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Effects of light availability on morphology, growth and biomass allocation of *Fagus sylvatica* and *Quercus robur* seedlings

Ignacio Sevillano [a,b,*], Ian Short [a], Jim Grant [c], Conor O'Reilly [b]

[a] Teagasc Forestry Development Department, Teagasc Ashtown Food Research Centre, Ashtown, Dublin 15, Ireland
[b] UCD Forestry, School of Agriculture and Food Science, University College Dublin, Belfield, Dublin 4, Ireland
[c] Statistics and Applied Physics, Research Operations Group, Teagasc Ashtown Food Research Centre, Ashtown, Dublin 15, Ireland

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ABSTRACT

The survival, morphological, and growth responses of European beech (*Fagus sylvatica* L.) and pedunculate oak (*Quercus robur* L.) seedlings to different light intensities, from full sunlight to heavy shade, were studied over two growing seasons in a shadehouse experiment. Although shade treatments significantly affected seedling growth, they did not influence seedling survival. Both growth and biomass increased as light intensity increased. Diameter growth of oak seedlings was higher than that of beech. Beech and oak seedlings showed typical acclimation to shade, including greater specific leaf area and height to diameter ratios, and lower leaf thickness and root:shoot ratios with increasing shade. Beech seedlings exhibited greater specific leaf area, and lower leaf thickness and root:shoot ratios than oak seedlings. In spite of the greater growth at full sunlight, the results from this study suggest that beech and oak seedlings would have high survival rates and would acclimate well if underplanted below overstories that reduce the available light to as low as 28% of full light.

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1. Introduction

Silviculture is an old discipline which must be adapted to address different forest management challenges, such as sustainability and multi-purpose objectives. Although natural regeneration is preferred and is the most common method of replacing forests on a worldwide scale (Savill et al., 1997), it is not always successful or practical. In these cases, underplanting may be a feasible alternative regeneration method. In Ireland, planting is the most common method of establishment (Woodlands of Ireland). Underplanting in an existing stand is a common practice in Central Europe (Hawe and Short, 2012) and is carried out in shelterwoods and thinned stands (Lüpke et al., 2004). Underplanting has been applied for the enrichment of an existing stand, for the conversion of even-aged monocultures into more complex systems and for the rehabilitation of non-productive stands (Kenk and Guehne, 2001; Paquette et al., 2006). Therefore, one suggested method for improving under-performing broadleaf forests is thinning in conjunction with underplanting (Evans, 1984; Hawe and Short, 2012). An understory of trees will help control weed growth and give some flexibility in management.

In Europe many different silvicultural systems have been used for centuries, but in recent years there is increasing interest in Continuous Cover Forestry (CCF), which has gained in recognition worldwide as an alternative to clearfelling to promote tree species and structural diversity, and multi-objective forests (Hart, 1995; Department of Agriculture, Food and the Marine, 2014). CCF uses the control of light through thinning and includes those silvicultural systems in which there is a continuous maintenance of forest cover (Pommerening and Murphy, 2004). The shelterwood and selection systems are preferred in CCF since these systems are considered to meet some principles of close-to-nature silviculture (COFORD, 2003; Brang et al., 2014). The interest in broadleaf species and alternatives to clearfelling has now heightened the demand for research on how tree species develop under different light environments as a result of forest management intervention. The response of species to the light conditions is a complex function (Valladares et al., 2002), and understanding how light influences seedling survival and growth in the early years after planting may reveal important information for the management of broadleaf species.

Pedunculate oak (*Quercus robur* L.) and European beech (*Fagus sylvatica* L.) are two important trees in Europe and play a notable role in European forestry. These species vary in their shade

* Corresponding author at: Teagasc Forestry Development Department, Teagasc Ashtown Food Research Centre, Ashtown, Dublin 15, Ireland.
E-mail addresses: ignacio.sevillano@teagasc.ie (I. Sevillano), ian.short@teagasc.ie (I. Short), jim.grant@teagasc.ie (J. Grant), conor.oreilly@ucd.ie (C. O'Reilly).

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tolerance, with oak being considered less shade-tolerant than beech at the seedling stage (Brzeziecki and Kienast, 1994). However, Welander and Ottosson (1998) suggested that one-year-old seedlings of oak and beech adapted similarly to low light conditions. Seedlings from nurseries, adapted to higher light before underplanting, may experience planting shock, but there is little information on this aspect for underplanted stock compared with stock planted on open forest sites. Therefore, responses to change in light intensity may be different from that of naturally regenerated plants. The performance of oak (Ziegenhagen and Kausch, 1995; Welander and Ottosson, 1998) and beech (Welander and Ottosson, 1997; Tognetti et al., 1998) seedlings can be influenced by previous and current light conditions. Beech responds well to thinning, but, if thinning or clearfelling is carried out suddenly in a previously shaded stand, the cambium may die as a result (Savill, 2013). Beech is one of the most suitable species for underplanting and the prescription involves underplanting after the first thinning of the overstorey (COFORD, 2002b).

While various studies have addressed the response of beech or oak to light availability (Madsen, 1994; Tognetti et al., 1994, 1998; Gross et al., 1996; Aranda et al., 2001), little research has been done with these two species under similar environmental conditions (Welander and Ottosson, 1998; Valladares et al., 2002). The responses of different species to light availability under a forest canopy are difficult to investigate since other factors may also vary and it can be difficult to find sites where the same species are present in the understory. Therefore, studies performed under artificial shade may be alternative approaches to investigate the response of various species to light intensity (Madsen, 1994).

The aim of this study was to investigate the impact on survival, growth and biomass allocation in beech and oak seedlings grown under different shade conditions. The different shade conditions were intended to mimic a range of underplanting conditions. The results were expected to provide information on the ecology and light adaptation of underplanted oak and beech seedlings, particularly in relation to CCF.

2. Material and methods

2.1. Study site and tree species

The study was conducted in a controlled-shade experiment located at Teagasc Ashtown Food Research Centre, Dublin 15, Ireland (53°22′45″N, 6°20′13″W, 40 m above sea level). Two year-old seedlings (1u1) of pedunculate oak (*Q. robur* L.) and three year-old (1u1u1) European beech (*F. sylvatica* L.) were purchased from a Coillte Nursery, Ardattin, Co. Carlow, Ireland (52°43′47″N, 6°41′13″W, 104 m above sea level) and planted at Teagasc Food Research Centre in March 2011. Because 1u1 beech seedlings of similar size to the oak seedlings (50–80 cm) were not available, 1u1u1 beech seedlings were used instead. The provenances used were according to recommendations in Ireland (COFORD, 2002a): beech provenance was Cirenceste Region 404, United Kingdom, origin unknown (51°43′0″N, 2°0′0″W, 140 m above sea level), and oak provenance was NL.S. Nuenen 03, Netherlands, origin unknown (51°29′9″N, 5°32′9″E, 20 m above sea level). The experimental area was fenced to exclude rabbits and hares. Weeding was carried out when required. The mean annual total rainfall in the region is 774 mm and the mean annual air temperature is 9.8 °C (all means are from the period 1981–2010). The weather conditions from 2011 to 2014, the period when this study was conducted, were similar with respect to temperature but differed in rainfall during the growing season (Table 1). Climate data were collected by an Automatic Weather Station (Met Éireann, Phoenix Park station) located 1.93 km away at an open site.

Table 1
Temperature (°C) and rainfall (mm) during the years of the study. Growing season was calculated considering the period from April to October.

Variable		Year			
		2011	2012	2013	2014
Temperature	Mean	10.4	9.8	9.9	10.4
	Growing season	13.2	12.4	13.2	13.6
Rainfall	Annual	675	869	711	885
	Growing season	287	564	282	336

The mean seedling heights were 61.1 ± 0.5 cm for *F. sylvatica* and 75 ± 0.6 cm for *Q. robur*. The mean stem diameters were 8.7 ± 0.1 mm for *F. sylvatica* and 7.3 ± 0.1 mm for *Q. robur*.

2.2. Experimental design and shade treatments

The experimental design was a randomised block design with split-plots: light as the whole plot factor and species as subplot factors, replicated across 5 blocks. This resulted in twenty plots (11 m long, 4.3 m wide and 2.9 m high, including the shading nets), each containing two subplots and corresponding to the two broadleaf species. Plots were spaced apart from each other to minimise any interaction effects. Forty-two seedlings were planted in each subplot at 0.5 × 0.5 m spacing to encourage the early onset of interplant competition. The subplot measurement area entailed 16 seedlings per species. Each subplot was surrounded by a buffer zone and included an additional line of plants.

Green polythene shade nets (Colm Warren Polyhouses Ltd., Kilmurray, Trim, Co. Meath, Ireland) were erected on frames to simulate different light environments (representing a spectrum of thinning intensities) in September 2012, about one year and half after the seedlings were planted. Four different light treatments were established in each block (one treatment per plot): full sunlight, light shade, medium shade and heavy shade. The proportion of photosynthetically active radiation (PAR) below the nets was calculated as the difference between readings taken simultaneously with a data logger, LI-1400 (LI-COR Inc., Lincoln, Nebraska), using a LI-190SA Quantum Sensor (LI-COR Inc., Lincoln, Nebraska) outside the plot and a LI-191SA Line Quantum Sensor (LI-COR Inc., Lincoln, Nebraska) inside the plot in October 2013. LI-COR quantum sensors monitored PAR in the 400–700 nm waveband. Soil water content (SWC, %) was measured in January 2014 in each plot to determine the amount of rainfall interception. Measurements were carried out in the corners and centre of the plot with a WET sensor and a moisture meter that allowed SWC measurement at a depth of 68 mm (Delta-T Devices Ltd., Cambridge, UK). Red/far-red ratio (R/FR) was measured in March 2014 with a Skye SKR 110 sensor connected to a display meter (Skye Instruments, Powys, UK) that reports quantum flux at 660 and 730 nm. In each light treatment of the first block, air temperature and relative humidity were recorded every 10 min from 26 May to 8 October during 2015 using dataloggers (SF-LOG-M, Solfranc Tecnologias SL, Tarragona, Spain) with shelter to prevent direct solar radiation and rainfall. Temperature and humidity loggers were located in the middle of each oak subplot (after checking there were no differences between oak and beech subplots), ~70 cm above-ground. The different light treatments averaged 100%, 62%, 51% and 28% of PAR. Because the measurements of the environmental conditions (SWC, temperature, etc.) were taken in different years of the experiment, it is not possible to test the correlation of those measurements to each other. A description of the conditions in the different treatments is shown in Table 2. The shadehouses had little effect on R/FR, as this ratio inside and outside the shadehouses was similar in the two intermediate treatments, and slightly lowered in the heavy shade treatment (Table 2). The

Table 2
Light properties, soil water content (SWC), air temperature (T) and relative humidity (RH) in the different shade environments. Data are the means ± standard errors.

Treatment	PAR (%)	R/FR	SWC (%)	T (°C)	RH (%)
Control (full sunlight)	100	1.00	47.7 ± 0.8	13.6	82.2 ± 0.1
Light shade	62	0.98	46.0 ± 0.9	13.6	82.4 ± 0.1
Medium shade	51	0.98	44.3 ± 0.9	13.7	81.1 ± 0.1
Heavy shade	28	0.92	39.8 ± 1.0	13.5	81.3 ± 0.1

rainfall interception in the soil decreased with increasing shade (Table 2). Air temperature and relative humidity did not differ among the different light environments.

2.3. Morphological measurements

Survival, seedling height and stem diameter at 3 cm above the ground were assessed during the dormant season before and after erecting the shadehouses (2011, 2012, 2013, 2014 and 2015). Height was measured from the ground to the highest point of the live crown (and drooping leaders were extended to full length for measurement). The height and diameter increments for each growing season were the differences in the two consecutive sets of values. Height:diameter ratios (H:D ratios) were calculated from recordings before starting the growing season as: height (mm)/stem diameter (mm). During the summer of 2014 the elongation of the main stem was measured at two different stages, June and August.

In 2013, dead or missing seedlings in the measurement area of each plot were replaced with randomly selected seedlings from the "spare area" of the same plot before the beginning of the growing season. If there were not enough plants in the spare line for each plot (light treatment) to be replaced, seedlings from a nearby plot with the same treatment were chosen.

2.4. Destructive sampling

Three plants of each species and treatment were randomly selected to carry out destructive measurements at the end of the study. Five leaves of each selected plant were harvested to analyse leaf area using a LI-3000 area meter (LI-COR Inc., Lincoln, Nebraska, USA). All leaf material was healthy and collected from the same position between 8:00 and 11:00 o'clock on 8th of October 2014. Leaves were placed in sealed plastic bags and stored in a cool box in the dark until further processing in the laboratory. Fresh weights of the selected leaves were measured, and they were dried at 80 °C for at least 48 h until constant weight was reached, after which the samples were reweighed. From these data, leaf size, leaf dry mass, specific leaf area (SLA) and leaf thickness (L_{th}) were calculated. SLA was determined as the leaf area divided by its oven-dry mass. L_{th} was estimated by dividing leaf fresh mass by leaf area, which allows to estimate leaf thickness from easily measured leaf traits and works well as an approximation (Vile et al., 2005; Pérez-Harguindeguy et al., 2013).

At the end of the experiment (February 2015) the selected seedlings were harvested and separated into stems, branches and roots. Seedlings were lifted by hand maintaining a soil core of 50 cm of diameter. Any remaining soil was removed by washing the roots. The stem was separated from the roots at the root collar, and the remaining dead leaves were removed along the branches. Samples were stored in bags and placed in a cold store until further processing. Samples were dried in an oven at 105 °C for at least 24 h until constant dry weight was obtained. Root mass, branch mass, stem mass, aerial biomass (branches plus stems, no leaves included), total biomass (above-ground plus below-ground mass, no leaves included) and root:shoot ratios were determined from these data.

2.5. Data analysis

All statistical analyses were performed with SAS 9.3 (SAS Institute Inc., Cary, NC, USA). Growth responses were analysed using the MIXED procedure of SAS. Dead seedlings were excluded. Fixed effects were light, species and their interaction. Random effects were block and block × light interaction; the latter to account for the split plot structure. For those parameters measured for the two years of the study (height, diameter and H:D ratios) and at different dates (elongation 2014), repeated measures models were used to account for correlations within plots. Following a significant effect or interaction, pairwise comparisons of least square means (Tukey's test) were used to detect treatment differences. All tests for significance were conducted at $p \leqslant 0.05$. Normal distribution of errors and homogeneity of variance were assessed graphically. Data with residuals that did not conform to assumptions of normality and/or homogeneity of variances were transformed using Box–Cox transformations (Box and Cox, 1964).

Additionally, Pearson correlation analyses were used to identify relationships between some morphological variables (height and growth) with biomass and SLA. Correlations between SLA and L_{th}; and aboveground biomass and root biomass were also carried out.

As survival was a binary response (alive or dead), maximum likelihood estimation was used to study relationships between survival and species, light conditions and species × light interaction, employing the LOGISTIC procedure of SAS.

A plasticity index (from 0 to 1) was determined for the parameters studied during the last growing season (growth, biomass and foliage characteristics). It was calculated as the difference between the maximum and the minimum mean values between the different light treatments divided by the maximum mean value (Valladares et al., 2002). This index allowed us to compare changes in variables expressed in different units.

3. Results

3.1. Tree survival

The study conducted during two growing seasons (2013 and 2014) showed that there were no significant differences in tree survival between species (p = 0.489 and 0.677 for the first and second growing season, respectively) or light treatments (p = 0.779 and 0.637 for the first and second growing season, respectively). Over the two growing seasons survival rates were always greater than 90% for the different species and light treatments.

3.2. Seedling growth

Seedling height increment (ΔHt) was significantly influenced by year, species × light, species × year and light × year interactions (Table 3). Beech seedlings had higher ΔHt (averaged over years) than oak seedlings at full sunlight but no significant differences were found between species and light treatment combinations for ΔHt (Table 4). While ΔHt (averaged over treatments) decreased in beech seedlings from the first to the second growing season, the opposite was found for oak seedlings. In 2013 the higher ΔHt was found in beech seedlings, but in 2014 ΔHt was higher in oak than in beech. With increasing shade, ΔHt (averaged over species) increased during 2013 but the opposite occurred in 2014, with significant differences between the heavy shade and full sunlight during both years of the study (Table 4).

Stem elongation in 2014 was significantly affected by species, light, month, species × light, species × month and light × month interactions (Table 3). While stem elongation (averaged over months) decreased with increasing shade for beech seedlings, no

Table 3
Repeated-measures analysis of variance testing (1) the effects of species (df = 1), light (df = 3), year (df = 1) and their interactions on height increment (ΔHt), diameter increment (ΔDia) and height to diameter ratio (H:D); (2) the effects of species, light, month (df = 1) and their interactions on main stem elongation during the growing season of 2014. Significant effects are in bold ($p < 0.05$).

Traits (1)	Species (S)	Light (L)	S × L	Year (Y)	S × Y	L × Y	S × L × Y
ΔHeight	0.290	0.307	**0.029**	**<0.001**	**<0.001**	**<0.001**	0.305
ΔDiameter	**<0.001**	**<0.001**	0.115	0.092	0.055	**0.011**	0.145
H:D	0.068	**<0.001**	0.105	**0.002**	0.778	0.719	0.386
Traits (2)	S	L	S × L	Month (M)	S × M	L × M	S × L × M
Elongation 2014	**0.030**	**0.023**	**0.002**	**0.007**	**<0.001**	**<0.001**	0.456

Table 4
Height increment (on a year basis) and elongation in 2014 (on a monthly basis) of beech and oak seedlings in the different light treatments. Data are the means. Where species × treatment interaction is significant, combination means followed by the same upper case letter are not significantly different ($n = 5$ reps). Where treatment × year (or treatment × month) interaction is significant, combination means followed by the same lower case letter are not significantly different ($n = 5$ reps).

Treatment	Species	Height increment (cm)			Elongation 2014 (cm)		
		2013	2014	Mean	June	August	Mean
100	Beech	42.75	41.8	42.27A	33.87	7.37	20.61A
	Oak	23.76	37.4	30.53B	14	17.18	15.53ABC
	Mean	33.26bc	39.55ab		23.90a	12.25cd	
62	Beech	45.87	34.46	40.07AB	25.84	6.9	16.3ABC
	Oak	36.36	45.36	40.77AB	13.12	26.82	19.95AB
	Mean	41.05ab	39.79ab		19.43ab	16.81bc	
51	Beech	43.45	28.24	35.81AB	20.12	7.24	13.67BC
	Oak	36.86	36.12	36.48AB	10.42	23.68	17.06ABC
	Mean	40.15ab	32.14bc		15.27bcd	15.46bcd	
28	Beech	48.43	21.11	34.67AB	14.47	6.57	10.41C
	Oak	38.82	36.53	37.61AB	7.66	28.11	17.89AB
	Mean	43.62a	28.66c		11.03d	17.27bc	

significant differences between treatments were found for oak seedlings (Table 4). Elongation decreased in beech seedlings from June to August but the opposite was found for oak seedlings, resulting in greater elongation in June for beech and greater elongation in August for oak regardless of light level (Table 4). While elongation (averaged over species) in June decreased with increasing shade, no differences between light treatments were found in August (Table 4).

Diameter increment (ΔDia) was significantly affected by species, light and light × year interaction (Table 3). ΔDia (averaged over treatments and years) was significantly greater in oak (4.91 ± 0.09 mm) than beech (3.80 ± 0.09 mm). ΔDia decreased with increasing shade but significant differences were not found between the intermediate treatments (Fig. 1A).

The H:D ratio was significantly affected by light and year (Table 3). The H:D ratio was significantly greater in 2014 (73.57 ± 1.17) than in 2013 (71.32 ± 1.16). Seedlings at full sunlight exhibited lower H:D ratios than seedlings in the other light treatments (Fig. 1B).

3.3. Biomass and foliage characteristics

Leaf size was more affected by decreasing light levels in oak than in beech, as indicated by the significant species × light interaction (Table 5). Leaf size of beech was not significantly different between the different light treatments while oak leaf size increased with decreasing light availability (Table 6). Oak leaves in the full sunlight were 27% smaller in area than those in the heavy shade. Although beech seedlings had generally smaller leaves in all the light treatments, significant differences between species were only found in the heavy shade treatment (Table 6). Unlike leaf size, the significant species × light interaction (Table 5) indicated that leaf mass in beech was more affected by decreasing light than in oak (Table 6). Leaf mass of beech decreased with decreasing light, with leaves in the heavy shade 43% lower in mass than those in the full sunlight (Table 6). Leaf mass was significantly greater in oak than in beech in the 51% and 28% of PAR (Table 6). The greatest difference in leaf characteristics between species was found in the heavy shade treatment, where oak leaves were

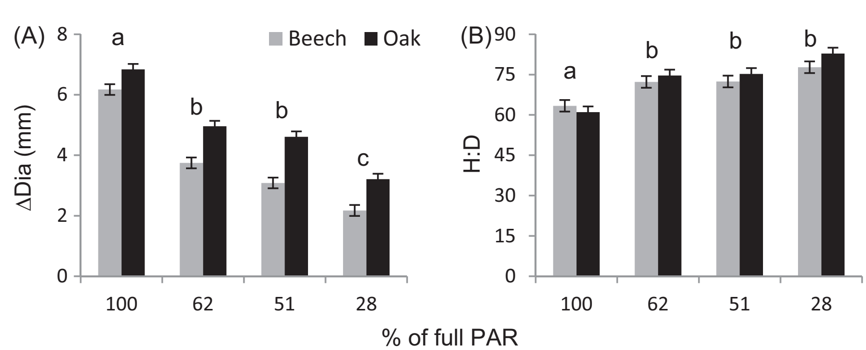

Fig. 1. Diameter increment (A) and height to diameter ratio (B) of beech and oak seedlings over two growing seasons for each PAR treatment. Bars indicate means and standard errors ($n = 5$ reps). Within a graph, different letters indicate significant differences between light treatments.

Table 5
Summary of analysis of variance for the main effects of species (df = 1), light (df = 3) and their interaction (df = 3) on growth, biomass and foliage characteristics. Significant effects are in bold ($p < 0.05$).

Traits	Species		Light		Species × light	
	F	*p*	*F*	*p*	*F*	*p*
Leaf size	39.84	**<0.001**	1.19	0.356	9.79	**<0.001**
Leaf mass	72.18	**<0.001**	2.32	0.128	4.20	**0.008**
Root mass	0.25	0.621	3.99	**0.035**	1.99	0.121
Branch mass	8.53	**0.010**	2.29	0.117	2.74	0.078
Stem mass	0.49	0.487	2.53	0.107	2.86	**0.041**
Aerial biomass	2.62	0.109	2.36	0.123	3.05	**0.032**
Total biomass	1.54	0.218	3.06	0.069	3.32	**0.023**
Root:shoot ratio	26.03	**<0.001**	6.20	**0.009**	0.30	0.824
SLA	50.51	**<0.001**	18.53	**<0.001**	0.63	0.595
Leaf thickness	155.61	**<0.001**	34.48	**<0.001**	0.59	0.624
Ht/StemMass	3.08	0.082	4.35	**0.027**	1.18	0.323

Table 6
Foliage characteristics of beech and oak seedlings grown under four percentages of PAR. Data are the means ± standard errors. Where species × treatment interaction is significant, combination means followed by the same letter are not significantly different ($n = 5$ reps). Where no interaction, species ($n = 10$ reps) or treatment ($n = 5$ reps) means followed by the same letter are not significantly different.

Variable	Light (PAR)	Beech	Oak	Treatment mean
Leaf size (cm^2)	100%	22.01 ± 1.49bc	22.82 ± 1.49bc	22.41 ± 1.26
	62%	20.74 ± 1.49bc	22.89 ± 1.49bc	21.82 ± 1.26
	51%	21.27 ± 1.49bc	26.48 ± 1.49ab	23.88 ± 1.26
	28%	19.02 ± 1.49c	31.06 ± 1.49a	25.04 ± 1.26
	Sp mean	20.76 ± 0.63	25.81 ± 0.63	
Leaf mass (g)	100%	0.14 ± 0.01ab	0.18 ± 0.01a	0.16 ± 0.01
	62%	0.12 ± 0.01bc	0.15 ± 0.01ab	0.13 ± 0.01
	51%	0.11 ± 0.01bc	0.17 ± 0.01a	0.14 ± 0.01
	28%	0.08 ± 0.01c	0.17 ± 0.01a	0.13 ± 0.01
	Sp mean	0.11 ± 0.01	0.17 ± 0.01	
SLA ($cm^2\ g^{-1}$)	100%	161.48 ± 8.76	132.89 ± 8.76	147.18 ± 6.61c
	62%	191.14 ± 8.76	151.32 ± 8.76	171.23 ± 6.61b
	51%	208.01 ± 8.76	158.17 ± 8.76	183.09 ± 6.61b
	28%	231.26 ± 8.76	186.02 ± 8.76	208.64 ± 6.61a
	Sp mean	197.97 ± 5.05a	157.10 ± 5.05b	
Leaf thickness (μm)	100%	148.8 ± 5.6	189.0 ± 5.6	168.9 ± 4.5a
	62%	125.6 ± 5.6	165.7 ± 5.6	145.7 ± 4.5b
	51%	112.0 ± 5.6	160.8 ± 5.6	136.4 ± 4.5b
	28%	102.3 ± 5.6	139.2 ± 5.6	120.8 ± 4.5c
	Sp mean	122.2 ± 3.8a	163.7 ± 3.8b	

63% greater in area and 113% heavier in mass than beech leaves (Table 6).

SLA and L_{th} were strongly influenced by species and light with no significant interaction between the two effects (Table 5). As expected, SLA increased with increasing shade (Table 6). L_{th} was significantly greater in oak than beech while the opposite was true for SLA (Table 6). L_{th} was significantly and negatively correlated with SLA for both species, showing a clear pattern of association between SLA and L_{th} (Fig. 2A).

Root mass was significantly influenced by light treatments, with seedlings at full sunlight averaging greater values than seedlings in the heavy shade (Tables 5 and 7). Beech seedlings allocated significantly greater biomass to branches than did oak seedlings (Tables 5 and 7). There was a significant interaction of species and light for stem, aerial and total biomass, indicating different responses to light treatments between species (Table 5). Stem, aerial and total biomass was significantly greater at full sunlight than heavy shade in beech seedlings, while no significant differences between treatments were found in oak seedlings (Table 7). The root:shoot ratio was significantly greater for seedlings grown in full sunlight and was higher in oak than in beech (Table 7). The length gained per unit of mass invested (calculated as the main stem length divided by stem dry weight, Ht/StemMass) increased with increasing shade (except in 51% of PAR), although the differences were only significant between the two extreme treatments, and was greater, but not significantly different, in oak than in beech (Tables 5 and 7). Shoot growth correlated strongly with root growth (Fig. 2B). Diameter and height at the end of the study were significantly and positively correlated with total biomass, but diameter was more strongly correlated with total biomass (Fig. 2C and D).

3.4. Morphological plasticity

Morphological plasticity in response to light diverged among species and variables studied (Table 8). Averaging the plasticity index for all variables showed a value 31% higher in beech than oak.

4. Discussion

In this study survival rates of oak and beech were not affected by shade and both species had low mortality over the two growing seasons. Greater mortality in the less shade-tolerant species (oak) was expected in the heavy shade as lower survival rates than those of shade-tolerant species have been reported for these species in previous studies in controlled (Walters and Reich, 1996) and natural conditions (Pacala et al., 1994; Gemmel et al., 1996; Chen, 1997; Kaelke et al., 2001). However, Paquette et al. (2006) reported that survival of underplanted temperate deciduous species was not affected by overstory density.

Height growth after erecting shadehouses increased with increasing shade level during the first growing season, but it decreased during the second growing season. Similar to the trend found during the second growing season, several studies have reported a decline in height growth with increasing shade (King, 1994; Chen, 1997). Čater et al. (2012) also reported height increment with increasing light availability for beech seedlings underplanted below Norway spruce (*Picea abies* L. (Karst.)) canopy. The greater height growth under shade found during the first growing season may suggest that the expected decline in height increment with shade may be time dependent (Kennedy et al., 2007). The fact that the seedlings were grown at full sunlight for a number of growing seasons before being exposed to shade may have delayed the response to treatment, as height growth might be more affected by previous than by current light conditions (Welander and Ottosson, 1997, 1998). When height growth for species in each year was averaged, it declined in beech and increased in oak from the first to the second growing season. Height increment was significantly different between species only at full sunlight, with beech having greater height increment than oak over the two seasons. Diameter growth decreased with increasing shade and was greater in oak than beech. This decline in diameter increment with increasing shade has been widely reported for beech and oak seedlings growing in natural (Gemmel et al., 1996; Löf, 2000; Einhorn et al., 2004; Balandier et al., 2007; Ní Dhubháin, 2010) and controlled conditions (Ammer, 2003). Löf et al. (2007) found the same trend in diameter growth for oak but they did not find an additional growth response at higher light levels for beech. In contrast to the results from this study, Van Hees and Clerkx (2003) found that shading levels of 30% of full sunlight had no effect on root collar diameter in oak and beech seedlings.

The H:D ratios of beech and oak during both years of the study were higher in all shade levels than at full sunlight, with no differences between species. The fact that H:D ratios were greater with increasing shade might suggest that seedlings under shade

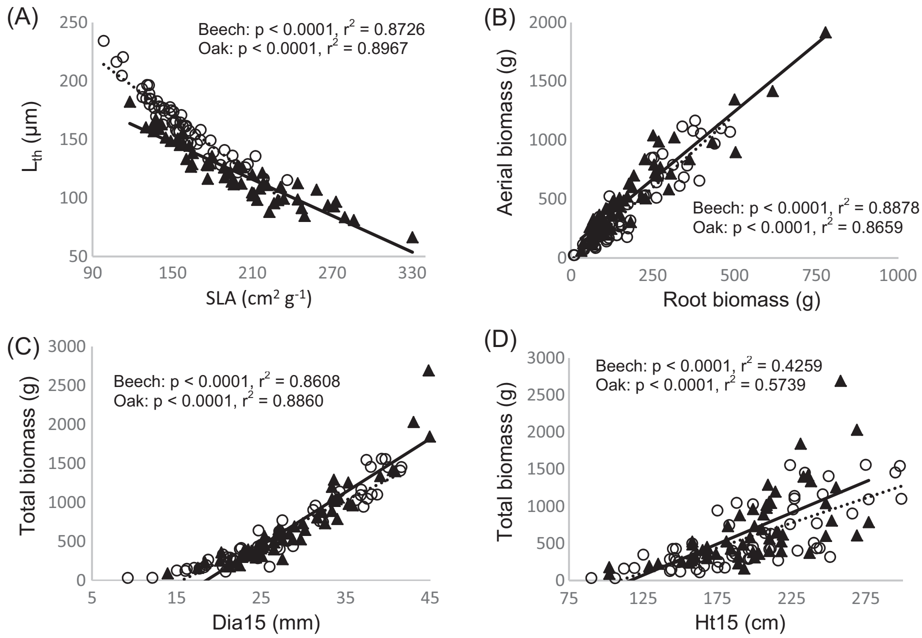

Fig. 2. Correlations between specific leaf area (SLA) and leaf thickness (L_{th}) (A); aerial biomass and root biomass (B); total biomass and final diameter (C), and final height (D). Solid triangles and continuous lines indicate beech seedlings; open circles and dotted lines indicate oak seedlings.

Table 7
Biomass characteristics of beech and oak seedlings grown under four percentages of PAR. Data are the means ± standard errors. Where species × treatment interaction is significant, combination means followed by the same letter are not significantly different (*n* = 5 reps). Where no interaction, species (*n* = 10 reps) or treatment (*n* = 5 reps) means followed by the same letter are not significantly different.

Variable	Light (PAR)	Beech	Oak	Treatment mean
Root mass (g)	100%	322.95 ± 33.58	197.59 ± 33.58	260.27 ± 25.16a
	62%	176.17 ± 33.58	167.1 ± 33.58	171.64 ± 25.16ab
	51%	144.42 ± 33.58	225.12 ± 33.58	184.77 ± 25.16ab
	28%	99.96 ± 33.58	117.22 ± 33.58	108.59 ± 25.16b
	Sp mean	185.87 ± 12.42a	176.76 ± 12.42a	
Branch mass (g)	100%	293.31 ± 36.99	107.29 ± 36.99	200.30 ± 27.93a
	62%	215.91 ± 36.99	124.99 ± 36.99	170.45 ± 27.93a
	51%	197.19 ± 36.99	183.82 ± 36.99	190.50 ± 27.93a
	28%	109.3 ± 36.99	103.28 ± 36.99	106.29 ± 27.93a
	Sp mean	203.93 ± 13.62a	129.84 ± 13.62b	
Stem mass (g)	100%	475.69 ± 54.94a	294.99 ± 54.94ab	385.34 ± 41.32
	62%	306.72 ± 56.14ab	254.58 ± 54.94ab	280.65 ± 41.72
	51%	270.89 ± 54.94ab	379.16 ± 54.94ab	325.02 ± 41.32
	28%	194.90 ± 54.94b	218.11 ± 54.94ab	206.5 ± 41.32
	Sp mean	312.05 ± 18.97	286.71 ± 18.75	
Aerial biomass (g)	100%	768.99 ± 88.39a	402.29 ± 80.48ab	585.64 ± 66.66
	62%	502.21 ± 90.67ab	379.56 ± 80.48ab	440.89 ± 67.43
	51%	468.08 ± 80.48ab	562.98 ± 80.48ab	515.53 ± 66.66
	28%	304.19 ± 80.48b	321.38 ± 80.48b	312.79 ± 66.66
	Sp mean	510.87 ± 31.39	416.55 ± 30.98	
Total biomass (g)	100%	1091.94 ± 119.24a	599.88 ± 119.24ab	845.91 ± 89.44
	62%	657.05 ± 122.37ab	546.66 ± 119.24ab	601.85 ± 90.49
	51%	612.49 ± 119.24ab	788.10 ± 119.24ab	700.30 ± 89.44
	28%	404.15 ± 119.24b	438.60 ± 119.24b	421.38 ± 89.44
	Sp mean	691.41 ± 42.68	593.31 ± 42.12	
Ht/StemMass (cm g^{-1})	100%	0.67 ± 0.22	0.91 ± 0.22	0.79 ± 0.16a
	62%	0.79 ± 0.23	1.41 ± 0.22	1.10 ± 0.16ab
	51%	0.89 ± 0.22	1.10 ± 0.22	0.99 ± 0.16ab
	28%	1.13 ± 0.22	1.43 ± 0.22	1.28 ± 0.16b
	Sp mean	0.87 ± 0.10a	1.21 ± 0.10a	
Root:shoot ratio	100%	0.43 ± 0.03	0.55 ± 0.03	0.49 ± 0.02a
	62%	0.32 ± 0.03	0.48 ± 0.03	0.40 ± 0.02b
	51%	0.35 ± 0.03	0.45 ± 0.03	0.40 ± 0.02b
	28%	0.34 ± 0.03	0.44 ± 0.03	0.39 ± 0.02b
	Sp mean	0.36 ± 0.02a	0.48 ± 0.02b	

Table 8
Plasticity index in response to different light levels of beech and oak seedlings for the variable studied during the growing season of 2014.

Variable	Plasticity index		ΔBeech–oak
	Beech	Oak	
Leaf size	0.14	0.27	−0.13
Leaf mass	0.43	0.17	0.26
Root mass	0.69	0.48	0.21
Branch mass	0.63	0.44	0.19
Stem mass	0.59	0.42	0.17
Root:shoot ratio	0.26	0.20	0.06
SLA	0.30	0.29	0.01
L_{th}	0.31	0.26	0.05
ΔHt	0.49	0.20	0.29
ΔDia	0.60	0.49	0.11
H:D	0.17	0.28	−0.11
Ht/stem mass	0.41	0.36	0.05
Mean	0.42	0.32	0.10

prioritised the allocation of biomass to leader height growth at the expense of diameter growth. Prévosto and Balandier (2007) reported similar results for beech seedlings growing under strong competition and low light availability. This trend is also confirmed by the greater height growth per unit of stem biomass under the heavy shade observed in the current study, as found by Einhorn et al. (2004).

As expected, shoot elongation was greater in June and lower in August in beech than oak seedlings. In the early years, oak seedlings usually experience two periods of shoot growth (the initial elongation in May and June, and the lammas growth in July and August), while lammas growth in beech is much less common, with elongation taking place mainly in May and June (Evans, 1984).

The decrease in seedling dry mass with decreasing light quantity found in the current study is consistent with previous studies on the effect of shading on biomass production on beech, oak and other species (Loach, 1970; Welander and Ottosson, 1998; Ammer, 2003; Einhorn et al., 2004; Kennedy et al., 2007; Gardiner et al., 2009; Čater and Simončič, 2010; Brown et al., 2014). The only exception to that in the present study was for oak under 51% of PAR (medium shade), where seedling biomass was greater than in all the other treatments. As found by Ammer (2003), branch dry mass was greater in beech than oak, which might suggest a better ability of oak to prune naturally. In contrast, root mass or total biomass did not differ significantly between species in this study. Plants with higher root:shoot ratios can compete more effectively for soil nutrients, while those with lower root:shoot ratios can collect more light energy (Allaby, 1998). Kitajima (1994) reported that shade-intolerant species had lower root:shoot ratios. Although the root:shoot ratios in this study did not follow that pattern, they were consistent with findings on beech and oak in previous studies (Welander and Ottosson, 1998; Valladares et al., 2002; Ammer, 2003). Shading generally reduced root biomass more than aerial biomass, resulting in lower root: shoot ratios under shade than at full sunlight in this study. Many studies have found a reduction in root:shoot ratios with increasing shade (Welander and Ottosson, 1998; Valladares et al., 2002; Ammer, 2003; Van Hees and Clerkx, 2003; Kennedy et al., 2007; Čater and Simončič, 2010).

Increasing shade level increased SLA, which is a common response of plants to shade that has been well documented in beech and oak (Van Hees, 1997; Aranda et al., 2001; Valladares et al., 2002; Curt et al., 2005; Kunstler et al., 2005; Gardiner et al., 2009; Goisser et al., 2013). Similarly, L_{th} decreased with increasing shade, which has also been reported in other studies (St-Jacques et al., 1991; Ashton and Berlyn, 1994; Valladares et al., 2002). The acclimation of plants to shade results in larger and/or thinner leaves, as shown by the frequently reported higher SLA in shaded leaves (Abrams and Kubiske, 1990; Abrams and Mostoller, 1995). Thinner leaves typically capture more light per unit area than thicker leaves and distribute nitrogen, which plays an important role in healthy growth, over a larger leaf area optimising the light harvesting (Niinemets, 1997). The low SLA values at full sunlight was associated with great growth increment, which is in agreement with a previous study on beech seedlings (Curt et al., 2005). Rebbeck et al. (2012) also found greater SLA in foliage of northern red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.) when grown in low light but they found the opposite response in chestnut oak (*Quercus prinus* L.). Similar to our findings, Špulák (2011) found that beech seedlings planted under a young spruce (*Picea* sp.) stand experienced significantly greater SLA than seedlings found in a nearby gap. Shade-tolerant beech seedlings had greater SLA than less shade-tolerant oak seedlings (Table 6), a similar trend to that reported in previous studies of beech and oak seedlings (Valladares et al., 2002; Gardiner et al., 2009) and in other species differing in shade tolerance (Kitajima, 1994; Niinemets and Kull, 1994). The results of this study showed that the increase of SLA with increasing shade was associated with lighter leaves in beech and larger leaves in oak. Other studies agree with this observation where oak species maximised their light interception by increasing their leaf area in response to increasing shade levels (Callaway, 1992; Gardiner and Krauss, 2001). The strong correlation between L_{th} and SLA might suggest that L_{th} could be as useful as SLA as an indicator of plant light-use strategy.

Beech seedlings showed a greater morphological plasticity than oak, although it was not as great as that reported by Valladares et al. (2002). Kunstler et al. (2005) also observed that beech exhibited higher morphological plasticity than less shade-tolerant downy oak (*Quercus pubescens* Willd.) as a function of light. In contrast, Van Hees (1997) found a similar morphological plasticity between both species. The seedlings in the study of Van Hees (1997) were younger than those used in this study, so differences in the effect of shading on growth might increase as the plants age. The results reported herein are in agreement with Canham (1988), who suggested that shade-tolerant species generally show greater morphological plasticity than less tolerant ones.

In addition to light availability, there are other environmental factors that affect tree growth, such as water availability, light quality, nutrient levels and temperature. While water stress may not seem to be a major issue in Ireland due to the high and frequent rainfall, exposure can increase moisture stress despite the availability of water in the soil and is believed to be the main cause of poor field performance of broadleaved species newly planted in open fields. Frost damage is also a principal impediment in establishing some broadleaf species in open fields. Therefore, underplanting in an existing stand may be a good practice as the existing canopy will provide shelter for underplanted seedlings (Paquette et al., 2006; Dey et al., 2012; Hawe and Short, 2012). The nets used in this study did not modify light quality in the same way than a forest canopy might do, and the possible effects of other environmental factors should also be taken into consideration.

Light availability affected the growth of beech and oak seedlings in this study, with growth decreasing as shade increased, but it did not affect seedling survival. Therefore, low growth rates might be expected for seedlings underplanted into shade conditions, such as stands where silvicultural treatments different from clearfelling or heavy thinning are applied. The above findings suggest that oak seedlings would perform well under light conditions as low as 28% of PAR, acclimating to shade as well as beech seedlings. Differences in the responses in the intermediate treatments were small for most parameters in this study, probably because PAR did not differ sufficiently to elicit strong responses. Although the best growth and biomass accumulation in both species were found at full sunlight, beech and oak seedlings would be able to acclimate both morphologically and physiologically to allow them survive and grow well under alternative systems to clearfelling, such as shelterwood systems, or a wide range of thinning intensities. Although both species can tolerate shade levels as low as 28% of full sunlight, these species might also respond favorably to canopy openings, as suggested by others (Lüpke, 1998; Collet et al., 2001; Coll et al., 2003; Curt et al., 2005).

5. Conclusion

The results from this study confirm that light strongly affected seedling growth and morphology. The survival rates of beech and oak seedlings were not influenced by light availability and were greater than 90% during two growing seasons, regardless of the shade level applied. The decrease in light availability reduced diameter growth in beech and oak seedlings during both years of the study. Height increment increased as the level of shade was increased during the first growing season, but the opposite was found for the second growing season. Both species exhibited morphological acclimation to increasing levels of shade, such as by increasing SLA and H:D ratios and decreasing leaf thickness and root:shoot ratio. The acclimation of leaves to shade would increase the seedling ability to intercept light, while the changes in H:D and root:shoot ratios suggest that plants allocate more biomass to the above-ground than below-ground parts in response to shade. Based on these findings, both species may be suitable for underplanting under a wide range of shade levels (from light to heavy shade), although they showed a reduction in growth and biomass as the shade level increased.

Conflict of interest

The authors declare that there are no conflicts of interest.

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