



Effects of above- and below-ground competition from shrubs on photosynthesis, transpiration and growth in *Quercus robur* L. seedlings

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ABSTRACT

For a tree seedling to successfully establish in dense shrubbery, it must maintain function under heterogeneous resource availability. We evaluated leaf-level acclimation in photosynthetic capacity, seedling-level transpiration, and seedling morphology and growth to gain an understanding of the effects of above- and below-ground competition on *Quercus robur* seedlings. Experimental seedlings were established in a typical southern Swedish shrub community where they received 1 of 4 competition levels (above-ground, below-ground, above- and below-ground, or no competition), and leaf-level responses were examined between two growth flushes. Two years after establishment, first-flush leaves from seedlings receiving above-ground competition showed a maximum rate of photosynthesis (A_{\max}) 40% lower than those of control seedlings. With the development of a second flush above the shrub canopy, A_{\max} of these seedlings increased to levels equivalent to those of seedlings free of light competition. Shrubby competition reduced oak seedling transpiration such that seedlings exposed to above- and below-ground competition showed rates 43% lower than seedlings that were not exposed to competition. The impaired physiological function of oak seedlings growing amid competition ultimately led to a 60–74% reduction in leaf area, 29–36% reduction in basal diameter, and a 38–78% reduction in total biomass accumulation, but root to shoot ratio was not affected. Our findings also indicate that above-ground competition reduced A_{\max} , transpiration and biomass accumulation more so than below-ground competition. Nevertheless, oak seedlings exhibited the ability to develop subsequent growth flushes with leaves that had an A_{\max} acclimated to utilize increased light availability. Our findings highlight the importance of flush-level acclimation under conditions of heterogeneous resource availability, and the capacity of oak seedlings to initiate a positive response to moderate competition in a shrub community.

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1. Introduction

Temporal and spatial competition in plant communities has been studied intensively (e.g., Goldberg and Barton, 1992; Callaway, 1997). Nevertheless, a need for understanding the effects of competition and its directions is still evident, especially if we wish to utilize these mechanisms, for example, when restoring oak forests with high biodiversity (Callaway, 1995; Byers et al., 2006).

Abbreviations: DOY, day of year; PPF, photosynthetic photon flux density; A_{\max} , maximum gross CO₂ assimilation rate; A_{net} , maximum net CO₂ assimilation rate; A–Q, photosynthetic light response; A–C_i, photosynthetic CO₂ response; R_D, apparent dark respiration; k, convexity; A_{sat} , maximum CO₂ assimilation rate at infinite CO₂ availability; CE, carboxylation efficiency; I_c , light compensation point; Chl_a, chlorophyll a; Chl_b, chlorophyll b; Chl_{total}, total chlorophyll; Chl_{a/b}, chlorophyll a to b ratio; R:S ratio, root to shoot ratio; DWL, leaf dry weight; SLA, specific leaf area.

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It has been suggested that understory vegetation may be used to facilitate restoration of oak (*Quercus*) forests by reducing ungulate browsing or reducing interspecific competition from herbaceous vegetation on young oak seedlings (Vera et al., 2006; Gómez-Aparicio et al., 2004, 2005; Harmer et al., 2010). Conversely, interspecific competition from woody vegetation may simultaneously reduce oak seedling growth (Lorimer et al., 1994; Collet and Frochet, 1996; Collet et al., 1998). Given that the importance of the interactions with a shrub community is dependent on the physical and biological environments, it is likely that competition and facilitation concurrently influence oak seedlings. Likewise the relative impact of above- and below-ground resource availability may be highly context-dependent and shift over time (Callaway, 1995, 1992; Brooker et al., 2008).

We studied above- and below-ground competition from a shrub community on *Quercus robur* L. seedlings, a key overstory component in temperate broadleaved forests supporting many red listed species in southern Sweden (Hannon et al., 2000; Ranius and Jansson, 2000; Nordén et al., 2007). Native shrub communities in

mixed broad-leaved forests in southern Sweden are typically composed of saplings from overstorey species mixed with shrub species such as *Rubus* spp. and *Corylus avellana* L. (Brunet and von Oheimb, 1998). For oak seedlings to successfully establish and develop in a shrub community, seedlings have to acclimate to spatial heterogeneity of resource availability on a micro-habitat level (Beckage and Clark, 2003; Gómez-Aparicio et al., 2005; Dickie et al., 2006).

Changes in irradiance may be abrupt or gradual for oak seedlings, as overstorey gaps form or close. Above-ground competition can alter several leaf processes that in turn alter whole plant morphology (e.g., Givnish, 1988). At the leaf-level, acclimation to high light may initiate a change in pigment composition, light response and leaf morphology (Walters, 2005). For example, mature and newly developed *Quercus petraea* (Matt.) Liebl. leaves enhanced net CO₂ assimilation rate (A_{net}) and light-saturated rate of electron transport upon transfer to a high light environment (Rodríguez-Calcerrada et al., 2008). In addition, above-ground competition may reduce proportional carbon allocation to the roots, and thereby affect the root to shoot (R:S) ratio (Ågren and Ingestad, 1987; Ammer, 2003).

As with many oaks, *Q. robur* has the potential to produce multiple flushes during a growing season of favorable conditions (e.g., Löf, 2000; Welander and Ottosson, 2000). At the seedling level, multiple flushing can lead to heterogeneous light availability, potentially giving seedlings an opportunity to avoid shaded environments. Assuming that oak seedlings optimize their overall carbon gain, and light availability within the shrub canopy restricts this gain, it may be advantageous for oak seedlings to re-allocate resources such as photosynthates and nitrogen from first flush leaves in shade to second flush leaves in a high light environment (Lockhart et al., 2008). To our knowledge, no other studies have examined photosynthetic acclimation in oak leaves under the vertically heterogeneous shade in a shrub community.

Vapor pressure deficit and light availability are often held as the major drivers of plant transpiration and in turn carbon gain (Kramer and Boyer, 1995). It is, however, not only above-ground conditions that influence transpiration rate, but also below-ground competition for plant available water (Breda et al., 1995). Evaluating differences in total transpiration over a growing season may provide an indication of the strength of above- and below-ground competition from a shrub community. During periods when plant available water is limited, competing successfully for water may largely determine growth for seedlings in the humid, temperate regions of Central and Northern Europe (Löf, 2000; Ciais et al., 2005).

Shrub communities are known to modify chemical, physical and biological soil properties (e.g., Callaway, 1995; Brooker et al., 2008). Eliminating root competition from mature trees and shrubs, by trenching or cleaning, has been observed to stimulate growth in tree seedlings (e.g., Riegel et al., 1992; Beckage and Clark, 2003). However, these techniques may lead to an enhanced resource availability, either as dying roots decompose after trenching or as increased light availability after removal of competing neighboring vegetation. This could lead to overestimating strength of the competition (Coomes and Grubb, 2000). We therefore propose that above- and below-ground competition is better studied by combining a classic root-exclusion treatment (excluding below-ground competition) with an alternative method in which competing shrub vegetation is maintained but the canopy is bent away from the oak seedling (excluding above-ground competition).

The aim of this study was to evaluate the impact and strength of above- and below-ground competition from a shrub community on photosynthesis, transpiration and growth of *Q. robur* seedlings. Four different competition levels were established in a field experiment to mimic a southern Swedish broad-leaved forest shrub community. We asked the following questions; (1) How will above- and below-ground competition from a shrub community affect

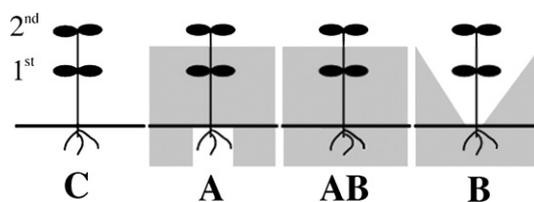


Fig. 1. Competition level design showing oak seedlings with two subsequent flushes. The grey area shows a general outline of the shrub community above- and below-ground. The competition levels were: no shrub vegetation (C), above-ground competition (A), both above- and below-ground competition (AB) and below-ground competition (B).

photosynthesis, transpiration and biomass accumulation in oak seedlings? (2) Will either above- or below-ground competition affect photosynthesis, transpiration and biomass accumulation more so than the other? (3) How will shading of lower leaves affect acclimation to high light in second flush leaves that overtop the shrub canopy? It has been observed and argued that forest trees acclimate to different competition scenarios by altering biomass accumulation through carbon allocation shifts (Kolb and Steiner, 1990; Ammer, 2003; Lockhart et al., 2008). We will therefore also discuss potentially advantageous acclimation strategies in connection to above- and below-ground competition from a shrub community.

2. Materials and methods

2.1. Experimental site

The experiment was established in a field located at the Swedish University of Agricultural Sciences, in Alnarp, Sweden (55°39'40"N, 13°05'04"E). The 30-year mean annual precipitation is 600 mm and the mean temperature spans from 1 °C in January to 16 °C in July (Anon., 2010). Soil in the field was sandy loam with increased clay content below 60 cm. Prior to establishment of the experiment; vegetation occupying the field was primarily different species of *Sorbus* spp. and grasses. To prepare the site for the experiment, it was cleared in early spring 2007 and planted with *Melilotus albus* Medik. In October 2007, the field was sprayed with glyphosate (Roundup, Monsanto, USA) then plowed in preparation for planting.

2.2. Experimental design

Sixteen, 5 m × 5 m plots were delineated in the field to establish four separate blocks of four plots each. Blocks were established 3 m apart and plots within blocks were established 1 m apart. In December 2007, 25 two-year-old, bareroot *Q. robur* seedlings (mean basal diameter of 9 mm, mean plant height of 68 cm and 18–22 cm long roots) were planted on a 1 m × 1 m spacing in each plot. At this same time, plots in each block were randomly assigned a competition level (Fig. 1). The four competition levels examined in this study included: A – above-ground competition; B – below-ground competition; AB – above- and below-ground competition; and, C – control. These competition levels were initiated by planting seedlings of various shrubs and trees within plots designated to receive competition. A mixture of 35% *Rubus idaeus* L., 25% *Betula pendula* Ehrh., 20% *C. avellana* L., 10% *Fraxinus excelsior* L. and 10% *Populus tremula* L. was planted in designated plots at a density of 12 stems per m² equally distributed within plots. To provide only above-ground competition to oak seedlings in competition level A, planting holes for the oak seedlings were lined with open-ended polyethylene bags (0.2 mm thick, 20 cm diameter, 80 cm length) (Icopal AB, Sweden) that served as a barrier to root ingrowth. To provide only below-ground competition to oak seedlings in com-

petition level B, the canopy of competing vegetation was held away from the shoots of oak seedlings with metal wires. The shrub community was gently bent, without damaging shrubs to form a 50 cm diameter gap. Oak seedlings in plots assigned competition level AB received both above- and below-ground competition from the established competitors, while plots assigned competition level C were kept free of all vegetation other than the planted oak seedlings. Mean plant height of oak seedlings and neighboring shrub vegetation were 76 and 96 cm, respectively, at the start of the experiment. The survival rate at the end of 2009 was higher than 99% for seedlings under all competition levels. All plots were manually weeded to remove herbaceous vegetation during the 2008 and 2009 growing seasons. Oaks were treated with Candit® (BASF, Germany) three times during the spring of 2009 to reduce fungal (*Erysiphe* sp., *Microsphaera* sp.) infections on leaves.

2.3. Environmental measurements

Photosynthetic photon flux density (PPFD) was measured with Minikin QT sensors (EMS, Brno, Czech Republic) every 5 min at one point per competition level 85 cm above groundline. Soil water content was measured from the surface to a depth of 15 cm using Time Domain Reflectometry (TDR) (Moisture point, E.S.I. Environmental Sensors Inc., Canada) at 6 points per competition level every other week. In competition level A, soil water content was measured inside the barrier formed by the polyethylene bags. Precipitation was collected using a Vantage Pro 2 weather station (Davis Instruments, USA). These environmental measurements were conducted from April to October 2009.

2.4. Gas exchange measurements

Photosynthetic light response ($A-Q$) and photosynthetic CO_2 response ($A-C_i$) curves were measured with a Ciras-2 portable photosynthesis system and an automatic leaf cuvette (PP-Systems, USA) during July and early August, 2009. Fully developed leaves in the middle of first and second flushes were selected on randomly chosen oak seedlings that met certain requirements. In competition levels A and AB, seedlings were selected only if the first flush was inside the shrub canopy and the second flush overtopped the shrub canopy (Fig. 1). Approximately 75% of the seedlings independent of competition level met these requirements. Measurements were conducted on sample leaves between 0800 and 1600 h. The evening before a sample leaf was measured, oak seedlings were covered to eliminate light exposure, and seedlings were watered to prevent moisture stress during sampling. Fifty-six leaves on 28 plants were measured to complete the sampling.

$A-Q$ was measured by controlling light level with a LED light source, and recording CO_2 assimilation rate as it stabilized at PPFDs of 0, 1600, 800, 400, 200 and $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ under a reference CO_2 concentration of 375 ppm. $A-C_i$ response data was collected on the same sample leaves immediately following $A-Q$ measurements. For $A-C_i$ response measurements, PPFD in the cuvette was maintained at $800 \mu\text{mol m}^{-2} \text{s}^{-1}$, and reference CO_2 concentrations were adjusted to 0, 100, 200, 400, 800 and 1600 ppm. A new leaf was selected if inhibition was observed during any part of $A-Q$ or $A-C_i$ measurements. Air temperature inside the cuvette tracked ambient air temperature ($25.5 \pm 0.2^\circ\text{C}$) and cuvette humidity was maintained at 50% of ambient humidity during all gas exchange measurements.

2.5. Transpiration measurements

Oak seedling transpiration was estimated with sap-flow measurements conducted on 12 seedlings using commercially available EMS-type gauges (T 4.2, EMS, Czech Republic) (Čermák et al., 2004).

For each competition level, three gauges were installed at heights ranging from 25 to 43 cm above the groundline where stems were straight, free of foliage and knots below gauges, and diameters ranged from 7 to 12 mm. Foam and weather shields provided thermal insulation of stem gauges. Additionally, stem tissue below gauges in competition level C was covered with aluminum foil to reflect direct sunlight. This was not necessary for the other competition levels since surrounding vegetation shaded those oak stems. Measurements were taken at 1 min intervals with average values stored every 10 min from 22 June to 3 September 2009. Heat loss from sensors was estimated at 0300 h while actual sap-flow was assumed to be zero with baseline subtraction in the software (Mini32, EMS, Czech Republic).

2.6. Leaf characteristics and seedling biomass

After gas exchange measurements, sample leaves were harvested to determine specific leaf area (SLA) and pigment content. Pigments were measured using modified protocols from Barnes et al. (1992) and Lichtenthaler (1987). Two, 7 mm diameter leaf disks free of major veins, were sampled immediately after leaves were harvested. Chlorophyll a (Chl_a), b (Chl_b) and carotenoids were extracted in dimethyl sulfoxide (DMSO) overnight at 65°C . The concentration was measured spectrophotometrically using a Beckman DU 650 spectrophotometer at $\lambda = 664.9, 648.2$ and 407.0 nm . SLA of sample leaves was calculated as leaf area over leaf dry weight (DWL). At the end of the 2009 growing season, all 12 seedlings sampled for sap-flow were harvested and separated into root, shoot and leaf components. Leaves were separated according to flush and leaf area was measured with a Li-3100C Area Meter (Li-Cor Inc., USA). Oak roots were harvested by excavating roots $>2 \text{ mm}$ diameter typically to a depth of 0.7 m below which the soil texture shifted to a higher clay content. Sampling concentrated on roots thicker than 2 mm in diameter because the greatest proportion of root biomass for oak seedlings is typically tap- and lateral-root biomass. This root biomass is also generally found in the upper 50 cm, of the soil (Jackson et al., 1996; Löf, 2000; Collet et al., 2006). After processing, all seedling tissue components were dried at 70°C then weighed. R:S ratio was calculated as root over shoots (including leave) biomass.

2.7. Data handling and statistical analyses

$A-Q$ and $A-C_i$ curves were fit using Photosyn Assistant software version 1.2 (Dundee Scientific, UK). This software utilizes a function described by Prioul and Chartier (1977) to model photosynthetic $A-Q$. Based on $A-Q$ curves, the maximum rate of photosynthesis (A_{max}), apparent dark respiration (R_D) and convexity (k) were modeled. This software also utilized a function described by Olsson and Leverenz (1994) to estimate carboxylation efficiency (CE) and a maximum CO_2 assimilation rate at infinite CO_2 (A_{sat}).

Competition level and flush effects on $A-Q$, $A-C_i$ response variables and leaf characteristics were tested using a generalized linear model (GLM) procedure, with a least squares mean separation. The independent factors used in the analysis were competition level (4), flush (2) and their interactions (8). The model initially included plant as an explanatory factor, however as model-outputs were unaffected by this factor it was not used in the final model. Oak seedling daily transpiration rate was calculated using total seedling sap-flow and leaf area. Daily leaf areas, used in the calculation of transpiration rate, were interpolated from leaf area measurements and timing of growth flushes. Second flush leaves in all competition levels expanded and matured between 2 July and 21 July 2010. Differences in biomass and transpiration between competition levels were analyzed for significance using a GLM procedure. Distribution assumptions were tested using the Kolmogorov–Smirnov

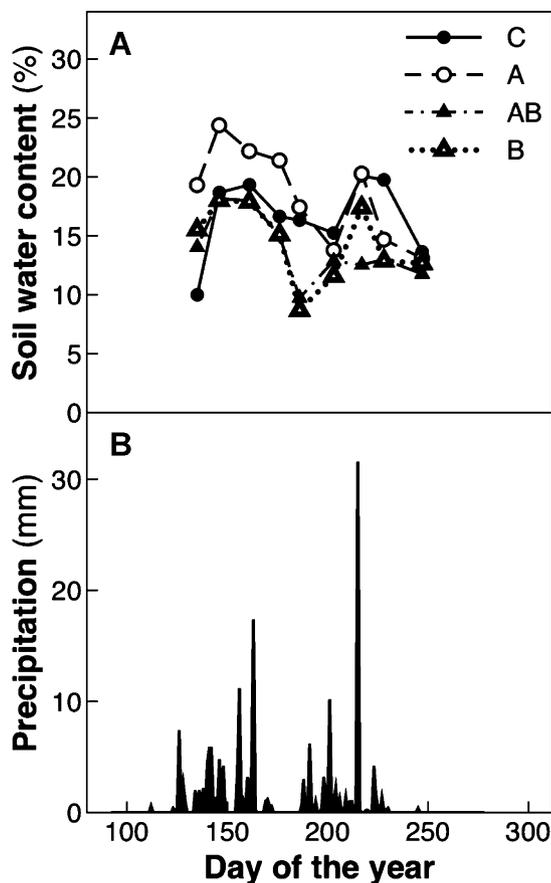


Fig. 2. Soil water content in the topsoil (0–15 cm) (A) of the four levels; C control, A above-ground competition, AB above- and below-ground competition and B below-ground competition and daily accumulated precipitation (B) in Alnarp, Sweden from April (day of the year = 91) to October (day of the year = 304) 2009.

normality-test and a Bartlett's test (Bartlett, 1937). Variables that did not meet this assumption were normalized using a Box-Cox transformation. A Satterthwaite-approximation was added to the model for heteroscedasticity consistent standard errors if needed. All statistical analyses were conducted using SAS 9.2 (SAS Institute Inc., USA) at significance levels of 0.05, 0.01 and 0.001 m

3. Results

3.1. Climate

Daily PPFD between June and mid-September 2009 averaged $17.5 \text{ mol m}^{-2} \text{ day}^{-1}$ for competition level C. As shrub community foliage expanded, light availability for oak seedlings decreased in competition levels B, A and AB to 80, 60 and 50% of full light, respectively. For each competition level, oak seedlings experienced the highest PPFD during midday. Soil water content from May to September ranged between 10 and 25% and differed among competition levels ($P < 0.05$). From mid-May to the beginning of July (day of year (DOY) 146–176), soil water content was significantly greater for oak seedlings in competition level A than competition levels C, AB, and B. Towards the end of the 2009 growing season, soil water content in competition level A became similar to that in the other competition levels (Fig. 2A). As the growing season progressed, soil water content increased following major rain events. Conversely, low precipitation during July (DOY 186) was followed by a drop in soil water content in all competition levels. This decrease in soil water content was greater in plots with shrubs compared to competition level C (Fig. 2). For example soil water content decreased

11% for seedlings under competition level A, but only 4% for control seedlings between May 26 (DOY 146) and July 5 (DOY 186) 2009. Compared to the 30-year mean (Anon., 2010), growing season precipitation was normal in 2009 (Fig. 2B).

3.2. Gas exchange

A–Q curves derived from oak leaves were substantially affected by competition from shrub vegetation. Flush and competition level differences in photosynthesis, carboxylation and dark respiration rates are shown in Fig. 3 and Table 1. First flush leaves on seedlings from competition level C maintained a significantly ($P < 0.05$) higher A_{net} rate on an area basis than first flush leaves that developed under shade of competitors in levels A and AB (Fig. 3A). A–Q curves for second flush leaves were similar and independent of competition level (Fig. 3B). Neither competition level nor flush affected A–Q calculated on a leaf mass basis (results not shown).

A–Q variables modeled using the empirical A–Q curves shown in Fig. 3 resulted in a higher A_{max} for first flush leaves in competition level C than levels A and AB (Fig. 3 and Table 1). Second flush leaves showed no differences regardless of competition level. Competition level and flush interacted to influence R_D . Neither competition level nor flush determined k (Table 1) or the light saturation point (data not shown). The light compensation point (I_c), on the other hand, was affected by the interaction of competition level and flush ($P < 0.05$) and ranged between 7.4 and $59.8 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in first and 31.2 – $53.4 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in second flush leaves. A_{sat} , generated from A– C_i curves, was significantly lower in first flush leaves than second flush leaves for oak seedlings in competition level A. CE was greatest in first flush leaves of control seedlings (Table 1).

3.3. Transpiration rates

Accumulated oak seedling transpiration for control seedlings averaged 28 L from June 23 (DOY 174) to September 2 (DOY 245), 2009. Competition from shrubs reduced ($P < 0.05$) whole seedling transpiration in competition levels B, A, and AB to 73, 66 and 56%, respectively, of control seedling transpiration. Transpiration rates estimated on a leaf area basis also differed between competition levels ($P < 0.05$). Daily mean transpiration rate was highest ($4.4 \text{ g dm}^{-2} \text{ day}^{-1}$) in oak seedlings receiving competition level C compared with 3.3, 2.9 and $2.5 \text{ g dm}^{-2} \text{ day}^{-1}$ in levels B, A and AB, respectively. Diurnal patterns of oak seedling transpiration generally followed daily courses of light availability (Fig. 4). In addition, during the period of decreasing soil water content between June 10 (DOY 161) and July 22 (DOY 203) (Fig. 2A), mean daily transpiration rates showed slightly higher or equal values in competition level B than levels A and AB (data not shown).

3.4. Biomass accumulation and leaf characteristics

At the end of the 2009 growing season, competition from shrub vegetation had strongly reduced leaf number, DWL and oak seedling biomass (Table 2). Seedling biomass in competition levels B, A, and AB was 62, 33 and 22%, respectively, of that in seedlings from level C. In addition, oak seedlings exposed to only root competition (competition level B) had a higher number of leaves, DWL and total plant biomass than seedlings in competition levels A and AB. A similar trend was also found for stem basal diameter, but mean seedling height was not influenced by competition. At the end of the growing season, seedlings averaged 132 cm tall while competing vegetation averaged 110 cm tall.

Competition level did not influence seedling R:S ratio, but did negatively impact seedling leaf area (Table 3). Total leaf area of seedlings in competition levels C, B, A and AB were 1.04, 0.42, 0.29 and 0.27 m^2 , respectively. This effect was more pronounced in the

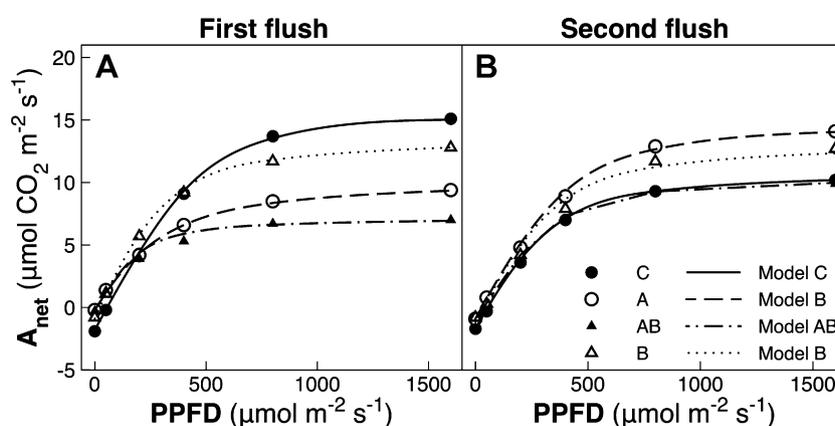


Fig. 3. Photosynthetic light response curves of *Q. robur* leaves measured (points) and modeled (lines) with and without competition from shrub vegetation in an open field in Alnarp, Sweden. The net CO₂ assimilation rate (A_{net}) at different PPFDs, for first flush leaves (A) and second flush leaves (B) calculated on a leaf area basis. Values are means from 7 seedlings per competition level and model variables are given in Table 1.

Table 1

Modeled photosynthetic light response curve parameters on a leaf area basis determined for first and second flush leaves from oak seedlings in four competition levels; (C) control, (A) above-ground competition, (AB) above- and below-ground competition and (B) below-ground competition. Means ($n = 7$) with SE in parentheses. Significant differences ($\alpha = 0.05$) between means are indicated with different letters. In variables that had a significant interaction between competition level (columns) and flush (rows), different letters indicate significant differences between flush-specific means. Whereas, if the interaction was not significant separation of means are given on competition level- and flush-means.

Variable	Competition level				Flush mean
	C	A	AB	B	
A_{max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)					
1st flush	17.7 (0.7)a	10.5 (0.5)bc	7.5 (1.2)c	14.5 (0.8)ab	12.5 (0.8)
2nd flush	12.6 (1.8)abc	15.9 (1.4)ab	11.6 (1.3)bc	14.5 (1.5)ab	13.6 (0.8)
Competition level mean	15.1 (1.2)	13.2 (1.0)	9.6 (1.0)	14.5 (0.8)	
R_D ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)					
1st flush	-1.8 (0.2)a	-0.2 (0.1)d	-0.3 (0.1)d	-0.9 (0.1)cd	-0.8 (0.1)
2nd flush	-1.7 (0.2)ab	-0.9 (0.2)cd	-1.1 (0.2)bc	-1.3 (0.3)abc	-1.3 (0.1)
Competition level mean	-1.8 (0.1)	-0.6 (0.1)	-0.7 (0.1)	-1.1 (0.2)	
k					
1st flush	0.889 (0.044)	0.613 (0.116)	0.773 (0.052)	0.786 (0.048)	0.765 (0.039)
2nd flush	0.807 (0.051)	0.837 (0.060)	0.845 (0.026)	0.796 (0.109)	0.822 (0.032)
Competition level mean	0.848 (0.034)	0.725 (0.003)	0.809 (0.030)	0.791 (0.003)	
I_c ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)					
1st flush	59.8 (11.1)a	7.4 (3.7)cd	8.5 (2.0)d	24.0 (4.9)bcd	24.9 (5.1)
2nd flush	53.4 (3.2)a	31.2 (6.0)abc	38.6 (9.9)ab	43.1 (11.5)ab	41.6 (4.2)
Competition level mean	56.6 (8.0)	19.3 (6.7)	23.6 (9.1)	33.6 (9.3)	
A_{sat} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)					
1st flush	30.7 (2.7)ab	16.1 (1.6)b	17.8 (3.4)ab	25.8 (2.1)ab	22.6 (1.7)
2nd flush	19.3 (1.8)ab	31.7 (3.8)a	24.4 (3.5)ab	28.5 (6.8)a	26.7 (2.3)
Competition level mean	25.0 (2.2)	23.9 (2.9)	21.1 (2.5)	29.5 (3.6)	
CE					
1st flush	3.8 (1.0)a	1.3 (0.1)b	1.2 (0.4)b	1.9 (0.3)ab	2.1 (0.3)
2nd flush	1.0 (0.1)b	1.5 (0.1)b	1.3 (0.3)b	1.5 (0.4)b	1.4 (0.1)
Competition level mean	2.4 (0.6)	1.4 (0.1)	1.3 (0.2)	1.8 (0.2)	

Statistical output from the generalized linear model when testing competition level and flush effect on light response. A_{max} (maximum gross CO₂ assimilation rate): competition level ($P < 0.001$); flush (n.s.); competition level \times flush ($P < 0.001$). R_D (apparent dark respiration): competition level ($P < 0.001$); flush ($P < 0.001$); competition level \times flush ($P < 0.05$). k (convexity): competition level (n.s.); flush (n.s.); competition level \times flush (n.s.). I_c (light compensation point): competition level ($P < 0.001$); flush ($P < 0.001$); competition level \times flush ($P < 0.05$). A_{sat} (maximum CO₂ assimilation rate at infinite CO₂ availability): competition level (n.s.); flush (n.s.); competition level \times flush ($P > F = 0.01$). CE (carboxylation efficiency): competition level (n.s.); flush (n.s.); competition level \times flush ($P > F = 0.01$).

Table 2

Means (SE in parentheses) of biomass and morphological characteristics in oak seedlings ($n = 3$) in four competition levels; (C) control, (A) above-ground competition, (AB) above- and below-ground competition and (B) below-ground competition. Significant differences ($\alpha = 0.05$) between competition levels within rows are indicated with different letters.

Variable	Competition level				F-value	P-value
	C	A	AB	B		
Number of leaves	1113 (137)a	179 (47)c	135 (8)c	395 (47)b	27.96	<0.001
Leaf weight (g)	83 (9)a	16 (3)c	13 (1)c	30 (2)b	50.42	<0.001
Total biomass (g)	362 (17)a	118 (15)c	82 (12)c	225 (26)b	47.60	<0.001
Root to shoot ratio	1.2 (0.2)	0.9 (0.2)	0.9 (0.1)	0.9 (0.1)	0.03	n.s.
Plant height (cm)	133 (14)	121 (7)	122 (4)	152 (21)	1.20	n.s.
Basal diameter (mm)	19.7 (3.1)ab	12.7 (1.5)b	14.0 (0.6)ab	21.5 (1.3)a	5.53	<0.05

Table 3
Oak leaf characteristics by flush position from seedlings grown under four different competition levels; (C) control, (A) above-ground competition, (AB) above- and below-ground competition and (B) below-ground competition (mean with SE in parentheses). Values for leaf area and specific leaf area (SLA) are means from the three seedlings per level that were used for sap-flow measurements. SLA and $\text{Chl}_{a/b}$ have been Box–Cox transformed before testing, untransformed values are given. Significant differences ($\alpha = 0.05$) between means are indicated with different letters. In variables that had a significant interaction between competition level (columns) and flush (rows), different letters indicate significant differences between flush-specific means. Whereas, if the interaction was not significant separation of means are given on competition level- and flush means.

Variable	Competition level				Flush mean
	C	A	AB	B	
Leaf area (m^2)					
1st flush	0.56 (0.06)a	0.22 (0.00)c	0.16 (0.02)c	0.37 (0.04)ab	0.33 (0.05)
2nd flush	0.48 (0.07)a	0.07 (0.03)c	0.11 (0.04)c	0.05 (0.03)c	0.18 (0.06)
Total leaf area	1.05 (0.12)	0.29 (0.04)	0.27 (0.06)	0.43 (0.05)	
SLA ($\text{cm}^2 \text{g}^{-1}$)					
1st flush	129.2 (8.7)	187.4 (4.3)	192.1 (8.7)	149.5 (9.8)	164.5 (8.6)a
2nd flush	124.8 (4.7)	140.4 (10.8)	241.0 (56.4)	102.3 (25.8)	152.1 (20.9)a
Competition level mean	127.0 (4.5)a	163.9 (11.7)ab	216.5 (27.8)b	125.9 (16.2)a	
$\text{Chl}_{\text{total}}$ ($\mu\text{g cm}^{-2}$)					
1st flush	111.7 (5.1)	109.9 (6.3)	100.9 (4.7)	107.9 (7.1)	107.6 (2.9)a
2nd flush	112.9 (4.9)	120.3 (5.8)	113.2 (7.5)	123.7 (8.9)	117.5 (3.4)b
Competition level mean	112.3 (3.4)a	115.1 (4.4)a	107.1 (4.6)a	115.8 (5.9)a	
$\text{Chl}_{a/b}$					
1st flush	2.5 (0.2)a	2.0 (0.1)ab	1.8 (0.1)b	1.9 (0.2)b	2.0 (0.1)
2nd flush	1.5 (0.1)b	1.6 (0.1)b	1.6 (0.1)b	1.6 (0.1)b	1.6 (0.0)
Competition level mean	2.0 (0.2)	1.8 (0.1)	1.7 (0.1)	1.7 (0.1)	
Carotenoids ($\mu\text{g cm}^{-2}$)					
1st flush	25.8 (1.1)	21.7 (1.3)	19.4 (1.3)	22.6 (1.3)	22.4 (0.7)a
2nd flush	26.2 (1.4)	27.2 (1.4)	24.9 (1.9)	28.1 (1.4)	26.6 (0.8)b
Competition level mean	26.0 (0.8)a	24.5 (1.2)ab	22.2 (1.3)b	25.4 (1.2)ab	

Statistical output from the generalized linear model when testing competition level and flush effect on leaf characteristics.

Leaf area: competition level ($P < 0.001$); flush ($P < 0.001$); competition level \times flush ($P < 0.05$). SLA: competition level ($P < 0.01$); flush (n.s.); competition level \times flush (n.s.). $\text{Chl}_{\text{total}}$: competition level (n.s.); flush ($P < 0.05$); competition level \times flush (n.s.). $\text{Chl}_{a/b}$: competition level (n.s.); flush ($P < 0.001$); competition level \times flush ($P < 0.05$). Carotenoids: competition level ($P < 0.05$); Flush ($P < 0.001$); competition level \times flush (n.s.).

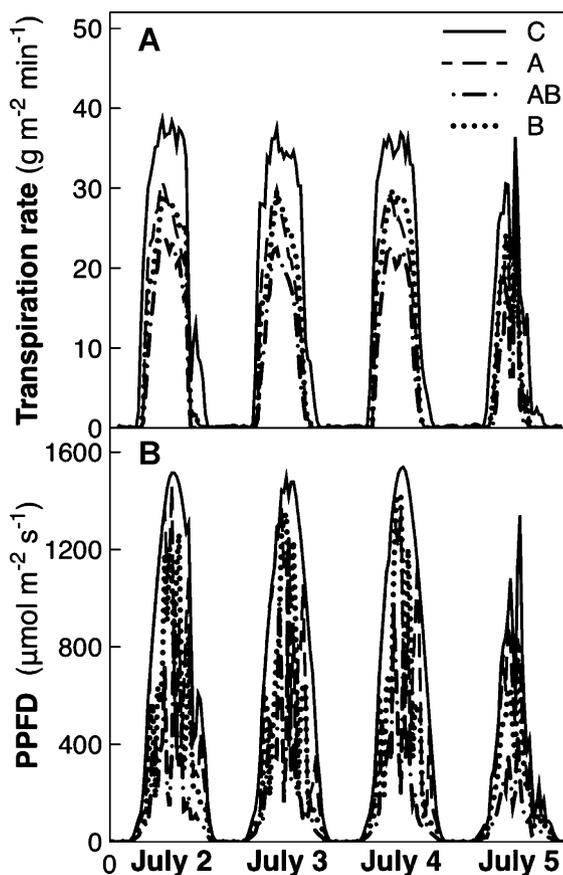


Fig. 4. Example courses of mean transpiration rates per oak seedling leaf area estimated using sap-flow (A) and photosynthetic photon flux density (PPFD) (B) from July 2 to July 5, 2009.

second flush, where leaf area in levels B, A and AB were only 10–23% of leaf area in level C. SLA was higher for oak seedlings receiving competition level AB than those receiving competition levels B and C ($P < 0.001$). Oak root excavation at the end of the experiment showed little root spiraling (less than 5% of root biomass) for oak seedlings in competition level A.

Competition from shrub vegetation did not affect the total chlorophyll ($\text{Chl}_{\text{total}}$) content, but second flush leaves generally had more ($P < 0.05$) chlorophyll than first flush leaves (Table 3). With the exception of first flush leaves of seedlings grown under competition level A, interspecific competition resulted in a higher Chl_b content (results not shown). Chlorophyll a to b ratios ($\text{Chl}_{a/b}$) were determined by the interaction of competition level and flush. $\text{Chl}_{a/b}$ were similar in first and second flush leaves that developed under competition levels A, AB and B. Even though $\text{Chl}_{\text{total}}$ content was similar in first and second flush leaves from competition level C, $\text{Chl}_{a/b}$ were lower in second flush leaves than first flush leaves (Table 3). Carotenoid content was lower in leaves from competition level AB than in C, and second flush leaves had a higher carotenoid content than first flush leaves.

4. Discussion

Several interesting results were found in this study that add to our understanding of competitive interactions between shrubs and *Q. robur*. Generally, competition levels that decreased resource availability also decreased oak seedling photosynthesis, transpiration and growth. Our results suggest that even though both above- and below-ground interspecific competition reduced seedling growth, competition for light appeared to have the largest effect. Biomass accumulation was reduced mainly by reducing leaf area and thereby light interception. A consistent trend through the physiological and morphological variables measured in this study was that the severity of competition levels could be ranked as following; $\text{AB} > \text{A} > \text{B} \gg \text{C}$. For example, total biomass was almost

40% lower in oak seedlings under competition level B than C (Table 2). This finding corroborates earlier reports on several tree species (Ziegenhagen and Kausch, 1995; Gardiner and Hodges, 1998; Welander and Ottosson, 1998; Bovard et al., 2005; Gardiner et al., 2009) that indicate light availability has a strong effect on seedling photosynthesis, transpiration and growth.

A–Q curves of *Q. robur* in this study were similar to earlier reported values, indicating that little photoinhibition occurred during the measurements (e.g., Gardiner et al., 2009). The first flush of control seedlings developed typical sun leaves with a greater A_{\max} and R_D on an area basis, than first flush leaves that developed within shrub canopies under competition levels A and AB. Even though oak seedlings in the latter competition levels developed their first flush leaves in the shade, they developed a second flush overtopping the shrub canopy. These leaves from the second flush had similar A–Q curves as first flush leaves of control seedlings, indicating oak seedlings have the capacity to adjust their photosynthetic apparatus to a vertically heterogeneous light environment. However, differences between flushes within A and AB seedlings were generally not significant, potentially reflecting that the light environment of the lower first flush leaves may have affected the development of the photosynthetic apparatus of the subsequent flush leaves. Hanson et al. (1986) reported that net photosynthesis was similar in first and second flush leaves of *Q. rubra* grown in a high-light environment, whereas photosynthetic activity was reduced in the third flush. In a later paper they showed that development of consecutive flushes and leaves affected photosynthetic activity of lower leaves (Hanson et al., 1988). However, evaluation of the effects from above-ground competition on photosynthetic light response, calculated on a leaf mass basis revealed no differences between flush position or competition level. This finding may also indicate a lack of significant below-ground competition from the shrub community.

Though competition for light appeared to have the strongest effect in our study, below-ground competition also affected oak seedling growth by reducing leaf area, leaf number, transpiration and total biomass. For example, the reduced biomass of oak seedlings in competition level B, in comparison with control seedlings, was most likely a result of reduced leaf area. This, in turn, may have been a partial consequence of reduced water and/or nutrient availability early in the 2009-growing season when low precipitation could have reduced photosynthate production during second flush leaf development. Examining below-ground competition in this study by excluding or including below-ground competition allowed us to evaluate the effects from two perspectives. For example, total biomass in competition level A was not higher than that for oak seedlings under competition level AB. By contrast, oak seedlings under competition level B had a higher total biomass than seedlings from both levels A and AB, although it was lower than in control seedlings. This illustrates that a weak competition interaction may be difficult to evaluate if a stronger competition interaction affects the plant simultaneously (Coomes and Grubb, 2000).

In this study, seedlings established in competition level A were kept free from root ingrowth by the 80 cm plastic bags. Because these bags were open on the bottom to allow for soil drainage, we cannot exclude the possibility that soil moisture and fertility were affected by competing vegetation below this point. However our results do not support that competition below 80 cm was significant.

To maintain a comparable below-ground competitive strength in competition level AB and B, shrub folia were bent away, thereby eliminating shade during most of the day in level B. We can, however, not exclude the possibility that a reduced light availability affected oak seedlings in competition level B. Since first and second flush leaves under competition level B had a similar A_{\max} ,

we assume that possible shading had a minor impact on photosynthetic capacity. This is supported by van den Boogaard et al. (2001), who showed that the daily light integral affected photosynthetic capacity in tomato (*Lycopersicon esculentum* Mill.) more so than the highest daily PPFD encountered by the leaf (Dean et al., 1982; Gardiner et al., 2001). Evaluating potential light competition from shrubs by only observing A–Q curves in isolation may be insufficient, but diurnal shading events may be detected in seedling transpiration rates.

Daily average transpiration rate may be used to estimate strength of competition (Čermák et al., 2004). Assuming that the transpiration rate (leaf area basis) was not restricted by self shading, the loss in transpiration rate caused by below- and above-ground competition in competition level B and A were about 24 and 34%, respectively, of level C. It is, however, likely that the strength of below-ground competition may be overestimated, as seedlings in competition level B likely received shade during the early morning and late afternoon. Together, this indicates, that above-ground competition from the shrub community was stronger than below-ground competition.

There is often a near-linear relationship between water use and dry matter production in plants (e.g., de Wit, 1958). This concurs with our findings from the different competition levels. However, our sap-flow measurements were only conducted during part of the 2009 growing season, while seedling biomass accounted for two years of growth (2008 and 2009).

The year of this study was a normal precipitation year, but during a drought we would expect that the relationship between seedling transpiration and soil water content to become stronger (Löf, 2000; Welander and Ottosson, 2000). We did not observe decreased transpiration rates during a short period of decreasing soil water content in the topsoil. This indicates that lower soil depths were not affected enough to influence oak seedling transpiration. However, most nutrients are normally present in the topsoil and since nutrient supply to the root surface is limited by soil moisture level (Barber, 1962; Nye and Tinker, 1977), the brief period of low moisture may have influenced nutrient acquisition and seedling growth in our study.

In contrast to most herbaceous plants that develop fewer deep roots, shrub and tree species develop both shallow and deep roots that could compete for plant available water with oak seedlings on a broader spatial scale (Stone and Kalisz, 1991; Canadell et al., 1996). Thus, during years of low precipitation and severe soil droughts, below-ground competition from shrubs might be of more importance than observed in this study. Predicting the severity of below-ground competition from a shrub community may therefore be highly complex as it is dependent on species, climate and soil resource availability (Callaway et al., 1991; Callaway, 1995).

In our study, oak seedlings accumulated approximately 42% of their total biomass below-ground regardless of competition level. Though the shrub community had a negative effect on overall seedling growth, it did not invoke a shift in apparent biomass distribution. In contrast, van Hees (1997) and Ammer (2003) who also used transplanted seedlings reported decreasing R:S ratios in *Q. robur* seedlings receiving artificial shade. Using a natural shrub canopy to provide shade, as in this study, has the advantage of providing a natural quality (red to far-red ratio) of light, that is known to affect stem elongation and pigment composition (Murchie and Horton, 1997; Ammer, 2003; Franklin, 2008). It may also induce carbon allocation from below-ground tissues to leaves and stems (Lockhart et al., 2008). A plausible explanation for our finding is that oak seedling leaves become sinks for carbon only below a critical light level, and shading from the shrub canopy in this experiment was not severe enough to stimulate such a response. In support for this, seedlings of all competition levels developed a second flush suggesting that the shrub community may have imposed only

moderate competition strength upon the oak seedlings (Löf, 2000; Welander and Ottosson, 2000).

Q. robur is considered a light demanding species (Ellenberg, 1988). Consequently low light levels are often cited as a limitation to seedling growth and survival (Harmer and Morgan, 2007). Growing tall and overtopping the shrub canopy, thereby partially escaping a shaded environment, is likely to be beneficial to oak seedlings. In this experiment the observations that oak seedling heights were similar for all competition levels and total biomass and basal diameter were lower in seedlings receiving competition, suggests that seedlings allocated resources to overtop competition and avoid a shady environment.

A total removal of neighboring shrub competitors may therefore be unnecessary when regenerating oak. Practices that account for the competitive abilities of oak seedlings could provide cost savings when regenerating oak. However, in order to develop silvicultural guidelines we need to resolve how the relative height and species composition of a shrub community affects oak seedlings survival and growth.

5. Conclusions

We found that shrub vegetation reduced the overall carbon assimilation and thereby growth of *Q. robur* seedlings. We further demonstrated that above-ground competition for light reduced seedling photosynthetic capacity, transpiration and total biomass more so than below-ground competition. Neither above- nor below-ground competition affected carbon accumulation to an extent that shifted the R:S ratio. Independent of competition levels, *Q. robur* developed a second flush and these leaves that overtopped the shrub canopy had the photosynthetic capacity to utilize increased light availability. Overall, these results suggest that *Q. robur* seedlings have the capacity to acclimate and respond positively to moderate competition from a shrub community, so long as the competitors are not able to overtop and shade the developing regeneration.

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