Effects of shade on growth, biomass allocation and leaf morphology in European yew (*Taxus baccata* L.)

Philip M. Perrin^{1, 2} and Fraser J. G. Mitchell¹

(1)Department of Botany, Trinity College Dublin, University of Dublin, Dublin 2, Ireland

(2)Present address: BEC Consultants Ltd., Ground Floor Offices, Loft 31, South Cumberland Street, Dublin 2, Ireland

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Abstract

The impact of shade on the growth of European yew (*Taxus baccata* L.) saplings was investigated over a three-year period using artificial shading to simulate four different light regimes (3, 7, 27 and 100 % relative photosynthetic photon flux density, RPPFD). There was no mortality attributable to shading even under the 3 % RPPFD treatment. Increasing shade was positively associated with specific leaf area, leaf length, leaf width and total chlorophyll content, but negatively associated with plant height, stem diameter, total dry weight and root to leaf and shoot ratio. Discoloration of the foliage occurred in plants grown in 100 % RPPFD conditions (resulting in reduced growth rates) and those transferred to 100 % RPPFD conditions after being shade-acclimated for 2 years. Evidence suggests that *T. baccata* has the ability to regenerate beneath a lighter canopy but beneath denser canopies gap dynamics will play an important role in facilitating successful regeneration and this needs to be reflected in management of natural populations of this declining species.

Keywords

Artificial shading Biomass allocation Leaf morphology Natural regeneration
Taxus baccata

Introduction

European yew (*Taxus baccata* L.) is widely regarded as a species in decline across continental Europe (e.g. Hofman 1970; Bugała 1978; Leuthold 1980; Majer 1981; Svenning and Magård 1999; García et al. 2000; Dhar et al. 2006) and is even at risk of becoming regionally extinct (Schirone et al. 2010). The species is afforded legal protection in some European countries (e.g. Poland) and yew-dominated woods in Britain and Ireland are listed as priority habitats under Annex I of the EU Habitats Directive (European Commission 2007). Poor rates of regeneration have been reported from many natural populations and this has been related to several factors including seed predation (Hulme 1996), winter frosts (Iszkuło 2010), autotoxicity (Semagina 1983) and herbivore browsing (Mysterud and Østbye 2004; Perrin et al. 2006; Farris and Filigheddu 2008).

Light conditions and canopy density are, however, known to be key considerations affecting yew regeneration (Iszkuło and Boratyński 2004, 2006). Yew regenerates most readily in thorny scrub where plants receive relatively high light levels, but are mechanically protected from browsing animals (Watt 1926; Tittensor 1980; Hulme 1996; García et al. 2000; Farris and Filigheddu 2008). Perrin et al. (2006) found that in Ireland, in the absence of browsing animals, yew regenerated beneath the lighter, deciduous canopy of sessile oak (*Quercus petraea* (Matt.) Liebl.), but not beneath the denser, evergreen canopy of yew. Svenning and Magård (1999) reported that sexual activity, strobilus production and recruitment to the sapling stage were all reduced beneath dense canopy, and the felling of beech (*Fagus sylvatica* L.) and opening up of the canopy were considered by Hulme (1996) to be responsible for strong yew sapling recruitment in a northern England woodland. Gap dynamics and overstory mortality are therefore particularly important considerations for yew regeneration in forests with dense canopies.

Despite favouring these higher light conditions for regeneration, yew is regarded as a shade-tolerant species (Bugala 1978; Brzezicki and Kienast 1994; Thomas and Polwart 2003). Shade tolerance is the minimum light level required for survival, but Valladares and Niinemets (2008) have argued that rather than this being an absolute value it is a relative concept affected by other biotic or abiotic factors such as drought, waterlogging and herbivory, with tolerance to this interaction also influenced by length of the growing season. Many species with shade tolerance exhibit a functional trade-off with lower tolerances to drought and waterlogging, but *T. baccata* is unusual, particularly amongst gymnosperms, in being both shade-tolerant and drought-tolerant (Niinemets and Valladares 2006).

Despite interactions with other stress factors, species-relative shade tolerance rankings remain fairly constant (Valladares and Niinemets 2008). In forest communities in Ireland and Britain where *T. baccata* occurs, yew is ranked as one of the most shade-tolerant of tree species present, whereas in examples of stands in central and Eastern Europe, there are several species with similar or stronger shade tolerance (Table 1).

Table 1

Ellenberg indicator values for light requirement for the main tree species in four European forest communities in which *Taxus baccata* occurs

Reenadinna Wood, SW Ireland (Perrin et al. 2006)*		Taxus baccata woodland of the British National Vegetation Classification (Rodwell 1991)*	
<i>Corylus avellana</i>	4	<i>Fagus sylvatica</i>	3
<i>Taxus baccata</i>	4	<i>Acer pseudoplatanus</i>	4
<i>Euonymus europaeus</i>	5	<i>Taxus baccata</i>	4
<i>Fraxinus excelsior</i>	5	<i>Fraxinus excelsior</i>	5
<i>Ilex aquifolium</i>	5	<i>Ilex aquifolium</i>	5
<i>Crataegus monogyna</i>	6	<i>Crataegus monogyna</i>	6
<i>Sorbus aucuparia</i>	6	<i>Sambucus nigra</i>	6
<i>Betula pubescens</i>	7	<i>Sorbus aria</i>	6
<i>Quercus robur</i>	7	<i>Quercus robur</i>	7
Stiwollgraben, Austria (Dhar et al. 2006)**		Knyazhdvir Nature Reserve, W Ukraine (Iszkulo et al. 2005)**	
<i>Abies alba</i>	3	<i>Abies alba</i>	3
<i>Fagus sylvatica</i>	3	<i>Acer campestre</i>	3
<i>Acer pseudoplatanus</i>	4	<i>Fagus sylvatica</i>	3
<i>Fraxinus excelsior</i>	4	<i>Acer pseudoplatanus</i>	4
<i>Taxus baccata</i>	4	<i>Prunus avium</i>	4
<i>Ulmus glabra</i>	4	<i>Taxus baccata</i>	4
<i>Picea abies</i>	5	<i>Acer platanoides</i>	5
<i>Sorbus aria</i>	6	<i>Picea abies</i>	5
<i>Pinus sylvestris</i>	7	<i>Cornus sanguineus</i>	7
<i>Larix decidua</i>	8	<i>Corylus avellana</i>	6
		<i>Sambucus nigra</i>	7

This scale varies for woody plants from 3 to 9 where 3 indicates plants found in shade and 9 indicates plants found in full light

* Signifies values are from Hill et al. (2004)

** Signifies values are from Ellenberg et al. (1992)

Phenotypic plasticity tends to be low overall in shade-tolerant plants, for example, they show limited elongation in low light conditions, but they can have considerable plasticity in some features which optimise light capture (Valladares and Niinemets 2008). These include increased chlorophyll content and producing a greater leaf surface area per unit dry mass under shade conditions (Niinemets 2010). Hallik et al. (2009) showed that, within key plant functional types, mean leaf dry mass per area of woody temperate species decreased with increasing shade tolerance. Under low light conditions, both shade-tolerant and shade-intolerant species have been shown to allocate proportionately less biomass to roots (e.g. Reich et al. 1998).

The aim of the experiment reported in this paper was to add to our knowledge of natural regeneration in yew by investigating the impact of shade on the growth, biomass allocation and leaf morphology adaptations of *T. baccata* saplings.

Methods

The experiment was conducted on an open plot at Trinity College Botanic Gardens, Dublin, Ireland (latitude 53° 20' N, longitude 6° 15' W). Young, bare-rooted *T. baccata* saplings grown from seed and approximately 35 cm in height were sourced from a commercial nursery. These were planted in 23 cm diameter plastic pots in a general purpose peat-based compost and randomly allocated to one of five shade treatments (n = 24 per treatment). Levels of shading were achieved by growing plants beneath wooden frames (3.05 m × 2.05 m × 1.15 m) covered on all side by layers of green plastic shade netting (Gardman). The photosynthetic photon flux density (PPFD) available in each treatment was measured on a uniformly overcast day using a quantum sensor (model LI-189, LI-COR Biosciences). This was used to quantify the PPFD available in each shaded treatment relative to the PPFD available for the unshaded control treatment, that is, relative photosynthetic photon flux density (RPPFD) (Table 2). The experiment was run over 3 years. In four treatments (A–D), the same shade conditions were maintained in each treatment throughout the experiment but in the fifth treatment (E), plants were grown under heavy shade for 2 years and then transferred to 100 % RPPFD shortly after bud burst in May of the third growing season. This was achieved by removing the shade frame and was intended to simulate canopy removal. An uncovered gap at the bottom of the frames permitted air circulation. Plants were watered by hand as required throughout the experiment and during the growing season plants were fed regularly with a standard liquid NPK plant feed. Global radiation and temperature data for the duration of the experiment are presented in Table 3 (Met Éireann, unpublished data for Dublin Airport 13 km N of the experimental site).

Table 2

Relative photosynthetic photon flux density (RPPFD) available to plants in each shade treatment

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Relative photosynthetic photon flux density (RPPFD) available to plants in each shade treatment

Treatment	Shading	RPPFD (%)
A	None (control)	100
B	Low	27
C	Medium	7
D	Heavy	3
E	Heavy (for first and second growing seasons)	3
	None (for third growing season)	100

Table 3

Mean global radiation and temperature data from Dublin Airport for 2000–2002

Parameter	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept
Daily global radiation (J cm ⁻²)	241	513	842	1,259	1,807	1,696	1,560	1,367	965
Daily maximum temperature (°C)	8.1	9.2	10.1	11.4	15.4	17.2	18.9	19.3	17.1
Daily minimum temperature (°C)	2.1	2.0	2.9	3.1	6.4	8.8	10.5	10.7	8.0

Data from Met Éireann

The experiment was initiated in February 2000. At that time the height of each plant (from level of root collar to highest living bud) and the stem diameter 2 cm above the root collar were measured. After the first growing season, in December 2000, the height of all plants was re-measured and eight plants from treatments A, B, C and D were randomly selected for harvest. From each harvested plant, twenty leaves were removed, five from the midpoint of each of the top four lateral shoots of current-year growth. These sampled leaves were scanned using a standard PC scanner and the resulting digitised leaf images were analysed using the Scion Image software (Scion Corporation) to obtain the mean area, length and width of leaves from each plant. The dry weight of sampled leaves, remaining new leaf and shoot biomass, old leaf and shoot biomass and root biomass for each harvested plant was measured after drying material in an oven for 72 h at 75 °C. Combined measurements were made for leaf and shoot biomass. Eight plants were also removed from treatment E to keep the number of plants per treatment equal and the plants remaining in each treatment were repositioned to maintain plant density.

After the second growing season, in January 2002, the height and basal diameter of all plants were re-measured. Eight plants were again randomly selected and removed from each treatment and biomass and leaf measurements were

recorded as detailed above for treatments A, B, C and D. In addition, chlorophyll content was measured from bulked leaf samples from three plants randomly selected from each of treatments A, B, C and D (approximately fifteen leaves per treatment). Following determination of fresh weight, chlorophyll was extracted with 80 % acetone from ground samples and extracts were centrifuged at $500 \times g$. Replicated measurements ($n = 5$) of the light absorbance of these samples at a wavelength of 652 nm were made using a spectrophotometer. Total chlorophyll content was then calculated following Hall and Rao (1994). After the third growing season, in late 2002, the height and basal diameter of all remaining plants were again re-measured.

Data were investigated using ANOVA with Tukey's HSD post hoc test.

Results

No mortality attributable to the effects of shade occurred during the experiment. In winter 2000, after the first growing season, foliage of plants in the control group (treatment A) developed a bronzy discoloration on the upper surface, possibly as a result of frost or exposure. This resulted in poor growth of these plants in the second and third growing seasons. Exposure of plants in treatment E to full light at the start of the third growing season resulted in a rapid bleaching effect of the foliage.

At the start of the experiment, there were no significant differences in mean height between the treatments (Fig. 1a, $P = 0.183$). After the first growing season, plants in treatment B (light shade) were significantly taller than plants under medium and heavy shade treatments (Fig. 1b, $P = 0.002$). No significant differences in height occurred at the end of the second growing season (Fig. 1c, $P = 0.147$). At the end of the third growing season, the poorly growing plants in treatment A were significantly shorter than those in treatments B (light shade) and C (medium shade) (Fig. 1d, $P = 0.008$). Although there was no significant difference in height between plants in treatments B, C and D, there was a trend of decreasing height with increasing shade. Exposure of plants in treatment E to full light conditions after two growing seasons in heavy shade did not result in a significant difference in height compared with treatment D, where plants had remained in heavy shade for all three seasons.

Fig. 1

Mean height (cm) of yew saplings grown under different shade treatments: a at start of experiment; b after first growing season; c after second growing season; d after third growing season. Percentages indicate RPPFD available to each treatment, with treatment E being 3 % RPPFD in graphs (a), (b) and (c) and 100 % in graph (d). Vertical bars indicate se. Within each graph, lower-case letters indicate homogeneous subsets according to Tukey's HSD post hoc test

Basal diameter did not differ significantly at the start of the experiment (Fig. 2a, $P = 0.388$) but after two growing seasons shading had clearly had an effect, with this measurement being significantly smaller as shade increased (Fig. 2b, $P < 0.001$). A similar pattern occurred after the third growing season (Fig. 2c, $P < 0.001$). Exposure of plants in treatment E to full light conditions after two growing seasons in heavy shade resulted in a trend for markedly greater basal diameter after the third growing season compared with treatment D.

Fig. 2

Mean basal diameter (mm) of yew saplings grown under different shade treatments: a at start of experiment; b after second growing season; c after third growing season. Percentages indicate RPPFD available to each treatment, with treatment E being 3 % RPPFD in graphs (a) and (b) and 100 % in graph (c). Vertical bars indicate se. Within each graph, lower-case letters indicate homogeneous subsets according to Tukey's HSD post hoc test

Mean total dry weight of plants harvested after the first growing season differed significantly between treatments (Table 4) with plants under the heavy shading (treatment D) being less than half the weight of the unshaded controls (treatment A). Root to leaf and shoot dry weight ratio also differed significantly between treatments after the first growing season with leaves and shoots comprising a smaller proportion of total dry weight in the unshaded plants (treatment A) and plants under low shade (treatment B) than in the other treatments. After the second growing season, these patterns had become more pronounced with plants in treatment D being less than a third of the dry weight of plants in treatment A, and with root to leaf and shoot ratio declining significantly with increasing shade.

Table 4

Dry weight proportions and root to leaf and shoot ratio of yew saplings grown under different shade treatments for one and two growing seasons

Treatment	New leaves and shoots (%)	Old leaves and shoots (%)	Roots (%)	Root: leaf and shoot	Total (g)
After first growing season					
A	16.5 ± 1.5a	30.9 ± 3.0a	52.6 ± 4.5a	1.13 ± 0.07a	103.9
B	17.7 ± 1.5a	31.9 ± 2.5a	50.4 ± 4.6a	1.02 ± 0.07a	86.3
C	18.0 ± 1.4a	41.4 ± 3.2ab	40.6 ± 4.2a	0.68 ± 0.04b	52.2
D	10.5 ± 1.8b	47.9 ± 5.9b	41.6 ± 6.7a	0.70 ± 0.06b	36.3
<i>P</i>	**	*	n.s.	***	***
After second growing season					
A	2.5 ± 0.6a	42.2 ± 3.4a	55.3 ± 6.5a	1.22 ± 0.09a	148.3
B	9.4 ± 3.7ab	44.1 ± 8.9a	46.5 ± 8.0ab	0.97 ± 0.07a	106.2
C	11.8 ± 2.1b	50.1 ± 5.4a	38.1 ± 4.8ab	0.63 ± 0.07b	83.0
D	10.1 ± 1.4ab	61.6 ± 5.9a	28.3 ± 3.2a	0.41 ± 0.05b	46.6
<i>P</i>	*	n.s.	*	***	***

Values are presented with se. Within columns for each growing season, lower-case letters indicate homogeneous subsets according to Tukey's HSD post hoc test

ANOVA: * < 0.05, ** < 0.01, *** < 0.001, n.s. indicates not significant

Increased levels of shade resulted in a higher specific leaf area (SLA) (Table 5). This was due primarily to larger leaf area; leaves under heavier shade were both longer and wider than leaves under low shade or no shade. Chlorophyll content of foliage grown in the second year differed significantly between treatments (Table 6, $P < 0.001$) with higher levels of chlorophyll in the plants under medium and heavy shade.

Table 5

Mean leaf length (mm), width (mm), area (cm²), dry weight (mg) and specific leaf area (SLA; cm² g⁻¹) of current-year foliage from yew saplings grown under artificial shade for one and two growing seasons

Treatment	Length	Width	Area	Dry weight	SLA
After first growing season					
A	19.48 ± 0.47a	2.59 ± 0.04a	0.43 ± 0.02a	4.2 ± 0.2a	103.0 ± 3.4a
B	21.03 ± 1.27ab	2.75 ± 0.09ab	0.49 ± 0.05a	4.3 ± 0.5a	116.3 ± 6.2a
C	21.06 ± 1.26ab	2.92 ± 0.10ab	0.51 ± 0.05a	3.1 ± 0.4a	172.8 ± 8.5b
D	24.08 ± 1.14b	3.09 ± 0.17b	0.59 ± 0.04a	2.9 ± 0.3a	209.2 ± 11.7c
<i>P</i>	*	*	n.s.	*	***
After second growing season					
A	9.82 ± 0.97a	2.23 ± 0.12a	0.17 ± 0.03a	1.7 ± 0.4a	115.2 ± 6.0a
B	16.95 ± 2.48b	2.69 ± 0.14b	0.41 ± 0.08b	3.5 ± 0.8ab	122.5 ± 5.1a
C	19.52 ± 0.58bc	3.35 ± 0.08c	0.55 ± 0.02bc	3.7 ± 0.2b	149.6 ± 4.6b
D	24.02 ± 0.81c	3.45 ± 0.12c	0.71 ± 0.03c	3.5 ± 0.3ab	208.2 ± 10.2c
<i>P</i>	***	***	***	*	***

Values are presented with se. Within columns for each growing season, lower-case letters signify homogeneous subsets according to Tukey's HSD post hoc test

ANOVA: * < 0.05, *** < 0.001, n.s. indicates not significant

Table 6

Chlorophyll content (mg g⁻¹ fresh weight) of current-year leaves of yew saplings grown under different shade treatments for two growing season

Treatment	RPPFD (%)	Chlorophyll content
A	100	0.33 ± 0.42a
B	27	0.49 ± 0.11a
C	7	1.26 ± 0.07b
D	3	1.97 ± 0.06b

Values are presented with se. Lower-case letters indicate homogeneous subsets according to Tukey's HSD post hoc test

Discussion

The experiment demonstrated that *T. baccata* growing under shade conditions exhibits growth and leaf morphology adaptations. Saplings survived under 3 % RPPFD conditions for 3 years. However, smaller plants are apparently less able to survive in dense shade conditions; Iszkuło and Boratyński (2004) found that whilst seedlings of yew (less than 25 cm tall) were most frequent beneath conifer trees including mature yews, regeneration over 1 m in height was most frequent beneath a broadleaf canopy. Hence, survival rates of seedlings are higher under a lighter, deciduous broadleaf canopy.

After 3 years, there was a general trend of greater height and stem diameter with increasing light levels between treatments B, C and D. A correlation between height and light availability has been found in an in situ experiment with *T. baccata* seedlings beneath a deciduous canopy (Iszkuło et al. 2007). Conversely, in shade-intolerant species significant increases in height occur under lower light conditions, for example, pedunculate oak (*Quercus robur* L.) (Welander and Ottoson 1998). Root collar diameter increment has been found to decline with increased shade in other conifer species (Kennedy et al. 2007). Whilst transfer of plants from 3 % RPPFD to unshaded conditions did not significantly increase the height of plants (possibly due to the damage to foliage), there was a positive response in stem diameter.

Specific leaf area (SLA) is indicative of the light levels in which foliage has grown. Increases in SLA by plants grown under lower light levels have been reported for many conifer species covering a range of shade tolerance (Mitchell 1998; Reich et al. 1998; Awada et al. 2003; Qu et al. 2005). *T. baccata* evidently has a considerable plasticity in the morphology of new leaves with plants grown under heavy shade (3 % RPPFD) having almost twice the SLA of unshaded plants. Increasing SLA in *T. baccata* seedlings with decreasing light levels was observed by Iszkuło (2010) who also reported similar relative differences between shade treatments.

Increasing shade resulted in reduced total dry weight as found in other conifer studies (e.g. Khan et al. 2000; Qu et al. 2005). With increasing shade, biomass allocation was shifted from roots to leaves and shoots, a strategy characteristic of shade-acclimated plants (Givnish 1988). Whilst leaf and shoot biomass were not examined separately in the present study, Iszkuło (2010) reported that in *T. baccata* seedlings grown under artificial shade, leaf biomass allocation and shoot biomass allocation both increased with increasing shade. In contrast, Reich et al. (1998) found that for a range of tree species, increased shade caused a decrease in root biomass allocation and an increase in shoot biomass allocation, but no significant change in leaf biomass allocation, although that investigation was confined to 5 and 25 % light treatments. Whilst the magnitude of these changes in biomass allocation differed by species in Reich's study, there was no pattern in relation to shade tolerance, hence biomass allocation is not diagnostic of shade strategy.

Plants grown in unshaded conditions and shade-adapted plants transferred to unshaded conditions suffered from damage to foliage. Damage to the plants grown in treatment A (100 % RPPFD) may have been due to exposure to full sunlight, winter frosts or a combination of these factors. Yew populations in England achieve a maximum tolerance to cold in mid winter (January), but cold hardiness then declines rapidly, therefore plants are susceptible to spring frosts (Melzack and Watts 1980). Frost is a major cause of mortality of yew seedlings in Poland (Iszkuło 2010), but the climate in Ireland is much milder than that in Eastern Europe. As occurs in natural populations, the plants grown in the full sunlight treatment will have been more exposed than those grown under shade. Damage to the plants in treatment E following transfer appears to be due to the unsuitability of shade-adapted foliage to full sunlight conditions, possibly due to the development of a thin waxy cuticle in deep shade; this layer protects plant tissues from excessive insolation. When plants are transferred to a different light regime, *T. baccata* needles grown in previous years have been shown to have no acclimative ability in their size or mesophyll structure (Wyka et al. 2008). It has also been reported that, whilst yew seedlings growing in the shade of their parent trees produce dark green leaves, those occurring in the open grow little and have leaves that turn orangey-brown in colour (Smith 1980). Mitchell (1998) found that sun-grown *T. baccata* foliage had a higher SLA and foliar N content than Pacific yew (*T. brevifolia* Nutt.) and suggested that *T. baccata* was therefore more tolerant of full irradiance than *T. brevifolia*. Bugała (1978) states that yew plants grown in the shade and transplanted into the open do not survive. In contrast, there is good evidence that, within woodland, opening up of the canopy has a positive effect on yew regeneration (Mitchell 1988, 1990; Hulme 1996; Svenning and Magård 1999). This suggests that, whilst shade-adapted yew is able to respond with increased growth to the medium increases in light levels associated with the development of canopy gaps, such plants are less able to adapt to full sunlight conditions. This regeneration strategy is similar to the 'Oskar syndrome' described by Silvertown (1982) where a pool of juveniles can survive for many years under heavy shade waiting for a canopy gap to appear and can then exploit the gap ahead of new regeneration from other species.

Conclusions

Plants grown under low light conditions display reduced growth rates, and changes to leaf morphology, chlorophyll content and biomass allocation, but no mortality attributable to shade. This tolerance appears to enable *T. baccata*, in the absence of other limiting factors, to regenerate successfully beneath lighter canopies. However, denser canopies such as those cast by conifers including yew itself may inhibit regeneration. The management implications of this concur with the recommendations proposed by Czatoryski (1978) and Svenning and Magård (1999) and investigated by Dhar et al. (2006), where selective felling to create broken or thin canopy conditions may be a valid management tool for promoting regeneration in natural populations of yew where it occurs in the understory of

mixed forests. Where the aim is to re-establish or reinforce a population within woodland, underplanting beneath lighter canopies is also feasible.

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