A comparative study of physiological and morphological seedling traits associated with shade tolerance in introduced red oak (*Quercus rubra*) and native hardwood tree species in southwestern Germany

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Northern red oak (*Quercus rubra* L.), a moderately shade-tolerant tree species, is failing to regenerate throughout its native North American range, while successful recruitment in Central Europe has been observed since its introduction. To examine whether comparative photosynthetic performance could explain the regeneration success of this non-native species in Central Europe, we compared the physiological and morphological seedling traits of red oak with three co-occurring tree species under three canopy types in southwestern Germany. Native species included a moderately shade-tolerant native oak (*Quercus robur* L.) and two shade-tolerant species (*Acer pseudoplatanus* L. and *Carpinus betulus* L.). The photosynthetic traits of non-native red oak seedlings were similar to those reported for this species in the native range, where shade-tolerant competitors readily outperform red oak under low light conditions. However, compared with native shade-tolerant species in Europe, red oak seedlings photosynthesized efficiently, especially under closed canopies and in small canopy gaps, exhibiting high photosynthetic capacity, low leaf dark respiration and leaf-level light compensation points that were similar to the more shade-tolerant species. The superior net carbon gain of red oak seedlings at low and moderate light levels was likely facilitated by high leaf areas and reflected by seedling dry masses that were greater than the observed native European species. A competitive advantage for red oak was not evident because relative height growth was inferior to seedlings of co-occurring species. In North America, the inability of seedlings to compete with shade-tolerant tree species in deeply shaded understories is central to the problem of poor oak recruitment. Our study suggests that the ability of non-native red oak to perform equally well to native shade-tolerant species under a variety of light conditions could contribute to the consistent success of red oak regeneration in Europe.

**Keywords**: European forests, introduced species, invasive species, morphological plant traits, physiological plant traits, regeneration dynamics, seedling growth, shade tolerance.

**Introduction**

Northern red oak (*Quercus rubra* L.) is an economically important, moderately shade-tolerant tree species native to eastern North America (*Sander 1990*). While this species is failing to regenerate in many locations throughout its native range (*Crow 1988, Abrams 1992, Lorimer et al. 1994*), red oak has been readily regenerating in Central European forests since its introduction in the mid-18th century (*Bauer 1953, Vansteenkiste 1967*).
et al. 2005, Major et al. 2013). Light is the environmental factor that most often limits the growth of regenerating red oak (Abrams 1992, Dey and Parker 1997). As such, the availability of this resource often regulates the success of red oak regeneration. Increased competition with shade-tolerant species is a significant factor contributing to the decline of red oak dominance in mesic hardwood forests throughout its native range (Lorimer 1984, Loftis 1990, Desmarais 1998, Van Lear 2004, Dech et al. 2008). Here, fire suppression is thought to be a major contributing factor to the recent proliferation of fire-sensitive shade-tolerant tree species and the poor recruitment of fire-adapted mid-tolerant species such as red oak (Lorimer 1984, Abrams 1992). A reduced frequency in the development of canopy gaps, such as those formed following low-intensity fires, prevents development of the moderate light conditions needed to promote the recruitment of red oak seedlings to upper forest strata (Lorimer et al. 1994). Under low light conditions, relatively high positive carbon gain and rapid growth favours shade-tolerant species that can easily overtop mid-tolerant oaks (Lorimer 1993, Walters et al. 1993).

In Europe, red oak also typically grows with shade-tolerant species. In fact, shade-tolerant ‘admixture’ or ‘trainer’ species have often been planted with red oak to maintain the quality of the latter by reducing epicormic branching (Lüpke 1998, Major et al. 2013). Furthermore, fires such as those needed to promote successful regeneration in North America are rare in the forests of Central Europe (Tinner et al. 2005), yet prolific natural regeneration of red oak has been extensively observed on a regular basis with minimal silvicultural promotion, in contrast to the intensive management needed to regenerate red oak in North America. In Europe, the density of red oak seedlings can exceed that of all other hardwood species combined even under closed (>90% canopy closure) canopy conditions and oak seedlings are typically taller than similarly aged seedlings of native tree species (Major et al. 2013). Prolific regeneration of red oak has raised the question of whether this non-native species is an aggressive invader in Central European forests (Chmura and Sierka 2005, Vor 2005). Detrimental effects of the spread of non-native red oak on native biodiversity have been reported (Reinhardt et al. 2003, Winter et al. 2009) and eradication policies have been implemented in some regions (Vansteenkiste et al. 2005). In addition, concern has been expressed that red oak is displacing native tree species including indigenous oaks such as pedunculate oak (Quercus robur L.); however, respective reports are often anecdotal with few data provided (Protopopova et al. 2006, Riepsás and Straigytė 2008, Marozas et al. 2009, Kiedrzyński et al. 2011).

The striking difference between native and introduced ranges in the recruitment potential of red oak has been described in previous studies (Steiner et al. 1993, Major et al. 2013). It is believed, for example, that owing to regular thinning in managed European forests, red oak, a gap specialist, is able to form a dense layer of advanced regeneration and occupy canopy openings aggressively (Scholz 1952, Kline and Cottam 1979, Steiner et al. 1993, Kaelke et al. 2001). Therefore, it appears that regeneration of red oak in Europe is not limited by light availability to the same extent as that of populations in the native range. A higher shade tolerance of red oak in Central Europe compared with North America has been proposed as a possible explanation for the discrepancy in regeneration success (Vor 2005). A recent study also suggested that in Europe, red oak might not be subjected to the high degree of competition from shade-tolerant species (Major et al. 2013) as has been observed in North America (Abrams 1996).

Possible differences in the relative shade tolerance of red oak in Europe and North America can be addressed by comparing the photosynthetic light responses within introduced and native populations of this species. Such information for red oak relative to sympatric shade-tolerant tree species could offer insights into the degree of light limitation and potential competition to which regenerating red oak would be subjected, and could confirm the role that differences in shade tolerance may play in the success of red oak in Europe. Ecophysiological studies examining the photosynthetic light response of red oak and sympatric shade-tolerant species have been conducted in North America (e.g., Bazzaz and Carlson 1982, Jurik et al. 1988, Kubiske and Pregitzer 1996, Parker and Dey 2008); however, little is known about the light response characteristics of non-native red oak in Europe.

In this study, we compared growth, morphology and photosynthetic performance as an indication of the relative shade tolerance in seedlings of non-native red oak and three common co-occurring hardwood species found in mixed deciduous forests of southwestern Germany, to address the following questions:

(i) In Europe, how does the photosynthetic performance of non-native red oak seedlings compare with co-occurring native tree species and published reports based on red oak seedlings in North American forests?
(ii) Relative to co-occurring European species, how does the photosynthetic performance in red oak seedlings respond to varying light conditions?
(iii) How are the photosynthetic traits of non-native red oak seedlings and those of co-occurring European species related to leaf morphology and biomass allocation patterns?

Materials and methods

Study site
This study was conducted in the South and North Mooswald forest districts close to the western outskirts of Freiburg im Breisgau, in southwestern Baden-Wuerttemberg, Germany (48°00′ N, 07°46′ E). The area is characterized by a warm
Atlantic climate with a mean annual temperature of ~11 °C, mean January and July temperatures (coldest and warmest months) of 0.9 and 19.3 °C, respectively, and 185 days per year above 10 °C (Bläsing 2008). The mean annual precipitation is ~870 mm, with the majority occurring during the growing season between May and September (~450 mm; Gauer and Aldinger 2005). Situated in a former floodplain area of the river Dreisam, a gleyc cambisol (Michéli et al. 2006) has developed from the alluvial deposits (silicate gravel), which are covered by a layer of loess of variable thickness (Villinger 2008). The well-drained soil is highly decarbonized and of gravelly sandy texture. The terrain is flat and has an elevation of ~220–230 m above sea level.

The secondary and semi-natural forests of the study area comprise mainly hardwood species, including pedunculate oak, sycamore maple (Acer pseudoplatanus L.), European hornbeam (Carpinus betulus L.), small-leaved lime (Tilia cordata Mill.) and northern red oak. Hornbeam and lime trees usually form the mid- and understory beneath an overstory of more economically valuable species such as oak, ash and maple. In addition, a tall shrub layer is dominated by hazelnut (Corylus avellana L) and the introduced North American black cherry (Prunus serotina Ehrh.). From the pole stage onwards, forest stands are typically thinned from above on a regular basis every 5–10 years. Single-tree and group selection (gaps <0.5 ha in size) as well as patch cuttings (patches 0.5–1 ha) are used to naturally and artificially regenerate the forest. All species except lime can be found in the natural regeneration layer of older stands.

**Canopy treatments**

In July 2011, naturally established, undamaged seedlings between 75 and 125 cm in height of the non-native northern red oak and the native pedunculate oak, sycamore maple and hornbeam were selected and marked in 13 stands situated across the study area. According to established shade tolerance rankings, European hornbeam is the most shade-tolerant and pedunculate oak the least shade-tolerant species in this tree community (Niinemets and Valladares 2006, Ellenberg 2009). Red oak and sycamore maple are usually classified as mid-tolerant (e.g., Hein et al. 2008, Rebbeck et al. 2012). Elsewhere, the shade tolerance of sycamore maple has been described as being similar to that of hornbeam and greater than that of both red oak and pedunculate oak (Niinemets and Valladares 2006).

Study stands were selected to provide a range of light conditions at the height of the seedling layer and experimental populations of seedlings where the impacts of intraspecific competition were minimal. Consequently, three different types of forest canopy coverage were classified and investigated: (i) closed multi-layered canopies; (ii) small to mid-sized canopy gaps; and (iii) large canopy openings. At least five seedlings per species and canopy type were selected for analyses (Table 1). The total height and annual terminal shoot growth for 2011 of all seedlings were recorded. Hemispherical photographs taken above each seedling were analysed using WinScanopy software (Régent Instruments, Inc., Quebec, Canada) to determine irradiance levels. The total site factor (TSF) was estimated as a percentage of direct and diffuse photosynthetic photon flux densities (PPFDs) at the leaf level relative to PPFD under open-field conditions.

**Physiological, leaf-level traits**

In August 2011, the photosynthetic response of net CO₂ gas exchange to PPFD (light response curve) was determined for one fully developed and undamaged leaf of the upper terminal shoot of each seedling using a portable LI 6400 infrared gas analyser in conjunction with a 6400-02B LED light source (LI-COR, Inc., Lincoln, NE, USA). Leaves were completely wrapped in an opaque material for ~30 min prior to photosynthesis measurements. In accordance with Kuptz et al. (2010), light response curves were developed by measuring leaf gas exchange at PPFDs of 0, 20, 50, 100, 200, 500, 1000 and 1500 μmol m⁻² s⁻¹, with a minimum time of 3 min between the different light levels. The reference CO₂ concentration was set to 400 μmol mol⁻¹ with a constant gas flow of 500 μmol s⁻¹. Relative humidity and leaf temperature were kept at ~40% and 20 °C, respectively. Light response curves were fitted using CurveExpert 1.4 software (D.G. Hyams, Starkville, MS, USA) and the Morgan–Merrcer–Flodin function (Morgan et al. 1975).

Following Kazda et al. (1998) and Beaudet et al. (2000), photosynthetic performance was characterized by net CO₂ assimilation at light saturation (A₅₁₀₀, area-based photosynthetic capacity, μmol CO₂ m⁻² s⁻¹), leaf dark respiration (Aᵢ, μmol CO₂ m⁻² s⁻¹), leaf-level light compensation point (LCP, μmol photons m⁻² s⁻¹) and quantum efficiency (α, μmol CO₂ (μmol photons)⁻¹).

Table 1. Number of investigated seedlings (N, physiological measure-ments) and mean and standard deviation (n=5) for total site factor (TSF, %) and height (cm) of excavated seedlings (n=5, morphologi-cal measurements) per species and canopy type. QURU, northern red oak; ACPS, sycamore maple; CABE, European hornbeam; QURO, pedunculate oak.

<table>
<thead>
<tr>
<th>Canopy type</th>
<th>QURU</th>
<th>ACPS</th>
<th>CABE</th>
<th>QURO</th>
</tr>
</thead>
<tbody>
<tr>
<td>Closed canopy</td>
<td>10</td>
<td>5</td>
<td>9</td>
<td>7</td>
</tr>
<tr>
<td>Canopy gap</td>
<td>15</td>
<td>17</td>
<td>6</td>
<td>12</td>
</tr>
<tr>
<td>Large opening</td>
<td>11</td>
<td>8</td>
<td>12</td>
<td>5</td>
</tr>
<tr>
<td>Height</td>
<td>14</td>
<td>6.6</td>
<td>3.7</td>
<td>4.0</td>
</tr>
</tbody>
</table>

## Table 1. Number of investigated seedlings (N, physiological measure-ments) and mean and standard deviation (n=5) for total site factor (TSF, %) and height (cm) of excavated seedlings (n=5, morphologi-cal measurements) per species and canopy type. QURU, northern red oak; ACPS, sycamore maple; CABE, European hornbeam; QURO, pedunculate oak.
Comparative study of seedling traits associated with shade tolerance

A\textsubscript{1500} was defined as net CO\textsubscript{2} assimilation at a PPFD of 1500 \textmu mol m\textsuperscript{2} s\textsuperscript{-1} as estimated by light response measurements. A\textsubscript{0} was also directly derived from the light response measurements at a PPFD of 0 \textmu mol m\textsuperscript{2} s\textsuperscript{-1}. The LCP was determined at the intersection of the fitted light response curve with the x-axis (light axis). Alpha (\(\alpha\)) is a measure to quantify the capability of a species to effectively increase net CO\textsubscript{2} assimilation under very low light conditions as a result of raising irradiance levels (Weber et al. 1985). It was calculated as the slope of the near-linear portion of the response curve between PPFD levels of 0 and 100 \textmu mol m\textsuperscript{2} s\textsuperscript{-1}.

Morphological, plant-level traits

Following gas exchange measurements, the total leaf area (LA, cm\textsuperscript{2}) for each seedling was measured in the laboratory with the LI-3000A leaf area scanner (LI-COR, Inc.) after harvesting all leaves in the field. Total leaf dry mass was also determined. In accordance with Kazda et al. (2000), theoretical maximum photosynthesis of the whole plant (\textmu mol CO\textsubscript{2} s\textsuperscript{-1}) was calculated by multiplying LA and A\textsubscript{1500} measured for each individual seedling.

In March 2012, five of the previously measured seedlings of northern red oak, pedunculate oak, sycamore maple and hornbeam from each canopy type were fully excavated (Table 1). The dry masses of the above- and belowground portions of each excavated seedling were measured to calculate total dry mass (TDM, g).

The growth and morphological variables measured for all sampled seedlings comprised relative leader length (RLL, terminal shoot growth 2011 divided by total plant height 2010, cm cm\textsuperscript{-1}) and specific leaf mass (SLM, leaf dry mass divided by total LA, g cm\textsuperscript{-2}), while the root-to-shoot ratio (RSR, belowground dry mass divided by aboveground dry mass (leaves and shoots)) was computed for the subsample of excavated seedlings.

Phenotypic plasticity

Plasticity of physiological and morphological traits and total plasticity for each species were calculated based on the phenotypic plasticity index, PI\textsubscript{p} (Valladares et al. 2006). This index, ranging from zero to one, is the difference between the minimum and the maximum mean values of a trait among studied environmental treatments divided by the maximum mean value (Valladares et al. 2000). Here, PI\textsubscript{p} was calculated only for pairs of canopy conditions between which traits generally differed and not in cases where traits between two canopy types were similar. Mean plasticity was calculated for each species by averaging the indices of plasticity obtained for physiological, morphological or all traits combined.

Statistical analyses

All statistical analyses were performed using IBM SPSS 20.0 (IBM Corporation 2011). Because of the relatively small and unequal sample sizes, non-parametric statistics were used. Differences between species means per variable and canopy type, and means within species were analysed using the Kruskal–Wallis analysis of variance followed by a Games–Howell post hoc test (Ruxton and Beauchamp 2008).

Results

The average TSF was distinctly different among the three canopy treatments. Only a minor overlap between closed canopies and canopy gaps at TSF levels of 10–15% of open-field light conditions was observed. Consequently, seedlings exposed to TSF levels between 11 and 40% were classified as growing in canopy gaps (Table 1). Closed canopies and large canopy openings therefore refer to TSF levels <11% or >40%, respectively. Maximum and minimum TSF values of at least 70 and 5%, respectively, were measured for each studied species.

Physiological, leaf-level traits

Under closed canopies, northern red oak seedlings exhibited the highest A\textsubscript{1500} and \(\alpha\), as well as the lowest A\textsubscript{0} observed among all investigated species (Figure 1, Table 2). A similar finding was observed for red oak seedlings growing in canopy gaps; however, here, the A\textsubscript{1500} and \(\alpha\) values were similar to those found for sycamore maple. Over the three canopy types, LCPs for red oak did not differ from other species; however, variation was especially high for LCP data. Among the species studied, pedunculate oak seedlings seemed to be best adapted to high light conditions, as A\textsubscript{1500} and \(\alpha\) were greatest for this species in large canopy openings (Table 2). The apparently uncharacteristic trend found over the three canopy treatments for A\textsubscript{1500}, LCP and \(\alpha\) in European hornbeam could be partially the result of an unbalanced data structure. Only one of the six gap seedlings studied had TSF values between 20 and 40%.

Red oak and sycamore maple exhibited comparatively high A\textsubscript{1500} and \(\alpha\) values under medium TSF levels (30–50%, Figure 2), while a further increase was not observed in large openings. In contrast, hornbeam and pedunculate oak showed an increase in these two variables over the entire TSF gradient. In addition, in red oak seedlings, A\textsubscript{0} and LCP were significantly higher in large canopy openings than under a closed canopy. Although similar patterns were also evident for the other species, the observed differences among the canopy types were not statistically significant (Table 2).

Morphological, plant-level traits

Regardless of canopy type, red oak seedlings consistently had the greatest LA among studied species (Table 3). The SLM of red oak remained comparatively high in all canopy types. Beneath closed canopies and in canopy gaps, hornbeam had the significantly lowest SLM values (Table 3).

Superior LA and comparatively high A\textsubscript{1500} in red oak across all canopy types resulted in exceptionally high maximum total...
Figure 1. Modelled light response curves for the investigated tree species derived from seedlings growing in different canopy types. QURU, northern red oak; ACPS, sycamore maple; CABE, European hornbeam; QURO, pedunculate oak.

Table 2. Mean and standard deviation for $A_{1500}$ (µmol CO$_2$ m$^{-2}$ s$^{-1}$), $A_0$ (µmol CO$_2$ m$^{-2}$ s$^{-1}$), LCP (µmol photons m$^{-2}$ s$^{-1}$) and $\alpha$ (µmol CO$_2$ (µmol photons)$^{-1}$) per species and canopy type. Significant differences among means within a species are indicated by different lower-case letters. Significant differences among species means within a canopy type are indicated by different upper-case letters. QURU, northern red oak; ACPS, sycamore maple; CABE, European hornbeam; QURO, pedunculate oak.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Canopy type</th>
<th>QURU</th>
<th>ACPS</th>
<th>CABE</th>
<th>QURO</th>
<th>$P^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_{1500}$</td>
<td>Closed canopy</td>
<td>5.46 ± 1.2$^{AB}$</td>
<td>3.35 ± 0.9$^{A}$</td>
<td>2.84 ± 1.1$^{A}$</td>
<td>2.93 ± 2.1$^{AB}$</td>
<td>0.006</td>
</tr>
<tr>
<td>Canopy gap</td>
<td>8.91 ± 2.1$^{AB}$</td>
<td>7.97 ± 2.5$^{B}$</td>
<td>2.71 ± 1.5$^{A}$</td>
<td>6.63 ± 2.6$^{B}$</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>Large opening</td>
<td>9.98 ± 2.9$^{B}$</td>
<td>8.32 ± 3.1$^{B}$</td>
<td>8.15 ± 2.5$^{B}$</td>
<td>10.87 ± 1.9$^{C}$</td>
<td>0.117</td>
<td></td>
</tr>
<tr>
<td>$A_0$</td>
<td>Closed canopy</td>
<td>−0.55 ± 0.6$^{A}$</td>
<td>−0.64 ± 0.8$^{A}$</td>
<td>−0.76 ± 0.2</td>
<td>−0.64 ± 0.3</td>
<td>0.299</td>
</tr>
<tr>
<td>Canopy gap</td>
<td>−0.91 ± 0.7$^{AB}$</td>
<td>−0.98 ± 0.7$^{B}$</td>
<td>−0.87 ± 0.3</td>
<td>−0.87 ± 0.5</td>
<td>0.727</td>
<td></td>
</tr>
<tr>
<td>Large opening</td>
<td>−1.65 ± 1.1$^{B}$</td>
<td>−1.13 ± 0.4$^{B}$</td>
<td>−1.56 ± 1.1</td>
<td>−1.82 ± 2.1</td>
<td>0.902</td>
<td></td>
</tr>
<tr>
<td>LCP</td>
<td>Closed canopy</td>
<td>21.5 ± 19$^{A}$</td>
<td>16.8 ± 15</td>
<td>17.0 ± 5</td>
<td>27.1 ± 26</td>
<td>0.805</td>
</tr>
<tr>
<td>Canopy gap</td>
<td>25.0 ± 23$^{A}$</td>
<td>21.1 ± 17</td>
<td>33.2 ± 36</td>
<td>17.9 ± 12</td>
<td>0.795</td>
<td></td>
</tr>
<tr>
<td>Large opening</td>
<td>53.4 ± 25$^{B}$</td>
<td>18.2 ± 7$^{A}$</td>
<td>28.3 ± 20$^{AB}$</td>
<td>33.4 ± 45$^{AB}$</td>
<td>0.010</td>
<td></td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Closed canopy</td>
<td>0.027 ± 0.013</td>
<td>0.021 ± 0.012$^{A}$</td>
<td>0.021 ± 0.005$^{A}$</td>
<td>0.018 ± 0.007$^{A}$</td>
<td>0.541</td>
</tr>
<tr>
<td>Canopy gap</td>
<td>0.039 ± 0.016$^{B}$</td>
<td>0.040 ± 0.012$^{AB}$</td>
<td>0.021 ± 0.008$^{A}$</td>
<td>0.034 ± 0.013$^{AB}$</td>
<td>0.037</td>
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</tr>
<tr>
<td>Large opening</td>
<td>0.028 ± 0.014$^{A}$</td>
<td>0.036 ± 0.012$^{AB}$</td>
<td>0.040 ± 0.011$^{AB}$</td>
<td>0.046 ± 0.006$^{AB}$</td>
<td>0.035</td>
<td></td>
</tr>
</tbody>
</table>

$^1$Significance of differences between species means within canopy type.

$^2$Significance of differences between means within a species.
plant photosynthesis (Figure 3). No other species reached comparable values in a given canopy type, although the differences were not always statistically significant. Despite efficient carbon gain, red oak did not exhibit superior height growth (Table 3). On the contrary, RLL for red oak did not surpass that of any other species across all canopy types, with the exception of large openings where RLL of pedunculate oak was significantly lower than the introduced oak species.

Across all canopy types, TDM and RSR were greatest in red oak seedlings (Table 3).

Phenotypic plasticity
Statistically significant differences in physiological or morphological plasticity among species or between canopy types were not evident (Table 4).

Discussion
Our study in Central European forests showed that seedlings of non-native red oak photosynthesized efficiently, not only in canopy gaps but also under closed canopies. Under low and moderate light conditions, red oak appeared to outperform other studied species in terms of total plant net carbon gain. This was likely facilitated by its large LA. High net carbon gain in red oak was reflected in significantly high TDM; however, the relative height growth of red oak seedlings was lower than that in the two shade-tolerant species.

Considering the physiological and morphological traits associated with shade tolerance, many of our measured variables suggest that red oak tends more towards being a shade-tolerant rather than a shade-intolerant species (Valladares and Niinemets 2008), an observation that has also been reported in studies in North America (Kaelke et al. 2001, Rebbeck et al. 2012). Under closed canopies, $A_{1500}$ and $\alpha$ for red oak seedlings were similar or even higher than values for European hornbeam and sycamore maple, both known to be very shade-tolerant at the seedling stage (Hein et al. 2008, Ellenberg 2009). Likewise, $A_0$ in red oak seedlings growing under closed canopies was very low in comparison with other studied tree species. Only LCP values did not follow this pattern. Nevertheless, the measured LCP values coincide with light conditions at 1–2% of open-field irradiance levels (theoretical light saturation of 1500 $\mu$mol m$^{-2}$ s$^{-1}$).
Table 3. Mean and standard deviation for LA (cm²), SLM (g m⁻²), RLL (cm cm⁻¹), TDM (g) and RSR (g g⁻¹) per species and canopy type. Significant differences among means within a species are indicated by different lower-case letters. Significant differences among species means within a canopy type are indicated by different upper-case letters. QURU, northern red oak; ACPS, sycamore maple; CABE, European hornbeam; QURO, pedunculate oak.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Canopy type</th>
<th>QURU</th>
<th>ACPS</th>
<th>CABE</th>
<th>QURO</th>
<th>p²</th>
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<tbody>
<tr>
<td>LA</td>
<td>Closed canopy</td>
<td>1224 ± 576³</td>
<td>893 ± 299³</td>
<td>779 ± 362³</td>
<td>394 ± 309³</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>Canopy gap</td>
<td>1897 ± 819³</td>
<td>1542 ± 572³</td>
<td>961 ± 396³</td>
<td>651 ± 343³</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Large opening</td>
<td>2547 ± 1101³</td>
<td>1094 ± 739³</td>
<td>1287 ± 726³</td>
<td>1346 ± 549³</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.007</td>
<td>0.022</td>
<td>0.235</td>
<td>0.186</td>
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</tr>
<tr>
<td>SLM</td>
<td>Closed canopy</td>
<td>36.8 ± 5³</td>
<td>34.2 ± 8³</td>
<td>29.8 ± 3³</td>
<td>35.8 ± 3³</td>
<td>0.019</td>
</tr>
<tr>
<td></td>
<td>Canopy gap</td>
<td>44.0 ± 10³</td>
<td>45.8 ± 15³</td>
<td>31.1 ± 3³</td>
<td>45.1 ± 7³</td>
<td>0.006</td>
</tr>
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<td></td>
<td>Large opening</td>
<td>71.0 ± 9³</td>
<td>76.3 ± 12³</td>
<td>61.2 ± 2³</td>
<td>66.6 ± 4³</td>
<td>0.035</td>
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<td></td>
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<td>&lt;0.001</td>
<td>&lt;0.001</td>
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</tr>
<tr>
<td>RLL</td>
<td>Closed canopy</td>
<td>13.0 ± 1³</td>
<td>20.3 ± 14³</td>
<td>29.4 ± 16³</td>
<td>15.8 ± 15</td>
<td>0.091</td>
</tr>
<tr>
<td></td>
<td>Canopy gap</td>
<td>32.3 ± 17³</td>
<td>62.1 ± 28³</td>
<td>38.2 ± 20³</td>
<td>24.6 ± 21³</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Large opening</td>
<td>73.0 ± 42³</td>
<td>119.3 ± 47³</td>
<td>125.0 ± 51³</td>
<td>32.7 ± 11³</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td></td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.001</td>
<td>0.121</td>
<td></td>
</tr>
<tr>
<td>TDW³</td>
<td>Closed canopy</td>
<td>22.5 ± 8³</td>
<td>17.7 ± 8³</td>
<td>19.1 ± 15</td>
<td>13.4 ± 9³</td>
<td>0.345</td>
</tr>
<tr>
<td></td>
<td>Canopy gap</td>
<td>81.6 ± 33³</td>
<td>49.5 ± 16³</td>
<td>26.4 ± 7³</td>
<td>30.5 ± 10³</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Large opening</td>
<td>101.4 ± 62³</td>
<td>56.7 ± 20³</td>
<td>36.0 ± 15³</td>
<td>60.3 ± 22³</td>
<td>0.043</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.009</td>
<td>0.013</td>
<td>0.160</td>
<td>0.006</td>
<td></td>
</tr>
<tr>
<td>RSR³</td>
<td>Closed canopy</td>
<td>0.64 ± 0.19³</td>
<td>0.44 ± 0.05³</td>
<td>0.22 ± 0.05³</td>
<td>0.51 ± 0.13³</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>Canopy gap</td>
<td>0.72 ± 0.16³</td>
<td>0.40 ± 0.08³</td>
<td>0.36 ± 0.09³</td>
<td>0.69 ± 0.35³</td>
<td>0.021</td>
</tr>
<tr>
<td></td>
<td>Large opening</td>
<td>0.80 ± 0.27³</td>
<td>0.52 ± 0.18³</td>
<td>0.25 ± 0.10³</td>
<td>0.53 ± 0.14³</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.445</td>
<td>0.691</td>
<td>0.065</td>
<td>0.756</td>
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</tr>
</tbody>
</table>

¹Significance of differences between species means within canopy type.
²Significance of differences between means within a species.
³Derived from excavated seedlings (n = 5).

Our measurements of photosynthetic variables for red oak indicated either a similar or inferior performance to those measured for red oak in North America (Teskey and Shrestha 1985, Kubiske and Pregitzer 1996, Kaelke et al. 2001, Rebeck et al. 2012). This suggests that the regeneration success of red oak in Europe is not due to differences in photosynthetic performance of the native and non-native ecotypes. A key to the success of red oak in Europe, however, could relate to an enhanced photosynthetic performance relative to associated shade-tolerant species in the non-native range. While our study suggests this is the case with respect to sycamore maple and hornbeam, future studies should compare non-native red oak with European beech (Fagus sylvatica L.), one of the most shade-tolerant hardwoods in Europe but a species that was not a significant component of the forests in our study area (Hügin 1990, Ellenberg 2009).

Studies conducted in Central European forests have reported that seedlings of red oak are able to persist and slowly grow in relatively deep shade for prolonged periods (Vor 2005, Major 2011). This contrasts with findings in the native range where red oak seedlings showed limited survival in understory shade after 5–10 years (Crow 1992, Steiner et al. 1993). Relative to the closed-canopy understory light levels in this study, the irradiance values reported for North American red oak forests were similar (Crow 1992, Kaelke et al. 2001, Parker and Dey 2008). This supports suggestions that factors other than low light are responsible for the widespread regeneration failure in North American oaks (McEwan et al. 2011) or that red oak is not as limited by low light availability in Europe as it is in North America. The degree to which factors other than light affect the regeneration of red oak in Europe is unknown and needs further research. Absence of native pathogens, insects and...
other biotic sources of mortality, damage or growth reduction is one potential cause. Lower browsing pressure by deer in Central Europe could be a possible explanation, but there have been observations that herbivory by European roe deer (Capreolus capreolus L.) can have a negative impact on red oak growth and survival (Vor 2005). The impact of insect herbivory on red oak population dynamics in Europe has not been studied to our knowledge. It has been hypothesized that lower accumulations of leaf litter in North America when compared with Central Europe may provide poorer conditions for overwinter survival and germination of acorns in the species native range (Steiner et al. 1993).

Like sycamore maple, red oak appeared best adapted to irradiance levels found in canopy gaps. In both species, $A_{1500}$ for gap seedlings was significantly greater than the values observed under closed canopies. However, a further increase in $A_{1500}$ was not observed for seedlings in large canopy openings. Highest levels of $\alpha$ for red oak and sycamore maple were also observed under medium light conditions. These patterns for $A_{1500}$ and $\alpha$ support the premise that both red oak and sycamore maple are specialists of small gaps (Scholz 1952, Denslow 1980, Crow 1988, Hein et al. 2008, Collet et al. 2011). Comparable results for red oak, in which photosynthetic attributes and growth variables ‘plateaued’ at medium light levels, have also been reported in North American populations (Phares 1971, Kaelke et al. 2001). The combination of relatively high shade tolerance and rapid growth under moderate light conditions could offer a competitive advantage to red oak and contribute to successful regeneration. This ability has been proposed as a characteristic of invasive tree species (Martin et al. 2010) with similar attributes being described for Norway maple (Acer platanoides L.), a European tree that ranks among the most invasive species in North American forests (Reinhart et al. 2005, Paquette et al. 2012). However, our study did not reveal superior plasticity in red oak, supporting previous reports that species-specific traits define the success of non-indigenous plant species more so than plasticity (Godoy et al. 2011, Palacio-Lopez and Gianoli 2011, Van Kleunen et al. 2011, Matzek 2012).

Given the large LA and efficient photosynthesis, red oak appeared to optimize net carbon gain under closed canopies and in forest gaps to a greater extent than the other studied species (cf. Van Kleunen et al. 2011). As a likely consequence, TDM was greatest for red oak in all three canopy types. Red oak also allocated a comparatively large proportion of resources to the root system, thereby leading to a high RSR. The large RSR indicated that red oak might use efficient photosynthetic performance to favour stress tolerance through root development to facilitate resprouting that follows disturbances such as fire and herbivory (Rebeck et al. 2012). This observation also suggests that aboveground, the production of large LA is a persistence strategy used to maximize light interception in shaded environments until a canopy disturbance results in improved light conditions. Favouring allocation to storage and light interception consequently led to inferior height growth in red oak. The RLL was substantially lower for red oak than the more shade-tolerant species, sycamore maple and hornbeam, in all canopy types. The dominance of red oak regeneration in our study area thus does not appear to result from superior height growth which would allow seedlings to readily overtop individuals of other species.

Our study shows that under all light conditions, red oak consistently outperformed pedunculate oak for most measures of carbon acquisition and growth and could therefore be capable of outcompeting or displacing the native pedunculate oak (Riepšas and Straigytė 2008, Kiedrzyński et al. 2011). More research is required to examine the ecological impacts of the potential spread of red oak in Europe.

**Conclusions**

Compared with the traits measured in our study of shade-tolerant European species, non-native red oak did exhibit enhanced leaf area production and photosynthetic performance under closed forest canopies. It is likely that this ability contributes to the success of red oak regeneration at our study sites in the introduced range of this species and could impart enhanced competitive capability under low and moderate light levels.
Acknowledgments

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Conflict of interest

None declared.

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