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Light responses of yew (*Taxus baccata* L.); does size matter?

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Abstract

Key message Photosynthetic capacity of yew needles depends primarily on light environment, with little evidence that developmental stage is a determinant photosynthetic performance. However, needle morphology is mostly determined by plant size.

Abstract Populations of yew *Taxus baccata* are often characterized by a lack of natural regeneration and stands of this species have been afforded priority conservation status within the European Union. Light availability is known to be a key factor influencing recruitment dynamics in yew. To explore potential size-related responses to light, we investigated the distribution, photosynthetic efficiency and needle morphological traits in yew across a gradient of light availability at Atlantic oak woodland in southwest Ireland. Young plants were more common in shaded areas whereas saplings and juvenile yews were distributed in areas of higher light availability. Photosynthetic capacity of yew needles was found to depend primarily on light environment, with little evidence that the developmental stage is a determinant of photosynthetic performance. Photoinhibition was evident in needles sampled from high light environments across all demographic size classes. However, larger plants also showed particularly strong needle morphological responses (needle length, width,

thickness, and specific leaf area) to light levels, which were mostly lacking in seedlings. We conclude that there is a dual control of yew light responses; the efficiency of the photosynthetic light reactions is largely linked to the light environment in which the plants grew, while needle morphology is mostly determined by the size of the plants. The findings of this study highlight the importance of considering all life-history stages and multiple traits when evaluating species response to light availability.

Keywords Forest regeneration · Yew · *Taxus baccata* · Light availability · Photosynthesis · Conservation biology

Introduction

Light controls plant growth and development by facilitating photosynthesis and through a range of photoreceptor-mediated photomorphogenic processes. The quantity and quality of light are key factors in determining growth and survival in plant communities (Canham et al. 1990; Messier et al. 1999) and interspecific differences in shade tolerance are recognized as fundamental drivers of succession (Kobe et al. 1995; Lusk 2004; Lusk and Jorgensen 2013). While a shortage of light can compromise growth and survival, excessive irradiance can also negatively affect plant performance by causing photoinhibitory stress (Jansen et al. 1999). As a result, in forested landscapes an increase in canopy openness may cause severe stress to seedlings and saplings due to exposure to excessive radiation (Wayne and Bazzaz 1993; Mitamura et al. 2009).

Much of the research on growth and survival of plants subject to varying degrees of insolation has focused on shade tolerance of young seedlings (Niinemets and Valladares 2006). Some authors have, however, highlighted

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the need to adopt a life cycle view of the responses of plants to their light environments (Valladares and Niinemets 2008; Kunstler et al. 2009). Tree species may be subject to major changes in light quantity and quality during their lifetime, ranging from low light understory or gap conditions as seedlings, to fully exposed canopy conditions as adults. Changes in physiological and morphological traits of the photosynthetic apparatus, leaf and canopy structure of tree species will occur during development (Augsburger and Bartlett 2003). Furthermore, as plant size increases, a decreasing ratio of photosynthetic to non-photosynthetic biomass, and associated higher maintenance costs, may lead to a reduction in shade tolerance (Givnish 1988; Kunstler et al. 2009).

Yew *Taxus baccata* L. is a dioecious gymnosperm, occurring throughout Europe with scattered populations extending to North Africa and the Middle East (Thomas and Polwart 2003). Yew has declined over recent millennia and populations are now isolated or locally extinct in many areas (Dubreuil et al. 2008; Myking et al. 2009). Due to concern for the conservation status of natural populations of this species (Dhar et al. 2006; Iszkulo et al. 2009), several conservation and restoration programmes have been established (Dhar et al. 2007; Piovesan et al. 2009). The absence of natural regeneration has been attributed to a range of factors, including overgrazing by ungulates, seed predation, genetic isolation and intraspecific competition (Hilfiker et al. 2004; Perrin et al. 2006; Farris and Filihgeddu 2008; Piovesan et al. 2009; Devaney et al. 2013). Numerous authors have also reported that light availability is a key factor influencing recruitment dynamics in yew (Svenning and Magård 1999; Thomas and Polwart 2003; Iszkulo et al. 2007).

Yew is known to be one of the most shade-tolerant tree species of the European flora (Thomas and Polwart 2003; Iszkulo and Boratynski 2006). However, this perceived tolerance to low light conditions does not necessarily infer a requirement for shade and indeed, conflicting reports exist on the role of light in recruitment in yew. For example, Perrin and Mitchell (2013) demonstrated that under ex situ experimental light conditions, no mortality of yew saplings was attributable to heavy shade (<3 % daylight), yet Iszkulo (2010) reported high mortality of young yew seedlings under similar low light conditions (<2 % daylight). The absence of young seedlings from many areas is often credited to the dense shade cast by mature *Fagus* spp. and yew canopies (Watt 1926; Krol 1978; Rodwell 1991). Furthermore, increased canopy closure by 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). Conversely, recent evidence suggests that seedlings of yew are susceptible to photoinhibition when exposed to full

sunlight (Robakowski and Wyka 2009). Nevertheless, older yew saplings and adult trees are often located in areas of high light availability such as limestone pavement and cliff faces (Jackson and Sheldon 1949; Thomas and Polwart 2003; Myking et al. 2009). These findings suggest that the response of yew to light depends on the age and/or developmental stage. A number of studies have identified similar size-related light requirement transitions in other tree species during their development (Poorter et al. 2005; Coopman et al. 2008). With few notable exceptions (Iszkulo and Boratynski 2006) research to date has yet to assess possible size-related changes in the response of yew to light availability.

The objective of this study was to investigate potential size-related responses to light availability in yew. Specifically, we tested the following hypotheses: (1) the natural distribution of yew in consecutive developmental stages is differentially related to light availability (2) the relationship between activity of photosystem II in yew and light availability differs between developmental stages and (3) the relationship between needle morphological traits and light availability differs between developmental stages.

Materials and methods

Study site

The study was carried out at the Glengarriff Wood Nature Reserve (GWNR; 51° 45' N, 9° 34' W) in southwest Ireland. The GWNR is a 301 ha area situated in primarily forested hilly terrain with many rocky outcrops. In most areas of the reserve the underlying sandstone is covered by acidic peaty soil with some podsolization (Little 1994). Due to its coastal Atlantic location, the climate is mild and oceanic. The predominant habitat at the GWNR is semi-natural sessile oak woodland, of the association *Blechno-Quercetum petraeae*, an association listed in Annex I of the EU Habitats Directive (Council Directive 92/43/EEC). The principal canopy tree is *Quercus petraea* with *Ilex aquifolium*, *Betula pendula*, *Sorbus aucuparia*, *Salix* spp. and *Arbutus unedo* forming well-developed understory and shrubs layers. Frequent plants in the field layer include *Calluna vulgaris*, *Vaccinium myrtillus* and *Pteridium aquilinum*. Studies by (O'Neill 2003) and McKenna (2003) have noted a high incidence of seedlings and saplings of yew, generally located in the vicinity of mature adult conspecifics, which occur as infrequent understory trees.

The relationship between yew size and light availability

As part of a wider study (Devaney 2013) the spatial distribution and height of all yew individuals within a 1 ha

study area in the GWNR were recorded. For the current study, a stratified random sample ($n = 158$) of individuals were selected across four demographic size classes based on plant height: seedlings 0–0.20 m; young saplings 0.21–0.50 m; saplings 0.51–2 m; and juveniles >2–6 m. To examine the relationship between the occurrence of yew individuals within these size classes and light availability, the percentage of full daylight available at the top of each plant was recorded. Light availability was determined by measuring photosynthetic photon flux density (PPFD; $\mu\text{mol m}^{-2} \text{s}^{-1}$) above each plant, on a uniformly overcast day using a SKYE 200 Photosynthetically Active Radiation meter, whilst obtaining a simultaneous measurement in an open area. PPFD values for open areas ranged from 94–420 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during sampling. Relative full daylight availability was determined by calculating the ratio of light intensity above each plant to the light intensity recorded in the open area.

Chlorophyll-*a* fluorescence of yew needles in response to light availability

The same stratified random sample of plants was used to investigate the activity of photosystem II of photosynthesis in needles of yew growing in a range of light environments. Plants were categorised according to the light environment in which they grew: low light (LL), <5 % full daylight; medium light (ML), 5–20 % full daylight, and; high light (HL), >20 % full daylight. Within each of these light environments, plants were again selected from the four demographic size classes (seedlings 0–0.20 m; young saplings 0.21–0.50 m; saplings 0.51–2 m; and juveniles >2–6 m). Where sufficient replicates of plants in each treatment were not located in the study area, supplementary individuals were sampled from elsewhere within the GWNR. For example, low numbers of yew seedlings and young saplings were recorded growing in high light under natural conditions within the 1 ha study area. Therefore, supplementary plants were sampled from artificially open areas where canopy cover had been removed as part of forest management operations (>3 years prior to sampling). In total, 227 needles were sampled for analyses, with 15–20 replicates per treatment. In all cases, current year needles were collected from the uppermost shoot of each plant at the end of the growing season (late September/early October 2010). Mean maximum and minimum temperatures for the region in September 2010 were 18.3 and 11.3 °C, respectively, similar to 10 year averages for the period 2001–2010 (18.6–10.27 °C). For the 10 day period prior to sampling, there was a total of 37 sun hours (10 year average; 47.3 h) and 102.29 MJ m² global solar radiation (10 year average; 106.09 MJ m²) (Met Eireann, Unpublished data). Immediately after removal from the plant, needles were stored in Petri dishes with wetted

filter paper, covered with aluminium foil, and analysed within four hours. Chlorophyll-*a* fluorescence was measured using a modulated, imaging fluorometer equipped with ImagingWin software (IMAG-MAX/L with blue measuring light, PAM, EffeLtrich, Germany). Needles were dark-adapted for 2–4 h (including transport time) prior to measurement and then placed on damp filter paper on the fluorometer stage. A weak measuring light (<1 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was used to determine the minimum fluorescence obtained in the dark-adapted state (F_o). Maximum fluorescence (F_m) was determined for the dark-adapted state by applying a saturating pulse of white light. Maximum quantum efficiency of photosystem II was calculated as $(F_m - F_o)/F_m = (F_v/F_m)$, where F_v is variable fluorescence. The effective quantum yield of PSII (Φ_{PSII}), photochemical quenching (qP) and electron transport rate (ETR) were also measured. Needles were illuminated using the in-built LED with up to eight levels of actinic light (1–800 $\mu\text{mol m}^{-2} \text{s}^{-1}$), in order of increasing intensity. Needles were exposed for 20 s to each intensity, after which needles were exposed to a flash of saturating light. Analysis of acclimation kinetics showed that slow changes in chlorophyll fluorescence parameters occur over time-spans of many minutes. The 20 s acclimation period captures the fast initial change in these parameters. At each level of actinic light, quantum yield of PSII was calculated as $\Phi_{\text{PSII}} = (F_m' - F_s)/F_m'$ where F_s is steady state fluorescence (Genty et al. 1989). Photochemical quenching (qP) was calculated as $qP = (F_m' - F_s)/(F_m' - F_o')$ where F_o' was calculated as $F_o' = F_o/(F_v/F_m + F_o/F_m')$ following Oxborough and Baker (1997). The apparent rate of electron transport (ETR) was calculated as $\text{ETR} = \Phi_{\text{PSII}} \times 0.5 \times 0.84 \times \text{PPFD}$ (Maxwell and Johnson 2000).

Morphological differentiation of needles in relation to light availability

Current year needles used in the measurement of chlorophyll-*a* fluorescence parameters were used to investigate morphological characteristics. Needle thickness was measured using micro callipers. Needles were digitally scanned using a Hewlett Packard ScanJet 4300C and mean needle length, width and area was determined using ImageJ software. Dry weights of the needles were obtained after oven drying for 72 h at 50 °C and specific leaf area (SLA) was calculated as needle area: needle dry weight (cm² g⁻¹).

Statistical analysis

The relationship between the occurrence of yew in different size classes and light availability at the GWNR was assessed using one-way ANOVA with post hoc Bonferroni tests. Two-way ANOVA was used to test for significant

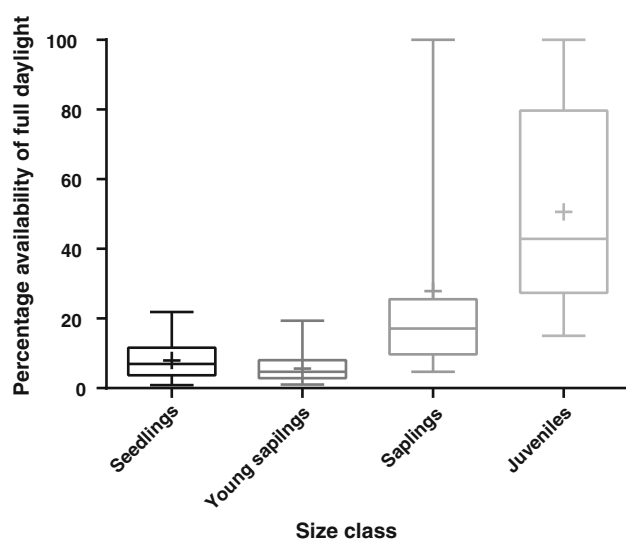


Fig. 1 The relationship between percentage availability of full daylight and the occurrence of yew in four demographic size classes; seedlings (0–0.20 m), young saplings (0.21–0.50 m), saplings (0.51–2 m) and juveniles (>2–6 m) in a 1 ha study area at the GWNr. Mean light availability at the top of plants was significantly higher for yew saplings and juveniles in comparison to seedlings and young saplings (one-way ANOVA, $F = 108.424$, $p < 0.001$). The box plots show the interquartile range (middle 50 % of data), with the median marked by a line, mean marked by *plus*, and the whiskers representing the full range of the data

differences between chlorophyll-*a* fluorescence parameters and needle morphological traits with respect to light environment (LL, ML, HL) and plant size (seedlings, young saplings, saplings, juveniles). Following Wyka et al. (2008), a single cardinal value for each light response curve was selected for statistical comparison of chlorophyll-*a* fluorescence parameters. For Φ_{PSII} and qP values were measured using an actinic light of $281 \mu\text{mol m}^{-2} \text{s}^{-1}$. The maximum value for ETR was used (ETR_{max}). Significant results were tested for pair-wise comparisons using Bonferroni post hoc tests. Prior to performing ANOVAs, variables were tested for normality and homogeneity of variances using Kolmogorov–Smirnov and Levene’s tests, with transformations applied wherever necessary. All data were analysed using SPSS (PASW® Statistics 17) software package. Figures were generated using GraphPad Prism software.

Results

The relationship between yew size and light availability

The relationship between the distribution of yew individuals in different size classes and light availability at the GWNr was assessed. 158 plants were sampled in total ranging in height from 0.07 m to 6 m. In general, seedlings

and young saplings were associated with low to medium light availability, whereas saplings and juvenile trees were commonly associated with higher light availability. The mean percentage of full daylight available to seedlings and young saplings was 7.9 and 5.6 % respectively (Fig. 1). In comparison, mean percentage of full daylight available to saplings and juveniles was 27.9 and 50.6 % respectively (Fig. 1). Overall, mean light availability was significantly higher for yew saplings and juveniles in comparison to seedlings and young saplings (one-way ANOVA, $F = 108.424$, $p < 0.001$, Fig. 1).

Chlorophyll-*a* fluorescence of yew needles in response to differing light availability

Light environment had a clear effect on measured chlorophyll-*a* fluorescence parameters of first year needles with values from HL environments being significantly different from other treatments (Table 1). Maximum quantum efficiency of photosystem II (F_v/F_m) was significantly reduced in yew needles growing in HL compared to those in LL and ML environments (Fig. 2; Table 1). Although the magnitude of F_v/F_m decrease in HL was less for juvenile individuals, size and interaction effects were not significant (Fig. 2; Table 1). High light environment had a significantly positive effect on the effective quantum yield of PSII ($\Phi_{\text{PSII}(281)}$) (Fig. 3; Table 1). Photochemical quenching ($qP_{(281)}$) was significantly higher for both HL and ML needles in comparison to LL needles. On average, photochemical quenching ($qP_{(281)}$) was found to be significantly greater for saplings in comparison to other size categories. A significant interaction between light environment and size was also recorded for $qP_{(281)}$ with differences between HL and LL values being greater for seedlings and young saplings compared to observed differences between HL and LL values for saplings and juveniles (Fig. 3; Table 1). For electron transport rate, ETR_{max} was significantly higher in HL needles compared to ML and LL needles.

Morphological differentiation of needles in relation to light availability

Univariate analysis revealed significant differences and interactions in macroscopic needle morphological traits with respect to light environment and size. Significant differences between size classes were observed for all measured needle morphological traits. In general, needles were longer, wider, and consequently, of greater surface area in larger plant size classes (saplings and juveniles). Conversely, SLA was significantly greater in seedlings with respect to other size classes (Tables 1, 2). Needle morphology was also affected by light environment, with LL and ML needles being significantly wider and having a

Table 1 Summary of two-way ANOVAs of chlorophyll-*a* fluorescence and needle morphological traits with light environment (LL; 0–5 % full daylight, ML; 5–20 % full daylight, and HL; >20 % full daylight) and demographic size class (seedlings–R1, young saplings–R2, saplings–R3, juveniles–R4) as main factors

		2-way ANOVA		Post-hoc Bonferroni tests		
		<i>F</i>	<i>P</i>	LL	ML	HL
Chlorophyll fluorescence						
<i>F_v/F_m</i>	Light environment	47.012	<0.001	a	a	b
	Size	2.464	0.063	–	–	–
	Interaction	1.57	0.157	–	–	–
Φ PSII ₍₂₈₁₎	Light environment	23.188	<0.001	a	a	b
	Size	2.107	0.101	–	–	–
	Interaction	1.681	0.128	–	–	–
<i>qP</i> ₍₂₈₁₎	Light environment	20.625	<0.001	a	b	b
	Size	24.649	<0.001	R3 > R1, R2, R4		
	Interaction	12.736	<0.001	–	–	–
ETR _{max}	Light environment	19.429	<0.001	a	a	b
	Size	0.424	0.736	–	–	–
	Interaction	1.072	0.381	–	–	–
Needle morphology						
Length	Light environment	2.388	0.095	–	–	–
	Size	13.384	<0.001	R4, R3 > R1, R2		
	Interaction	2.232	0.042	–	–	–
Width	Light environment	4.898	0.008	a	a	b
	Size	31.274	<0.001	R3 > R4 > R2 > R1		
	Interaction	2.145	0.048	–	–	–
Thickness	Light environment	9.606	<0.001	a	b	b
	Size	70.094	<0.001	R4 > R1, R2, R3		
	Interaction	12.166	<0.001	–	–	–
Surface area	Light environment	4.965	<0.001	a	a	b
	Size	16.374	<0.001	R4, R3 > R1, R2		
	Interaction	1.995	0.068	–	–	–
SLA	Light environment	9.369	<0.001	a	a	b
	Size	19.899	<0.001	R1 > R3 > R4		
	Interaction	1.906	0.082	–	–	–

Any two light environments sharing a common letter are not significantly different. Any post hoc significant differences between demographic size classes are also indicated

greater SLA than HL needles. For needle width, a weak interaction was found with respect to light environment and size class. Needles sampled from LL and ML had significantly greater surface area than HL needles. Light environment and plant size had a marked effect on needle thickness. Plants from HL and ML exhibited greater needle thickness than plants from LL environments (Tables 1, 2). A strong interaction between light environment and size occurred for needle thickness. Thickness was greater for HL and ML plants in sapling and juvenile size classes. Conversely, for seedlings, needle thickness was greatest in LL plants and lowest in HL plants.

Discussion

Light is a primary determinant of plant growth and survival (Walters and Reich 1996). However, due to the

heterogeneous distribution of light in the environment many species will be exposed to a range of light intensities over the course of their life cycle (Valladares and Niinemets 2008). In forests, tree seedlings are more likely to be growing in a shaded position, whilst mature individuals of many species will be exposed to the full intensity and spectrum of solar radiation. Thus, to understand plant light responses, a life-cycle view is required (Valladares and Niinemets 2008; Kunstler et al. 2009). Here, we explored the relationship between light availability and the distribution and growth of yew *Taxus baccata* L.

The relationship between yew size and light availability

At the GWNR, a large proportion of yew seedlings (0–0.20 m) and young saplings (0.21–0.50 m) were found under relatively low light availability- on average less than 7 % of full sunlight. In contrast, saplings and juveniles

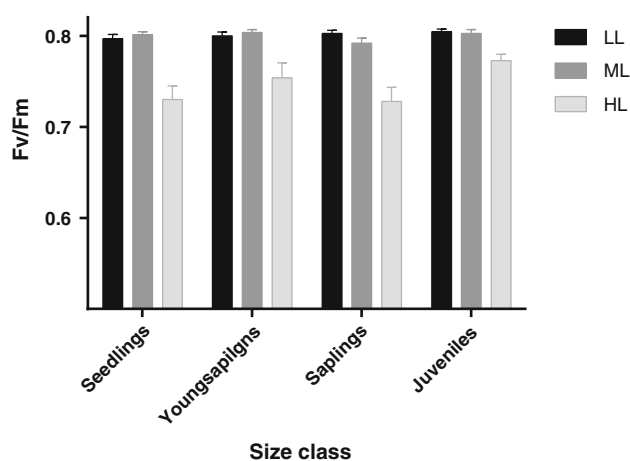


Fig. 2 Mean \pm 1 SE maximum quantum yield of fluorescence (F_v/F_m) for first year yew needles from four demographic size classes; seedlings (0–0.20 m), young saplings (0.21–0.50 m), saplings (0.51–2 m) and juveniles (>2–6 m). Needles were sampled from plants growing in three light environments; LL- <5 % full daylight; ML-5–20 % full daylight; HL- >20 % full daylight. Two-way ANOVA was used to assess differences within categories (Table 2)

were found in more illuminated conditions, where the light availability was often more than 50 % of full sunlight. This observation may reflect the dispersal pattern of yew seeds. Under natural conditions yew seeds are less likely to be deposited in open areas due to their dispersal mechanism (Martínez et al. 2008). Frugivorous birds (the primary dispersers of yew seeds) are attracted to perches on canopy trees and shrub vegetation and consequently seed deposition has been shown to be much greater beneath canopied areas than in open habitats (Smith 1980; Garcia et al. 2000, 2005; Farris and Filigheddu 2008). As yew height increases, it may grow above ground and understory shading vegetation and be gradually exposed to increased light

availability. A predictable vertical gradient of diminishing light availability is well-established in forest habitats with light being intercepted by consecutive leaf layers within the forest profile (Poorter et al. 2005; Thomas and Packham 2007). Consequently, in undisturbed conditions, tree seedlings will often be subject to greater light availability as they increase in height (Poorter et al. 2005). In our study, the reduced number of sapling and juvenile yews in shaded conditions suggests that light availability is a limiting factor in survival and recruitment of yew to later demographic stages. Studies by Iszkulo and Boratynski (2004, 2006) have indicated that despite the presence of yew seedlings in deep shade (<2 % full daylight), survival to later stages is stimulated by more open canopy conditions. Similar transitions of shaded seedlings to higher light areas in subsequent demographic stages, as seen in yew (Fig. 1) were demonstrated for a range of other tree species, such as *Nothofagus nitida* (Coopman et al. 2008) and *Aristotelia chilensis* (Lusk et al. 2008).

Size-dependent photosynthetic shade adaptation of yew needles

Given that yew seedlings are typically exposed to low light intensities, we asked whether this developmental stage is inherently photosynthetically shade-adapted. The question of whether an ontogenetic component of shade acclimation in yew exists has previously been posed by Wyka et al. (2008). To address this, we analysed photosynthetic parameters of seedlings, saplings and juveniles that grew in low, medium or high light environments.

In our study, it was found that the photosynthetic capacity of yew needles depends primarily on the light environment where the plant grew (Table 1). In general, seedlings growing in a particular light environment were

Table 2 Mean (\pm 1 SE) length (cm), width (cm), thickness (mm), surface area (cm^2) and specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) of first year yew needles sampled from range of light environments (LL, ML, HL) and size classes (seedlings, young saplings, saplings, juveniles)

Size class (m)	Light availability	Needle morphology				
		Length (cm)	Width (cm)	Thickness (mm)	Surface area (cm^2)	SLA ($\text{cm}^2 \text{g}^{-1}$)
Young seedlings	LL	1.31 \pm 0.08	0.21 \pm 0.01	0.24 \pm 0.01	0.24 \pm 0.02	204.7 \pm 15.5
	ML	1.50 \pm 0.09	0.19 \pm 0.01	0.22 \pm 0.01	0.26 \pm 0.02	169.6 \pm 19.2
	HL	1.48 \pm 0.08	0.21 \pm 0.01	0.16 \pm 0.02	0.25 \pm 0.03	154.5 \pm 8.56
Seedlings	LL	1.33 \pm 0.07	0.23 \pm 0.01	0.19 \pm 0.01	0.27 \pm 0.02	154.1 \pm 7.14
	ML	1.33 \pm 0.08	0.25 \pm 0.01	0.24 \pm 0.02	0.25 \pm 0.01	179.9 \pm 15.7
	HL	1.32 \pm 0.06	0.21 \pm 0.01	0.29 \pm 0.01	0.24 \pm 0.01	135.5 \pm 12.8
Saplings	LL	1.73 \pm 0.07	0.28 \pm 0.01	0.18 \pm 0.01	0.41 \pm 0.02	173.6 \pm 13.44
	ML	1.61 \pm 0.07	0.28 \pm 0.01	0.21 \pm 0.01	0.36 \pm 0.02	143.7 \pm 8.62
	HL	1.47 \pm 0.07	0.25 \pm 0.01	0.21 \pm 0.01	0.29 \pm 0.02	117.9 \pm 11.20
Juveniles	LL	1.69 \pm 0.14	0.24 \pm 0.01	0.30 \pm 0.02	0.34 \pm 0.04	117.8 \pm 5.9
	ML	1.89 \pm 0.1	0.26 \pm 0.01	0.36 \pm 0.01	0.37 \pm 0.03	96.8 \pm 7
	HL	1.57 \pm 0.07	0.23 \pm 0.01	0.39 \pm 0.01	0.29 \pm 0.01	92.2 \pm 3.2

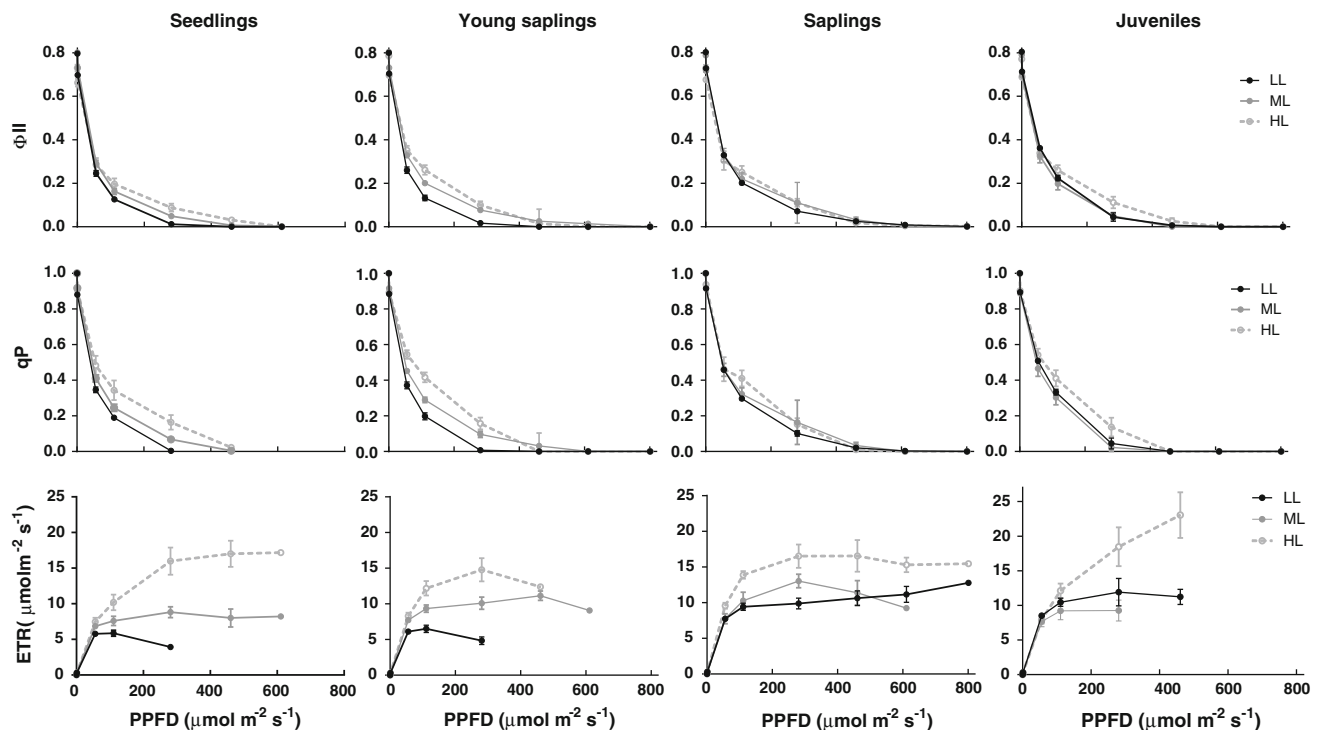


Fig. 3 Responses of chlorophyll-*a* fluorescence parameters in first year needles from three light environments (HL—dashed line, ML—Grey line, LL—Black line) and four size classes (seedlings, young saplings, saplings, juveniles). Points represent mean values (± 1 SE) from up to eight levels of actinic light (1–800 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

Statistical comparisons for Φ_{PSII} and qP were conducted at $\text{PPFD} = 281 \mu\text{mol m}^{-2} \text{s}^{-1}$ and the maximum values for ETR (ETR_{max}) were compared to assess differences within size class and light environment (Table 2)

photosynthetically indistinguishable from juveniles in the same light environment. There is little evidence that the developmental stage is an inherent determinant of photosynthetic performance, with the possible exception of a size-dependent effect on qP . Thus, based on a lack of significant interactions between light environmental and plant size (Table 1), yew plants acclimate to the light environment in which they occur, regardless of developmental stage. This finding is in contrast to other studies (Poorter et al. 2005; Coopman et al. 2008) that have indicated that the developmental stage itself is a determinant of photosynthetic performance. However, the degree to which photosynthetic capacity is mediated by development stage is likely to be species-specific with Poorter et al. (2005) recording all of the nine of their hypothesized height-light trajectories amongst 47 tropical tree species.

Interestingly, all yew plants displayed a decrease in the maximal efficiency of photosystem II (F_v/F_m) when growing in high light environments (Fig. 2). Such photoinhibition is caused when plants are subject to excess light beyond the photosynthetic capacity, leading to oxidative photodamage to photosystem II, and in some cases even a reduction in plant health (Mitamura et al. 2009). Conifers can be susceptible to photoinhibition, particularly

when canopy openness is abruptly increased, or when relatively high light intensities in late winter are accompanied by low temperatures that impede biochemical reactions (Ball et al. 1991; Oquist and Huner 1991; Robakowski and Wyka 2009). In general, photoinhibitory stress can be observed when plants are exposed to moderate to high light intensities in combination with drought conditions, low nutrient levels, low temperatures, or various other stressors (Valladares et al. 2005; Takahashi and Murata 2008). For this study, PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) above plants was not recorded on the day immediately before sampling. However, given that global solar radiation values and sunlight hours for the 10 day period prior to sampling (102.29 MJ m^{-2} and 37 h, respectively) were both lower than 10 year averages for the same period (106.09 MJ m^{-2} and 47.3 respectively), it is unlikely that climate conditions immediately prior to sampling were responsible for the observed potential photoinhibition in high light plants. For the current study, the question is raised whether the observed photoinhibitory effect (Fig. 2) directly reflects continued exposure to excess light, or rather a combined effect of high light with a secondary stressor. Devaney (2013) raised yew plantlets from seed *ex situ* under low (<5 % full daylight) and high light (100 % full daylight)

conditions and measured a number of growth and photosynthetic parameters, including F_v/F_m . In these plants, 7 weeks after germination, F_v/F_m was also lower when plants were grown at the highest light intensity, despite the optimised growth conditions with adequate supply of water and nutrients. Thus, although yew seedlings, saplings and juveniles effectively adjust photosynthetic performance in response to the light environment where they grow (Table 1), there seems to be a maximum light intensity above which individuals from these demographic size classes are subjected to photoinhibition. Mitchell (1998) examined acclimation of mature yew trees (>10 m) to high light conditions and found no evidence of photoinhibition. In fact, yew *T. baccata* was found to be more tolerant of exposure to full light than *T. brevifolia*. Future work will need to examine whether the lack of photoinhibition in mature yew trees is an acclimatory response (as observed for seedlings, saplings and juveniles), or whether a development-dependent change in light-utilisation occurs between juvenile and mature stages.

It remains to be established to what extent photoinhibition affects overall performance of yew at higher light intensities. Evidence from the literature is contradictory. It has been reported that yew increases its growth rate in high light conditions (Svenning and Magård 1999; Thomas and Polwart 2003). In an experiment examining light limitation of yew seedlings in Poland, Iszkulo et al. (2007) found a positive correlation between seedling height increase and light availability. However, during the experiment, maximum light availability recorded in the study area was <35 % of full daylight, and hence, growth at high light intensities was not evaluated. In an ex situ study of light availability and yew growth, Perrin and Mitchell (2013) demonstrated that although yew plants grown below 27 % full daylight displayed a positive correlation between light availability and height increase, growth was suppressed in treatments exposed to 100 % of full daylight. Hence it is possible that yew offspring are capable of increasing growth under intermediate shade conditions but in higher light environments (>30–40 % daylight), photoinhibition of needles will lead to a reduction in growth.

Size-dependent morphological responses to light availability in yew needles

Needles exhibited variations in morphology depending on both light environment where plants grew and their size (Table 1). Needle size (length and width) is predominantly dependent on the size of the yew individual (Table 1). Needle structure is an important determinant of light capture, and therefore photosynthetic performance. This creates an interesting dichotomy; the efficiency of the photosynthetic light reactions is largely linked to the light

environment in which the plants grew, but needle area is mostly determined by the size of the plants. During the life cycle of yew, needle surface area will increase with plant size (Table 2), and this will be matched by an increase in light availability, as larger plants are exposed to more light (Fig. 1). The size-dependent increase in needle surface area may reflect the overall balance between above and below-ground biomass, i.e. larger individuals with a larger root system can develop and maintain greater needle surface area (Reich et al. 1998).

In this study, changes in needle thickness and related SLA were influenced by light environment and plant size. SLA decreases with both increasing plant size and increasing light availability. Mitchell also found that SLA was reduced in needles of yew trees growing in full sunlight (Mitchell 1998). In other coniferous species similar reductions in SLA in response to exposure to full sunlight were observed (Tucker and Emmingham 1977; Mitchell and Arnott 1995). Increases in SLA are associated with exposure to low light in many tree species and this response can be interpreted as an attempt to maximise light capture (Rozendaal et al. 2006). Conversely, decreases in SLA are often associated with growth under higher light intensities and drought acclimation in woody species (Monclus et al. 2006). In our study, the SLA data can be interpreted in the context of environmental pressure to increase light capture in small plants in low light environments, and to decrease transpiration in larger plants in high light environments. Thus, the lower thickness and higher SLA of needles of yew seedlings compared to juvenile yews, irrespective of light environment, suggests that seedlings are morphologically inherently shade-adapted.

For needle thickness, a strong interaction between plant size and light environment was evident with larger plants following expected patterns of greater thickness in higher light but seedlings being of lowest thickness in high light and greatest thickness in low light. The absence of shading vegetation for high light seedlings may have led to exposure to higher temperatures. Decreases in needle thickness in gymnosperms maybe related to increased atmospheric temperature (Luomala et al. 2005). However, for yew, potential size-dependent responses to environmental stresses other than light availability remain untested.

Yew regeneration and light availability

Our data show a strong association between seedlings and young saplings and shade, and hence, the question arises whether shade is a prerequisite for natural regeneration. Natural regeneration of yew seedlings is mostly absent in high light environments (Watt 1926; Smith 1980). Indeed, Watt (1926), recorded only one seedling in a grazer-excluded

grassland area which was located near abundant mature yew trees at the South Downs in England. The relationship between recruitment success in yew and the presence of shade-giving shrubs has been highlighted in the literature (Smith 1980; Garcia et al. 2000; Farris and Filigheddu 2008). For example, the development of yew-dominated woodland in the British Isles is commonly associated with the presence of shrub species such as *Crataegus monogyna* and *Ilex aquifolium* (Rodwell 1991). In Mediterranean habitats, work by Garcia and others (Garcia et al. 2000; Farris and Filigheddu 2008) has also outlined the facilitation of yew regeneration by nurse plants. Nurse plants can facilitate yew recruitment by providing multiple microsite benefits such as increased seed input and protection from herbivore damage (Garcia and Obeso 2003; Garcia et al. 2005; Farris and Filigheddu 2008). The extent to which shaded conditions afforded by shrub species contribute to yew growth and development in early life history stages is not clear.

To enable effective conservation and silvicultural programs for tree species, further research is required to clarify the extent to which light availability regulates both photosynthetic capacity and needle morphology, and consequently species growth and distribution. The data in this paper highlight the importance of considering multiple plant traits and developmental stages when evaluating species environmental responses and distribution patterns.

Author contribution statement All authors conceived and designed the work presented in this paper, and contributed substantially to analysis and interpretation of data. J.L.D. carried out field sampling, with assistance from P.M.W. Chlorophyll fluorescence and needle morphology work was carried out and analysed by J.L.D., with assistance from M.A.K.J. The manuscript was prepared and edited by J.L.D., P.M.W., and M.A.K.J.

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