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

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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.

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

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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