods, Glencar, 1911."

" In Beaufort woods and two or three fine trees by Dunloe Castle, 1901; sparingly on the west side of the Purple Mountain, 1904, and very sparingly above Lough Gouragh in the Hag's Glen, Reeks, 1911; in the Glencar valley and on the east side of Caragh Lake near the Sugarloaf, 1913."

" About Fermoyle, Brandon Bay, 1905."

" Plentiful about all the Killarney Lakes and most of their islands as well as about the Long Range &c., 1888-1914, sparingly in Glenflesk, 1904."

" Frequent in Ballyseedy demesne east of Tralee, 1890."

" About Ardfert Abbey, &c., 1907; in Ballinruddery demesne near Listowel, 1899."

" About Lislaughtin Abbey near Ballylongford, 1904."

"From sea-level, to 1,275 feet above Lough Gouragh, Reeks, and to 1,550 feet beside Lough Glad on the Purple Mountain....most probably cannot claim to be native in some of the stations given above."

Flora of County Wicklow. ***Brunker (1950)***

"Native. Rocky places and woods. Rare. A small tree."

" Poulaphuca '34!"

" Kilmacanogue '23! Powerscourt '24 !"

" In the rough wood at Avondale ('99 ITB); in the graveyard at Glendalough '24; one seedling on a rock scarp in the oakwood, half-way from Lough Dan to Lough Tay '39! "

" Head on Altidore Glen '23!; in Glenealy Wood behind Ballyfree House '39!; some very large old trees in Rossanna Demesne, by the river, below Ashford '47!"

" By Avonmore River above Woodenbridge '26!; in Kilmacrea Pass '26!; some very large old trees between the Castle and the Church at Dunganstown '30!; at the abbey at Wickow '42! ; in the churchyard at Redcross '47!"

APPENDIX II

LICHENS OF REENADINNA WOOD

Compiled from British Lichen Society (1996) and Sanderson (1996)

B.L.S. No. [a]	Species	Location [b]	Abundance on *Taxus* [c]
2001	*Abrothallus bertianus**	on *P. glabratula*	
0034	*Acrocordia gemmata*	T	R
0049	*Anisomeridium polypori (=Anisomeridium nyssaegenum)*	T	R
0072	*Arthonia cinnabarina*	C	
0094	*Arthonia ilicina*	C	
1584	*Arthopyrenia ranunculospora*	?	
0146	*Biatora epixanthoides*	Fx	
0204	*Buellia disciformis*	T	O, lig
1557	*Byssoloma marginatum*	T	O
0183	*Catillaria atropurpurea*	T	R
0318	*Catillaria pulverea*	T	R, lig
0410	*Cladonia pyxidata*	T	R
0453	*Collema nigrescens*	C	
0457	*Collema subflaccidum*	C	
1027	*Degelia atlantica*	C	
1029	*Degelia plumbea*	C	
0490	*Dimerella lutea*	T	F
0489	*Dimerella pineti*	T	R
0504	*Enterographa crassa*	T	O
0541	*Gyalecta truncigena*	T	A
0547	*Gyalideopsis anastomosans*	T	R
0582	*Hypogymnia physodes*	T	F, lig
0657	*Lecanora intumescens*	Q	
0658	*Lecanora jamesii*	T	R
0820	*Lepraria incana*	T,C	O, lig
1629	*Lepraria lobificans*	T	O
0828	*Leptogium brebissonii*	T,C	O
0830	*Leptogium burgessii*	C,B	
0832	*Leptogium cochleatum*	C	
0834	*Leptogium cyanescens*	C	
0836	*Leptogium hibernicum*	C	
0839	*Leptogium lichenoides*	T	O
0857	*Lobaria pulmonaria*	T,C	O
0858	*Lobaria scrobiculata*	C	
0856	*Lobaria virens*	T,C	A
0551	*Loxospora elatinia*	T	R, lig
0871	*Micarea alabastrites*	T	O, lig
0887	*Micarea prasina*	T	O
0910	*Mycoblastus sterilis*	T	R, lig
0917	*Nephroma laevigatum*	C,S	
0920	*Normandina pulchella*	T,C	O
0945	*Opegrapha corticola*	T	R

0962	*Opegrapha sorediifera*	T	R
0966	*Opegrapha viridis*	T,C	O, lig
0943	*Opegrapha vulgata*	T	R
0972	*Pachyphiale carneola*	T	O
0974	*Pannaria conoplea*	Fx	
0980	*Pannaria rubiginosa*	C	
0989	*Parmelia crinita*	T	R
0998	*Parmelia glabratula subsp. fuliginosa*	T	R
1008	*Parmelia perlata*	T	R
1013	*Parmelia revoluta*	T	R, lig
1015	*Parmelia saxatilis*	T	R
1022	*Parmelia sulcata*	T	O, lig
1028	*Parmeliella parvula*	C	
1031	*Parmeliella testacea*	C, Fx	
1032	*Parmeliella triptophylla*	C	
1042	*Peltigera horizontalis*	C	
1050	*Peltigera praetextata*	C	
1058	*Pertusaria amara* f. *amara*	?	
1083	*Pertusaria multipunctata*	?	
1087	*Pertusaria pertusa*	?	
1181	*Porina leptalea*	T	R, lig
1222	*Pyrenula dermatodes*	B	
1224	*Pyrenula macrospora*	C	
1225	*Pyrenula occidentalis*	C	
1234	*Ramalina farinacea*	T	R, twig
1342	*Skyttea nitschkei**	on *Thelotrema* sp.	
2281	*Sticta canariensis / dufourii***	T, C, Fx	F
1367	*Sticta fuliginosa*	C	
1368	*Sticta limbata*	C	
1369	*Sticta sylvatica*	C	
-	*Strigula sp. (taylorii?)*	?	
1410	*Thelotrema lepadinum*	T	F, lig
1412	*Thelotrema petractoides (= Thelotrema subt.)*	C	
1469	*Usnea cornuta*	?	
1960	*Xerotrema megalospora***	T	lig
1172	*Zamenhofia coralloides*	T	O
1178	*Zamenhofia hibernica*	T	R
1671	*Zamenhofia rosei*	T	R

* lichenicolous fungi
** non-lichenized fungi
a British Lichen Society Catalogue Number
b T = *Taxus baccata,* Fx = *Fraxinus excelsior,* B = *Betula pubescens,* Q = *Quercus* spp., S = *Salix* spp., C = *Corylus avellana*
c A = abundant, F = frequent, O = occasional, R = rare,
lig lignicolous (growing on wood not bark)

Appendix III

Species abbreviations used in Ordinations

ABIEALBA	*Abies alba*
ACERPSEU	*Acer pseudoplatanus*
AGROCANI	*Agrostis canina*
AGROCAPI	*Agrostis capillaris*
AJUGREPT	*Ajuga reptans*
ANTHODOR	*Anthoxanthum odoratum*
ARBUUNED	*Arbutus unedo*
ARUMMACU	*Arum maculatum*
ASPECYNA	*Asperula cynanchica*
ASPLADIA	*Asplenium ruta-muraria*
ASPLCETE	*Asplenium adiantum-nigrum*
ASPLRUTA	*Asplenium ceterach*
ASPLTRIC	*Asplenium scolopendrium*
ASPLSCOL	*Asplenium trichomanes*
ATHYFELI	*Athyrium felix-femina*
AVENPUBE	*Avenula pubescens*
BETUPUBE	*Betula pubescens*
BLECSPIC	*Blechnum spicant*
BRACSYLV	*Brachypodium sylvaticum*
BRIZMEDI	*Briza media*
CALLVULG	*Calluna vulgaris*
CAMPROTU	*Campanula rotundifolia*
CAREFLAC	*Carex flacca*
CAREPULI	*Carex pulicaris*
CARESYLV	*Carex remota*
CARREMO	*Carex rostrata*
CARROST	*Carex sylvatica*
CARLVULG	*Carlina vulgaris*
CENTRUBE	*Centranthus ruber*
CIRCLUTE	*Circaea lutetiana*
CIRSARVE	*Cirsium arvensis*
CLEMVITA	*Clematis vitalba*
CONOMAJU	*Conopodium majus*
CORYAVEL	*Corylus avellana*
COTOINTE	*Cotoneaster integrifolia*
CRATMONO	*Crataegus monogyna*
CYTISCOP	*Cytisus scoparia*
DACTFUSC	*Dactylis glomerata*
DACTGLOM	*Dactylorhiza fuschii*
DATHDECU	*Dathonia decumbens*
DESCFLEX	*Deschampsia flexuosa*
DIGIPURP	*Digitalis purpurea*
DRYAOCTO	*Dryas octopetala*
DRYOAEMU	*Dryopteris aemula*
DRYOAFFI	*Dryopteris affinis*
DRYODILI	*Dryopteris dilitata*
DRYOFILI	*Dryopteris filix-mas*
ENDYNONS	*Endymion non-scripta*
EPIPATRO	*Epipactis atrorubens*
ERICCINE	*Erica cinerea*
ERICTETR	*Erica tetralix*
EUONEURO	*Euonymus europaea*
EUPHHYBE	*Euphorbia hyberna*
EUPHRASI	*Euphrasia spp.*
FAGUSYLV	*Fagus sylvatica*

FILIVULG	*Filipendula vulgaris*
FRAGVESC	*Fragaria vesca*
FESTRUBR	*Festuca rubra*
FRAXEXCE	*Fraxinus excelsior*
GALISAXA	*Galium saxatile*
GALIPALU	*Galium palustre*
GALISTER	*Galium sterneri*
GERAMOLL	*Geranium molle*
GERAROBE	*Geranium robertianum*
GERASANG	*Geranium sanguinuem*
GEUMURBA	*Geum urbanum*
HEDEHELI	*Hedera helix*
HIERACIU	*Hieracium spp.*
HOLCLANA	*Holcus lanatus*
HYMETUNB	*Hymenophyllum tunbridgense*
HYPEANDR	*Hypericum androsaemum*
HYPEPULC	*Hypericum pulchrum*
HYPORADI	*Hypochoeris radicata*
ILEXAQUI	*Ilex aquifolium* (field layer)
ILEXAQUI	*Ilex aquifolium* (understorey)
JUNCBULB	*Juncus bulbosus*
JUNCCONG	*Juncus conglomeratus*
JUNCEFFU	*Juncus effusus*
JUNICOMM	*Juniperus communis*
LATHMONT	*Lathyrus montanus*
LINUCATH	*Linum catharticum*
LISTOVAT	*Listera ovata*
LOLIPERE	*Lolium perenne*
LONIPERI	*Lonicera periclymenum*
LOTUCORN	*Lotus corniculatus*
LUZUMULT	*Luzula multiflora*
LUZUSYLV	*Luzula sylvatica*
MALUSYLV	*Malus sylvestris*
MELIUNIF	*Melica uniflora*
MOLICAER	*Molinia caerulea*
MYCEMURA	*Mycelis muralis*
OXALACET	*Oxalis acetosella*
PILOOFFI	*Pilosella officinarum*
PINUSYLV	*Pinus sylvestris*
PLANLANC	*Plantago lanceolata*
POAPRATE	*Poa pratensis*
POLYPODI	*Polypodium spp.*
POLYSETI	*Polystichum setiferum*
POLYVULG	*Polygala vulgaris*
POTEEREC	*Potentilla erecta*
POTESTER	*Potentilla sterilis*
PRIMVULG	*Primula vulgaris*
PRUNAVIU	*Prunus avium*
PRUNSPIN	*Prunus spinosa*
PSEUMENZ	*Pseudotsuga menziesii*
PTERAQUI	*Pteridium aquilinum*
QUERCUS	*Quercus spp.*
QUERPETR	*Quercus petraea*
RANUBULB	*Ranunculus bulbosus*
RANUREPE	*Ranunculus repens*
RHAMCATH	*Rhamnus cathartica*
RHODPONT	*Rhododendron ponticum* (field layer)
RHODPONT	*Rhododendron ponticum* (understorey)
ROSA	*Rosa spp.*
ROSACANI	*Rosa canina*

ROSAPIMP	*Rosa pimpinellafolia*
ROSARUBI	*Rosa rubiginosa*
RUBIPERE	*Rubia peregrina*
RUBUFRUT	*Rubus fruticosus*
SALIAURI	*Salix aurita*
SALICINE	*Salix cinerea*
SANIEURO	*Sanicula europaea*
SAXISPAT	*Saxifraga spathularis*
SENEJACO	*Senecio jacobea*
SESLCAER	*Sesleria caerulea*
SOLIVIRG	*Solidago virgaurea*
SONCASPE	*Sonchus asper*
SORBARIA	*Sorbus aria agg.*
SORBAUCU	*Sorbus aucuparia* (field layer)
SORBAUCU	*Sorbus aucuparia* (understorey)
SUCCPRAT	*Succisa pratensis*
TARAOFFI	*Taraxacum officinale*
TAXUBACC	*Taxus baccata*
TEUCSCOR	*Teucrium scorodonia*
THYMPRAE	*Thymus praecox*
ULEXEURO	*Ulex europaeus*
ULMUGLAB	*Ulmus glabra*
VACCMYRT	*Vaccinium myrtillus*
VEROOFFI	*Veronica chamaedrys*
VEROCHAM	*Veronica officinale*
VIBUOPUL	*Viburnum opulus*
VICISEPI	*Vicia sepium*
VIOLRIRE	*Viola riviniana / reichenbachiana*