



Sprouts of shoot-clipped oak (*Quercus alba* and *Q. robur*) germinants show morphological and photosynthetic acclimation to contrasting light environments

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Abstract

Sprouting by woody plants can increase species resilience to disturbance and foster regeneration during periods with little recruitment from seed. Though sprouting often plays a critical role in oak forest regeneration, there is little information available on sprouting capacity and sprout physiology at the seedling stage, particularly for new germinants. This study compared sprouting capacity and sprout photosynthesis of shoot-clipped germinants of two temperate oaks established in contrasting light environments. We studied the North American *Quercus alba* and the European *Q. robur*, both are in the section *Quercus* and appear to share similar biological and ecological requirements. Sprouting capacity for both species was enhanced under high light availability (29% more sprouts per plant), a response not previously noted for oak germinants. Seedling sprouts acclimated to high light with a 34% decrease in leaf area ratio, a 56% increase in leaf mass per area, and a 49% increase in the light-saturated maximum photosynthetic rate. Though both species appeared similarly adapted to shoot loss, a greater sprouting capacity (29% more sprouts per plant) and plant-level net photosynthesis (73% higher) was observed for *Q. robur*, regardless of light environment. As naturally regenerated oak seedlings in forest understories often experience disturbance or stress resulting in shoot loss or die-back, our results highlight the importance of the light environment during early plant development. Our comparison of temperate oaks from different continents should facilitate exchange of successful stand regeneration practices within the range of temperate oak forests.

Keywords Disturbance · Management · Oak · Photosynthesis · Shade tolerance · Sprouting

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Introduction

Sprouting is an important trait among many woody plants that enables survival following natural or anthropogenic disturbance (Bond and Midgley 2001; Clarke et al. 2010). Tree species capable of sprouting may do so adventitiously, or more commonly from dormant buds banked along the stem and root collar (Del Tredici 2001; Klimesová and Klimes 2007). Species with high sprouting capacity are not only more resilient to disturbance, they can also tolerate longer periods with little or no recruitment from seed (Bond and Midgley 2001). However, sprouting capacity can vary at different developmental stages of the tree, often with greatest capacity exhibited by relatively vigorous young trees, saplings, and seedlings (Bellingham and Sparrow 2000; Del Tredici 2001).

Oak-dominated (*Quercus* spp.) forests are common in temperate, subtropical, and Mediterranean regions of Eurasia and the Americas (Johnson et al. 2018). They provide important ecosystem services, such as wood production, soil protection, and preserved water quality (Löf et al. 2016). Moreover, many oak-based ecosystems are of great importance for biodiversity conservation (Ranius et al. 2008; Rodewald and Abrams 2002). Currently, the extent of oak-dominated forests is much lower in many regions than in previous centuries, this being a consequence of forest degradation, deforestation, and changing climate (Dey et al. 2019; Lindbladh and Foster 2010). Furthermore, widespread failure of oak regeneration and the subsequent loss of the oak component in forests has been reported across Eurasia and the Americas (Abrams 2003; Annighöfer et al. 2015; Petersson et al. 2019; Takahashi et al. 2003). Though heavy masting is often followed by substantial germination, seedlings can fail to establish for a variety of reasons. Young oak seedlings are particularly susceptible to damage from herbivores (Bonfil 1998; Frost and Rydin 1997; Gómez et al. 2003). And, insufficient understory light and competition from shade-tolerant species can also contribute to poor seedling vigor and reduce oak regeneration success (Jensen and Löf 2017; Lorimer et al. 1994; Petersson et al. 2019).

In eastern North America, the oak regeneration issue has been linked in part to changed disturbance regimes such as that which followed the effective fire suppression during the last century (Abrams 1992; Brose et al. 2001; Nowacki and Abrams 2008). Today, prescribed burns are used extensively in the United States to regenerate and restore oak ecosystems—burning is used in combination with stand thinning to reduce competition and increase light availability (Brose et al. 2014; Dey and Hartman 2005). These management practices favor oaks that show a persistent ability to sprout following top kill, which can give them a competitive advantage over competing vegetation less resilient to fire damage (Brose et al. 2013; Del Tredici 2001; Gould et al. 2007; Weigel and Peng 2002). A high sprouting capacity has also been documented for European oaks (Garcia and Retana 2004; Leonardsson and Götmark 2015; Matula et al. 2012), but, their resiliency to fire is less clear. Despite biological and ecological similarities between many North American and Eurasian oaks, there are few comparative studies that include species from both continents, especially studies on sprouting capacity (but see Zhang et al. 2019). This limits knowledge transfer and adoption of management practices proven effective in other regions.

Light is, of course, a vital resource for plant survival and growth, and the effects of light availability on oak seedling biology have received considerable study (e.g. Jensen et al. 2012; Kuehne et al. 2014; Rebbeck et al. 2011; Rodríguez-Calcerrada et al. 2008; Sevillano et al. 2016). Observations indicate their large acorns allow for seedling establishment in relatively dark understories, but light demands increase once energy reserves of the cotyledons are exhausted (Johnson et al. 2018; Rebbeck et al. 2012). Oak seedlings

generally benefit from relatively high light availability, but minimum light requirements and functional optima are species-specific (Brose and Rebbeck 2017; Rebbeck et al. 2012; Rodríguez-Calcerrada et al. 2008) and dependent on plant developmental stage. For example, *Q. rubra* L. and *Q. ilex* L. sprouts have demonstrated higher photosynthetic capacity than intact trees growing in the same light environment (Fleck et al. 1996, 1998; Kruger and Reich 1993b). This greater photosynthetic capacity is attributed to shifts in root to shoot balance that improve water and nutrient availability to sprouts as compared to intact plants (Fleck et al. 1998; Peña-Rojas et al. 2005). There is, however, little information available on sprouting capacity, sprout morphology, and sprout physiology during early seedling development, especially in relation to environmental conditions. This is surprising as seedling sprouts often play a critically important role in oak forest regeneration (Del Tredici 2001).

We studied sprouting capacity and leaf-level photosynthetic response in oak germinants established in contrasting light environments. This work included two species, the North American white oak (*Q. alba* L.) and the European pedunculate oak (*Q. robur* L.). Both are temperate white oaks (section *Quercus*), and they appear to have some similar biological and ecological characteristics, such as sprouting after shoot damage or mortality (Leonardsson and Götmark 2015; Weigel and Peng 2002) and intermediate light requirements at the seedling stage (Rebbeck et al. 2012; Welander and Ottosson 1998). The North American *Q. alba* is known to be fire adapted and its regeneration can sometimes benefit from prescribed burning (Abrams 2003; Dey 2014). The response to fire is less clear for *Q. robur*, but it is known to sprout following top kill (Leonardsson and Götmark 2015). In this study, we clipped the shoots of new germinants to emulate damage caused by disturbance. Previous work has demonstrated that method of top kill does not influence sprouting response, nor sprout physiology (Fleck et al. 1996; Hmielowski et al. 2014). The purpose of this research was to study the response of oak germinants to shoot clipping. We set out to study two species of similar biological and ecological characteristics, one native to temperate forests of North America and the other native to Europe. Specific objectives were to investigate how light environment affects: (1) sprouting capacity, i.e. number and size of sprouts per plant, and sprout development; and, (2) carbon acquisition potential, i.e. leaf characteristics and photosynthetic function. Results from this research will provide a better understanding of how new oak germinants respond morphologically and physiologically to shoot loss. This should yield implications that contribute to the development of management practices supporting improved sustainability of oak-dominated forests.

Materials and methods

Experimental design

The research was conducted in a greenhouse located at the Center for Bottomland Hardwoods Research, USDA Forest Service, Stoneville, MS, USA. The experiment was established as a completely random design with factorial arrangement of two factors (species and light) each with two levels. Treatment combinations were “*Q. alba* × low light”, “*Q. alba* × high light”, “*Q. robur* × low light”, and “*Q. robur* × high light”, and each combination was replicated three times. Each replicate consisted of 30, 2.3-L pots filled with a commercial potting mix and the replicates were randomly assigned locations on benches in the greenhouse.

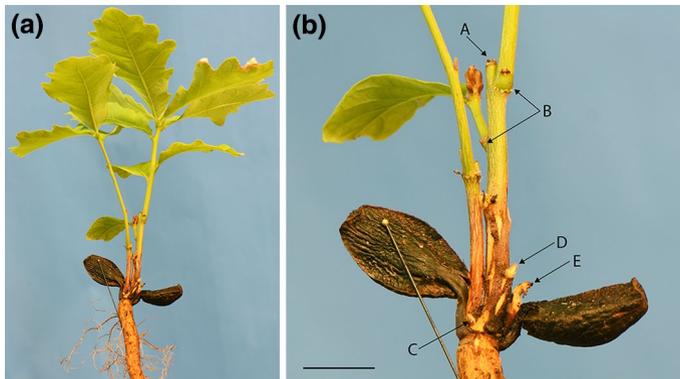


Fig. 1 **a** *Quercus robur* seedling sprout with depleted cotyledons still attached, and **b** close-up. The original stem was cut 2 cm above the soil line (A), and in this case released two sprouts that originated from buds along the stem (B) and one sprout that originated from a bud at the cotyledonary node (C). Also, note the expanded stem bud that did not develop into a sprout (D) and the underdeveloped sprout originating from a bud at the right cotyledonary node (E). The black line in (b) provides a 1 cm scale

On 2 March 2018, one acorn was sown in each pot and during the following weeks moisture of the potting mix was maintained near saturation to encourage germination. Acorns were graded and selected for consistency in size within a species, because there is a positive relationship between acorn size and growth of the first flush (Ke and Werger 1999; Quero et al. 2007). Average fresh weights were 5.9 ± 0.2 g and 8.7 ± 0.3 g for *Q. alba* acorns and *Q. robur* acorns, respectively. Ambient light in the greenhouse was supplemented with high pressure sodium lamps programed to provide a 15-hour diurnal period. Replicates of the high light treatment level received full ambient and supplemental light. Photosynthetically active radiation (PAR) averaged $365 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ between 05.00 and 20.00 h, with a maximum PAR of $805 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Replicates of the low light treatment level were shaded using 80% neutral density shade cloth, and PAR averaged $70 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ during the diurnal period, with a maximum PAR of $185 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. These light levels correspond to approximately 90% and 18% of light available under field conditions in southern Sweden, respectively (Jensen et al. In preparation; Welander and Ottosson 1998). Temperature in the greenhouse averaged 26.0 °C with daily averages ranging between 22.7 and 31.4 °C over the 3-month course of the study.

To induce sprouting, seedlings were stem-clipped at 2 cm above the soil when they were at the end of stem elongation and beginning leaf expansion of the initial growth flush (Fig. 1) (Hanson et al. 1986). Seedlings reached this targeted developmental stage between 26 March and 24 April 2018. At time of clipping, *Q. alba* seedlings averaged 9.8 ± 1.5 cm tall and weighed 0.6 ± 0.05 g in low light replicates, and 9.8 ± 0.2 cm tall weighing 0.5 ± 0.03 g in high light replicates. Seedlings of *Q. robur* averaged 15.4 ± 0.4 cm tall and weighed 0.7 ± 0.08 g in low light replicates, and 10.0 ± 0.6 cm tall weighing 0.4 ± 0.09 g in high light replicates. Near 100% of the germinants sprouted after clipping. We did not study intact seedlings in this experiment because our objectives were to draw comparison of sprouting capacity and carbon acquisition potential for germinants of two species, not to assess growth and carbon acquisition of seedlings versus sprouts. The potting mix in each

pot was kept well-watered throughout the experiment to avoid water stress. No pests or pathogens were observed during the eleven-week experimental period.

Seedling sprouting capacity, morphology, and leaf characteristics

Ten plants per replicate (120 plants total) were randomly selected to quantify seedling sprouting capacity, morphology, and leaf characteristics. This was conducted between 26 April and 18 May 2018, as individual plants reached the 1-Lag stage of development, i.e. the interval between completion of the first growth flush and the onset of the next (Hanson et al. 1986). We defined seedling sprouting capacity as the number and size of sprouts produced per plant. Plants were harvested and separated into various tissue types (roots, original stems, stem sprouts (i.e. sprouts originating from dormant buds along the stem), cotyledon node sprouts (i.e. sprouts originating at the cotyledonary node), and leaves), and data on number of sprouts, sprout origin (i.e. stem or cotyledonary node sprout), sprout length (± 0.1 cm) and sprout diameter (± 0.1 mm) were recorded (Fig. 1). Total plant leaf area was measured using a LI-3100 leaf area meter (Li-Cor Inc., NE, USA). Thereafter, plant tissues were dried at 70 °C and their weight was recorded when measurements reached a constant. Root mass ratio (RMR) was calculated as root dry weight over the total above-ground biomass including leaves (g g^{-1} dry weight). Leaf area ratio (LAR) was calculated as total leaf area over total plant biomass including leaves (cm g^{-1} dry weight). Leaf mass per area (LMA) was calculated as total dry leaf mass over total leaf area (g m^{-2}). Relative growth rate (RGR_{mass}) was calculated for each plot replicate as:

$$\text{RGR}_{\text{mass}} = \ln(\text{final.biomass}) - \ln(\text{initial.biomass})$$

where final.biomass was the average total dry plant biomass per replicate at the final harvest (ten plants per replicate) and initial.biomass was the average total dry plant biomass including leaves per replicate at time of clipping (three plants per replicate).

Photosynthetic response

Leaf gas exchange was measured to construct photosynthetic light response (A/PPFD) and internal CO_2 response (A/C_i) curves. From each replicate, three plants with a dominant stem-sprout were randomly selected for measurement. This was conducted between 27 April and 18 May 2018 as the randomly selected plants reached the 1-Lag stage of development. For each seedling sprout, gas exchange measurements were conducted on a fully developed median leaf from the dominant stem sprout. The evening before measurement, sample plants were moved from the greenhouse to a dark room and soil was watered to moisture holding capacity. This ensured that dark respiration (R_d) was determined without photorespiration and that there were no restrictions in stomatal conductance. Gas exchange measurements were conducted with a LI-6800FL portable photosynthesis system using the 6 cm^2 leaf chamber (Li-Cor Inc., NE, USA). To collect data for building A/PPFD curves, net photosynthesis was measured at 0, 1600, 800, 400, 200, and 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (PAR) with a cuvette environment that maintained leaf temperature at 25 °C, reference CO_2 concentration at 400 ppm, and vapor pressure deficit near 1.5 kPa. Data to construct A/C_i curves were collected from the same sample leaves immediately following A/PPFD measurements. For this we maintained saturating light ($1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) in the cuvette

and recorded A at each of 12 sequentially adjusted reference CO_2 concentrations (400, 300, 200, 100, 50, 400, 550, 650, 800, 950, 1200, 1600 ppm). For both curves, measurements were taken when steady state photosynthesis was reached (the water vapor differential was less than $0.5 \mu\text{mol}$ and carbon dioxide differential was less than $1 \mu\text{mol}$ for more than 20 s). Following gas exchange measurement, each sample plant was harvested and processed according to the procedures described above for quantifying sprouting capacity and leaf characteristics. Leaves sampled for gas exchange were individually processed for area and dry weight. Before gas exchange measurements, total chlorophyll content of the sample leaf was measured using a CCM-300 chlorophyll content meter (Opti-Science Inc., NH, USA). Total chlorophyll concentration per leaf mass ($\text{Chl}_{\text{total}}$) was calculated by multiplying measured area based chlorophyll content (mg m^{-2}) with the specific leaf area ($\text{m}^2 \text{g}^{-1}$) for each sample leaf.

Calculations and statistical analysis

A/PPFD curves were fitted by applying a nonrectangular hyperbola-based model:

$$A_N = \frac{\phi_{(\text{PPFD}_0)} * \text{PPFD} + A_{\text{gmax}} \sqrt{(\phi_{(\text{PPFD}_0)} * \text{PPFD} + A_{\text{gmax}})^2 - 4\theta * \phi_{(\text{PPFD}_0)} * \text{PPFD} + A_{\text{gmax}}}}{2\theta} - R_d$$

using Microsoft Excel 2016 (Lobo et al. 2013; Prioul and Chartier 1977), where A_N is the net photosynthesis rate, ϕ_{PPFD_0} is the quantum yield at $\text{PPFD}=0 \mu\text{mol m}^{-2} \text{s}^{-1}$, PPFD is the photosynthetic photon flux density, A_{gmax} is the maximum gross photosynthesis rate, θ is convexity, and R_d is the dark respiration rate. This provided estimates of the light-saturated maximum photosynthetic rate (A_{max}), daytime dark respiration (R_d), light compensation point (I_c), and quantum efficiency (ϕ). We estimated plant-level net photosynthesis (A_{net}) by inserting diurnal light availability data into each A/PPFD model developed for respective photosynthesis sample plants, and adjusting for total plant leaf area. This estimation assumes that plants were not affected by self-shading; it is therefore possible that A_{net} was overestimated, particularly in the high light environment. PAR under each treatment level was measured continually through the experimental period with quantum sensors. We randomly selected the modeled A_{net} output from one sunny day at the end of the study period for analysis. A/C_i curves were fit to the FvCB model according to Gu et al. (2010) through leafweb.org/. For the A/C_i analyses, R_d was fixed at the estimated R_d from the A/PPFD analyses while I_c was not fixed. This provided estimates of maximum carboxylation rate ($V_{c,\text{max}}$) and maximum electron transport rate (J_{max}).

Plot replicate averages were calculated for all variables and used in the following analyses. Multivariate analysis of variance (MANOVA) was used to provide protection against the possibility of a type I error of treatment effects for plant morphology and leaf variables (total biomass, leaf biomass, stem biomass, root biomass, RGR_{mass} , RMR , number of sprouts per plant, mean sprout length, leaf size, plant leaf area, number of leaves per plant, LAR , LMA , and $\text{Chl}_{\text{total}}$) and leaf-level photosynthesis response variables (A/PPFD and A/C_i response variables). Due to the large number of response variables in relation to the sample size, two separate principal component analyses (PCA) were used to reduce the number of dimensions (Fig. S1). The MANOVA was then performed on the PCs that together explained at least 90% of the variance (PC1-PC3 for plant morphology and leaf variables, and PC1-PC2 for photosynthesis variables). Light, species, and interaction effects on the separate plant morphology and

leaf variables were analyzed using two-way ANCOVA and mean comparisons were conducted using the “emmeans” function (Russell 2018). Total plant dry biomass at time of clipping was included as a covariate to control for acorn size between the two species. Light, species, and interaction effects on the separate photosynthesis variables, as well as RGR_{mass} and Chl_{total} , were analyzed using two-way ANOVA and mean comparisons were conducted using Tukey’s honestly significant difference. Distribution assumptions were tested using the Shapiro–Wilk normality test, the Breusch–Pagan test (for ANCOVA), and Levene’s test (for ANOVA); all variables met test assumptions. All statistical analyses were done using R version 3.5.0 (R Core Team 2017). Significance was determined at an alpha level of 0.05.

Results

Seedling sprouting capacity, morphology, and leaf characteristics

Results of the MANOVA for plant morphology and leaf variables showed significant treatment effects for light and species (Table S1). The covariate of total plant dry biomass at time of clipping, included to control for differences in acorn size between the two species (Ke and Werger 1999; Quero et al. 2007), was not significant in ANCOVA analyses (Table S1).

Total plant biomass, leaf biomass, and root biomass was similar for the species, but differed by light environment (Table 1, Table S1). For both species, plants receiving high light accumulated 44% more total biomass, 43% more leaf biomass, and 48% more root biomass than plants raised in low light. Stem biomass differed between the species with *Q. robur* averaging 44% more stem mass than *Q. alba*. Stem biomass for both species was greatest (28% greater) in the high light environment (Table 1, Table S1). The proportional distribution of biomass within seedling sprouts, as measured by RMR, was affected neither by light nor species (RMR ranged between 1.01 ± 0.04 and $1.11 \pm 0.08 \text{ g g}^{-1}$ for all treatment combinations) (Table S1). However, both species increased LAR about 51% when raised in low light versus high light (Table 2, Table S1).

The RGR_{mass} was similar for the species, but plants receiving high light had 79% greater RGR_{mass} than plants raised in low light (Table 1, Table S1). *Q. robur* developed 29% more sprouts per plant than *Q. alba*, and both species developed 29% more sprouts per plant in the high light environment versus the low light environment (Table 1, Table S1). Sprouts originated from dormant buds along the stem (stem sprouts) and at the cotyledonary node (cotyledonary node sprouts) (Fig. 1). Stem sprouts were more common than cotyledonary node sprouts for both species regardless of light environment—stem sprouts comprised 95% of all sprouts produced by *Q. robur* and 76% of *Q. alba* sprouts. *Q. robur* sprouts averaged 37% longer than *Q. alba* sprouts, but there was no difference in average sprout length between light environments (Table 1, Table S1).

The number of leaves per plant for *Q. robur* was almost twice that of *Q. alba*, but *Q. alba* leaves were 47% larger than *Q. robur* leaves (Table 2, Table S1). Both species produced about 36% more leaves per plant in the high light environment, while average leaf size increased about 42% under low light. Total leaf area was similar for both species when plants were grown in high light, but *Q. robur* developed 43% more total leaf

Table 1 Plant morphology characteristics of seedling sprouts (mean \pm SE) of two oak species grown in either a low or a high light environment

Variable	Light environment		Species mean
	Low	High	
Total biomass (g)			
<i>Q. alba</i>	1.31 \pm 0.05	2.30 \pm 0.22	1.81 \pm 0.24 ^a
<i>Q. robur</i>	1.96 \pm 0.18	2.30 \pm 0.17	2.13 \pm 0.13 ^a
Treatment mean	1.64 \pm 0.17 ^a	2.30 \pm 0.12 ^b	
Stem biomass (g)			
<i>Q. alba</i>	0.20 \pm 0.01	0.34 \pm 0.02	0.27 \pm 0.03 ^a
<i>Q. robur</i>	0.37 \pm 0.03	0.40 \pm 0.04	0.39 \pm 0.02 ^b
Treatment mean	0.29 \pm 0.04 ^a	0.37 \pm 0.03 ^b	
Leaf biomass (g)			
<i>Q. alba</i>	0.46 \pm 0.01	0.78 \pm 0.05	0.62 \pm 0.08 ^a
<i>Q. robur</i>	0.62 \pm 0.05	0.76 \pm 0.05	0.69 \pm 0.04 ^a
Treatment mean	0.54 \pm 0.04 ^a	0.77 \pm 0.03 ^b	
Root biomass (g)			
<i>Q. alba</i>	0.65 \pm 0.05	1.19 \pm 0.14	0.92 \pm 0.14 ^a
<i>Q. robur</i>	0.96 \pm 0.11	1.14 \pm 0.08	1.05 \pm 0.07 ^a
Treatment mean	0.81 \pm 0.09 ^a	1.2 \pm 0.07 ^b	
RGR _{mass} (g g ⁻¹)			
<i>Q. alba</i>	0.83 \pm 0.13	1.53 \pm 0.07	1.18 \pm 0.17 ^a
<i>Q. robur</i>	1.05 \pm 0.20	1.82 \pm 0.18	1.43 \pm 0.21 ^a
Treatment mean	0.94 \pm 0.11 ^a	1.68 \pm 0.11 ^b	
Total sprouts (number)			
<i>Q. alba</i>	1.5 \pm 0.1	1.9 \pm 0.2	1.7 \pm 0.1 ^a
<i>Q. robur</i>	1.9 \pm 0.03	2.5 \pm 0.2	2.2 \pm 0.2 ^b
Treatment mean	1.7 \pm 0.1 ^a	2.2 \pm 0.2 ^b	
Average sprout length (cm)			
<i>Q. alba</i>	7.6 \pm 0.6	6.6 \pm 0.5	7.1 \pm 0.4 ^a
<i>Q. robur</i>	11.3 \pm 0.2	8.1 \pm 0.8	9.7 \pm 0.8 ^b
Treatment mean	9.4 \pm 0.9 ^a	7.3 \pm 0.5 ^a	

Species or light treatment means followed by different letters are significantly different ($P < 0.05$). No species \times light treatment interactions were significant

area than *Q. alba* in low light (Table 2, Table S1). *Q. alba* leaves were 10% heavier per unit area than *Q. robur* leaves, but LMA for both species was greatest in the high light environment (Table 2, Table S1). $\text{Chl}_{\text{total}}$ was 64% greater in the low light environment, while there were no differences in $\text{Chl}_{\text{total}}$ between species (Table 2, Table S1).

Photosynthetic response

Photosynthetic light and CO_2 response curves for *Q. alba* and *Q. robur* seedling sprouts were substantially affected by the light environment (Fig. 2, Table S2). Plants raised in the high light environment developed leaves with a 49% greater A_{max} , 70% greater I_c , and 67% greater R_d than plants raised in low light (Fig. 2a, Table 3). *Q. alba* and *Q. robur* registered

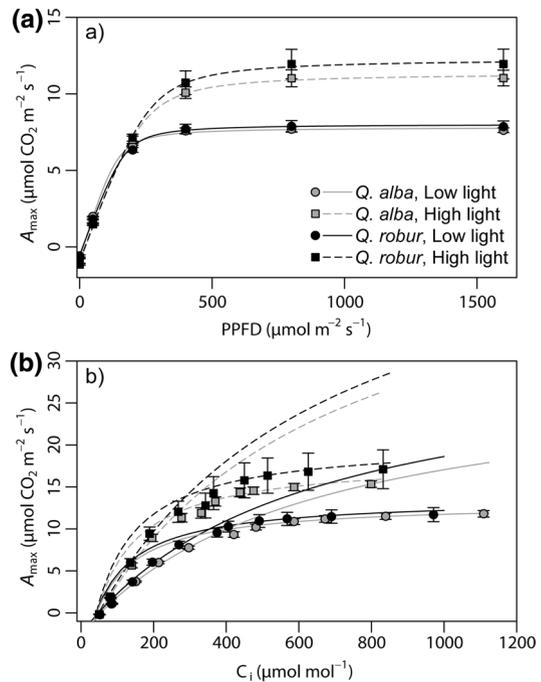
Table 2 Leaf characteristics of seedling sprouts (mean ± SE) of two oak species grown in either a low or a high light environment

Variable	Light environment		Species mean
	Low	High	
Leaves (number)			
<i>Q. alba</i>	5.5 ± 0.3	8.2 ± 0.9	6.8 ± 0.7 ^a
<i>Q. robur</i>	11.0 ± 0.2	14.4 ± 1.2	12.9 ± 0.9 ^b
Treatment mean	8.3 ± 1.2 ^a	11.3 ± 1.5 ^b	
Leaf size (cm ²)			
<i>Q. alba</i>	23.4 ± 2.0	17.6 ± 1.2	20.5 ± 1.7 ^a
<i>Q. robur</i>	17.0 ± 0.3	10.8 ± 0.4	13.9 ± 1.4 ^b
Treatment mean	20.2 ± 1.7 ^a	14.2 ± 1.6 ^b	
Plant leaf area (cm ²)			
<i>Q. alba</i>	127 ± 3 ^A	136 ± 9 ^A	131 ± 5
<i>Q. robur</i>	181 ± 6 ^B	149 ± 8 ^{AB}	165 ± 8
Treatment mean	154 ± 12	143 ± 6	
LMA (g m ⁻²)			
<i>Q. alba</i>	35.3 ± 0.3	57.1 ± 1.2	46.2 ± 4.9 ^a
<i>Q. robur</i>	33.8 ± 1.1	50.8 ± 1.4	42.3 ± 3.9 ^b
Treatment mean	34.6 ± 0.6 ^a	54.0 ± 1.6 ^b	
LAR (cm ² g ⁻¹)			
<i>Q. alba</i>	95 ± 5	61 ± 3	78 ± 8 ^a
<i>Q. robur</i>	96 ± 6	66 ± 2	81 ± 7 ^a
Treatment mean	95 ± 3 ^a	63 ± 2 ^b	
Chl _{total} (mg g ⁻¹)			
<i>Q. alba</i>	10.5 ± 0.5	6.0 ± 0.2	8.2 ± 1.0 ^a
<i>Q. robur</i>	10.5 ± 1.1	6.8 ± 0.4	8.7 ± 1.0 ^a
Treatment mean	10.5 ± 0.5 ^a	6.4 ± 0.3 ^b	

Where species × light treatment interactions are significant, combination means followed by different uppercase letters are significantly different ($P < 0.05$). Where there is no significant interaction, species or light treatment means followed by different lowercase letters are significantly different ($P < 0.05$)

similar rates of A_{max} and I_c , but R_d rates were 29% greater in *Q. alba* than in *Q. robur*. For ϕ , the response was similar for both species in the high light environment, but ϕ was 20% greater for *Q. alba* than *Q. robur* in low light (Fig. 2a, Table 3). For *Q. alba*, ϕ was 17% higher in the low light environment versus the high light environment. Seedling sprouts raised in the high light environment were modeled to have a 256% greater A_{net} than those raised in the low light environment, and *Q. robur* seedling sprouts were modeled to have a 73% greater A_{net} than *Q. alba* (Table 3, Table S2). The two species shared similar rates of $V_{c,max}$ and J_{max} , but $V_{c,max}$ rose 66% and J_{max} rose 45% when leaves developed in high light as opposed to low light (Fig. 2b, Table 3, Table S2).

Fig. 2 Photosynthetic light response curves (a) and photosynthetic CO₂ response curves (b) of *Quercus alba* and *Q. robur* leaves measured (points) and modeled (lines) in low and high light environments. Values are mean \pm SE for each species and light environment combination, and modeled functional variables are given in Table 3



Discussion

We set out to compare sprouting capacity of shoot-clipped germinants of two temperate oak species (section *Quercus*: *Q. alba* and *Q. robur*) indigenous to different continents, and to determine the role of light availability in sprouting capacity and sprout photosynthesis. Sprouting can promote plant survival under stressful conditions caused by factors such as light limitation, herbivory, pathogens, drought or fire damage; and, seedling sprouts are often the predominant form of oak reproduction in forest understories in North America (Del Tredici 2001; Johnson et al. 2018). Seedling sprouts have received less attention in Europe, but may be of equal importance in the regeneration pool. By directly comparing allopatric species with similar biological and ecological characteristics, we aim to facilitate knowledge transfer that supports development and adoption of successful regeneration practices for improved sustainability within the range of temperate oak forests.

Sprouting capacity of oak germinants

Both oaks examined in this study displayed a high sprouting capacity after shoot clipping despite the young age and early ontogeny of seedlings. This is consistent with previous observations on sprouting by more developed seedlings in the first year of growth, including *Q. alba* and *Q. robur* (Andersson and Frost 1996; Cain and Shelton 2000; Huddle and Pallardy 1996; Verdaguer et al. 2000; Zhang et al. 2019). In our study, sprouting capacity of *Q. robur* appeared greater than that of *Q. alba* as indicated by the number of sprouts per plant and the accumulated stem biomass. This may reflect an inherent difference in

Table 3 Photosynthetic response of seedling sprouts (mean \pm SE) of two oak species grown in either a low or a high light environment

Variable	Light environment		Species mean
	Low	High	
A_{\max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)			
<i>Q. alba</i>	7.5 \pm 0.2	10.8 \pm 0.5	9.2 \pm 0.8 ^a
<i>Q. robur</i>	7.7 \pm 0.4	11.7 \pm 1.0	9.7 \pm 1.0 ^a
Treatment mean	7.6 \pm 0.2 ^a	11.3 \pm 0.5 ^b	
R_d ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)			
<i>Q. alba</i>	0.7 \pm 0.03	1.0 \pm 0.04	0.9 \pm 0.07 ^a
<i>Q. robur</i>	0.5 \pm 0.07	0.9 \pm 0.04	0.7 \pm 0.10 ^b
Treatment mean	0.6 \pm 0.06 ^a	1.0 \pm 0.03 ^b	
I_c ($\mu\text{mol photons m}^{-2}$)			
<i>Q. alba</i>	13.3 \pm 0.3	22.0 \pm 1.3	17.7 \pm 2.0 ^a
<i>Q. robur</i>	11.7 \pm 1.4	20.3 \pm 0.5	16.0 \pm 2.0 ^a
Treatment mean	12.5 \pm 0.7 ^a	21.2 \pm 0.7 ^b	
ϕ ($\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photons)			
<i>Q. alba</i>	0.055 \pm 0.000 ^A	0.047 \pm 0.002 ^B	0.051 \pm 0.002
<i>Q. robur</i>	0.046 \pm 0.000 ^B	0.046 \pm 0.001 ^B	0.046 \pm 0.0003
Treatment mean	0.051 \pm 0.002	0.046 \pm 0.001	
A_{net} ($\text{mmol CO}_2 \text{ day}^{-1}$)			
<i>Q. alba</i>	2.2 \pm 0.4	6.8 \pm 0.7	4.5 \pm 1.1 ^a
<i>Q. robur</i>	3.3 \pm 0.1	12.4 \pm 2.2	7.8 \pm 2.3 ^b
Treatment mean	2.7 \pm 0.3 ^a	9.6 \pm 1.6 ^b	
$V_{c,\max}$ ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)			
<i>Q. alba</i>	29.7 \pm 1.3	49.8 \pm 2.7	39.7 \pm 4.7 ^a
<i>Q. robur</i>	32.1 \pm 0.8	52.8 \pm 4.6	42.4 \pm 5.1 ^a
Treatment mean	30.9 \pm 0.9 ^a	51.3 \pm 2.5 ^b	
J_{\max} ($\mu\text{mol electrons m}^{-2} \text{ s}^{-1}$)			
<i>Q. alba</i>	55.7 \pm 1.2	77.4 \pm 1.9	66.6 \pm 5.0 ^a
<i>Q. robur</i>	56.8 \pm 3.3	85.6 \pm 11.1	71.2 \pm 8.3 ^a
Treatment mean	56.2 \pm 1.6 ^a	81.5 \pm 5.3 ^b	

Where species \times light treatment interactions are significant, combination means followed by different uppercase letters are significantly different ($P < 0.05$). Where there is no significant interaction, species or light treatment means followed by different lowercase letters are significantly different ($P < 0.05$)

sprouting capacity between the species. It is important to note that the *Q. robur* acorns used in this study were on average 48% heavier than those of *Q. alba*, so our observation of superior sprouting capacity by *Q. robur* could be tied to acorn mass (Ke and Werger 1999; Quero et al. 2007). However, we accounted for this difference in acorn size in our analyses of plant morphology and leaf characteristics. And, we found no species difference in RGR_{mass} , though high light availability did enhance RGR_{mass} . This suggests that the light environment was of greater importance to seedling sprout development than was the species difference in acorn size. Yet, another observation to consider was that, most cotyledons of harvested *Q. robur* appeared sound and functional, while those of *Q. alba* had begun to decompose. Considering all evidence, we cannot resolve if the superior sprouting capacity of *Q. robur* we observed was due to an inherent difference in sprouting capacity, a species

difference in cotyledon longevity, or a coincidental difference in acorn size. These observations on cotyledon longevity did not appear to differ between light environments for either species.

High light availability enhanced sprouting capacity of both oaks, and this is consistent with previous studies on sprouting by deciduous tree seedlings in relation to light (Kabeya et al. 2003; Kabeya and Sakai 2005; Longbrake and McCarthy 2001). Our study, however, appears to be the first to demonstrate this response for recent oak germinants. Enhanced sprouting capacity as promoted by high light availability has been attributed to root system development (Longbrake and McCarthy 2001) and accumulation of carbohydrate stores (Kabeya et al. 2003; Kabeya and Sakai 2005). In this respect, sprouting capacity is largely determined by the light environment of the plant prior to stem loss. However, this does not explain our finding because root biomass for both species was greatest in the low light environment (65% greater) at time of clipping (data not shown). Interestingly, we did observe root mass to be greatest among seedling sprouts in the high light environment at the end of our study. Our observations demonstrate plasticity in sprout development of shoot-clipped oak germinants that is attributable to the light environment of the developing seedling sprout rather than the light environment prior to clipping. Indeed, significant morphological plasticity relative to light availability is consistently reported for other oaks (Jensen et al. 2012; Rebbeck et al. 2011; Rodríguez-Calcerrada et al. 2008).

Impact of light environment on plant morphology

Plants growing in shaded environments could be expected to prioritize photosynthate allocation to support light capture. Several studies on temperate deciduous species, including oaks, have found that low light availability leads to a decreased RMR and an increased LAR (Brose and Rebbeck 2017; Gardiner et al. 2009; Jensen et al. 2012; Rebbeck et al. 2011; Sevillano et al. 2016). In the current study, however, light availability did not affect the RMR of either species. This is likely an effect of the clipping treatment that necessitated germinants prioritize photosynthate allocation to shoot development. This conclusion is supported by Kruger and Reich (1993a) who found that *Q. rubra* sprouts growing in 50% of full light accumulated less root mass than did seedlings when measured after first-flush leaf expansion. In contrast, we observed LAR of oak seedling sprouts to be consistent with findings reported for oak seedlings (Jensen et al. 2012; Rebbeck et al. 2011; Welander and Ottosson 1998). In the respective light environments, we found no significant species difference in the plant-level morphological response following shoot destruction. This supports the notion that *Q. alba* and *Q. robur* have similar biological and ecological characteristics and would therefore be expected to respond in a similar way to disturbance.

Leaf plasticity relative to light environment

Along with plant-level morphological acclimation, some temperate deciduous species show strong leaf plasticity relative to light availability (Abrams and Kubiske 1990; Gardiner et al. 2009; Kuehne et al. 2014). LMA has been recognized as a trait which links morphological acclimation to light availability with leaf physiological function—LMA is typically positively correlated with photosynthetic capacity on a leaf area basis (Abrams and Kubiske 1990; Ellsworth and Reich 1992; Zhang et al. 2018). We observed the lowest LMA when *Q. alba* and *Q. robur* leaves developed in low light. This was accompanied

by high $\text{Chl}_{\text{total}}$ in both species. These observations are consistent with previous studies on oak seedlings and saplings that exhibit plasticity to light availability (Gardiner et al. 2009; Jensen et al. 2012; Rodríguez-Calcerrada et al. 2007; Zhang et al. 2018). The low LMA and high $\text{Chl}_{\text{total}}$ we observed for the low light environment indicates that both oaks acclimate leaf morphology to improve efficiency of light capture. Furthermore, LMA of *Q. alba* was greater than that of *Q. robur*. This species difference in LMA may be indicative of species-specific light requirements as described for other temperate broadleaf trees (Abrams and Kubiske 1990; Niinemets and Kull 1994). In other words, the lower LMA of *Q. robur* suggests a level of plasticity that may convey greater tolerance to shaded environments than *Q. alba*. However, we found no species difference in $\text{Chl}_{\text{total}}$.

Photosynthetic acclimation

Related to the observed plasticity in LMA and $\text{Chl}_{\text{total}}$, leaves of both oaks studied showed photosynthetic acclimation to light availability. Leaf-level photosynthetic capacity for both species was greatest in the high light environment. Several studies have supported the generalization that leaves which develop under high light availability exhibit greater area-based A_{max} , R_d , I_c , V_{cmax} , and J_{max} than those which develop under low light availability (Gardiner et al. 2009; Jensen et al. 2012; Rebbeck et al. 2012; Rodríguez-Calcerrada et al. 2007; Rzigui et al. 2017; Zhang et al. 2018). However, seedlings of three oaks, one of which is *Q. alba*, have previously shown limited photosynthetic and growth responses to shading in their first year (Rebbeck et al. 2011, 2012). It was suggested that cotyledonary reserves can compensate for resource limitations during early seedling growth. This contrasts with our results, which indicate that the light environment has an immediate effect on photosynthesis of young seedling sprouts. Photosynthetic capacity observed in our study indicates that cotyledonary reserves in *Q. alba* and *Q. robur* may not sufficiently compensate for simultaneous shoot loss and light limitation, and in this respect young oak seedling sprouts might be less shade tolerant than seedlings during their first growing season. However, further studies that directly compare young oak seedling sprouts and intact seedlings are needed to verify this suggestion.

As expected for both species, daily plant-level net photosynthesis (A_{net}) was much greater in seedling sprouts raised in the high light environment compared to those raised in the low light environment. However, A_{net} for *Q. robur* seedling sprouts was almost two times greater than for *Q. alba*, suggesting that *Q. robur* seedling sprouts have a greater carbon acquisition potential. This difference in A_{net} during sprouting was likely facilitated by the greater plant leaf area and lower R_d of *Q. robur*. It also likely explains why *Q. robur* seedlings sprouts out-grew *Q. alba* seedling sprouts, but we cannot completely eliminate the impact of greater acorn size for *Q. robur* (Bonfil 1998). Still, the greater A_{net} of *Q. robur* may indicate that it can acclimate to a wider range of light environments and have a higher long-term survival rate in low light environments compared to *Q. alba*, particularly during the early stages of regeneration.

Conclusion

We have demonstrated that germinants of both *Q. alba* and *Q. robur* sprout vigorously following top kill. To our knowledge, this is the first study to demonstrate a connection between sprouting capacity, as indicated by the number of sprouts per plant and accumulated biomass, and light environment for oak germinants. Furthermore, oak seedling sprouts of both species showed substantial morphological and physiological plasticity to the light environment, despite the young age and early ontogeny at time of clipping. At the plant level, light availability altered proportional distribution of leaf area, but not biomass, such that plants grown in a shaded environment developed a morphology consistent with enhanced light gathering. Similar morphological acclimation was found at the leaf-level, where plasticity in LMA and $\text{Chl}_{\text{total}}$ were associated with photosynthetic acclimation to the light environment, both at the leaf and plant level. In contrast to previous studies on oak seedlings during their first growing season (cf. Rebbeck et al. 2012), oak seedling sprouts that developed in high light exhibited a greater photosynthetic capacity than seedling sprouts in low light. We suggest that cotyledonary reserves may not sufficiently compensate for shoot loss when light availability is low. As naturally regenerated oak seedlings in forest understories often experience herbivory, frost damage, fire damage, or stress factors that results in shoot loss or die-back, our results highlight the importance of the light environment during early plant development and regeneration.

While the allopatric species we studied appeared similarly adapted to shoot loss, *Q. robur* displayed a greater sprouting capacity and plant carbon acquisition potential than *Q. alba*, regardless of the light environment. This may indicate that *Q. robur* seedling sprouts can more successfully acclimate to a wider range of light environments. The lower LMA, lower R_d , and greater A_{net} of *Q. robur* suggest that it may tolerate shaded environments more readily than *Q. alba*. Nevertheless, our results indicate that management practices developed to regenerate the respective species could be successfully applied to the other as well. However, field experiments in the respective ranges of each species are needed for a more complete understanding of seedling sprout development in their natural environments.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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