

Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: Natural regeneration and stand dynamics

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Abstract

Woodland dominated by *Taxus baccata* is one of the rarest of European woodland types and has priority habitat status under Annex I of the EU Habitats Directive, yet little is known about its stand dynamics or the effects of long-term grazing. The abundance of naturally regenerating seedlings and saplings was monitored over a 32-year period in exclosures in a yew-wood and a neighbouring oakwood in the Killarney National Park, southwest Ireland. Both woods are heavily grazed by introduced sika deer (*Cervus nippon*). Mortality, recruitment and growth of adult trees were monitored over a 20-year period. Comparison was made with unfenced plots adjacent to each of the exclosures. Regeneration in the yew-wood exclosures was chiefly by *Ilex aquifolium*, *Sorbus aucuparia* and *Fraxinus excelsior*. No *Taxus baccata* saplings were recorded and seedlings of this species were very rare throughout the duration of the experiment. *Taxus baccata* trees which died during the 20-year monitoring period were significantly smaller than those which survived, indicating that self-thinning is occurring and the wood in its present form may be of relatively recent origins. Changes in adult tree species composition suggest that yew woodland in Ireland may develop from a yew-hazel scrub woodland sere. A variety of species regenerated in the oakwood exclosures, including *Taxus baccata*, and dense holly thickets formed in several areas. *Quercus petraea* failed to regenerate beneath the oak canopy. We conclude that chronic heavy grazing in the Killarney woodlands strongly influences the natural regeneration of several tree species. Research into the scientific manipulation of grazing levels in temperate woodlands is required. However, grazing intensity is not the only factor affecting regeneration, canopy conditions in particular are also likely to be of high significance, and this should be reflected in management plans.

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1. Introduction

Grazing animals can have major impacts on the vegetation of semi-natural woodlands (Mitchell and Kirby, 1990). Natural regeneration of tree species can be impeded or precluded by the eating of vulnerable seedlings and saplings (e.g. Linhart and Whelan, 1980; Pigott, 1983; Putman et al., 1989; Latham and Blackstock, 1998) although susceptibility to browsing can vary considerably between species (Gill and Beardall, 2001). Established trees may be damaged by activities such as bark stripping (e.g. Larner, 1977) and, in the long term, the effects of grazing can impact markedly on the stand structure and composition of woodlands (e.g. Peterken and Tubbs, 1965). Heavy grazing pressure is a feature of many types of woodland

in Ireland, particularly within the rugged landscapes of the National Parks (Kelly, 2000; Higgins, 2001). This is cause for serious concern given the very limited area of semi-natural woodland remaining in Ireland, estimated at covering 1.1% of the country (Higgins et al., 2004). The Killarney National Park, Co. Kerry, possesses some of the best remaining examples of semi-natural woodland in Ireland (Kelly, 1981; Kelly and Iremonger, 1997), including two woodland types of international importance: yew woodland and acidophilous oak woodland. Kelly (1981) highlighted that a conspicuous feature of these woods was the extreme scarcity of natural regeneration of any tree species.

Woodland dominated by *Taxus baccata* L. (common yew)¹ is one of the rarest of European woodland types and is largely restricted to southern England and western Ireland. The unique nature of these woodlands has afforded them priority habitat

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¹ Botanical nomenclature in this paper follows Stace (1997).

status under Annex I of the EU Habitats Directive (Fossitt, 2000). Irish yew-woods differ markedly from those on the chalk downlands of southern England studied by Watt (1926) and Tittensor (1980), in that they are found on areas of karst limestone pavement rather than chalk. They thus have more geologically in common with the yew-woods on Magnesian limestone found in the coastal dunes of Co. Durham, northeast England (Hulme, 1996). A striking feature of yew-woods is the extreme paucity of the field layer and the scarcity of shrubs or regenerating saplings, which Rodwell (1991) attributes in English woods to the heavy shade cast by the dense canopy. It has been unclear to what degree grazing is influential in this regard in the case of Irish yew-woods as little is known about their structural dynamics. The reasons for the dominance of yew are also unclear as in most woodland on such terrain in Ireland (e.g. the Burren, Co. Clare), *Corylus avellana* is dominant, *Fraxinus excelsior* is abundant and *T. baccata* is rare (Kelly and Kirby, 1982).

The acidophilous oakwoods of Ireland and Britain that are dominated by *Quercus petraea* (sessile oak) with an *Ilex aquifolium* understorey and *Blechnum spicant* in the field layer, also have Annex I status. They tend to occur in high rainfall western areas, particularly in the uplands, and are characterised by the variety and abundance of bryophytes, lichens and filmy ferns (Hymenophyllaceae) which include species with restricted Atlantic distributions (Ratcliffe, 1968). A general account of these woods in Ireland has been given by Kelly and Moore (1975) and of the Killarney oakwoods by Kelly (1981).

Fenced exclosures have often been used to examine the effects that grazing is having on natural regeneration in woodland (e.g. Latham and Blackstock, 1998; Sykes, 1992) and fencing is frequently used as a management tool in areas where grazing is a problem. This paper describes natural regeneration and changes in stand structure in relation to fencing in two semi-natural woodlands, a yew-wood and an oakwood, in southwest Ireland over a period of 32 years. There have now been several long-term ecological monitoring studies conducted in a range of woodland types in Britain, for example, *Quercus robur*–*Betula pubescens* woodland (Mountford et al., 2000), *Q. robur*–*F. excelsior* woodland (Kirby et al., 1996), *Q. robur*–*Fagus sylvatica* woodland (Putman et al., 1989), *Q. petraea*–*B. pubescens* woodland (Pigott, 1983), *Q. robur*–*F. excelsior*–*Tilia* spp. woodland (Peterken and Jones, 1987, 1989) and *Pinus sylvestris* woodland (Gong et al., 1991; Sykes, 1992). However, 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 18 year period. Furthermore, there have been few other ecological studies of comparable duration in Ireland, the notable exception being the Tomies oakwood study of Kelly (2000, 2002). Our aims were to investigate the effects that long-term deer exclusion would have on the abundance and growth of seedlings and saplings, in particular those of the canopy dominants *T. baccata* and *Q. petraea*. In addition, we aimed to examine the changes in stand structure that occurred during this period with regards to recruitment and mortality.

2. Methods

2.1. Study area

The study was conducted in the woodlands of the Muckross Peninsula in the Killarney National Park, southwest Ireland (Fig. 1) between 1969 and 2001. The vegetation of these woods has been described in detail by Kelly (1981). The peninsula is low-lying with an altitude of 17–30 m. It is divided by a geological boundary, separating Carboniferous Limestone to the east from Devonian Old Red Sandstone to the west. The limestone area supports Reenadinna Wood (longitude 9°30', latitude 52°1'), a *Taxus baccata*-dominated woodland, about 25 ha in size and located on a series of outcropping limestone reefs. The soil in the grykes on these reefs has a pH around 6.8. Kelly (1981) classified the vegetation as a facies of the *Corylo*–*Fraxinetum* association (Braun-Blanquet and Tüxen, 1952). The canopy is low (6–14 m in height) and in most areas no appreciable understorey is present. *Fraxinus excelsior* and *Corylus avellana* are frequent, especially where pockets of soil have accumulated, and occasionally *C. avellana* replaces *T. baccata* as the canopy dominant. The field layer is typically very sparse, but a luxuriant bryophyte carpet covers the surface of the limestone. The outcrops are fringed by areas of wet woodland dominated by a mixture of *Betula pubescens*, *F. excelsior* and *Salix cinerea* ssp. *oleifolia*.

The sandstone area supports Camillan Wood (longitude 9°32', latitude 52°1'), a *Quercus petraea*-dominated woodland of about 20 ha. The oak canopy is 13–25 m in height with an evergreen understorey (5–10 m in height) of *Ilex aquifolium*. Scattered individuals of *B. pubescens* and *Sorbus aucuparia* are frequent and *Arbutus unedo* is common around the woodland margins. The soil is podzolised with deep mor humus cover and a pH around 4.5. The vegetation has been classified as part of the *Blechno*–*Quercetum* association typical of acidophilous oakwoods in upland Ireland (Kelly, 1981). The invasive alien *Rhododendron ponticum* is widespread throughout Camillan Wood despite ongoing attempts to control it.

Early ecological accounts of the Killarney woods indicate relatively moderate grazing levels (Watts, 1984), but grazing levels have been much higher in recent decades. Sika deer (*Cervus nippon* Temminck) were introduced to the park in 1865, and the population has expanded considerably since then (Higgins et al., 2001). Grazing has been further increased by the presence of feral goats and trespassing sheep. This is in addition to the pressure exerted by the native grazers, red deer (*Cervus elaphus* L.) and Irish hare (*Lepus timidus hibernica* L.), the main natural predators of which, wolf (*Canis lupus* L.) and golden eagle (*Aquila chrysaetos* L.), are no longer present. Population estimates for sika deer are not available for the whole course of this study, but Larner (1977) recorded densities on the peninsula of 0.51 animals ha⁻¹ in 1970 and 0.82 animals ha⁻¹ in 1975. Higgins et al. (1996) reported lower (but still relatively high) densities of 0.18 animals ha⁻¹ in 1991 and 0.22 animals ha⁻¹ in 1996 for the Muckross area. The native red deer population in this area is much lower and is considered to have a relatively minor impact on the vegetation.

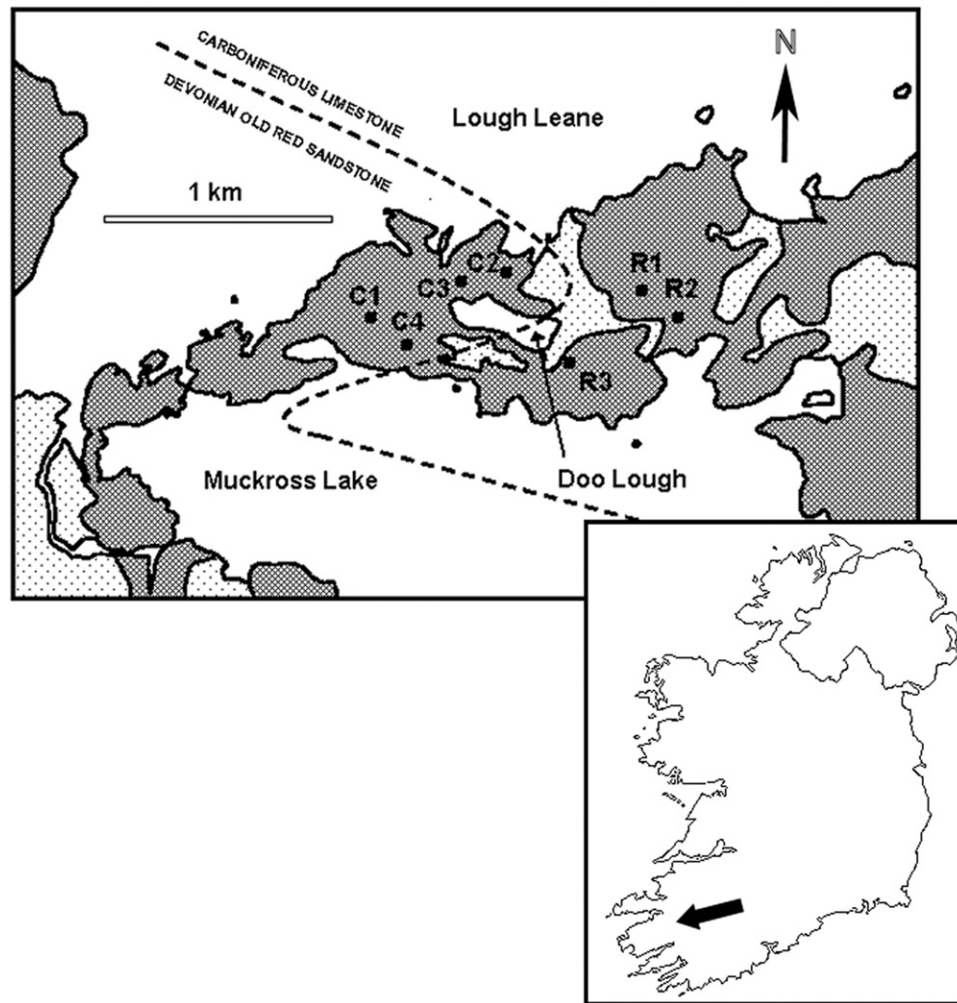


Fig. 1. Map of the Muckross Peninsula, Killarney National Park, showing the location of the deer exclosures. The dashed line indicates the geological boundary. Heavy shading indicates wooded areas and light shading indicates non-wooded terrestrial habitats. The arrow in the smaller map shows the location of the study site within Ireland.

The climate of the area is extreme oceanic, with cool summers and mild winters; for Killarney town, 6 km NNE of the peninsula, the mean maximum temperature of the hottest month is 19.3 °C and mean minimum of the coldest month is 3.1 °C (Met Éireann, unpublished data for the period 1961–1990). The mean number of frost days is 40 year⁻¹ and the mean rainfall at Muckross House, 0.5 km E of the peninsula is 1263 mm year⁻¹ (Met Éireann, unpublished data for the period 1931–1960).

2.2. Exclosure establishment

Four deer-proof exclosures were established in the winter of 1969–1970 (Table 1). Exclosures R1–R3 were erected on limestone outcrops in Reenadinna Wood, and situated to include a representative range of yew-wood stand types. Exclosure C1 was established in Camillan Wood, where three further exclosures were added in 1974–1975 (C2–C4). Exclosures C2 and C3 fenced off areas which had been

Table 1
Location, vegetation type and area of exclosed and unexclosed plots on the Muckross Peninsula, with date of exclosed plot establishment

Site	Location	Vegetation	Exclosed plot area (m ²)	Exclosed plot established	Unexclosed plot area (m ²)
R1	Reenadinna	<i>Taxus baccata</i> woodland	888	1969–1970	600
R2	Reenadinna	<i>Taxus baccata</i> – <i>Corylus avellana</i> woodland	764	1969–1970	600
R3	Reenadinna	<i>Taxus baccata</i> scrub woodland	1036	1969–1970	600
C1	Camillan	<i>Quercus petraea</i> – <i>Ilex aquifolium</i> woodland	1090	1969–1970	600
C2	Camillan	<i>Quercus petraea</i> – <i>Ilex aquifolium</i> woodland	959	1974	600
C3	Camillan	<i>Quercus petraea</i> – <i>Betula pubescens</i> woodland	260	1974	260
C4	Camillan	<i>Quercus petraea</i> – <i>Ilex aquifolium</i> woodland	225 ^a	1974–1975	225

^a This was a plot within a larger exclosure.

cleared of *R. ponticum* in 1972. The location of all exclosures is shown in Fig. 1.

Exclosure fences were approximately 2 m high, composed of wire stock netting topped with barbed wire and maintained throughout the course of the study. The exclosed plots were left unmanaged except for the removal of invasive exotics, in line with National Park policy. In Reenadonna Wood this consisted of the removal of three large *R. ponticum* bushes from exclosure R1 in the mid 1980s and the occasional removal of *Fagus sylvatica* seedlings. In Camillan Wood, *R. ponticum* is more of a problem and most of the plots have been subject to periodic management to this end. Outside the exclosures, there were no physical barriers to animal movement along the peninsula throughout the period that this experimental study was running.

2.3. Data collection

2.3.1. Seedlings and saplings

A base-line survey of natural regeneration in exclosures R1–R3 and C1 was conducted prior to fencing in 1969, and these exclosures were subsequently resurveyed at irregular (5–9 year) intervals until 1997 (Table 2). A restricted random sampling technique with 1 m × 1 m quadrats was employed, with new random co-ordinates being used for each survey. For all tree species the numbers of seedlings (height < 25 cm) and saplings (height ≥ 25 cm, DBH < 3.2 cm; BH = 1.3 m) present within each quadrat were recorded. The term juvenile will be used to refer to combined seedling and sapling data. To facilitate analysis the records spread over the years 1992–1994 (Table 2) were used combined as estimates for vegetation in 1993.

In summer 2001, to permit a comparison of grazed and ungrazed woodland, an unfenced site was established adjacent to each exclosure (Table 1). To avoid edge effects and paths worn by deer around exclosures, unfenced sites were positioned 2–3 m away from the fenceline. Due to the large size of exclosure C4, a 15 m × 15 m plot was established within the western part of this exclosure. Natural regeneration in all exclosed and unexclosed plots was again surveyed using a restricted random sampling method. In both woods sixty 1 m × 1 m quadrats were recorded in each treatment. In addition, the heights of all juvenile trees within each quadrat

were measured and an effort was made to locate and measure all juvenile *T. baccata* within each plot area.

2.3.2. Adult trees

In 1981 the adult tree class (DBH ≥ 3.2 cm) in exclosures R1–R3 and C1 was surveyed. Species, number of adult stems, DBH and position co-ordinates were recorded. In 2001, the adult tree class in all exclosures and unexclosed plots was re-surveyed. For exclosures R1–R3 and C1, maps drawn from the 1981 dataset were used to re-identify trees and note recruits and losses. The high abundance of *I. aquifolium* adults of DBH 3.2–6.1 cm in exclosure C2 necessitated that this class was subsampled using the 1 m × 1 m quadrats.

2.4. Data analysis

All statistical analysis was conducted using SPSS for Windows (SPSS Inc., Chicago). Linear regression analysis was used to test for changes over time; quadratic models could not be successfully fitted to the data. One-way ANOVA was used to test for differences in regeneration between fenced and unfenced plots in 2001. A variety of analyses were employed to test the adult tree data; where χ^2 analysis was used, likelihood-ratio tests were employed in preference to the Pearson statistic, as recommended by Sokal and Rohlf (1995).

3. Results

3.1. Seedlings and saplings

3.1.1. Reenadonna yew-wood

Between 1969 and 2001, the most frequent juveniles in the yew-wood exclosures were of *Ilex aquifolium*, *Fraxinus excelsior* and *Sorbus aucuparia* (Fig. 2). The density of *I. aquifolium* seedlings changed little during this period, whilst that of *S. aucuparia* declined slightly. *F. excelsior* seedlings increased significantly in density ($P = 0.039$, $R^2 = 0.17 \pm 2.5$, data for 1969–2001). *I. aquifolium* sapling density increased during the first 11 years of deer exclusion ($P = 0.001$, $R^2 = 0.10 \pm 1.1$, data for 1969–1980) but subsequently declined. *S. aucuparia* saplings showed a similar but delayed response ($P = 0.040$, $R^2 = 0.03 \pm 1.8$, data for 1969–1985). Saplings of *F. excelsior* were first recorded in 1985 and subsequently increased in density ($P < 0.001$, $R^2 = 0.06 \pm 0.5$, data for 1969–2001). Seedlings and saplings of *Betula pubescens*, *Crataegus monogyna*, *Corylus avellana* and *Euonymus europaeus* were also occasionally recorded during this period but at very low densities (<0.05 m⁻²). Notably, no *Taxus baccata* saplings and only three *T. baccata* seedlings were found, one each in 1980, 1993 and 2001 (in each year, overall density m⁻² = 0.02).

Seedling and sapling tree data displayed striking differences between fenced and unfenced plots in 2001. For *I. aquifolium* seedlings were more abundant in the unfenced sites (Fig. 3a), whereas for this species and for both *F. excelsior* and *S. aucuparia*, saplings were more abundant in the fenced sites (Fig. 3b). Consequently, for all three species

Table 2
Surveys of natural regeneration in exclosures R1–R3 and C1, 1969–1997

Year	Exclosures surveyed	No. of 1 m ² quadrats
1969	R1	8
	R2	12
	R3	10
	C1	9
1974	R1–R3, C1	10 per exclosure
1980	R1–R3, C1	15 per exclosure
1985	R1–R3, C1	15 per exclosure
1992	R3	15
1993	C1	15
1994	R1–R2	15 per exclosure
1997	C1	15

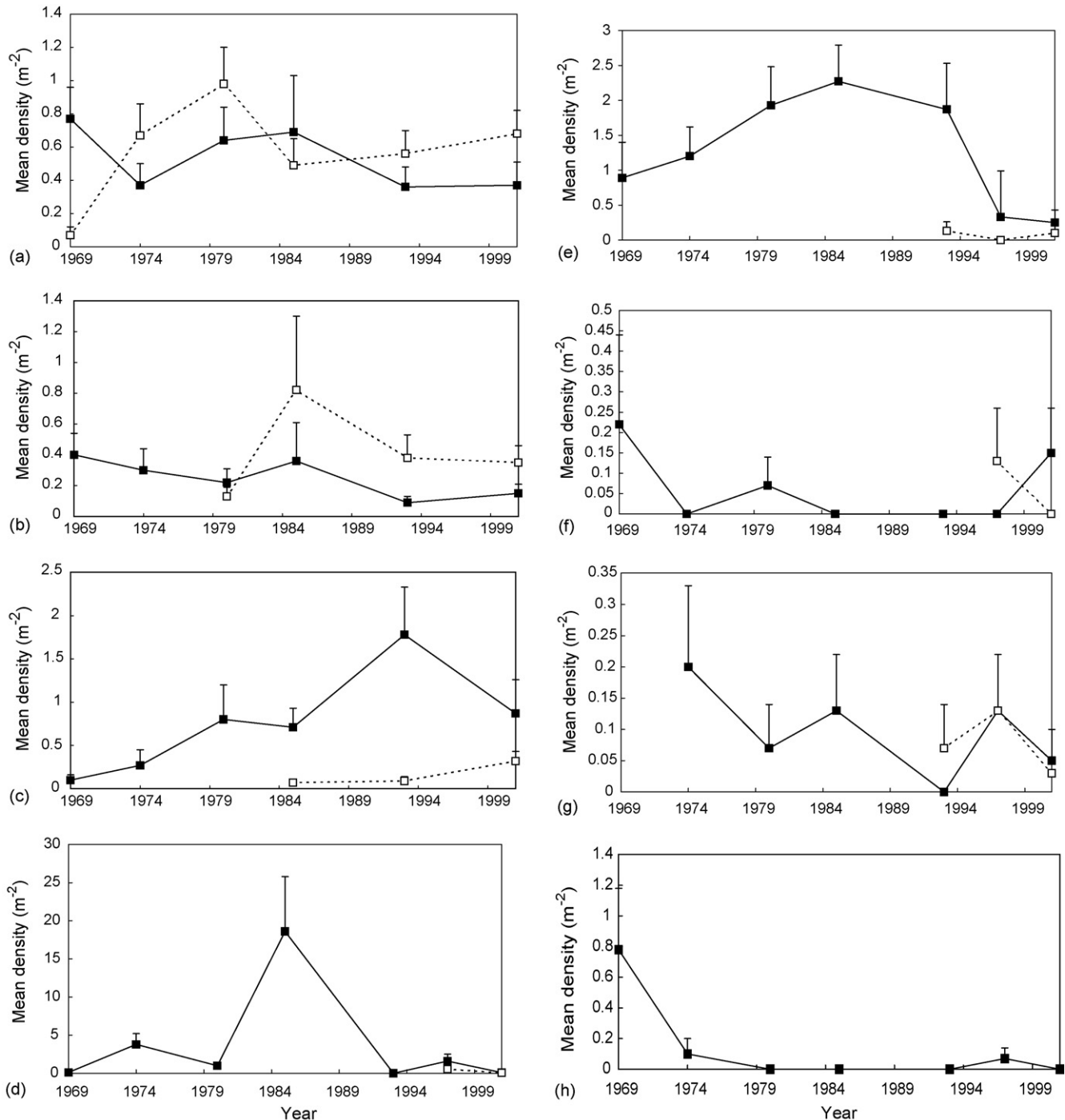


Fig. 2. Changes in densities of seedlings (closed squares) and saplings (open squares) between 1969 and 2001 of (a) *Ilex aquifolium*, (b) *Sorbus aucuparia* and (c) *Fraxinus excelsior* in Reenadinna Wood enclosures, and of (d) *Quercus petraea*, (e) *Ilex aquifolium*, (f) *Sorbus aucuparia*, (g) *Taxus baccata*, (h) *Betula pubescens* in Camillan Wood enclosure C1. Vertical bars indicate positive standard errors. Negative standard errors have been omitted for the sake of clarity.

mean juvenile height was greater in the fenced sites (Fig. 3c). No *T. baccata* saplings were recorded in either fenced or unfenced sites; the lack of significant difference between treatments in the density or height of *T. baccata* seedlings is influenced by this rarity.

3.1.2. Camillan oakwood

Between 1969 and 2001, oakwood data are only available for enclosure C1 (see Table 2), where the most frequent

seedlings and saplings were *Quercus petraea*, *I. aquifolium*, *S. aucuparia*, *T. baccata*, and *B. pubescens* (Fig. 2). There was considerable variation in the density of *Q. petraea* seedlings, with very high levels (18.6 seedlings m⁻²) recorded in 1985, due to the mast crop of 1984. This cohort may have produced the small number of saplings recorded in 1997 and 2001. *I. aquifolium* seedlings increased significantly following fencing ($P = 0.040$, $R^2 = 0.04 \pm 1.8$, data for 1969–1985). The subsequent decline was accompanied

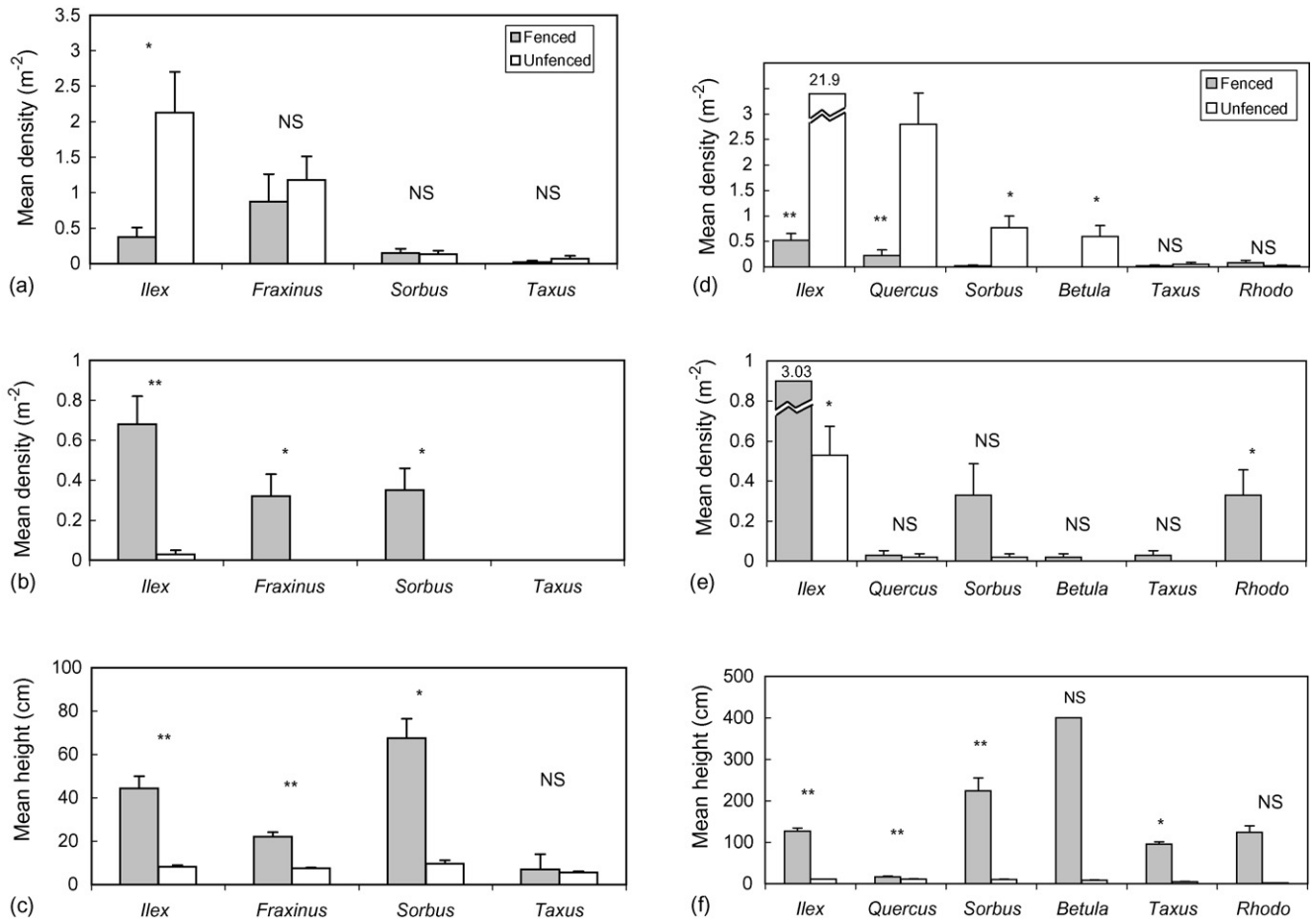


Fig. 3. Comparison of juvenile tree data for all fenced and unfenced plots in 2001. Reenadinna Wood data: (a) seedling density, (b) sapling density, (c) juvenile height. Camillan Wood data: (d) seedling density, (e) sapling density, (f) juvenile height. Labels indicate results of one-way ANOVA tests, ** $P < 0.001$, * $P < 0.05$, NS denotes not significant. Vertical bars indicate standard errors.

by the first recorded *I. aquifolium* saplings in 1993. *S. aucuparia* seedlings were infrequently recorded although saplings were recorded in 1997. Interestingly, *T. baccata* seedlings were not recorded prior to fencing, but subsequently were recorded fairly regularly at low densities and *T. baccata* saplings were recorded from 1993 onwards. *B. pubescens* seedlings declined in density following fencing ($P = 0.002$, $R^2 = 0.09 \pm 0.4$, data for 1969–2001); no *B. pubescens* saplings were recorded in this enclosure.

The survey of enclosures C1–C4 and the adjacent unfenced sites in 2001 revealed that seedlings of *I. aquifolium*, *Q. petraea*, *S. aucuparia* and *B. pubescens* were present at significantly higher densities in the unfenced plots (Fig. 3d), whereas saplings of *R. ponticum* and, in particular, *I. aquifolium* were far more abundant within the enclosures (Fig. 3e). There were no significant differences between treatment in the sapling densities of *Q. petraea*, *S. aucuparia*, *T. baccata*, or *B. pubescens*. The mean height of juveniles was significantly higher within the enclosures for *I. aquifolium*, *S. aucuparia*, *Q. petraea* and *T. baccata* (Fig. 3f). In the case of *Q. petraea* the difference was very slight but it was marked for the other species.

3.2. Adult trees

3.2.1. Reenadinna yew-wood

Between 1981 and 2001, the total density of adult trees in the Reenadinna enclosures decreased substantially whilst total basal area increased (Table 3). The overall mortality rate was 15.9% but there were significant differences in mortality between species ($P < 0.001$, likelihood-ratio χ^2 -test). *S. aucuparia*, *B. pubescens* and *C. avellana* exhibited the highest rates with a complete turnover in the *S. aucuparia* tree population. *F. excelsior* and *T. baccata* exhibited low mortality. The 1981 diameter of yew trees which died during this period ($0.08 \text{ m} \pm 0.03$) was significantly smaller than the diameter of those which survived ($0.25 \text{ m} \pm 0.13$; $P < 0.001$, one-way ANOVA); *T. baccata* was the only species which exhibited such a relationship.

Of all adult trees present in 2001, 5.5% were new recruits. There were highly significant differences in recruitment success between species ($P < 0.001$, likelihood-ratio χ^2 -test), with *I. aquifolium*, *S. aucuparia* and *C. avellana* forming the majority of recruits, and *T. baccata*, *F. excelsior* and *Q. robur* failing to produce any new adult trees. Regeneration via basal sprouting was largely limited to *C. avellana*, with a trend towards an

Table 3
Changes in stand structure of exclosures R1–R3 and C1 between 1981 and 2001

	No. of adult trees		Density (trees ha ⁻¹)		Basal area (m ² ha ⁻¹)		Mortality		Recruitment		Mean radial inc. (cm year ⁻¹)
	1981	2001	1981	2001	1981	2001	% of all losses	% of species	% of all recruits	% of species	
Exclosures R1–R3											
<i>Taxus baccata</i>	252 (64.8)	230 (66.3)	937.5	855.7	53.50 (88.1)	57.29 (90.0)	37.1	9.1	0.0	0.0	0.030 ± 0.003 ^{ab}
<i>Corylus avellana</i>	37 (9.5)	30 (8.6)	137.6	111.6	1.56 (2.6)	1.15 (1.8)	16.1	27.0	15.8	10.0	nc
<i>Fraxinus excelsior</i>	31 (8.0)	29 (8.4)	115.3	107.9	1.38 (2.3)	1.93 (3.0)	3.2	6.5	0.0	0.0	0.066 ± 0.007 ^{ab}
<i>Ilex aquifolium</i>	27 (6.9)	35 (10.1)	100.4	130.2	0.56 (0.9)	0.63 (1.0)	4.8	11.1	57.8	31.4	0.027 ± 0.006 ^{ab}
<i>Betula pubescens</i>	21 (5.4)	4 (1.2)	78.1	14.9	1.38 (2.3)	0.56 (0.9)	29.0	85.7	5.3	25.0	0.074 ± 0.031 ^a
<i>Crataegus monogyna</i>	10 (2.6)	8 (2.3)	37.2	29.8	0.11 (0.2)	0.11 (0.2)	4.8	20.0	5.3	12.5	0.014 ± 0.007 ^b
<i>Quercus robur</i>	8 (2.1)	7 (2.0)	29.8	26.0	2.27 (3.7)	2.01 (3.2)	1.6	12.5	0.0	0.0	0.041 ± 0.012 ^{ab}
<i>Sorbus aucuparia</i>	2 (0.5)	3 (0.9)	7.4	11.2	0.03 (0.05)	0.01 (0.02)	3.2	100.0	15.8	100.0	nc
<i>Euonymus europaeus</i>	1 (0.3)	1 (0.3)	3.7	3.7	0.01 (0.02)	0.01 (0.02)	0.0	0.0	0.0	0.0	nc
All species	389	347	1447.2	1290.9	60.75	63.69	–	15.9	–	5.5	–
Exclosure C1											
<i>Ilex aquifolium</i>	116 (80.6)	90 (77.6)	1064.2	825.7	18.36 (33.3)	16.25 (29.3)	92.9	22.4	0	0	0.021 ± 0.006
<i>Quercus petraea</i>	25 (17.4)	24 (20.7)	229.4	220.2	36.63 (66.3)	39.13 (70.5)	3.6	4.0	0	0	0.037 ± 0.012
<i>Sorbus aucuparia</i>	3 (2.0)	2 (1.7)	27.5	18.3	0.22 (0.4)	0.16 (0.2)	3.6	33.3	0	0	0.004 ± 0.012
All species	144	116	1321.1	1064.2	55.21	55.54	–	19.4	–	0	–

Figures in parentheses are percentages. For mean radial increment, superscript letters indicate homogeneous subset according to Tukey's HSD post hoc test. nc indicates not calculated.

increasing number of stems per adult hazel tree between 1981 (median = 2, mean = 2.65) and 2001 (median = 3, mean = 3.23; $P = 0.095$, Mann–Whitney test).

These species-specific differences in mortality and recruitment resulted in a trend towards an overall change in the adult tree species composition in the Reenadonna exclosures ($P = 0.093$, likelihood-ratio χ^2 -test), with an increase in the percentage of *I. aquifolium* (+3.2%), *T. baccata* (+1.5%) and *F. excelsior* (+0.4%) and a decrease in the percentage of *B. pubescens* (–4.2%) and *C. avellana* (–0.9%). Changes in the diameter frequency distribution of *T. baccata* between 1981 and 2001 were significant ($P = 0.032$, Kolmogorov–Smirnov test) due to the lack of recent recruitment and the high mortality of the younger trees. There was however no significant difference in the diameter frequency distribution of *T. baccata* between fenced and unfenced plots in 2001 ($P = 0.103$, Kolmogorov–Smirnov test), indicating that deer exclusion had not had a significant effect on adult yew stand structure, nor was there a significant difference in adult tree species composition between exclosed and unexclosed plots (Table 4; $P = 0.169$, likelihood-ratio χ^2 -test).

Radial growth rate between 1981 and 2001 was calculated for individual trees and it was found that there were significant differences between species means (Table 3; $P < 0.001$, one-way ANOVA). *B. pubescens* was the fastest growing tree although *F. excelsior* also displayed a high growth rate. *T. baccata* had a growth rate of 0.03 cm year⁻¹, comparable to that of *I. aquifolium* and *Q. robur*, whilst *C. monogyna* was the slowest growing tree. *C. avellana* was excluded from this analysis as individual stems could not be re-identified with confidence. *S. aucuparia* and *E. europaeus* were excluded due to insufficient numbers.

3.2.2. Camillan oakwood

In exclosure C1, total density of adult trees decreased substantially between 1981 and 2001, but the change in total basal area was minimal (Table 3). Overall mortality was 19.4%, but *I. aquifolium* and *S. aucuparia* exhibited much higher mortality rates than *Q. petraea* ($P = 0.045$, likelihood-ratio χ^2 -test). There was no recruitment to the adult tree class, but abundant basal sprouting resulted in a significant increase in the mean number of adult stems per holly tree between 1981 (median = 1, mean = 1.12) and 2001 (median = 1, mean = 1.60; $P < 0.001$, Mann–Whitney test). Despite the loss of a large number of holly trees the overall change in the adult tree species composition was not significant ($P = 0.782$, likelihood-ratio χ^2 -test). Neither were there significant differences between species in radial growth rate ($P = 0.429$, one-way ANOVA).

At sites C1–C4, there were highly significant differences in adult tree species composition between fenced and unfenced plots (Table 4; $P < 0.001$, likelihood-ratio χ^2 -test), primarily owing to the much greater *I. aquifolium* density in the exclosures. In addition, there were several species present within the exclosures that were absent from the unfenced plots, including *Alnus glutinosa*, *Arbutus unedo*, *Frangula alnus*, *Juniperus communis*, *Salix cinerea* and *T. baccata*. There was a highly significant difference in diameter frequency distribution

Table 4

Comparison of stand structure in fenced and unfenced plots in Reenadinna Wood (R1–R3) and Camillan Wood (C1–C4) in 2001

	Density (trees ha ⁻¹)				Basal area (m ² ha ⁻¹)			
	Reenadinna		Camillan		Reenadinna		Camillan	
	Fenced	Unfenced	Fenced	Unfenced	Fenced	Unfenced	Fenced	Unfenced
<i>Taxus baccata</i>	855.65	694.44	23.68	–	57.30	47.04	0.10	–
<i>Ilex aquifolium</i>	130.21	138.89	2470.40	504.45	0.63	0.80	15.07	13.31
<i>Fraxinus excelsior</i>	107.89	111.11	–	5.93	1.92	4.61	–	0.10
<i>Corylus avellana</i>	111.61	127.78	–	–	1.14	1.15	–	–
<i>Crataegus monogyna</i>	29.77	16.67	–	–	0.11	0.17	–	–
<i>Euonymus europaeus</i>	3.72	–	–	–	0.01	–	–	–
<i>Betula pubescens</i>	14.88	27.78	51.30	65.28	0.54	0.85	4.69	2.96
<i>Quercus robur</i>	26.04	11.11	–	–	2.01	1.25	–	–
<i>Quercus petraea</i>	–	–	122.34	148.37	–	–	32.53	35.57
<i>Sorbus aucuparia</i>	11.16	38.89	59.19	5.93	0.01	0.27	0.22	0.05
<i>Arbutus unedo</i>	–	–	3.95	–	–	–	0.01	–
<i>Alnus glutinosa</i>	–	–	19.73	–	–	–	0.10	–
<i>Frangula alnus</i>	–	–	3.95	–	–	–	0.01	–
<i>Juniperus communis</i>	–	–	3.95	–	–	–	0.03	–
<i>Rhododendron ponticum</i>	–	–	7.89	–	–	–	0.01	–
<i>Salix cinerea</i>	–	5.56	15.79	–	–	0.85	0.02	–
<i>Prunus avium</i>	–	5.56	–	–	–	0.05	–	–
<i>Malus sylvestris</i>	–	–	–	5.93	–	–	–	0.10
All species	1290.92	1177.78	2782.16	735.91	63.67	57.04	52.79	51.89

for *I. aquifolium* between fenced and unfenced plots ($P < 0.001$, Kolmogorov–Smirnov test), with many more young trees being present within the fences.

4. Discussion

4.1. Yew stand dynamics

Mitchell (1990a) showed via pollen analysis that a substantial *T. baccata* population has existed on the Muckcross Peninsula for about the last 5000 years, but suggested that the yew-wood in its present form may have arisen following the cessation of agricultural and industrial activities on the peninsula in the late eighteenth century. The evidence from the present study, that self-thinning of smaller stems and individuals is still occurring within the yew population, supports the idea of relatively recent origins. Barkham (1978) observed a similar pattern amongst *Q. robur* on Dartmoor; this is the aggradation phase of the model for forest development following major disturbance proposed by Bormann and Likens (1979). The mean radial growth rate for *T. baccata* from this study (0.03 cm year⁻¹) is markedly less than those reported by Hulme (1996) for English yew-woods of 0.10 cm year⁻¹. The skeletal soils on the limestone pavement of Reenadinna (Kelly, 1981) provide a likely explanation for the lower growth rate here.

Changes in tree species composition suggest that the wood is developing from scrub woodland in which *C. avellana* was prominent, at least locally, to a state more strongly dominated by *T. baccata* and *F. excelsior*. *C. avellana* is a constant associate of *T. baccata* in Irish semi-natural habitats (Perrin, 2002) and far more abundant than either *J. communis* or *C. monogyna*, which Watt (1926) showed served as spiny nurse

shrubs to yew saplings in southern England. *C. avellana* is absent from the floristic table for W13 *Taxus baccata* woodland presented by Rodwell (1991); however, Hulme (1996) reports it as present in the limestone yew communities in Co. Durham. Furthermore, there is palaeoecological evidence for *C. avellana* scrub being a seral precursor to *T. baccata* dominated woodland in southern England (Peglar, 1993; Waller and Hamilton, 2000).

4.2. Natural regeneration

Despite being highly toxic to some animals, particularly cattle and horses, yew foliage is freely eaten by deer, goats, hares and rabbits (Watt, 1926; Edlin, 1965; Rodwell, 1991; Thomas and Polwart, 2003). Mysterud and Østbye (2004) found that roe deer browsing pressure was strongly limiting yew recruitment in Norwegian nature reserves. Deer browsing is clearly limiting *T. baccata* regeneration in Camillan Wood; a striking finding of this study was the occurrence of several vigorous *T. baccata* saplings within the oakwood exclosures and the recruitment of *T. baccata* to the adult tree class in some of these exclosures. Similarly, self-sown *T. baccata* 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 and on some of the small, ungrazed islands in the Killarney lakes, as was described by Turner and Watt (1939). Ferguson and 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. Interestingly, *T. baccata* regeneration was not recorded in the experimental exclosures in Tomies Wood in the northwest of the National Park (Kelly, 2000, 2002) possibly because of a lack of seed sources in the vicinity. In Reenadinna

Wood, deer browsing alone is not responsible for the paucity of *T. baccata* regeneration because regeneration was negligible within the exclosures. *T. baccata* is reported as being a highly shade tolerant species (Packham and Harding, 1982; Rodwell, 1991; Brzeziecki and Kienast, 1994; Thomas and Polwart, 2003) and saplings grown experimentally under artificial shade develop several of the morphological adaptations characteristic of shade-tolerance (Perrin, 2002). This tolerance permits the species to regenerate freely beneath a deciduous canopy, but apparently is insufficient to permit regeneration beneath the heavy year-round shade cast by the evergreen yew-wood canopy. Svenning and Magard (1999) found recruitment to the sapling stage was reduced under dense canopy in Denmark. Mitchell (1990b) found evidence that *T. baccata* may act as a gap opportunist, although it has so far failed to take advantage of the main canopy gap event that occurred during the course of the present study, the demise of a small group of *B. pubescens* in exclosure R3. It has also been suggested that yew-woods regenerate primarily from the margins where light conditions are more favourable (Watt, 1926; Smith, 1980). This is difficult to assess at Reenadinna, where the yew-wood occupies almost all of the exposed limestone reefs, being bordered by either marsh, lake or managed grassland. Evidence from this study does, however, support the theory that light conditions within yew-woods are not favourable to regeneration of *T. baccata*.

Fencing in Camillan failed to promote *Q. petraea* regeneration significantly, supporting the findings of previous studies that oak does not freely regenerate beneath an oak canopy, at least in more oceanic regions (cf. Kelly, 2002; Krahl-Urban, 1959). Restriction of *Q. petraea* 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 and Kausch, 1995). Failure of fencing to promote oak regeneration within woodland was similarly found by Barkham (1978) at Wistman's Wood, Dartmoor and by Linhart and Whelan (1980) at Coed Gorswen, North Wales, where increased shade from *Rubus fruticosus* was thought to be partially responsible. Pigott (1983) recorded successful regeneration of *Q. petraea* under a canopy of the same species in his Pennines exclosure; however this woodland was only 5–12 m high and had an unusually favourable light regime.

Despite its spiny leaves, *I. aquifolium* is palatable to many species (Peterken and 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 *I. aquifolium* by sheep and deer is responsible for its scarcity in the shrub layer of many western oakwoods in Britain (Mitchell and Kirby, 1990; Mitchell et al., 1996). Even small *I. aquifolium* seedlings are remarkably tolerant to browsing, however, and Peterken and 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 50 cm high". This accurately describes several of the unexclosed Camillan plots where very high densities of small (<30 cm) gnarled *I. aquifolium* plants are almost the sole components of the field layer. Deer

exclusion appears to have released this high density bed of established plants with the result that impenetrable holly thickets have formed in many of the exclosures. In Tomies Wood, Kelly (2000) also found that dense holly thickets 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. *I. aquifolium* is a shade-tolerant species (Peterken and Lloyd, 1967) and evidently able to establish saplings under a closed oak canopy. In exclosure C1, *I. aquifolium* responded weakly to fencing in comparison with the other oakwood exclosures as regeneration here was almost entirely restricted to basal sprouting from mature *I. aquifolium* trees; this may have been due to higher competition in the field layer from *Vaccinium myrtillus* and *Luzula sylvatica* which were both abundant in this exclosure (Perrin, 2002). Kirby et al. (1994) reported that a dense *I. aquifolium* understorey formed in several English woods following the cessation of grazing. 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. *I. aquifolium* is evidently able to endure the shade of the yew-wood canopy as well as the scanty soil.

Marked increases in *F. excelsior* regeneration in the event of stock exclusion have been reported from British woods by Linhart and Whelan (1980) and Latham and Blackstock (1998). *F. excelsior* is a highly palatable species, but very resilient to browsing and able to compensate repeatedly for lost growth (Mitchell et al., 1996; Hester et al., 1996). Although fencing increased *F. excelsior* regeneration it did not respond as strongly as *I. aquifolium* or *S. aucuparia*; whilst ash seedlings are tolerant of canopy shade and may persist for many years, they do not make effective height growth until the occurrence of a canopy gap (Wardle, 1961). For example, Gardner (1975) found stunted *F. excelsior* saplings 15–28 years old beneath an ashwood canopy in Derbyshire.

Soil disturbance, typically by large herbivores, is known to be important for regeneration of *Betula* spp. (Kinnaid, 1974; Miles and Kinnaid, 1979; Pigott, 1983; Hester et al., 1996; Henderson et al., 1997), these are also light-demanding species. It is therefore unsurprising that *B. pubescens* responded poorly to the exclusion of deer in Camillan. In comparison, a dense birch stand developed in the exclosed clearfell in Tomies oakwood (Kelly, 2002).

S. aucuparia is regenerating successfully in the exclosures in both woodlands. Pigott (1983) noted that established rowan seedlings are more shade-tolerant than either birch or oak.

4.3. Management

The experiments in this paper have demonstrated that heavy grazing pressure, chiefly exerted by deer, is having a major impact on natural regeneration in Killarney National Park. The extreme scarcity of natural tree regeneration is distorting the natural ecology of the Killarney woods. High levels of grazing favour the regeneration of unpalatable species (e.g. the aliens *F. sylvatica* and *R. ponticum*) and also the canopy dominance of

long-lived trees, such as *T. baccata* and *Q. petraea*, which became established before the advent of high grazing pressure. The preponderance of oak in the acidic Killarney woods has undoubtedly been accentuated by 18th–19th century silviculture (Watts, 1984), but this preponderance is reinforced by 20th–21st century grazing levels. It may be speculated, based on the data presented, that a continuation of high grazing pressure in Reenadinna Wood will result in an increasingly monospecific canopy as *T. baccata* persists whilst shorter lived species decline.

The complete cessation of grazing via fencing, however, is now widely considered as undesirable, except as a short-term measure in heavily degraded or deforested areas (Hester et al., 2000), preferably whilst more lasting solutions are put in place. Grazing animals, namely red deer and the extinct wild boar (*Sus scrofa* L.), would have historically been present within Irish woodlands as an integral part of the ecosystem. Furthermore, whilst the sudden absence of grazing benefits established tree seedlings, the development of dense ground vegetation, moss and litter layers can prevent subsequent seedling establishment through the elimination of microniches (Miles and Kinnaird, 1979). 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 fairly long-term maintenance commitments (Sykes, 1992).

An alternative approach is to reduce animal numbers to levels where browsing of sapling stems is light, but trampling and grazing of the field layer is sufficient to allow continued seedling establishment. Manipulation of stocking density and seasonality of grazing can identify such thresholds for domestic herbivores (e.g. Hester et al., 1996; Mitchell et al., 1996). Where wild or feral herbivores are involved, systematic culling may be employed (e.g. Staines et al., 1995; Scott et al., 2000). Threshold densities will vary though with the species of grazer and the species of the regenerating tree.

However, the data presented here for *T. baccata* and *Q. petraea* demonstrate that regeneration success is not a simple function of grazing intensity. Other influential factors may include distance and abundance of seed sources (Scott et al., 2000; Smith, 2003) and post-dispersal seed predation (Hulme, 1996). Canopy cover in particular is likely to play an important role (e.g. Vickers and Palmer, 2000; Palmer et al., 2004). As found by Senn and Suter (2003), it is important not to assume that herbivore browsing is the only factor contributing to poor regeneration, which may be a variable and irregular process both spatially and temporally. Reenadinna Wood has an aggrading stand structure with adult tree mortality largely occurring within the smaller size classes. As a result, canopy gaps are likely to be small and infrequent. As the stand structure matures, it may be speculated that mortality of larger trees will increase and so will the occurrence of larger gaps. If grazing levels permit, this will lead to a change in patterns of regeneration.

5. Conclusions

This 32 year experiment has shown that natural regeneration of several species can occur beneath a yew-wood canopy in the

absence of grazing, although *T. baccata* itself is unable to do so. Natural regeneration of several species, including *T. baccata*, can occur beneath an oakwood canopy, although, as has been shown in other studies, *Q. petraea* is unable to do so. Chronic heavy grazing in and around the Killarney woodlands is strongly suppressing natural regeneration.

From the conclusions derived from Killarney we may draw wider implications for the management of other woodlands in temperate ecosystems subjected to heavy grazing. Information on threshold densities, and indeed on natural grazing levels, is required if woodland managers are to decide upon suitable stocking levels, and we strongly recommend future studies to investigate the effects of manipulation of grazing intensity on natural regeneration. It is important to recognise, however, that grazing is not the only factor influencing regeneration and we therefore also recommend that management plans for heavily grazed woodlands incorporate investigations into the reasons for regeneration failure.

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