Forest Ecology and Management 321 (2014) 52–60

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Spatial patterns of natural regeneration in stands of English yew (*Taxus baccata* L.); Negative neighbourhood effects

John L. Devaney [a,*], Marcel A.K. Jansen [a], Pádraig M. Whelan [a,b]

[a] School of Biological, Earth and Environmental Sciences (BEES), University College Cork, Ireland
[b] Environmental Research Institute (ERI), University College Cork, Lee Road, Cork, Ireland

ARTICLE INFO

Article history:
Available online 31 July 2013

Keywords:
Neighbourhood effects
Yew *Taxus baccata*
Natural regeneration
Forest management
Conservation

ABSTRACT

Understanding the mechanisms underlying spatial patterns of regeneration of tree species can improve the effectiveness of forest management and restoration activities. English yew (*Taxus baccata* L.) stands have declined across their native range and yew dominated woodlands have priority status under the EU Habitats Directive. Several conservation and restoration programmes for this species have been established. We investigated population structure and spatial distribution of natural regeneration of yew at six woodlands in the south and west of Ireland. Specifically, the influence of adult conspecific neighbourhood density, canopy cover and distance from seed source on regeneration was explored. Within each site, canopy openness, soil and vegetation characteristics were established. Weiner spatial analysis revealed that the density of conspecific adults was negatively related to the recruitment of yew juveniles. In addition, a significant negative relationship between presence of conspecific canopy cover and regeneration density was evident. Although seedlings and saplings were scarce directly beneath conspecifics, regeneration was highest in nearby areas suggesting that intermediate dispersal distance maximises recruitment probability. Yew regeneration was correlated with a number of habitat characteristics, particularly percentage cover of woody shrubs. Management operations should focus on regeneration around the edges of populations to conserve existing yew stands.

1. Introduction

Numerous studies have highlighted the importance of spatial patterns of recruitment for population dynamics of tree species (Barton, 1993; Stoll et al., 1994; Camarero et al., 2005). The spatial distribution of tree regeneration is influenced by a number of factors, but is principally controlled by mechanisms of seed dispersal and the availability of suitable microsites for germination and survival (Schupp, 1995; Nathan and Muller-Landau, 2000). The identification of factors influencing spatial patterns of natural regeneration is necessary to successfully design and implement conservation and management strategies for tree species and/or forested habitats (Rodriguez-Garcia et al., 2010).

It is well established that, in general, the quantity of dispersed seeds decreases as distance from the parent plant increases (Janzen, 1970). However, in many tree species a simple negative relationship between establishment of seedlings and distance from parent tree is not obvious (Wada et al., 2000). In some cases, density of regeneration is reduced in proximity to parent plants (Wada and Ribbens, 1997). Parent trees may promote or hinder germination and growth of juveniles and alter conditions for subsequent recruitment by modifying habitat characteristics such as light, vegetation composition and soil nutrient and water availability (Frelich et al., 1998; Nagashima, 1999). It has been proposed that for many tree species recruitment success is influenced by neighbourhood effects exerted by adult conspecifics (Janzen, 1970; Connell, 1971; Duncan, 1991; Frelich and Reich, 1999).

English yew (*Taxus baccata* L.) is a dioecious gymnosperm, occurring throughout Europe with scattered populations extending to North Africa and the Middle East (Lewandowski et al., 1995; Thomas and Polwart, 2003). While its geographic distribution remains wide, yew has declined over the last number of millennia, with populations becoming isolated or locally extinct in many areas (Dubreuil et al., 2008; Myking et al., 2009). Concerns have been raised regarding the conservation status of natural populations of the species (Dhar et al., 2006; Iszkulo et al., 2009; Linares, 2013). As a species, yew is now legally protected in many countries and is included in several national Red Data Books (Hageneder, 2007). Due to its rarity, yew dominated woodland has been afforded priority status under the EU Habitats Directive (European Commission, 2007). Indeed, programmes aimed at conserving and restoring yew populations have been established throughout its native range (Dhar et al., 2007; Piovesan et al., 2009).

Whilst extensive felling is undoubtedly a primary factor in the decline of yew (Tittensor, 1980; Svenning and Magård, 1999), an

* Corresponding author. Tel.: +353 214904617.
E-mail address: j.devaney@ucc.ie (J.L. Devaney).

0378-1127/$ - see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2013.06.060

absence of regeneration has been noted in extant populations (Garcia and Obeso, 2003; Mysterud and Ostbye, 2004). Recent research efforts have focused on the regeneration biology of yew, and particularly on identifying factors that may limit recruitment success such as seed predation, overgrazing by ungulates, genetic isolation and intraspecific competition (Hulme, 1996; Hilfiker et al., 2004; Perrin et al., 2006; Farris and Filigheddu, 2008; Piovesan et al., 2009). It has been proposed that high densities of adult conspecifics have a negative effect on recruitment success in yew (Piovesan et al., 2009). Watt (1926) reported that yew regeneration was poor beneath its own canopy and instead invaded areas around the edge of the wood amongst scrub species such as *Juniperus communis* L. and *Crataegus monogyna* Jacq. Smal and Fairley (1980) reported that up to 4 million yew seeds ha^{-1} fall each year on the ground in Reenadina Wood, an extensive yew woodland in southwest Ireland. Despite such high levels of seed input, Perrin et al. (2006) found that conspecific regeneration beneath yew canopies was almost entirely absent, even following the exclusion of herbivores. Several reasons for this lack of regeneration have been hypothesised including low light availability and autotoxicity (Smith, 1980; Svenning and Magård, 1999; Thomas and Polwart, 2003). However, the extent to which conspecific neighbourhood density and availability of suitable microsites influence spatial patterns of regeneration of yew remains poorly understood.

Previous studies have highlighted the effect of herbivory on the spatial distribution of yew regeneration, with recruitment being reduced in areas subject to large herbivore grazing (Mysterud and Ostbye, 1995, 2004; Perrin et al., 2006; Farris and Filigheddu, 2008; Perrin et al., 2011). To separate the effects of grazing from the regeneration process, the objective of this study was to investigate spatial patterns of regeneration in yew populations in the absence of heavy grazing pressure. The specific objectives were to: (i) determine the population structure of yew at six woodlands in Ireland; (ii) quantify the influence of adult neighbourhood density, canopy cover and distance from seed source on regeneration success; (iii) identify habitat characteristics associated with regeneration in yew. The findings are discussed in the context of conservation and restoration strategies of yew populations.

2. Methods

2.1. Study areas

Based on previous studies (McKenna, 2003; O'Neill, 2003; Perrin, 2003; O'Mahony, 2009) and preliminary field visits, six woodlands where yew was present as a canopy tree species were selected for study (Table 1). To investigate potential negative intraspecific neighbourhood effects, woodlands were selected to represent a gradient of adult yew density. This study aimed to investigate the spatial patterns of yew regeneration where grazing is minimal and therefore, only sites with low grazing pressure were chosen for assessment (Table 1).

Glengarriff is a 453.7 ha *Quercus petraea* (Matt.) Liebl. dominated woodland on sandstone bedrock in southwest Ireland. Individual adult yews are infrequent and generally occur on shallow soils as a sub-canopy species. Fota is a small (4.9 ha), dense, mixed broadleaf woodland where non-native *Fagus sylvatica* L. and *Acer pseudoplatanus* L. dominate the canopy. Adult yew are scattered throughout the understory. Occurring towards the eastern limit of the Burren landscape, the Castletaylor complex (74.4 ha) contains a diverse range of habitats including limestone pavement, orchid-rich calcareous grassland, and juniper scrub. The study site is composed of a 2.62 ha transitional scrub woodland of *Fraxinus excelsior* L., *Sorbus aria* L., and yew. Situated east of Askeaton, Co. Limerick, the Curraghchase woodland (378.3 ha) consists of mixed deciduous woods and conifer stands. Where the limestone bedrock becomes shallow, a 1.88 ha area of yew predominates along a steep river valley. Garryland is a 315.3 ha *Quercus robur* L. and *F. excelsior* woodland, occurring on shallow limestone soils, with large areas planted with *F. sylvatica* and other non-native tree species. Yew dominates on a number of small limestone outcrops ranging from 0.1 to 0.3 ha in size. Reenadina is recognised as the most extensive area of yew woodland in Ireland. Occurring within the predominantly acidophilus *Quercus petraea* dominated Killarney woodland (1188.5 ha), Reenadina is a 25 ha area of yew dominated woodland on outcropping limestone. The climate at all sites is extreme oceanic, with cool summers and mild winters. The mean maximum temperature of the hottest month ranges from 16.4 °C at Curraghchase to 15.3 °C at Fota (Met Eireann, unpublished data, 1981–2010). The mean minimum temperature of the coldest month ranges from 5.3 °C at Garryland to 7.4 °C at Glengarriff (Met Eireann, unpublished data, 1981–2010). Mean rainfall is highest at Reenadina (1557 mm $year^{-1}$) and lowest at Curraghchase (977 mm $year^{-1}$; Met Eireann, unpublished data, 1981–2010).

2.2. Population census

At each site, a plot of maximum size 60 × 60 m (0.36 ha) was established. At Fota and Garryland, plot size was limited due to boundary features such as roads and periodically inundated areas, which precluded seedling establishment. Plots were maintained at a minimum distance of 10 m from boundary features to minimise their effect on regeneration. At Reenadina, plot size was limited to 0.08 ha, as sampling took place within a permanent grazing exclosure of that size. The position and height of all yew individuals within each plot was recorded. Seedlings and saplings were classified into the following regeneration classes; seedlings (R1); 0–0.2 m, young saplings (R2); 0.2–0.5 m, saplings (R3); 0.5–2 m, juveniles (R4); 2–6 m. Adult trees were defined as yews greater than 6 m in height or with clear signs of sexual maturity.

2.3. Habitat characteristics

At each plot, 1–3 quadrats (0.01 ha) were randomly located to investigate habitat characteristics associated with natural regeneration in yew. If quadrats were intersecting, new random coordinates were generated to avoid any overlap. To determine percentage canopy openness within each quadrat, hemispherical photographs were taken at 50 cm above the surface of the soil using a fish-eye lens (Nikon Coolpix 5700 with Nikon FC-E9 fish

Table 1
Geographic location, plot size and habitat characteristics of study sites. Habitat type is based on Fossitt (2000) classification scheme.

No.	Site	Latitude/longitude	Size (ha)	Altitude (m)	Slope	Aspect	Soil type	Habitat type
1	Glengarriff	N 51°24.88′ W 009°54.63′	0.36	33	4	S	Peaty podzol	Oak – birch – holly woodland
2	Fota	N 51°88.96′ W 008°30.29′	0.13	8	10	NE	Grey brown podzolic	Mixed broadleaf woodland
3	Castletaylor	N 53°18.36′ W 008°81.06′	0.36	32	0	W	Rendzina/lithosol	Scrub woodland
4	Curraghchase	N 52°60.35′ W 008°87.00′	0.36	45	5	E	Rendzina/lithosol	Yew woodland
5	Garryland	N 53°08.12′ W 008°85.97′	0.16	31	2	SE	Rendzina/lithosol	Yew woodland
6	Reenadina	N 52°02.08′ W 009°51.48′	0.08	32	7	NW	Rendzina/lithosol	Yew woodland

eye converter). The camera was mounted on an upward-facing levelling device. Readings were taken at four uniformly spaced locations within quadrats and a mean percentage canopy openness value for each quadrat was calculated. To calculate values for percentage canopy openness, hemispherical photographs were analysed using Gap Light Analysis software (Frazer et al., 1999).

Soil cores were taken to a depth of 15 cm using a 5 cm diameter soil auger. As with canopy openness measurements, soil samples were taken at four uniformly spaced locations within each quadrat. Soil samples were immediately transferred to polythene bags and transported to the laboratory and stored at 4 °C. Following Allen (1989), pH was determined on fresh soil in aqueous suspension 1:2 soil: water ratio using an Orion 3 soil pH meter (Thermo Electron Co-operation, Singapore). Moisture content was measured gravimetrically by drying the soil at 40 °C to a constant weight (Allen, 1989). Soil depth was measured at four locations at each plot using a graduated steel rod (Dovciak et al., 2001). Above ground cover of vascular plants, total bryophyte cover, bare rock and bare soil was recorded in each quadrat according to the Domin scale (Dahl and Hadac, 1941).

2.4. Data analysis

Weiner spatial analysis (Weiner, 1984) was used to assess the influence of conspecific adult density on the spatial distribution of yew regeneration at the six woodlands. Following Wada and Ribbens (1997), plots were divided into 5 × 5 m subplots and neighbourhood influence W was calculated at the centre of each subplot. Weiner's neighbourhood influence statistic (Weiner, 1984) was calculated as:

$$W = \sum_{i=1}^{N} \frac{S_i}{d_i^2}$$

where N is defined as the total number of adult yew within 30 m of the centre of each subplot and d_i was calculated as the distance from the ith neighbour to the centre of the subplot. According to Weiner (1984), S_i is defined as size of the ith neighbour. Here, S_i is calculated as height of the ith neighbour. Following Bucci and Borghetti (1997), a yew Regeneration Index (RI) for each subplot was calculated as

$$RI = N^{*}AH$$

where N is density of yew regeneration m^{-2} (excluding adults) and AH is the average height of yew regeneration per subplot. The relationship between RI and distance to nearest conspecific adult was quantified. Due to non-normality of data, differences between RI at three distance classes (Near 0–5 m, Medium 5–15 m, and Far >15 m) were calculated using the non-parametric Kruskall–Wallis test for analysis of variance. *Post-hoc* Mann–Whitney U tests were applied where relevant. Spearman Rank correlation tests were carried out to explore relationships between habitat characteristics and yew regeneration variables. For analysis, Domin values were transformed to estimates of percentage cover using Currall's (1987) "Domin 2.6" method.

3. Results

3.1. Population structure

Natural regeneration was greater at sites with lower densities of adult conspecifics (Table 2, Fig. 1). A strikingly high density of yew seedlings and saplings were recorded at Glengarriff (Table 2). The population here was skewed towards young plants with >90% of plants being less than 1 m in height (Fig. 1). The yew population at Fota was dominated by young individuals, with densities of saplings and juveniles being greater than at other sites. At both Castletaylor and Curraghchase, most seedlings and sapling height classes were present, but at low densities (Fig. 1). A high density of adult yews were recorded at Garryland (94 ha^{-1}) and particularly Reenadina (475 ha^{-1}) (Table 2). However, only 81 and 26 regenerating individuals were recorded ha^{-1} at Garryland and Reenadina respectively, with saplings and juveniles being largely absent (Table 2).

Table 2
Total yew regeneration density ha^{-1} and regeneration density ha^{-1} at four regeneration classes (R1; 0–0.2 m, R2; 0.2–0.5 m, R3; 0.5–2 m, R4; 2–6 m) at study sites. Also indicated is no. of adult yew trees ha^{-1} at each site.

No.	Site	Yew regeneration ha^{-1}					Adult yew ha^{-1}
		Total	R1	R2	R3	R4	
1	Glengarriff	1962	631	717	592	22	3
2	Fota	753	38	77	308	331	15
3	Castletaylor	175	31	25	39	81	22
4	Curraghchase	281	19	28	100	133	25
5	Garryland	81	81	0	0	0	94
6	Reenadina	26	13	0	0	13	475
Mean		546	136	141	173	97	106

3.2. Spatial patterns of natural regeneration

Weiner spatial analysis revealed that yew regeneration was related to the density, size and proximity of adult conspecifics. Regeneration Index (RI) was highest in areas of neighbourhood influence (W) of between 0.01 and 1 (Fig. 2). With the exception of a number of subplots at Curraghchase, regeneration was absent in areas subject to a neighbourhood influence of greater than 1 (Fig. 2). Due to the high density of adult yews, neighbourhood influence (W) was highest at Garryland and Reenadina with values generally >1. RI was zero or minimal at these sites (Fig. 2), in contrast to other sites.

The direct relationship between yew RI and distance to nearest conspecific adult was also investigated (Fig. 3). Spatial distribution of regeneration followed a broadly similar curvilinear pattern at Glengarriff, Fota and Curraghchase (Fig. 3). In all areas, RI was low near (0–5 m) adult trees, increased to a maximum RI between 5 and 15 m and decreased in areas over ~20 m from nearest adult conspecific (Fig. 3). At Glengarriff, RI was significantly lower near adult trees when compared with medium and far distances ($H = 7.095$, $p = 0.029$) (Fig. 3). At Curraghchase, RI was significantly greater at medium distances when compared with areas near and far from adult yews ($H = 11.768$, $p = 0.003$) (Fig. 3). At Castletaylor, although RI was lowest in areas adjacent to adult trees, no clear spatial pattern of regeneration was apparent. At Garryland and Reenadina, due to the high densities of adult trees, no subplots were greater than 10 m away from adult yews and no spatial patterns of regeneration were evident.

3.3. Associations between yew regeneration and habitat characteristics

Correlation analysis revealed linkages between vegetation structure/composition at sites and yew RI (Table 3 and 4). However, the character of these relationships varied between regeneration classes (Table 4). Canopy cover of adult yew trees was negatively correlated with RI and density of yew saplings (R3). In contrast, the % canopy cover of broadleaf trees was positively correlated with yew regeneration at the sapling (R3) and juvenile (R4) stage (Table 4). Overall, yew regeneration (RI) was strongly correlated with shrub cover (Table 4). In particular, densities of young saplings (R2) and saplings (R3) were positively correlated with

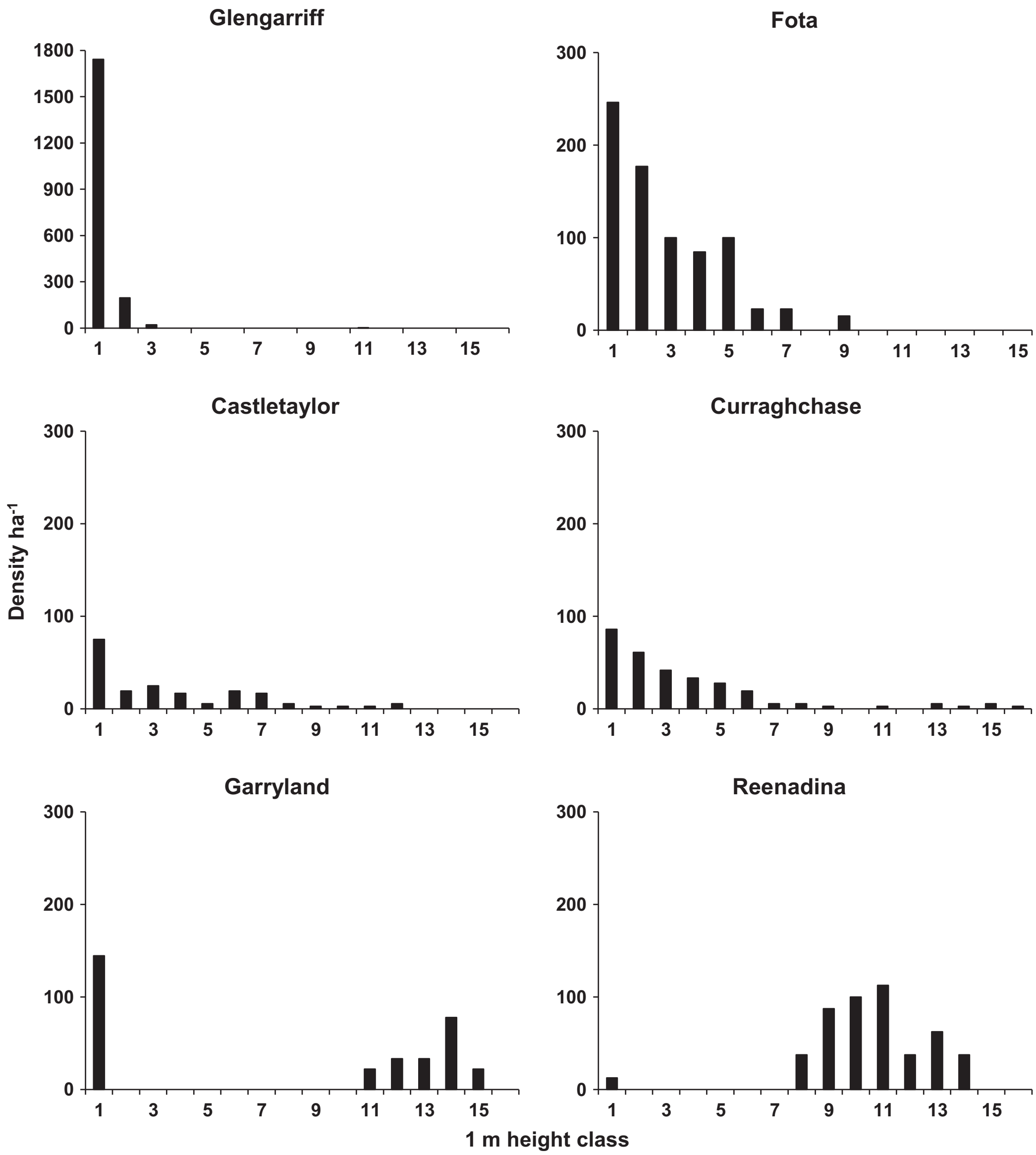

Fig. 1. Density (ha^{-1}) of yew in 1 m height classes at study sites. A different frequency axis was used for Glengarriff where regeneration was more abundant.

shrub cover. No such relationship was apparent for young seedlings (R1) and juveniles (R4; Table 4). The number of adult yew trees m^{-2} was negatively correlated with shrub cover (Table 4). RI was also positively correlated with percentage cover of forb species (Table 4). No significant correlations between densities of individual regeneration classes and forb cover was found, although we note borderline significance for the relationship between forb cover and densities of young sapling (R2) and saplings (R3) ($r = 0.736$, $p = 0.096$ and $r = 0.754$, $p = 0.084$ respectively). Density of young saplings was positively correlated with species richness. Conversely, density of adult trees was negatively correlated with species richness (Table 4). Despite the known association of yew woodland and limestone pavement habitat, density of large saplings (R3) was negatively correlated with bare rock. Juveniles (R4) were positively correlated with bryophyte cover (Table 4).

Percentage canopy openness varied amongst sites, from a dense closed canopy at Fota (11.22% openness) to an open canopy at Castletaylor (45.58% openness; Table 3). No relationship between canopy openness and regeneration was evident (Table 4). Soil pH was lowest at Glengarriff, an acidophilous oak woodland, and highest at Castletaylor (Table 4). In general, regeneration was more frequent in sites with a lower pH, although this relationship was not significant (Table 4). Similarly, no significant relationship between soil moisture and depth and yew regeneration was evident.

4. Discussion

4.1. Population structure

A high degree of variation in population structure and regeneration density between study sites was recorded. In particular, higher density of natural regeneration of young seedlings was recorded at Glengarriff. Compared to other areas where high levels of yew regeneration are reported (Hulme, 1996; Svenning and Magård, 1999; Giertych, 2000; Piovesan et al., 2009), a density of 1962 individuals' ha^{-1} exemplifies very high levels of yew regeneration. For example, in a study of a yew population in the Sierra Nevada

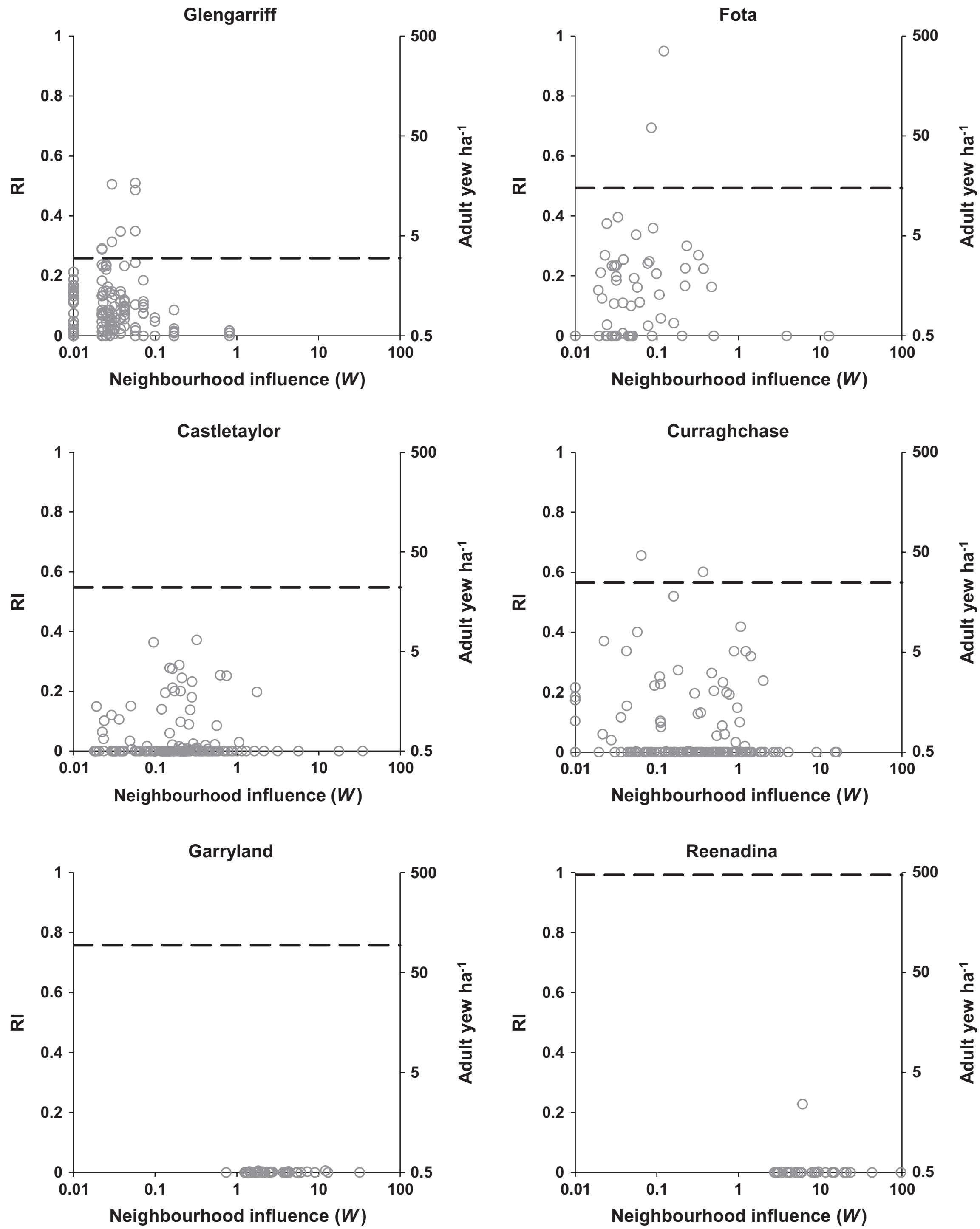

Fig. 2. Relationship between yew Regeneration Index (RI) and neighbourhood influence W at study sites. Dashed lines represent the density of adult yew trees ha^{-1} at each site, indicated on secondary y axis.

Mountains, Spain, Garcia et al. (2000) recorded densities of 287.9 individuals ha^{-1}. The high density of regeneration at Glengarriff is striking considering the probable low seed input due to the scarcity of adult yews at the site. Furthermore, the underlying sandstone geology of the Glengarriff area differs from the calcareous substrate commonly associated with areas of a high yew density. O'Neill (2003) previously noted the profusion of regeneration at Glengarriff, and attributed the abundance of yew seedlings and understory species such as *Ilex aquifolium* L. to management practices, specifically the removal of the invasive alien shrub *Rhododendron ponticum* L. As the population structure of yew at Glengarriff is highly skewed towards young individuals, the question remains as to whether these seedlings can cope sufficiently with competing species and achieve recruitment to the adult phase. In contrast, an almost complete absence of regeneration was recorded at Reenadina and Garryland. These sites represent fully developed yew dominated woodlands as described by the Habitats Directive (European Commission, 2007). The absence of regeneration at these sites, where the canopy is comprised almost entirely of yew, is comparable with other such woodlands in

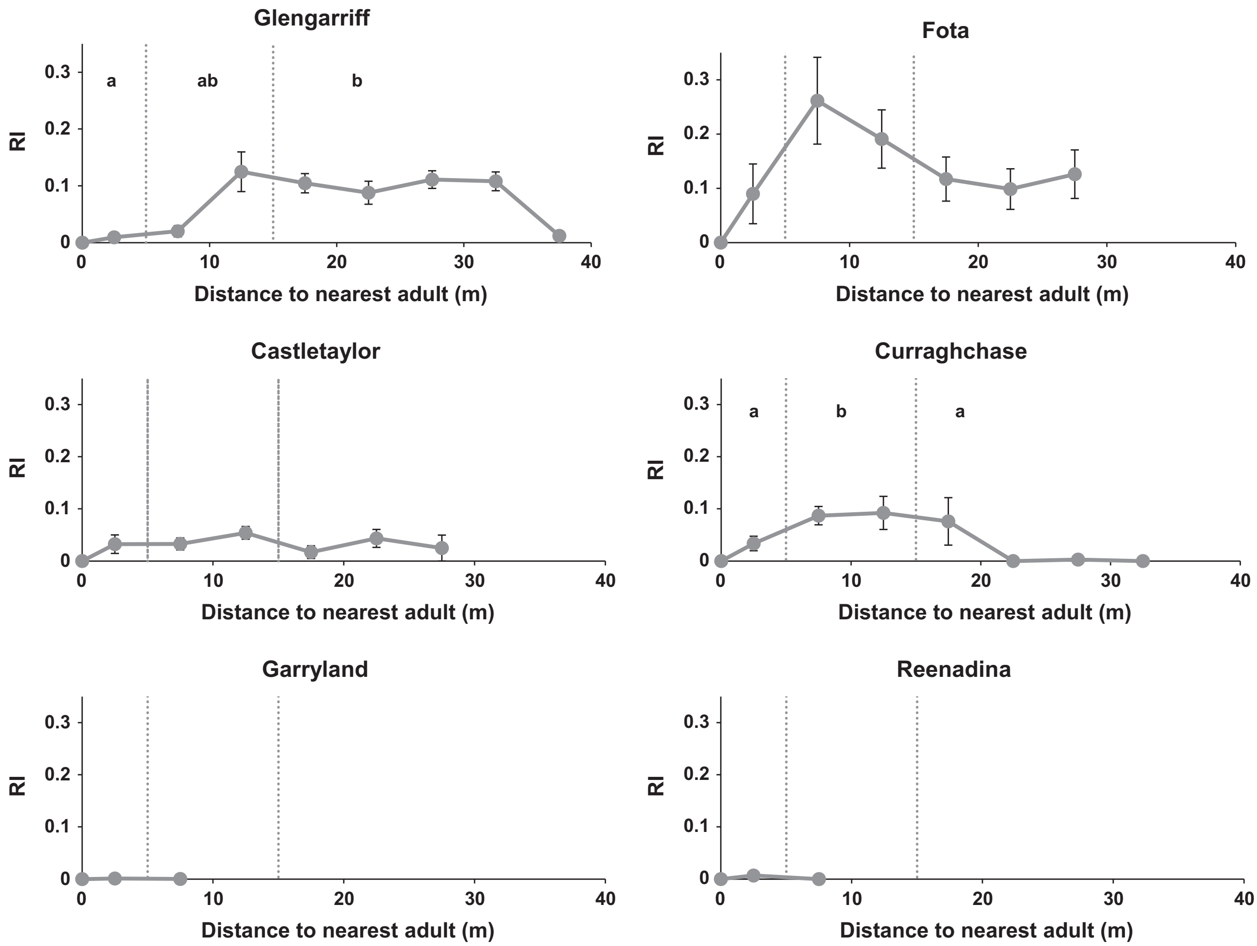

Fig. 3. Relationship between yew Regeneration Index (RI) and distance to nearest adult yew at study sites. Dashed lines represent categories of distance from adult trees (Near; 0–5 m, Medium; 5–15 m, Far; >15 m;). Kruskall–Wallis with *post hoc* Mann Whitney tests were performed to determine differences between RI densities within each distance category (Glengarriff $H = 7.095$, $p = 0.029$, Far > Near; Curraghchase $H = 11.768$, $p = 0.003$, Medium > Near, Far; relationship was not significant at other sites).

Britain (Watt, 1926; Williamson, 1978; Hulme, 1996). The presence of yews of all size classes at Curraghchase and Castletaylor suggest that these sites are representative of an intermediate seral stage in the development of yew woodlands, as described by Watt (1926) and Tittensor (1980).

4.2. Spatial patterns of natural regeneration

The density of parent trees within forests may determine the spatial pattern and density of conspecific regeneration by mediating habitat characteristics. The question has previously been raised as to the extent to which negative intraspecific neighbourhood effects operate in stands of yew (Dovciak, 2002; Piovesan et al., 2009). Our results show a clear negative influence of adult tree proximity and canopy cover on density of yew offspring. Dovciak (2002) reported similar trends in spatial patterning of regeneration whereby high seedling density was associated with presence of adult trees but the direct influence by parent trees lead to a reduction in seedling number. In a study of *Fagus-Taxus* woods in the central Apennines, Piovesan et al. (2009) reported that while a low density of adult trees favoured regeneration at local scales (~10 m), high densities of established adults had a negative effect on regeneration. In our study, the distribution of regeneration of yew around potential parents was broadly similar to patterns predicted by the Janzen–Connell hypothesis (Janzen, 1970; Connell, 1971). While yew saplings were excluded from areas directly beneath the canopy of adult trees, regeneration was highest in nearby areas (~30 m) suggesting that intermediate distance from parent trees increases the likelihood of recruitment. At intermediate distances, intraspecific competitive constraints are reduced while seed input may remain sufficiently high to maximise recruitment probability.

Negative intraspecific neighbourhood effects have been reported in other tree species, with escape from intraspecific competition commonly cited as driving spatial distribution patterns (He and Duncan, 2000; Dovciak et al., 2001). For example, in North American beech – maple forests Fox (1977) found that despite seed input of *Fagus grandifolia* Ehrh. and *Acer saccharum* Marsh. being greater beneath conspecifics, saplings were more likely to establish beneath the canopies of the heterospecifics i.e. reciprocal replacement. In British Columbia, Canada, He and Duncan (2000) found that *Pseudotsuga menziesii* Mirb. survival was significantly higher in less dense patches of conspecifics. Similarly, poor seedling survival of *Quercus* species beneath mature conspecific stands is frequently noted (Watt, 1919; Lorimer et al., 1994; Kelly, 2002). In a study of *Quercus crispula* Blume regeneration in northern Japan, Wada et al. (2000), recorded high levels of seedling mortality beneath conspecific canopy cover. Successful establishment of seedlings and saplings often occurs through edge regeneration, whereby recruitment is higher in areas away from parent trees.

Table 3
Canopy openness (CO), soil data and vegetation characteristics of study plots at six woodlands. Values represent mean (±S.E.) values from quadrats at each site.

Site	*n* plots	Soil pH	% Soil moisture	Soil depth	Species richness	% CO	Canopy cover (%)			Shrub cover (%)	Forb cover (%)	Grass cover (%)	Fern cover (%)	Bryophyte cover (%)	Bare rock (%)	Bare soil (%)
							Yew	Other conifers	Broadleaves							
Glengarriff	3	3.5 ± 0.0	60.6 ± 8.5	12 ± 1.9	15 ± 1.2	20.34 ± 1.0	2.33 ± 1.5	0.33 ± 0.3	38.5 ± 2.3	37.7 ± 5.5	84.6 ± 6.3	2.3 ± 1.4	0	7.6 ± 5.2	0	5.6 ± 3.1
Fota	3	4.8 ± 0.2	20.3 ± 2.3	10.8 ± 1.2	12 ± 1.7	11.27 ± 0.7	7.66 ± 3.2	2.33 ± 2.3	68.33 ± 6.1	8.1 ± 5.0	21.4 ± 5.2	0	0.36 ± 0.31	0	0.03 ± 0.0	28.3 ± 3.3
Castletaylor	3	7.1 ± 0.1	61.2 ± 3.4	3.1 ± 1.7	15 ± 1.2	45.57 ± 10.5	7.33 ± 3.8	14.66 ± 9.2	7.33 ± 7.3	17.7 ± 1.9	10.2 ± 3.4	22.3 ± 11.3	0.06 ± 0.03	23.1 ± 11.3	24.4 ± 10.5	0.8 ± 0.1
Curraghchase	3	6.2 ± 0.1	51.8 ± 10.3	7.7 ± 0.6	15 ± 1.2	19.73 ± 0.6	8 ± 3.2	0	54.46 ± 5.4	17.7 ± 2.8	36.4 ± 5.7	0	0.04 ± 0.03	3.3 ± 0.3	0.4 ± 0.0	26.3 ± 5.3
Garryland	1	5.2	45.0	13.6	11	14.6	80	0	2	3.1	16.1	0	0	40.5	2	15
Reenadina	1	6.2	58.2	6.2	10	25.9	65	0	6.1	3	13.1	0	0	95.1	5.6	2

4.3. Natural regeneration and habitat characteristics

Direct comparisons of yew regeneration density and vegetation structure/composition at study sites highlighted characteristics common to areas with high levels of natural regeneration. Notably, yew regeneration and cover of conspecific canopy was negatively correlated. A number of reasons for a lack of regeneration beneath conspecific canopy cover have been proposed. For example, the dense, year round shade cast by adult yews has been linked with the absence of regeneration at these habitats (Rodwell, 1991). Recent research suggests that yew is able to regenerate beneath lighter canopies but gap conditions may be important in facilitating successful regeneration beneath its own dense canopy. Similarly, shade from other shade-causing species such as *Fagus sylvatica* may lead to a reduction in strobilus production and recruitment to the sapling stage in yew (Svenning and Magård, 1999). However, in the present study however, no relationship between regeneration density and overall canopy openness was found.

The potential for autotoxic mechanisms to operate in yew populations has also been raised in the literature (Smith, 1980; Svenning and Magård, 1999). For example, Iszkulo and Boratynski (2006) reported that an allelopathic influence of parent yew trees could negatively impact on seedling density beneath a conspecific canopy. The release of allelochemicals by yew would not be surprising, as the tree contains a range of secondary metabolites including taxoids and other diterpenoids for which cytotoxic activity has been reported (Appendino et al., 1992; 1993). Although the potential autotoxicity of yew has been repeatedly highlighted, until this is tested experimentally it "must remain an open question" (Smith, 1980).

The density of natural regeneration of yew and the abundance of shrubs were positively correlated, particularly for younger yew regeneration classes. The relationship between recruitment success in yew and the presence of shrub vegetation has previously been highlighted in the literature (Smith, 1980; Garcia et al., 2000; Farris and Filigheddu, 2008). Although yew is capable of invading grassland, the presence of shrub vegetation is required to ensure the establishment of regeneration and subsequent colonisation (Smith, 1980; Tittensor, 1980). The development of yew dominated woodland in the British Isles is commonly associated with the presence of shrub species such as *C. monogyna* (Rodwell, 1991). Indeed, in the first detailed study on the formation of yew woodlands, Watt (1926) frequently recorded the dead remains of *J. communis* at the base of established yew trees. Similarly, in Mediterranean habitats, work by Garcia and others (Garcia et al., 2000; Garcia and Obeso, 2003; Farris and Filigheddu, 2008) has outlined the facilitation of yew regeneration by nurse plants. Fleshy-fruited shrubs may act as sites of regeneration "nucleation" or "recruitment foci" (Pausas et al., 2006). A high density of perching structures associated with some shrubs, in the form of horizontal branches, can lead to increased seed deposition by birds. Nurse shrubs are known to afford regenerating yew seedlings protection from herbivores (Farris and Filigheddu, 2008). In this study, grazing activity at all study sites was low or absent yet a clear correlation between the shrub cover and yew regeneration was found suggesting that other factors such as the provision of suitable microsites for germination and early establishment may also be important. Shrubs may provide shaded conditions required for growth of some seedlings of coniferous species, which can be subject to photoinhibition (Ball et al., 1991; Oquist and Huner, 1991). Recent research suggests that yew regeneration may be subject to photoinhibition, particularly and younger life stages (Robakowski and Wyka, 2009).

Although shrub cover is positively correlated with yew regeneration, particularly at the seedling and sapling stage, adult yews were negatively correlated with shrub cover. Similarly, species

Table 4
Summary statistics from correlation analysis of habitat variables and yew regeneration (RI; Regeneration Index, R1; 0–0.2 m, R2; 0.2–0.5 m, R3; 0.5–2 m, R4; 2–6 m) and adult yew trees at the six study sites. Analysis was performed on mean values of variables from each site ($n = 6$).

Variable	Regeneration					Adult trees
	RI	R1	R2	R3	R4	
% CO	−0.2	0.145	0.029	−0.232	−0.088	−0.058
Soil pH	−0.371	−0.261	−0.235	−0.522	0.353	0.029
% Soil moisture	0.086	0.406	0.294	0.029	0.003	−0.319
Soil depth	0.257	0.493	0.059	0.203	−0.353	−0.029
Species richness	0.754	0.559	0.821*	0.676	0.582	−0.868*
Canopy cover						
Yew	−0.866*	−0.736	−0.794	−0.829*	−0.464	0.754
Other conifers	−0.02	0.313	0.313	0.455	0.37	−0.277
Broadleaves	0.647	0.029	0.677	0.829*	0.812*	−0.638
Shrub cover	0.943**	0.551	0.971**	0.812*	0.618	−0.958**
Forb cover	0.829*	0.319	0.736	0.754	0.265	−0.638
Grass cover	0.304	0.549	0.435	0.309	0.157	−0.463
Fern cover	0.213	−0.462	0.188	0.339	0.75	−0.216
Bryophyte cover	−0.771	−0.771	0.116	−0.677	0.812*	0.638
Bare rock	−0.769	−0.232	−0.647	−0.814*	−0.177	0.493
Bare soil	0.371	−0.261	0.177	0.377	0.353	−0.145

* Correlation is significant at the 0.05 level.
** Correlation is significant at the 0.01 level.

richness was positively correlated with seedling density, but negatively correlated with the presence of adult conspecifics. It is clear that conditions associated with natural regeneration of yew are dissimilar from those associated with high densities of adult trees. Discordance between factors influencing early growth of seedlings and recruitment to later life stages is not uncommon in tree species. In mixed deciduous and conifer forests in British Columbia, Coates (2002) found that conditions favourable to the germination and establishment of young seedlings differed to those favouring growth and survival of older seedlings and saplings. The author concluded that the abundance and composition of tree species within these forests is more likely controlled by differences between growth and survival niches than by regeneration niches.

No relationship between soil conditions and yew regeneration were recorded in this study. This finding, and the negative influence of dense yew canopy on regeneration, supports the hypothesis proposed by Linares (2013). Linares (2013) suggests that water availability is limiting yew regeneration at the southern margin of the species distribution, but shade may be more important in temperate areas.

4.4. Conclusions and implications for management and conservation

Results from this study provide insight into the structure and functioning of one of Europe's rarest forest types – yew woodland. Our study of regeneration dynamics in yew populations has shown that: (1) high densities of conspecific adults are negatively related to the recruitment likelihood of yew regeneration; (2) yew regeneration is reduced beneath conspecific canopies; (3) yew regeneration is correlated with woody shrub cover, although the strength of this relationship varies with life history stage. Information such as this, regarding the factors influencing regeneration of yew, will inform future conservation and management efforts.

Despite the long-lived nature of the species, many of the most extensive yew woodlands are thought to be single generation stands of relatively recent origin (Tittensor, 1980; Mitchell, 1990). Woodlands such as Reenadina and others may have developed following the cessation of agricultural practices leading to gradual colonisation of yew until canopy closure. This study shows that this precludes any subsequent conspecific regeneration. As discussed by Watt (1926) and others (Williamson, 1978; Thomas and Packham, 2007) the continued existence of a yew woodland is largely dependent on regeneration around the edges of the wood. Under natural conditions, yew woodlands can be viewed as even aged stands "moving" across the landscape via edge regeneration (Newbould, 1960; Thomas and Polwart, 2003).

Due to the negative neighbourhood influences reported here, the promotion of regeneration (natural and assisted) under conspecific canopies should be avoided. Although regeneration was scarce directly beneath adult yew trees, regeneration was highest in nearby areas, suggesting that intermediate dispersal distance maximises recruitment probability. Areas adjacent to existing yew stands are most likely to represent optimal sites for regeneration and, where possible, should be managed for this purpose. Density of yew regeneration was related to shrub cover which highlights a potential facilitative relationship. The creation of shrub vegetation in areas bordering yew populations may enhance recruitment through increased availability of suitable microsites, as well as affording seedlings protection from grazers.

Numerous studies have highlighted the negative effect of grazing on the establishment of yew regeneration (Mysterud and Ostbye, 1995, 2004; Perrin et al., 2006; Farris and Filigheddu, 2008). This study has shown that where grazing is naturally or artificially low, high levels of yew regeneration may occur; however, this is dependent on other factors such as density of adult conspecifics and canopy species. As the findings of this study are based on sites where herbivory is limited, management recommendations proposed here may be most relevant where grazing pressure is low, or active management of grazers is on-going.

Acknowledgements

The authors thank Dr. Grace Cott, Fergus McAuliffe, Flor Spaans and Alan O'Connor for their assistance in fieldwork. We are grateful to the National Parks and Wildlife Service and Coillte Teoranta for access to woodlands. This study was funded by a University College Cork departmental postgraduate fellowship.

References

Allen, S., 1989. Chemical analysis of ecological materials. Blackwell Scientific Publications, London.

Appendino, G., Cetin Özen, H., Fenoglio, I., Gariboldi, P., Gabetta, B., Bombardelli, E., 1993. Pseudoalkaloid taxanes from *Taxus baccata*. Phytochemistry 33, 1521–1523.

Appendino, G., Gariboldi, P., Pisetta, A., Bombardelli, E., Gabetta, B., 1992. Taxanes from *Taxus baccata*. Phytochemistry 31, 4253–4257.

Ball, M., Hodges, V., Laughlin, G., 1991. Cold-induced photoinhibition limits regeneration of snow gum at tree-line. Funct. Ecol., 663–668.
Barton, A.M., 1993. Factors controlling plant distributions: drought, competition, and fire in montane pines in Arizona. Ecol. Monogr., 367–397.
Bucci, G., Borghetti, M., 1997. Understory vegetation as a useful predictor of natural regeneration and canopy dynamics in *Pinus sylvestris* forests in Italy. Acta Oecol. 18, 485–501.
Camarero, J.J., Gutiarrez, E., Fortin, M.J., Ribbens, E., 2005. Spatial patterns of tree recruitment in a relict population of *Pinus uncinata*: forest expansion through stratified diffusion. J. Biogeogr. 32, 1979–1992.
Coates, K.D., 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia. Canada. For. Ecol. Manage. 155, 387–398.
Connell, J., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynamics and Populations. Centre for Agriculture Publishing and Documentation, Wageningen.
Currall, J., 1987. A transformation of the Domin scale. Plant Ecol. 72, 81–87.
Dahl, E., Hadac, E., 1941. Strandgesellschaften der Insel Ostoy im Oslofjord. Nytt. Mag. Naturvidens 82, 251–312.
Dhar, A., Ruprecht, H., Klumpp, R., Vacik, H., 2006. Stand structure and natural regeneration of English yew (*Taxus baccata* L.) at Stiwollgraben in Austria. Dendrobiology 56, 19–26.
Dhar, A., Ruprecht, H., Klumpp, R., Vacik, H., 2007. Comparison of ecological condition and conservation status of English yew population in two Austrian gene conservation forests. J. For. Res. 18, 181–186.
Dovciak, M., 2002. Population dynamics of the endangered English yew (*Taxus baccata* L.) and its management implications for biosphere reserves of the western Carpathians. Final report of young scientist Award, Division of Ecological Sciences, UNESCO.
Dovciak, M., Frelich, L.E., Reich, P.B., 2001. Discordance in spatial patterns of white pine (*Pinus strobus*) size classes in a patchy near a boreal forest. J. Ecol. 89, 280–291.
Dubreuil, M., Sebastiani, F., Mayol, M., González-Martínez, S.C., Riba, M., Vendramin, G.G., 2008. Isolation and characterization of polymorphic nuclear microsatellite loci in *Taxus baccata* L. Conserv. Genet. 9, 1665–1668.
Duncan, R.P., 1991. Competition and the coexistence of species in a mixed podocarp stand. J. Ecol., 1073–1084.
EuropeanCommission, 2007. Interpretation manual of European Union Habitats – EUR27. DG Environment, European Commission.
Farris, E., Filigheddu, R., 2008. Effects of browsing in relation to vegetation cover on common yew (*Taxus baccata* L.) recruitment in Mediterranean environments. Plant Ecol. 199, 309–318.
Fossitt, J., 2000. A guide to habitats in Ireland. Heritage Council, Kilkenny.
Fox, J.F., 1977. Alternation and coexistence of tree species. Am. Nat., 69–89.
Frazer, G.W., Canham, C., Lertzman, K., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York 36.
Frelich, L.E., Reich, P.B., 1999. Minireviews: neighborhood effects, disturbance severity, and community stability in forests. Ecosystems 2, 151–166.
Frelich, L.E., Sugita, S., Reich, P.B., Davis, M.B., Friedman, S.K., 1998. Neighbourhood effects in forests: implications for within stand patch structure. J. Ecol. 86, 149–161.
Garcia, D., Obeso, R.J., 2003. Facilitation by herbivore mediated nurse plants in a threatened tree, *Taxus baccata*: local effects and landscape level consistency. Ecography 26, 739–750.
Garcia, D., Zamora, R., Hódar, J.A., Gómez, J.M., Castro, J., 2000. Yew (*Taxus baccata* L.) regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments. Biol. Conserv. 95, 31–38.
Giertych, P., 2000. Factors determining natural regeneration of yew (*Taxus baccata* L.) in the Kornik Arboretum. Dendrobiology 45, 31–40.
Hageneder, F., 2007. Yew a History. Sutton Publishing, Stroud.
He, F., Duncan, R.P., 2000. Density-dependent effects on tree survival in an old growth Douglas fir forest. J. Ecol. 88, 676–688.
Hilfiker, K., Gugerli, F., Schütz, J.P., Rotach, P., Holderegger, R., 2004. Low RAPD variation and female-biased sex ratio indicate genetic drift in small populations of the dioecious conifer *Taxus baccata* in Switzerland. Conserv. Genet. 5, 357–365.
Hulme, P., 1996. Natural regeneration of yew (*Taxus baccata* L.): microsite, seed or herbivore limitation? J. Ecol., 853–861.
Iszkulo, G., Boratynski, A., 2006. Analysis of the relationship between photosynthetic photon flux density and natural *Taxus baccata* seedlings occurrence. Acta Oecol. 29, 78–84.
Iszkulo, G., Jasiska, A.K., Giertych, M.J., Boraty ski, A., 2009. Do secondary sexual dimorphism and female intolerance to drought influence the sex ratio and extinction risk of *Taxus baccata*? Plant Ecol. 200, 229–240.
Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. Am. Nat., 501–528.
Kelly, D.L., 2002. The regeneration of *Quercus petraea* (sessile oak) in southwest Ireland: a 25-year experimental study. For. Ecol. Manage. 166, 207–226.
Lewandowski, A., Burczyk, J., Mejnartowicz, L., 1995. Genetic structure of English yew (*Taxus baccata* L.) in the Wierzchlas Reserve: implications for genetic conservation. For. Ecol. Manage. 73, 221–227.
Linares, J.C., 2013. Shifting limiting factors for population dynamics and conservation status of the endangered English yew (*Taxus baccata* L., Taxaceae). For. Ecol. Manage. 291, 119–127.
Lorimer, C.G., Chapman, J.W., Lambert, W.D., 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol., 227–237.
McKenna, B., 2003. An Inventory of *Arbutus unedo* (Arbutus) and *Taxus baccata* (Yew) at Glengarriff Wood Nature Reserve – a GIS approach. University College Cork, Cork.
Mitchell, F., 1990. The history and vegetation dynamics of a yew wood (*Taxus baccata* L.) in SW Ireland. New Phytol. 115, 573–577.
Myking, T., Vakkari, P., Skrøppa, T., 2009. Genetic variation in northern marginal *Taxus baccata* L. populations. Implications for conservation. Forestry 82, 529.
Mysterud, A., Ostbye, E., 1995. Roe deer *Capreolus capreolus* feeding on yew *Taxus baccata* in relation to bilberry *Vaccinium myrtillus* density and snow depth. Wildl. Biol. 1, 249–253.
Mysterud, A., Ostbye, E., 2004. Roe deer (*Capreolus capreolus*) browsing pressure affects yew (*Taxus baccata*) recruitment within nature reserves in Norway. Biol. Conserv. 120, 545–548.
Nagashima, H., 1999. The processes of height-rank determination among individuals and neighbourhood effects in *Chenopodium album* L. Stands. Ann. Bot. 83, 501.
Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol. Evol. 15, 278–285.
Newbould, P.J., 1960. The Age and Structure of the Yew Wood at Kingley Vale. Report, Wye. UK.
O'Mahony, T., 2009. Wildflowers of Cork City and County. Collins Press, Cork.
O'Neill, F.H., 2003. Regeneration of Native Oak Woodland following *Rhododendron ponticum* L. clearance from Glengarriff Woods Nature Reserve, Co. Cork, Ireland. University College Cork, Cork.
Oquist, G., Huner, N., 1991. Effects of cold acclimation on the susceptibility of photosynthesis to photoinhibition in Scots pine and in winter and spring cereals: a fluorescence analysis. Funct. Ecol., 91–100.
Pausas, J.G., Bonet, A., Maestre, F.T., Climent, A., 2006. The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields. Acta Oecol. 29, 346–352.
Perrin, P., 2003. The ecology of yew (*Taxus baccata*) in Ireland. University of Dublin.
Perrin, P.M., Kelly, D.L., Mitchell, F.J.G., 2006. Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: natural regeneration and stand dynamics. For. Ecol. Manage. 236, 356–367.
Perrin, P.M., Mitchell, F.J.G., Kelly, D.L., 2011. Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: Changes in ground flora and species diversity. For. Ecol. Manage. 236, 2328–2337.
Piovesan, G., Presutti Saba, E., Biondi, F., Alessandrini, A., Di Filippo, A., Schirone, B., 2009. Population ecology of yew (*Taxus baccata* L.) in the Central Apennines: spatial patterns and their relevance for conservation strategies. Plant Ecol. 205, 23–46.
Robakowski, P., Wyka, T., 2009. Winter photoinhibition in needles of *Taxus baccata* seedlings acclimated to different light levels. Photosynthetica 47, 527–535.
Rodriguez-Garcia, E., Juez, L., Bravo, F., 2010. Environmental influences on post-harvest natural regeneration of *Pinus pinaster* Ait. in Mediterranean forest stands submitted to the seed-tree selection method. Eur. J. For. Res. 129, 1119–1128.
Rodwell, J.S., 1991. British Plant Communities, Woodlands and Scrub. Cambridge University Press, Cambridge, UK.
Schupp, E.W., 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. Am. J. Bot., 399–409.
Smal, C., Fairley, J., 1980. The fruits available as food to small rodents in two woodland ecosystems. Ecography 3, 10–18.
Smith, C.J., 1980. Ecology of the English chalk. Academic Press, London.
Stoll, P., Weiner, J., Schmid, B., 1994. Growth variation in a naturally established population of *Pinus sylvestris*. Ecology, 660–670.
Svenning, J., Magård, E., 1999. Population ecology and conservation status of the last natural population of English yew *Taxus baccata* in Denmark. Biol. Conserv. 88, 173–182.
Thomas, P., Packham, J.R., 2007. Ecology of woodlands and forests: description, dynamics and diversity. Cambridge Univ Press, Cambridge.
Thomas, P., Polwart, A., 2003. *Taxus baccata* L. J. Ecol. 91, 489–524.
Tittensor, R., 1980. Ecological history of yew Taxus baccata L. in southern England. Biol. Conserv. 17, 243–265.
Wada, N., Murakami, M., Yoshida, K., 2000. Effects of herbivore bearing adult trees of the oak *Quercus crispula* on the survival of their seedlings. Ecol. Res. 15, 219–227.
Wada, N., Ribbens, E., 1997. Japanese maple (*Acer palmatum* var. matsumurae, Aceraceae) recruitment patterns: seeds, seedlings, and saplings in relation to conspecific adult neighbors. Am. J. Bot. 84, 1294–1294.
Watt, A., 1919. On the causes of failure of natural regeneration in British oakwoods. J. Ecol., 173–203.
Watt, A., 1926. Yew communities of the South Downs. J. Ecol. 14, 282–316.
Weiner, J., 1984. Neighbourhood interference amongst *Pinus rigida* individuals. J. Ecol., 183–195.
Williamson, R., 1978. The great yew forest: the natural history of Kingley Vale. Macmillan, London.