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Conspecific negative density dependence in a long-lived conifer, yew *Taxus baccata* L.

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Abstract

Conspecific negative density dependence in tree species can have major consequences for structuring of communities, yet in temperate forests this phenomenon remains largely unexplored. We investigated density-dependent recruitment in the long-lived conifer yew (*Taxus baccata* L.), for which low levels of regeneration have been linked with reduced light availability beneath conspecific canopies and speculative autotoxic effects. We combined in situ assessment of yew regeneration in a temperate forest in southwest Ireland with ex situ pot experiments to assess whether light and/or beneath conspecific canopy conditions inhibit the germination and early growth of yew. In field experiments, recruitment was related to distance from adult conspecifics, with higher levels of regeneration found in areas not beneath yew canopies. However, reduced light availability beneath the dense yew canopy was not responsible for this pattern, with abundant seedlings found in areas of equivalent or even lower light availability. Pot experiments showed that seedling survival was highest in deep shade treatments. Experiments also demonstrated that the addition of yew needles negatively affected seedling growth, but not seed germination. Together, our results suggest that under natural forest conditions, the absence of regeneration beneath mature yew canopies, often attributed to low light availability, may at least be partly related to substances in yew canopy or leaf leachates.

Keywords Janzen–Connell · Negative plant–soil feedbacks · Natural regeneration · Autotoxicity

Introduction

Diversity of tree species in forests has a beneficial influence on multiple ecosystem services (Gamfeldt et al. 2013). Consequently, elucidating processes governing tree diversity has been a major focus of ecology (Connell et al. 1984; Hubbell et al. 1999; McMahon et al. 2011). For example,

conspecific negative density-dependent mortality (CNDD; or the Janzen–Connell hypothesis; Janzen 1970; Connell 1971), whereby juvenile recruitment is reduced in proximity to adults of the same species, is a leading explanation for the preservation of forest tree diversity (Harms et al. 2000; Johnson et al. 2012). Indeed, it has been proposed that for many tree species, recruitment success is largely dependent on the cumulative effects of neighbouring conspecifics (Duncan 1991).

Traditionally, patterns of CNDD are thought to be driven by host-specific enemies, including specialist seed predators, herbivores and soil pathogens (Fragoso 1997; Packer and Clay 2000). However, the extent to which canopy effects and leaf leachates contribute to CNDD remains poorly understood. For example, canopy trees may alter conditions that are critical for subsequent conspecific recruitment by modifying light penetration, nutrient availability and litter quality (Frelich et al. 1998; Nagashima 1999; Ehrenfeld et al. 2005). Established canopies also alter the soil chemical environment, including through autotoxic (the inhibition of conspecific growth via the release of chemicals into the

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environment) processes (Fernandez et al. 2008), which may drive patterns of species-specific negative plant–plant feedbacks observed in natural and agricultural systems (Johnson et al. 2012; Mazzoleni et al. 2015a, b).

English yew (*Taxus baccata*, hereafter yew) is a dioecious gymnosperm with a stress-tolerant life strategy, being exceptionally long-lived (> 1000 years) and capable of growing in a range of edaphic and light conditions (Thomas and Polwart 2003). Yew generally occurs as a scattered understory tree in European temperate and Mediterranean forests, but may form closed canopy monospecific stands in some cases (Perrin and Mitchell 2013). Recently, much research attention has focused on yew, owing to the production of paclitaxel, a diterpene derivative (Sze et al. 2008), used widely in the treatment of a variety of cancers (Goodman and Walsh 2001). Despite its pharmaceutical value, yew is a species in decline across much of its native range and is currently the focus of several conservation actions (Dhar et al. 2007; Piovesan et al. 2009; Peragón et al. 2015). The observed decline of yew has been attributed to seed predation (Sanz and Pulido 2014), reduction in genetic variation (Hilfiker et al. 2004; Dubreuil et al. 2010) and overgrazing by ungulates (Perrin et al. 2006; Farris and Filigheddu 2008). Dense shade cast by mature yew trees has also been suggested as a cause of low beneath-canopy regeneration (Linares 2013); however, evidence for light limitation of the widely considered deep-shade-tolerant yew is equivocal (Svenning and Magård 1999; Iszkulo et al. 2007; Robakowski and Wyka 2009; Perrin and Mitchell 2013). Negative neighbourhood effects have been cited as an explanation for poor regeneration in yew populations, with seedling recruitment often low in proximity to high densities of adult conspecifics (Piovesan et al. 2009), and specifically beneath mature yew canopies (Devaney et al. 2014). In yew-dominated forests, a lack of conspecific seedlings beneath the canopy is striking given the quantity of seed rain; Smal and Fairley (1980) estimated that up to 4 million yew seeds ha^{-1} fall on the ground in a yew woodland each year, deposited via avian seed dispersal or directly from the tree.

Autotoxic behaviour of yew has been speculated upon in the literature (Smith 1980; Svenning and Magård 1999; Thomas and Polwart 2003). Yew species produce high levels of phenolics (Brzezinska and Kozłowska 2008), compounds often associated with autotoxicity, as well as a range of secondary metabolites including taxoids and other diterpenoids for which cytotoxic activity has been reported (Appendino et al. 1992, 1993). Moreover, the yew congener *Taxus brevifolia* shows allelopathic potential in both field and laboratory assays, which has speculatively been attributed to secondary chemicals in senescent needles that are leached easily from leaf litter by rain (Moral and Cates 1971). Studies of other species have demonstrated that allelopathic substances can also be leached from intact canopies (Lorenzo et al. 2011) or

accumulate over time in beneath-canopy soils (Zhang et al. 2011). To date, however, experimental evidence regarding potential negative effects of yew needles and/or beneath-canopy soils on conspecific regeneration is lacking.

In this study, we couple assessment of yew recruitment patterns in a temperate deciduous forest in southwest Ireland with *ex situ* experiments to assess whether low light availability, conspecific needle addition and/or beneath-yew canopy soils inhibit the germination and early growth of seedlings. First, we addressed whether yew regeneration was more strongly related to proximity to mature trees or light availability at three large experimental forest plots. Secondly, we simulated natural conditions by testing to what extent beneath-yew canopy soils and yew needles affected seed germination and growth of yew seedlings under varying light intensities.

Materials and methods

Yew recruitment patterns

We assessed spatial patterns of yew recruitment at Glengarriff Wood (51°45'N, 9°34'W), a 301 ha temperate deciduous forest in southwest Ireland. The Old Red Sandstone geology of the area is generally covered by acidic peaty soil with some podzolization. Due to its Atlantic coastal location, the climate is mild and oceanic with a mean minimum winter temperature of 7.4 °C and mean annual rainfall of 2001 mm year^{-1} (Met Eireann, unpublished data, 1981–2010). The predominant habitat is seminatural sessile oak woodland (*Quercus petraea*) with yew generally occurring as a scattered sub-canopy tree. We established 0.36-ha (60 × 60 m) sampling plots at three sites within Glengarriff Wood: Drumaclarig (DR, 51°45'18"N, 9°33'59"W), Fisherman's Walk (FW, 51°45'09"N, 9°33'36"W) and Lady Bantry's Lookout (LB, 51°45'04"N, 9°33'57"W). Sites were broadly comparable in soil characteristics and vegetation communities (Supplementary text, Table S1). Plots were centred on a single isolated mature yew tree. During the autumn prior to study, a preliminary site assessment was carried out and focal trees were chosen based on the following set of criteria: (i) mature yew trees > 10 m in height, (ii) healthy female trees with good crown vitality and an abundance of seeds, and (iii) located at least 100 m from other adult conspecifics. Canopy cover of each adult was determined by recording maximum canopy radius at 20° intervals around the tree base. To assess spatial patterns of recruitment around these seed sources, the location of all yew individuals within plots was determined using a compass and a grid of tape measures with intersections every 2 m. Height (distance from the ground to highest living apical bud) and root collar diameter of all yews were also

recorded. Low densities of deer at Glengarriff (Devaney et al. 2014) facilitated the study of recruitment patterns in the absence of heavy browsing damage, which can strongly influence yew regeneration (Perrin et al. 2006; Farris and Filigheddu 2008). Nonetheless, we also noted the occurrence of ungulate herbivore damage (i.e. 0 = no damage, 1 = damage) on all individuals. To assess variation in light availability throughout our plots, photosynthetically active radiation (PAR) was recorded using a SKYE 200 PAR meter. On uniformly overcast days, PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was recorded at 0.3 m above ground level on a 2 m grid within the plots (total of 2700 readings). A measurement in an open area was simultaneously obtained, and relative (%) light availability within the experimental area was calculated. The distribution of light availability in each plot was interpolated using the inverse distance weighting interpolation (IDW) algorithm in ArcGIS 10.1 (Fig. 1).

Effects of yew needles and beneath-canopy soil on germination and growth of conspecifics

In a second experiment, we assessed whether soil beneath yew canopies and/or the addition of yew needles affected conspecific germination and growth in ex situ pot experiments. Experiments were conducted at an open plot research area at the School of Biological, Earth and Environmental Sciences, University College Cork, Ireland ($51^{\circ}53'56''\text{N}$,

$8^{\circ}29'22''\text{W}$). For germination experiments, ripe seeds were obtained from mature trees at Killarney National Park ($52^{\circ}01'15''\text{N}$, $9^{\circ}31'01''\text{W}$) during autumn, then washed and sieved to remove the aril. Seeds were buried to a depth of 1 cm in 1 L pots ($n = 10$ seeds per pot, 9 pots per treatment, total $n = 360$). Seeds were assigned to two soil treatments; soil was taken from directly beneath the canopy of adult yew trees or soil from mixed canopies. For yew canopy soil treatments, six soil samples were taken beneath the canopy of ten adult yew trees at Glengarriff Wood using a 5 cm diameter soil auger and mixed thoroughly. For mixed canopy soils, six samples were taken from 10 random locations beneath canopies of oak (*Quercus petraea*), birch (*Betula* spp.) and holly (*Ilex aquifolium*), the dominant canopy and understory species in the area. For the needle addition treatment, leaf input was based on field observations (i.e. the average quantity of green yew needles beneath yew canopies per equivalent surface area of 1 L pot). We added 1.5 g of green yew needles (collected from the canopy of the mature trees used in our field study) to half of the pots every 8 weeks. This allowed us to expose seeds to leachates from green needles (i.e. canopy leachates) and, because needles degraded over time, leachates from decomposing needles. However, it is recognized that green needles can be different from senescent needles and leaf litter as a result of nutrient resorption and/or changes in quality and quantity of secondary metabolites (Moral and Cates 1971; Hashoum et al. 2017).

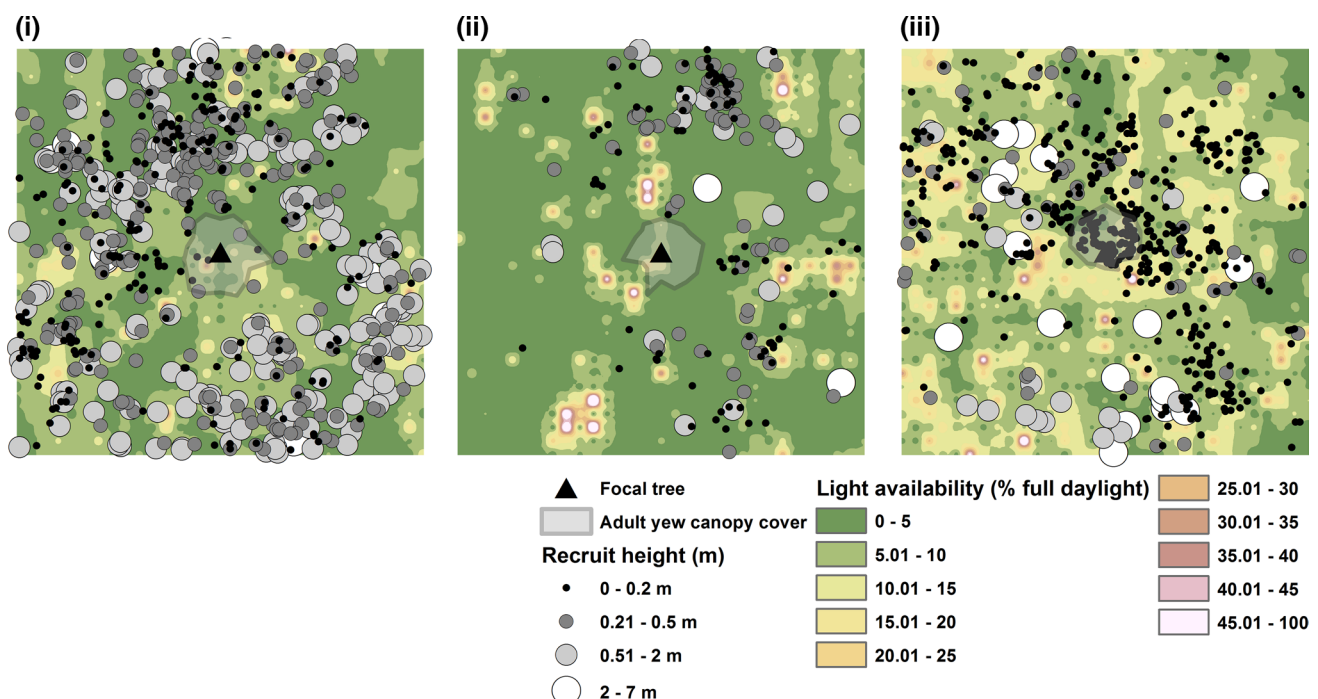


Fig. 1 Spatial distribution of yew regeneration in four size categories relative to light availability at three 60×60 m plots at Glengarriff Wood [(i) DR, (ii) FW, (iii) LB]

Therefore, the experimental design did not allow us to specifically test potential autotoxic effects of yew leaf litter. Control pots received no needle addition. Pots were assigned to three light availability treatments; 5, 18 and 70% of full daylight using multiple layers of polypropylene shade fabrics erected on frames. Germination was recorded on a weekly basis for 24 months. Germination was defined as the emergence of any part of the seedling above the soil surface.

Finally, we investigated the effects of beneath-yew canopy soil, yew needle addition, and light availability on yew seedling growth. Seedlings were obtained from a nursery at Killarney National Park, planted in 1 L pots, and assigned to soil, needle addition and light treatments as described previously ($n = 13$ per treatment, total $n = 156$). Seedlings were planted in the spring, and survival and shoot height increase were monitored every 12 weeks for 12 months.

Data analysis

Differences in light availability between sites were assessed using one-way ANOVA. Generalized linear models (GLMs) were used to assess whether yew height was related to proximity to mature conspecifics and/or light availability. For each site, we modelled yew height as a response to distance from a mature conspecific tree, light availability at plant location (derived from interpolated GIS maps) and their interaction, adopting a gamma distribution with log-link functions. Next, we used GLMs to test whether proximity to mature conspecifics and light availability predicted yew regeneration densities. To do this, we divided each site into 5×5 m subplots ($n = 432$, 144 per site) and quantified the density of yew individuals within. We used GLMs to assess the response of yew regeneration density in subplots to distance from mature conspecific and average subplot light availability. For yew density GLMs, a Poisson distribution and log-link function were adopted. Significance of each variable in all GLMs was tested using likelihood ratio tests of reduced versus full models.

For pot germination experiments, we used logistic regression (*glmer* in R package *lme4*) to assess differences between treatments. We assessed the binary outcome of germination (i.e. 0 = no germination, 1 = germination) using soil type, needle addition, light availability and all two-way interactions as fixed effects and pot as a random effect. Next, we used fixed effects logistic regression to assess differences in survival of three-year-old seedlings between treatments. For logistic regressions, χ^2 and p values were calculated using likelihood ratio tests of reduced versus full models. For seedlings that died during the experiment, we also tested whether time of death differed between treatments using linear regressions. Finally, for living seedlings, we asked whether our treatments could successfully predict growth over the 12-month

experimental period. Using linear regression, we assessed the effect of soil, needle addition and light on relative growth rate of seedlings, calculated as $(\overline{\ln H_2} - \overline{\ln H_1}) / (t_2 - t_1)$ where $\overline{\ln H_2}$ and $\overline{\ln H_1}$ are means of the natural logarithm transformed plants heights at time t_2 and t_1 . All calculations were performed in R 2.13.1.

Results

Yew recruitment patterns

Plant height differed between sites, with a greater proportion of smaller individuals at LB ($p < 0.001$, Fig. 1, Fig. S1). At sites DR and LB, yew height showed a positive curvilinear relationship with distance, being tallest at intermediate distances from adult conspecifics ($p < 0.001$, Fig. 2, Table 1). At FW, distance from the adult conspecific did not influence plant height ($p = 0.189$, Fig. 2, Table 1), although no regeneration was recorded < 5 m from the focal tree. Light availability was higher at LB with an average of 9.07% full daylight compared to 5.4% at DR and 4.4% at FW ($F = 127.1$, $p < 0.001$). At all sites, seedlings were frequent in areas experiencing $< 3\%$ daylight. Plant height was related to light only at DR ($p = 0.002$, Fig. 2, Table 1), where effects of light and distance on plant height were interactive ($p = 0.002$, Table 1), with taller individuals occurring in areas of both intermediate light availability and distances from conspecific adults.

Regeneration density was significantly related to distance to the mature conspecific focal tree at all sites (Fig. S2, Table S2). Regeneration density generally followed a Janzen–Connell distribution at sites DR and FW, occurring at low density close to adults and at highest densities at intermediate distances (Fig. S2). At site LB, density was negatively related to distance ($p < 0.001$, Fig. 1, Fig. S2, Table S2). Across sites, seedlings were either absent or very small in close proximity to adults (Figs. 1 and 2). Only five yews were found directly beneath the adult yew canopy at DR, with one seedling recorded beneath the yew canopy at FW. In contrast, a high density (93) of yew seedlings were found beneath the adult yew canopy at LB; however, the average height of these was only 0.08 m (Figs. 1 and 2). Regeneration density was related to light at all sites, but the nature of this relationship differed between sites (Fig. S2, Table S2). In total, we recorded 706, 179 and 641 yew recruits at DR, FW and LB, respectively. Grazing damage was low across sites (3% of yew individuals). Height and root collar diameter were

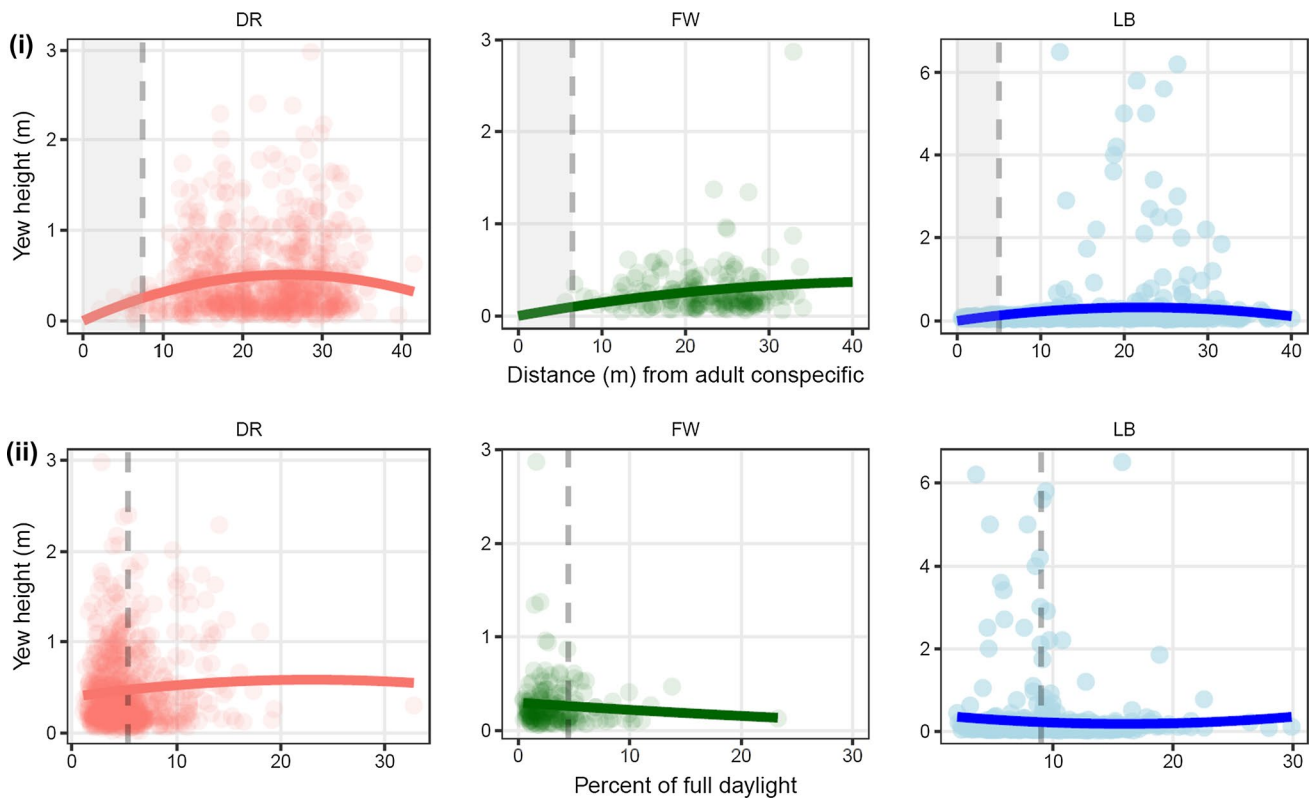


Fig. 2 Relationship between yew height and (i) distance from mature conspecific and (ii) average light availability at three sites in Glengarriff Wood. The grey area on (i) represents that average canopy radius of mature conspecifics used in our study. The dashed line in (ii) rep-

resents the average per cent light availability beneath the canopy of mature conspecifics used in our study. Effects on distance, light and site on yew height were analysed using GLMs (Table 1)

Table 1 Parameters from a generalized linear model predicting yew height as a function of distance to mature conspecific (distance), percentage of full daylight availability (light) well as their interaction

Site	<i>df</i>	Deviance	Residual <i>df</i>	Residual deviance	<i>P</i> value
DR					
Full model	–	–	705	517.19	–
Distance	– 2	– 11.764	704	514.1	< 0.001
Light	– 2	– 10.519	704	512.85	0.002
Distance × light	– 1	– 7.1089	704	509.44	0.002
FW					
Full model	–	–	178	94.36	–
Distance	– 2	– 2.7303	177	93.098	0.1894
Light	– 2	– 1.114	177	91.482	0.5072
Distance × light	– 1	– 0.53747	176	90.905	0.4183
LB					
Full model	–	–	640	957.49	–
Distance	– 2	– 109.46	639	948.21	< 0.001
Light	– 2	– 16.917	639	855.66	0.288
Distance × light	– 1	– 13.463	638	852.21	0.159

Significant predictors (highlighted in bold) represent those that when removed from the full model led to a significant reduction in deviance from the observed frequencies (based on a likelihood ratio test)

correlated, showing a polynomial relationship ($r^2 = 0.74$, $p < 0.001$, Fig. S3).

Effects of yew needles and soil on germination and growth of conspecifics

In pot experiments, germination first occurred after 17 months and continued until month 19, after which no

further germination was observed. Overall, 48% of seeds germinated during the experiment. Germination of yew seedlings was reduced in soil collected from beneath mixed oak, birch and holly canopies compared to soil from directly beneath yew canopies ($p < 0.001$, Fig. 3, Table 2). The addition of yew needles to pots had no effect on germination, both in mixed canopy and beneath-yew canopy

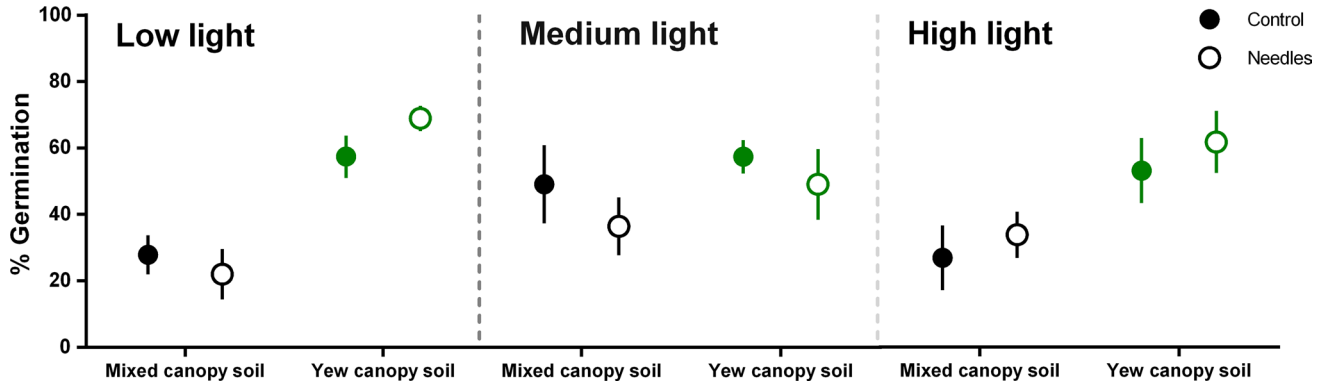


Fig. 3 Mean (\pm SE) per cent germination of yew seeds after 20 months in soil (mixed canopy and yew canopy), needle addition (control and yew needles) and light availability (low, 5% full daylight; medium, 18% full daylight; and high, 70% full daylight) treatments

Table 2 Summary of model results for logistic (germination and seedling survival) and linear (seedling RGR) regressions

Treatment	Germination		Seedling survival		Seedling RGR	
	Deviance	<i>p</i>	Deviance	<i>p</i>	<i>F</i>	<i>p</i>
Soil	– 30.456	< 0.001	– 3.068	0.546	1.844	0.178
Needles	– 1.982	0.738	– 4.213	0.377	5.099	0.027
Light	– 9.176	0.164	– 13.978	0.029	0.217	0.805
Soil \times needles	– 0.117	0.732	– 0.042	0.837	0.011	0.916
Soil \times light	– 5.844	0.058	– 2.847	0.240	0.434	0.649
Needles \times light	– 1.836	0.399	– 1.881	0.390	0.733	0.484

For logistic regression likelihood ratio tests, deviance from full model is indicated for each treatment
Significant treatment effect *p* values are highlighted in bold

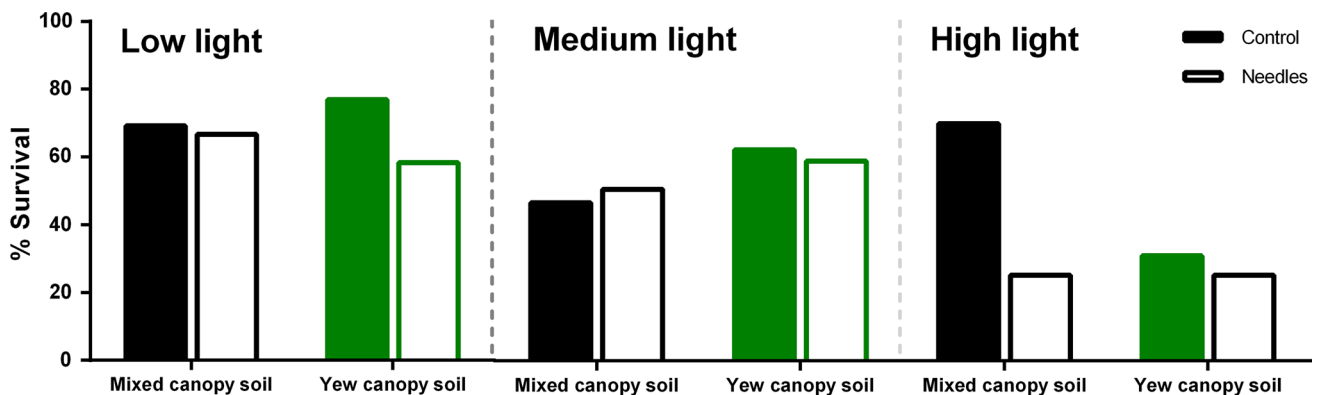


Fig. 4 Percentage survival of three-year-old yew seedlings after 12 months in soil (mixed canopy and yew canopy), needle addition (control and yew needles) and light availability (low, 5% full daylight; medium, 18% full daylight; and high, 70% full daylight) treatments

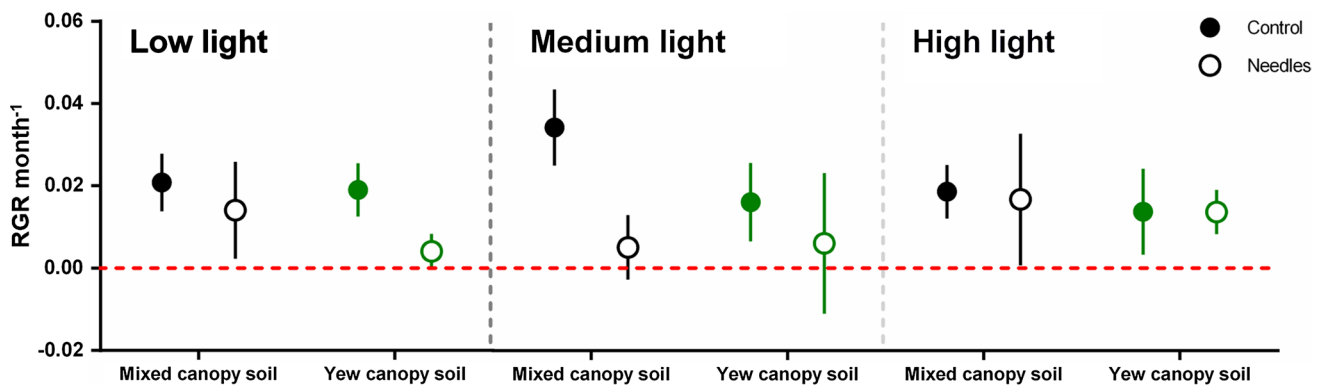


Fig. 5 Mean (\pm SE) relative growth rate (RGR month⁻¹) of three-year-old yew seedlings after 12 months in soil (mixed canopy and yew canopy), needle addition (control and yew needles) and light

availability (low, 5% full daylight; medium, 18% full daylight; and high, 70% full daylight) treatments

soils (Fig. 3, Table 2). Similarly, germination showed little variation across light treatments.

Survival of yew seedlings over 12 months was significantly reduced in high light conditions ($p = 0.029$, Fig. 4, Table 2). Time of death of seedlings did not differ between treatments ($F = 0.81$, $p = 0.51$). In contrast to the germination experiments, the addition of yew needles negatively affected RGR of seedlings ($F = 5.099$, $p = 0.027$, Fig. 5).

Discussion

In forests, neighbourhood effects are known to alter competitive dynamics through the modification of key habitat characteristics (Frelich et al. 1998; Gómez-Aparicio and Canham 2008). Canopy species therefore play a central role in determining microsite suitability for germination and establishment of seedlings (Molofsky and Augspurger 1992; Sariyildiz et al. 2005) often leading to patterns of CNDD. By combining field data with ex situ experimental studies, we show that patterns of CNDD in yew are more likely related to plant–plant feedbacks than low light availability beneath dense yew canopies.

In many European populations, low levels of yew regeneration have been linked with competition from shading *Fagus* and *Carpinus* species (Averdieck 1971; Svenning and Magård 1999; Deforce and Bastiaens 2007), with reduced interspecific competition leading to increased growth (Ruprecht et al. 2010). Indeed, the absence of seedlings beneath conspecifics has been attributed to low light penetration through the dense evergreen yew canopy (Watt 1926; Rodwell 1991). In our study, average light availability beneath mature yew canopies was 6.76% of full daylight, yet yew regeneration was abundant in areas receiving < 3% of full daylight. Furthermore, in ex situ experiments, seedling survival was higher in shaded treatments (< 5% of full

daylight) compared to high light treatments. Naturally occurring yew seedlings at Glengarriff Wood have been shown to be photoinhibited at high light availabilities, being unable to adequately cope with excess light beyond the photosynthetic capacity (Devaney et al. 2015). Photoinhibition can cause oxidative photodamage to photosystem II in leaf tissues, which may cause a reduction in overall plant health. Differences in population structure (i.e. the low rate of recruitment of young seedlings to later life stages) at LB may have been related to seedling exposure to high light conditions at that site. In contrast, the occurrence of yew seedlings in low light environments at all study sites, coupled with growth and survival of seedlings in heavily shaded ex situ experimental treatments, suggests that low light availability is not a primary factor in the preclusion of seedling regeneration observed in many areas, most notably beneath conspecific canopy cover.

Although plant height was not related to distance from adult tree at site FW, regeneration was still precluded from beneath the conspecific canopy, indicating that CNDD might have occurred at all sites. CNDD is often associated with an increase in host-specific soil pathogens (Packer and Clay 2000), but beneath-yew canopy soils did not lower yew germination rates in our ex situ experiments. In fact, yew seed germination was reduced in mixed oak canopy soil relative to soil taken from directly beneath mature yew canopies. Alteration of the soil environment by oak and yew canopies has previously been reported. Howard et al. (1998) found that soil from under oak trees had a lower carbon and nitrogen content relative to soils from under a yew canopy, as well as higher concentrations of some phenolic acids associated with allelopathy, including vanillic acid. Increased seed predation by animals beneath conspecific tree canopies has also been linked with CNDD (Nathan and Casagrandi 2004). Although seed predation was not measured in our field study, previous experiments have indicated that vertebrate

seed predation is unlikely to drive patterns of CNDD in yew populations (Hulme 1996; Hulme and Borelli 1999; Sanz and Pulido 2014). Low levels of recruitment have also been linked with ungulate herbivory (Mysterud and Østbye 2004; Perrin et al. 2011), but given that evidence of deer browsing in our study was low at all sites, we assumed that grazing was not a principal driver of recruitment patterns in this case.

Regeneration failure in yew has previously been linked with potential toxicity of canopy and/or leaf litter leachates (Smith 1980; Thomas and Polwart 2003). In our experiments, the addition of yew needles had no effect on germination of conspecific seeds, but did cause a reduction in seedling growth. This finding is consistent with García and Ramón Obeso (2003), who found that while seed rain, germination and emergence beneath yew canopies are common, first-year survival of seedlings was reduced compared to beneath heterospecific canopies. The effect of yew needles, but not yew soils, on seedling growth in our study suggests that potential CNDD effects may be linked with leaching of labile compounds from living or decomposing needles, rather than the gradual accumulation of persistent phytotoxins in the soil environment. The leaching of potentially toxic chemicals from canopies during rainfall has been identified for other species, for example (Lorenzo et al. 2011), and negative autotoxic effects of adult conspecifics are prevalent among gymnosperms (Sinkkonen 2007); bark, needles, litter and root/mycorrhizal exudates can inhibit the germination of seeds and/or growth and development of seedlings (Ruan et al. 2011, 2016). Examples of life-stage specific responses to autotoxicity exist in other conifers; leaf litter of mature *Pinus halepensis* affects the growth of conspecific seedlings negatively but not seed germination (Fernandez et al. 2008). Although yew needle addition did not impact seedling survival after twelve months, given that yew is one of the slowest growing tree species in Europe (Dhar et al. 2006), it is possible that prolonged exposure to needle effects is required to induce mortality in established seedlings. The occurrence of young seedlings of maximum height of 0.15 m beneath conspecific canopies in our field study further suggests that potential beneath-canopy effects do not limit germination, but do reduce long-term growth and recruitment to later life stages. A limitation of our study design, however, is that physical effects of needle addition cannot be accounted for. The addition of needles may have created darker, moister conditions for seeds relative to control treatment. Nonetheless, given that pots were watered to capacity and light treatments did not affect germination, it is unlikely that physical effects of needles influenced germination rates.

While the chemicals involved in the observed effect of green needles remain unknown, autotoxicity is often associated with phenolic compounds of various types (Inderjit 1996; Li et al. 2010). For example, in bioassays on needle

constituents of *Picea schrenkiana*, Ruan et al. (2016) identified the specific phenolic 3,4-dihydroxyacetophenone as having autotoxic potential. High levels of phenolic compounds have been recorded in yew foliage (Brzezinska and Kozłowska 2008), and a toxic effect of the phenolic phytochemical coumarin on growth of young yew seedlings has been reported (Nandi et al. 1996). Similarly, diterpenoids, which also occur in yew needles, have recently been linked with directly mediating antagonistic plant–plant interactions (Xu et al. 2012). Further research is required to ascertain potential autotoxicity of phenolic and diterpenoid constituents that occur in high quantities in yew foliage and litter. Throughout Europe, limits on regeneration of yew have been shown to vary with site and environmental conditions (Ruprecht et al. 2010), ranging from reduced water availability in many southern populations, to overgrazing, light conditions and low temperature stress in northern Europe (Linares 2013). It is likely, however, that negative beneath-canopy effects occur throughout the range, although the extent to which potential autotoxicity is the limiting factor for recruitment may vary with site conditions (including soil type).

Conclusions

CNDD in yew may explain the maintenance of even-aged monoculture stands such as those protected under the EU Habitat Directive (European Commission 2007) as “*Taxus baccata* woods of the British Isles”. Yew-dominated stands are thought to develop following a change in land management regimes such as the cessation of grazing pressure (Tittensor 1980). High levels of initial colonization and recruitment in areas of scrub vegetation are followed by the development of mature stands and the subsequent exclusion of conspecific regeneration. Age-related density-dependent mortality may play an important role in preserving resource availability for established conspecifics, rather than maintaining local tree species richness as observed widely in tropical forest systems. We propose that the absence of regeneration beneath mature yew canopies, often attributed to low light availability, may at least partly be related to phytotoxic substances in leaf leachates. Such negative plant–plant feedbacks have been linked with observed patterns of conspecific negative density-dependent mortality in other species (Bonanomi et al. 2008). Suppression of intraspecific competition through potential autotoxic process may be particularly relevant for long-lived stress-tolerant species (Mayol et al. 2015) that grow in resource-poor environments. Further exploration of autotoxicity in trees species and its role in governing patterns of CNDD in forest communities is required.

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References

- Appendino G, Gariboldi P, Pisetta A, Bombardelli E, Gabetta B (1992) Taxanes from *Taxus baccata*. *Phytochemistry* 31:4253–4257
- Appendino G, Özen HC, Fenoglio I, Gariboldi P, Gabetta B, Bombardelli E (1993) Pseudoalkaloid taxanes from *Taxus baccata*. *Phytochemistry* 33:1521–1523
- Averdieck F (1971) Postglacial history of yew-tree (*Taxus baccata* L.) in northwestern Germany. (In German with English abstract). *Flora* 160:28–42
- Bonanomi G, Rietkerk M, Dekker SC, Mazzoleni S (2008) Islands of fertility induce co-occurring negative and positive plant–soil feedbacks promoting coexistence. *Plant Ecol* 197:207–218
- Brzezinska E, Kozłowska M (2008) Effect of sunlight on phenolic compounds accumulation in coniferous plants. *Dendrobiology* 59:3–7
- European Commission (2007) Interpretation manual of European Union Habitats—EUR27. DG Environment, European Commission, Brussels
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dyn Popul* 298:312
- Connell JH, Tracey J, Webb LJ (1984) Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecol Monogr* 54:141–164
- Deforce K, Bastiaens J (2007) The Holocene history of *Taxus baccata* (yew) in Belgium and neighbouring regions. *Belg J Bot* 140:222–237
- Devaney JL, Jansen MA, Whelan PM (2014) Spatial patterns of natural regeneration in stands of English yew (*Taxus baccata* L.); Negative neighbourhood effects. *For Ecol Manag* 321:52–60
- Devaney JL, Whelan PM, Jansen MA (2015) Light responses of yew (*Taxus baccata* L.); does size matter? *Trees* 29:109–118
- Dhar A, Ruprecht H, Klumpp R, Vacik H (2006) Stand structure and natural regeneration of *Taxus baccata* 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
- Dubreuil M, Riba M, González-Martínez SC, Vendramin GG, Sebastiani F, Mayol M (2010) Genetic effects of chronic habitat fragmentation revisited: strong genetic structure in a temperate tree, *Taxus baccata* (Taxaceae), with great dispersal capability. *Am J Bot* 97:303–310
- Duncan RP (1991) Competition and the coexistence of species in a mixed podocarp stand. *J Ecol* 79:1073–1084
- Ehrenfeld JG, Ravit B, Elgersma K (2005) Feedback in the plant–soil system. *Annu Rev Environ Resour* 30:75–115
- 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
- Fernandez C, Voirit S, Mévy J-P, Vila B, Ormeno E, Dupouyet S, Bousquet-Mélou A (2008) Regeneration failure of *Pinus halepensis* Mill.: the role of autotoxicity and some abiotic environmental parameters. *For Ecol Manag* 255:2928–2936
- Fragoso JM (1997) Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *J Ecol* 85:519–529
- Frellich LE, Sugita S, Reich PB, Davis MB, Friedman SK (1998) Neighbourhood effects in forests: implications for within-stand patch structure. *J Ecol* 86:149–161
- Gamfeldt L, Snäll T, Bagchi R, Jonsson M, Gustafsson L, Kjellander P, Ruiz-Jaen MC, Fröberg M, Stendahl J, Philipson CD (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat Commun* 4:1340
- García D, Ramón Obeso J (2003) Facilitation by herbivore-mediated nurse plants in a threatened tree, *Taxus baccata*: local effects and landscape level consistency. *Ecography* 26:739–750
- Gómez-Aparicio L, Canham CD (2008) Neighbourhood analyses of the allelopathic effects of the invasive tree *Ailanthus altissima* in temperate forests. *J Ecol* 96:447–458
- Goodman J, Walsh V (2001) The story of taxol: nature and politics in the pursuit of an anti-cancer drug. Cambridge University Press, Cambridge
- Harms KE, Wright SJ, Calderón O, Hernández A, Herre EA (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–495
- Hashoum H, Santonja M, Gauquelin T, Saatkamp A, Gavinet J, Greff S, Lecareux C, Fernandez C, Bousquet-Mélou A (2017) Biotic interactions in a Mediterranean oak forest: role of allelopathy along phenological development of woody species. *Eur J For Res* 136:699–710
- 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
- Howard P, Howard D, Lowe L (1998) Effects of tree species and soil physico-chemical conditions on the nature of soil organic matter. *Soil Biol Biochem* 30:285–297
- Hubbell SP et al (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554–557
- Hulme PE (1996) Natural regeneration of yew (*Taxus baccata* L.): microsite, seed or herbivore limitation? *J Ecol* 84:853–861
- Hulme PE, Borelli T (1999) Variability in post-dispersal seed predation in deciduous woodland: relative importance of location, seed species, burial and density. *Plant Ecol* 145:149–156
- Inderjit (1996) Plant phenolics in allelopathy. *Bot Rev* 62:186–202
- Iszkulio G, Lewandowski A, Jasinska AK, Dering M (2007) Light limitation of growth in 10-year-old seedlings of *Taxus baccata* L. (European yew). *Pol J Ecol* 55:827–831
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Johnson DJ, Beaulieu WT, Bever JD, Clay K (2012) Conspecific negative density dependence and forest diversity. *Science* 336:904–907
- Li ZH, Wang Q, Ruan X, Pan CD, Jiang DA (2010) Phenolics and plant allelopathy. *Molecules* 15:8933–8952
- Linares JC (2013) Shifting limiting factors for population dynamics and conservation status of the endangered English yew (*Taxus baccata* L., Taxaceae). *For Ecol Manag* 291:119–127
- Lorenzo P, Palomera-Pérez A, Reigosa MJ, González L (2011) Allelopathic interference of invasive *Acacia dealbata* Link on the physiological parameters of native understory species. *Plant Ecol* 212:403–412
- Mayol M et al (2015) Adapting through glacial cycles: insights from a long-lived tree (*Taxus baccata*). *New Phytol* 208:973–986
- Mazzoleni S et al (2015a) Inhibitory and toxic effects of extracellular self-DNA in litter: a mechanism for negative plant–soil feedbacks? *New Phytol* 205:1195–1210
- Mazzoleni S et al (2015b) Inhibitory effects of extracellular self-DNA: a general biological process? *New Phytol* 206:127–132

- McMahon SM, Metcalf CJ, Woodall CW (2011) High-dimensional coexistence of temperate tree species: functional traits, demographic rates, life-history stages, and their physical context. *PLoS ONE* 6:e16253
- Molofsky J, Augspurger CK (1992) The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73:68–77
- Moral RD, Cates RG (1971) Allelopathic potential of the dominant vegetation of western Washington. *Ecology* 52:1030–1037
- Mysterud A, Østbye E (2004) Roe deer (*Capreolus capreolus*) browsing pressure affects yew (*Taxus baccata*) recruitment within nature reserves in Norway. *Biol Cons* 120:545–548
- Nagashima H (1999) The processes of height-rank determination among individuals and neighbourhood effects in *Chenopodium album* L. stands. *Ann Bot* 83:501–507
- Nandi SK, Palni LMS, Rikkari H (1996) Chemical induction of adventitious root formation in *Taxus baccata* cuttings. *Plant Growth Regul* 19:117–122
- Nathan R, Casagrandi R (2004) A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen–Connell and beyond. *J Ecol* 92:733–746
- Packer A, Clay K (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404:278–281
- Peragón JLN, Matias LFB, Simón JP (2015) Restoration of European yew (*Taxus baccata* L.) in Mediterranean mountains: importance of seedling nursery fertilization and post-planting light levels. *For Syst* 24:041
- Perrin PM, Mitchell FJ (2013) Effects of shade on growth, biomass allocation and leaf morphology in European yew (*Taxus baccata* L.). *Eur J For Res* 132:211–218
- Perrin PM, Kelly DL, Mitchell FJ (2006) Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: natural regeneration and stand dynamics. *For Ecol Manag* 236:356–367
- Perrin PM, Mitchell FJ, Kelly DL (2011) Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: changes in ground flora and species diversity. *For Ecol Manag* 262:2328–2337
- Piovesan G, Saba EP, 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
- Rodwell JS (1991) British plant communities, woodlands and scrub. Cambridge University Press, Cambridge
- Ruan X, Li Z-H, Wang Q, Pan C-D, Jiang D-A, Wang GG (2011) Autotoxicity and allelopathy of 3, 4-dihydroxyacetophenone isolated from *Picea schrenkiana* needles. *Molecules* 16:8874–8893
- Ruan X et al (2016) Effects of climate warming on plant autotoxicity in forest evolution: a case simulation analysis for *Picea schrenkiana* regeneration. *Ecol Evol* 6:5854–5866
- Ruprecht H, Dhar A, Aigner B, Oitzinger G, Klumpp R, Vacik H (2010) Structural diversity of English yew (*Taxus baccata* L.) populations. *Eur J For Res* 129:189–198
- Sanz R, Pulido F (2014) Post-dispersal seed depletion by rodents in marginal populations of yew (*Taxus baccata*): consequences at geographical and local scales. *Plant Species Biol* 29:E48–E54
- Sariyildiz T, Anderson J, Kucuk M (2005) Effects of tree species and topography on soil chemistry, litter quality, and decomposition in Northeast Turkey. *Soil Biol Biochem* 37:1695–1706
- Sinkkonen A (2007) Modelling the effect of autotoxicity on density-dependent phytotoxicity. *J Theor Biol* 244:218–227
- Smal C, Fairley J (1980) The fruits available as food to small rodents in two woodland ecosystems. *Ecography* 3:10–18
- Smith CJ (1980) Ecology of the English chalk. Academic Press, London
- Svenning J-C, Magård E (1999) Population ecology and conservation status of the last natural population of English yew *Taxus baccata* in Denmark. *Biol Cons* 88:173–182
- Sze DM, Miller K, Neilan B (2008) Development of taxol and other endophyte produced anti-cancer agents Recent patents on anti-cancer drug discovery. *Recent Pat Anti-Cancer Drug Discov* 3:14–19
- Thomas P, Polwart A (2003) *Taxus baccata* L. *J Ecol* 91:489–524
- Tittensor RM (1980) Ecological history of yew *Taxus baccata* L. in southern England. *Biol Conserv* 17:243–265
- Watt A (1926) Yew communities of the South Downs. *J Ecol* 14:282–316
- Xu M, Galhano R, Wiemann P, Bueno E, Tiernan M, Wu W, Chung IMM, Gershenzon J, Tudzynski B, Sesma A (2012) Genetic evidence for natural product-mediated plant–plant allelopathy in rice (*Oryza sativa*). *New Phytol* 193:570–575
- Zhang S, Zhu W, Wang B, Tang J, Chen X (2011) Secondary metabolites from the invasive *Solidago canadensis* L. accumulation in soil and contribution to inhibition of soil pathogen *Pythium ultimum*. *Appl Soil Ecol* 48:280–286