ORIGINAL PAPER

Photosynthetic performance, height growth, and dominance of naturally regenerated sessile oak (*Quercus petraea* [Mattuschka] Liebl.) seedlings in small-scale canopy openings of varying sizes

Tobias Modrow[1] · Christian Kuehne[3] · Somidh Saha[2] · Jürgen Bauhus[1] · Patrick L. Pyttel[1]

Abstract

Small-scale harvesting methods as practised in close-to-nature forestry may disadvantage the regeneration of more light-demanding tree species such as most oaks and thus cause regeneration failure. Conducted in south-western Germany, this study examined photosynthetic performance and height growth of naturally regenerated 7-year-old sessile oak (*Quercus petraea* [Mattuschka] Liebl.) seedlings growing in artificially established and fenced canopy openings varying from 0.05 to 0.2 ha in size. We quantified the influence of solar radiation and competing vegetation within gaps on total height, height increment, and dominance of oak seedlings. Measurements were taken on plots systematically established along a north–south transect through gaps. Plot-level solar radiation levels within canopy openings quantified using the total site factor (TSF) were between 20% at southerly positions within small openings and up to 75% of open-field conditions at the centre of larger gaps. Photosynthetic performance, total height, and shoot length of the studied oak seedlings increased with increasing solar radiation. However, height increment and total height did not improve substantially when radiation levels increased from 20 to 50% TSF. Yet, highest levels of oak dominance, where oaks were the tallest individual at a plot, were found around 50% of TSF. Under the conditions at our research site, canopy openings of at least 0.2 ha in size appear necessary to successfully establish natural oak regeneration. Irrespective of gap size, the competition to oaks by woody species needs to be controlled to reduce the risk of regeneration failure.

Keywords Sessile oak · Natural regeneration · Forest gap · Light availability · Interspecific competition

Introduction

Pedunculate and sessile oak (*Quercus robur* L. and *Q. petraea* (Mattuschka) Liebl., respectively) are among the economically and ecologically most valuable hardwood tree species in Central Europe (Ellenberg and Leuschner 2010). Managed mature pedunculate and sessile oak forests are known for their high-quality timber while old oak

trees provide habitat for rare and endangered fauna (Ziesche 2010). The two relatively storm-resistant and moderately drought-tolerant oak species (Kunz et al. 2018) are likely to increase in importance as the climate warms in Central Europe (Bolte et al. 2009; Hanewinkel et al. 2013). As part of an adaptive strategy to address predicted long-term changes in prevailing climatic conditions, forest administrations of many German federal states aim at significantly increasing the proportion of oaks, mostly by converting conifer stands into mixed forest with a high proportion of deciduous tree species (Landeskompetenzzentrum Forst Eberswalde 2009; Frischbier et al. 2010; Vasconcelos 2012).

Until several decades ago, oak was mostly artificially regenerated by sowing or planting (Burschel and Huss 1997). However, high costs of site preparation, planting, fencing, and tending have been a matter of concern. As a result, European foresters and scientists are motivated to seek alternatives to the conventional row planting approach for establishing oak stands such as oak cluster planting

✉ Patrick L. Pyttel
patrick.pyttel@waldbau.uni-freiburg.de

1 Chair of Silviculture, Albert-Ludwigs-Universität Freiburg, 79085 Freiburg i. Br., Germany

2 Institute for Technology Assessment and Systems Analysis (ITAS), Postfach, 3640, 76021 Karlsruhe, Germany

3 School of Forest Resources, University of Maine, 5755 Nutting Hall, Orono, ME 04469-5755, USA

schemes (Saha et al. 2017), where oak is introduced to a site, and the use of natural regeneration methods, where oaks are already a canopy species (Kühne et al. 2014).

The renewed focus on silvicultural systems that allow for natural regeneration is further enforced by the widespread implementation of the close-to-nature forest management (CTNFM) paradigm on public forest land across Central Europe (Diaci 2006). The avoidance of large canopy openings is a major principle of CTNFM which, however, discriminates against more light-demanding tree species including oak (Bauhus et al. 2013). Small-scale reproduction methods such as patch and group selection cuttings have resulted in mixed regeneration outcomes, often causing failure in the long-term establishment of oak seedlings (Spellmann 2001; Lüpke 2008). Based on previous studies (Bruciamacchie et al. 1994; Dobrowolska 2008) and practical observations (Jacobee 2004; Timal et al. 2014), regenerating oak in smaller canopy openings seems to be possible in principal. More shade-tolerant tree species such as European beech (*Fagus sylvatica* L.) or European hornbeam (*Carpinus betulus* L.), however, can outgrow and eventually outcompete oak regeneration if light levels are unfavourable over a longer time period (Lüpke and Hauskeller-Bullerjahn 1999; Valladares et al. 2002). The manipulation of light conditions thus is a major silvicultural approach to promote survival and growth of oak seedlings (Röhrig et al. 2006; Diaci et al. 2008).

Light requirements of young deciduous woody plants usually increase with increasing plant size (Givnish 1988; Valladares and Niinemets 2008). This holds especially true for oak seedlings that appear to be fairly shade-tolerant throughout the first few years, which is partly attributable to the comparatively large amount of available resources stored in the acorn (Grime 1966; Ziegenhagen and Kausch 1995). Once these seed resources are depleted, light levels need to be sufficiently high to assure continued growth and survival. According to Röhrig et al. (2006), oak regeneration is able to persist in shady forest understories at light levels of about 15% of open-field conditions over several years while levels > 20% are necessary for continuous height growth (see also Newbold and Goldsmith 1981; Ligot et al. 2013). Oak seedlings competing with more shade-tolerant tree species and/or vigorous ground vegetation, however, require higher light levels in order to become and remain a dominant component of the tree regeneration layer (Lüpke and Hauskeller-Bullerjahn 2004). Irrespective of the competition intensity oak seedlings are exposed to, heavy browsing pressure by ungulates is likely to result in regeneration failure in oak stands (Annighöfer et al. 2015).

Many previous studies have focussed on photosynthetic performance and growth of oak seedlings under mostly controlled, experimental conditions (e.g. Vernay et al. 2016). In contrast, published studies examining naturally regenerated oak seedlings exposed to interspecific competition in forest canopy gaps are rare (Dobrowolska 2008; Diaci et al. 2008; Brezina and Dobrovolny 2011). In addition, findings of these published studies are equivocal with regard to the influence of light availability on oak growth performance (e.g. Brezina and Dobrovolny 2011; Ligot et al. 2013).

Based on the identified knowledge deficits, this study assessed photosynthetic performance and height growth of naturally established sessile oak seedlings growing in fenced small canopy openings. We addressed the following research questions: (1) how do solar radiation availability vary with gap size and location within gap, (2) how do varying solar radiation levels affect the photosynthetic performance of oak seedlings, (3) how does oak height increment vary under differing light conditions, and (4) how does the combined effect of light availability and competing vegetation influence oak dominance within the regeneration layer?

Methods

Study site

The study site is located in the northern part of the German federal state of Baden-Württemberg near the city of Heilbronn (49° 09′ 03″ N, 09° 22′ 49″ E) on a plateau 330 m above sea level. The area has a mean annual temperature of 10.3 °C and annual rainfall averages 860 mm (1981-2010, DWD 2016). Pelosols with a loamy to silty soil structure developed from the prevailing gypsum Keuper. The soils have a moderate water supply (available field capacity is between 50 and 90%) and are characterized by a medium to very high (lower soil horizons) cation exchange capacity and varying acidification (BKG 2016). The potentially natural forest community is mapped as a *Luzulo-Fagetum*, i.e. European beech forest with individual sessile oak trees mixed into the beech matrix (Ellenberg 2009).

All measurements were carried out in 2016. Growing season mean temperature and precipitation in 2016 and during the whole study period (2010–2016) were closely in line with long-term averages (Wetterzentrale 2019).

Based on the overall site characteristics as well as the weather conditions in 2016, we did not consider water and nutrient availability to be growth limiting factors neither during the study period nor in general.

The study site is dominated by approximately 160-year-old and 30 m tall sessile oak trees with an under- and midstory of mainly European beech and some hornbeam. Initially established as coppice with standards, high forest management at the study site started around the beginning of the last century. Total stand basal area prior gap creation was 22 m² ha⁻¹ with 80% oak and 20% European beech. Mean

annual increment (for a reference age of 100 years) at the site is 8 and 9 m³ ha⁻¹ year⁻¹ for oak and beech, respectively.

A heavy acorn mast in 2009 formed a dense oak seedling bank across the entire study site in the following spring. To use this mast event for partial regeneration of the stand, 15 canopy gaps of varying size were created by group selection harvesting in winter 2010/2011. The average distance between margins of neighbouring canopy gaps (edge to edge) was approximately 30 m (min 15 m, max 100 m). Oak seedling density, which was measured systematically around gap centres during the first growing season after the mast year, averaged 24 (0–178) seedlings m⁻². Accompanying tree species consisted mainly of European beech and amounted to 1 (0–13) seedlings m⁻². Oak and beech seedlings were similar in height averaging approximately 20 cm (Van Cleve 2012). Ground vegetation was sparse before gaps were created. Throughout the time of our experiment, concurrence vegetation was left unregulated in all canopy gaps. To prevent browsing, all gaps were fenced in early spring 2011.

Data collection

Gap size and oak growth

Margins of the artificially created forest canopy openings were defined by the position of bordering trees and their crown extension towards the gap centre (Runkle 1984). Hence, gap size was defined as a) canopy gap, i.e. the land surface area directly under the canopy opening and b) expanded gap, i.e. land surface area which extends to the bases of canopy trees bordering the opening (i.e. edge trees). Canopy gap area of the 15 openings studied here varied between 0.05 and 0.2 ha (Table 1).

A north–south-oriented belt transect of four metres in width was positioned in every gap during summer 2016. Circular sample plots with a radius of 2 m were systematically placed within these transects, i.e. the total number of sample pots per transect varied with total transect length. Sample plots were established every four, five, and six metres along gap transects less than 30 m, 30–40 m, and more than 40 m in length, respectively. A total of 159 sample plots were established across expanded gap areas with 70 of these 159 plots located within fenced canopy areas.

Total height and terminal shoot length (including Lammas shoot) of the five tallest oak seedlings in each sample plot were measured in August 2016. Maximum height of competing vegetation including separate measurements for *Rubus* spp. (*R. fruticosus* or *R. idaeus*) as well as height of the tallest competitor among other tree species within a radius of 1 m around each of the five tallest oaks was also recorded. Consequently, a *Rubus* spp. and an accompanying woody species competitor were individually assigned

Table 1 Canopy gap and expanded gap area (m²) as well as orientation and length of the longest gap transect and length of the north–south transect (m) within canopy gap areas

Area (m²)		Orientation	Length (m)	
Canopy gap	Expanded gap	Longest transect	Longest transect	North–south transect
484	962	NW–SE	29	23
504	1175	NE–SW	49	17
549	953	NE–SW	37	24
552	921	NE–SW	39	18
575	1131	NW–SE	40	31
657	1174	E–W	49	15
688	1546	N–S	38	32
705	1277	NW–SE	41	32
747	1383	NE–SW	37	27
756	1433	NE–SW	45	28
780	1253	NW–SE	34	28
932	1540	NE–SW	54	31
1224	1652	NW–SE	56	38
1649	2474	NW–SE	74	47
2143	3127	NE–SW	85	38

to each of the tallest five oak seedlings per plot. If the tallest oak seedling of a plot was superior in total height when compared to its respective *Rubus* spp. or woody species competitor, respectively, the plot was considered to be dominated by oak.

Light conditions

Solar radiation was quantified by evaluating individual hemispherical photographs taken directly above the terminal bud of the tallest oak seedling per plot. For taking photographs, a Canon EOS Digital Rebel XSi reflex camera (Canon, Ota, Tokyo, Japan) equipped with a Sigma 4.5 mm fisheye lens (Sigma, Rödermark, Germany) was used. If the tallest oak was shorter than other accompanying vegetation, additional photographs were taken directly above the vegetation layer in order to quantify radiation availability in relation to gap size and sample plot position within the gap. Transects were divided into same-sized northern, north-central, south-central, and southern sections, respectively, and sample plots assigned accordingly. Using the software WinSCANOPY (Régent Instruments Canada Inc. 2008), indirect site factor (ISF), direct site factor (DSF), and total site factor (TSF) were estimated from each photograph. TSF is the relative amount of incident diffuse radiation (ISF) plus the incident direct radiation (DSF) that penetrates the forest canopy during one growing season (April–September, Vilhar et al. 2014). TSF is thus quantified as the percentage of direct and

diffuse photosynthetic photon flux densities (PPFDs in μmol photons m^{-2} s^{-1}, i.e. photosynthetic active radiation) at the leaf level relative to PPFD under open-field conditions. All hemispherical photographs were taken in early July 2016.

Physiological measurements

Photosynthetic response of net CO_2 gas exchange to PPFD (light response curve) was determined for one randomly selected, fully developed, and undamaged leaf of the upper terminal shoot of a subsample of tallest oak seedlings. Using the infrared gas analysis system Li-6400 (Li-Cor Inc., Lincoln, NE, USA), measurements took place in early July 2016. Sample seedlings were selected with regard to TSF measured above the terminal bud of the tallest oak seedling per plot (see above) which varied between 5 and 74% across the 159 sample plots (Table 2). Dividing the observed TSF range into seven classes of equal width (5–14%, 15–24%, 25–34%, 35–44%, 45–54%, 55–64%, and 65–74%), five tallest oak seedlings from each TSF class were chosen randomly from fenced and non-fenced areas of all gaps. Overall, 35 leaves were evaluated in situ. Before measurements, leaves were wrapped in light reflecting aluminium and optically opaque plastic bags for a minimum of 30 min to create a completely dark and cool environment. Similar to Kuptz et al. (2010), light response curves were developed by measuring leaf gas exchange at PPFDs of 0, 20, 50, 100, 200, 500, 750, 1000, 1250, and 1500 μmol photons m^{-2} s^{-1} emitted by an intra-system light source (6400-02B, Li-Cor Inc., Lincoln, NE, USA) with a minimum time of 3 min between the different radiation levels. The measurements were taken in summer conditions between 10 a.m. and 6 p.m. During measurements, CO_2 concentration was kept constant at 400 ppm, while leaf temperature was maintained near 26 °C (25.9 mean ± 1.5 °C SD) and relative air humidity was maintained around 46% (45.7 mean ± 4.0% SD).

Data analysis

Light response curves for each TSF class were fitted by nonlinear least square regression using the CurveExpert 1.4 software (D.G. Hyams, Starkville, MS, USA) and the Multiple Multiplicative Factor Model (MMF-model, Bazzaz and Carlson 1982):

$$A = \frac{(a \times b) + (c \times PPFD^d)}{(b + PPFD^d)} \tag{1}$$

where A (μmol CO_2 m^{-2} s^{-1}) is assimilation, a, b, c, and d are estimated parameters and PPFD (μmol photons m^{-2} s^{-1}) is photosynthetic photon flux density (see above). Following Kazda et al. (1998), photosynthetic performance was characterized by net CO_2 assimilation at light saturation (area-based photosynthetic capacity A_{max} in μmol CO_2 m^{-2} s^{-1} at 1500 μmol photons m^{-2} s^{-1}) and leaf-level light compensation point (LCP, μmol photons m^{-2} s^{-1}). LCP was determined by solving Eq. (1) for PPFD with A set to zero (see Bazzaz and Carlson 1982; Lüttge and Kluge 2012).

Since most of the data were not normally distributed (tested by Kolmogorov–Smirnov test, $N > 50$), equality of population medians among classes was tested by applying the Kruskal–Wallis H test to compare more than two groups followed by a Mann–Whitney U post hoc test.

To evaluate the impact of solar radiation availability (TSF) on total height and terminal shoot length of oak seedlings, generalized linear models (GLMs) were developed. We used the identity link to connect the linear predictor (explanatory variables) with the expected values of the two gamma-distributed response variables (Zuur et al. 2009). Owing to collinearity between the independent variables TSF and height of competing vegetation, the latter variable was excluded from the models. Maximum likelihood estimation (MLE) was used for parameter estimation. Chi-square test and Wald test were applied to test the significance of the total model and predictor variables. All statistical analyses were performed at $P < 0.05$ and carried out using the software package SPSS 24.0 (IBM Corporation 2016).

Results

Solar radiation availability

Direct solar radiation measured along a north–south transect across the expanded gap area was asymmetrically distributed within canopy openings with significantly higher levels found at northern locations than at southern locations (Fig. 1). Indirect solar radiation was more uniformly

Table 2 Total number of plots and number of fenced plots within expanded gap areas of canopy openings examined in this study sorted by total site factor (TSF, %) class

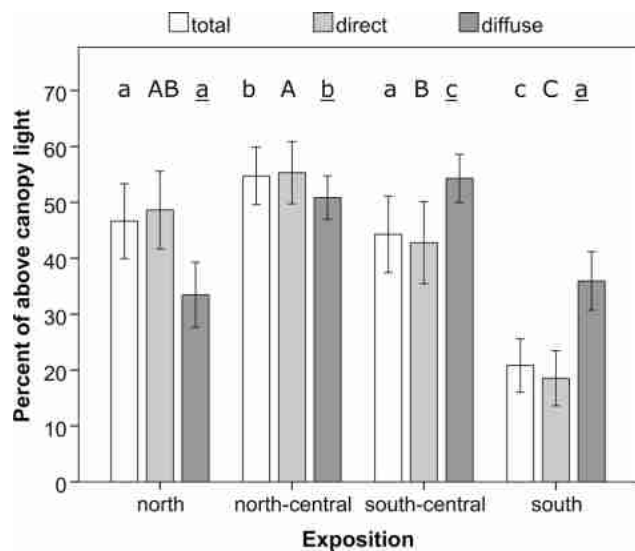| TSF # of plots	5–14	15–24	25–34	35–44	45–54	55–64	65–74
Total	37	29	25	18	20	11	19
Fenced	2	5	13	11	13	9	17

Fig. 1 Average and 95% confidence interval of total (white), direct (grey), and indirect (dark grey) solar radiation levels above the vegetation at various locations within 15 artificial canopy openings of varying sizes quantified using total (TSF), direct (DSF), and indirect site factor (ISF), respectively. Different lower case, upper case, and underlined lower case letters represent statistically significant differences in TSF, DSF, and ISF levels among locations within gaps, respectively
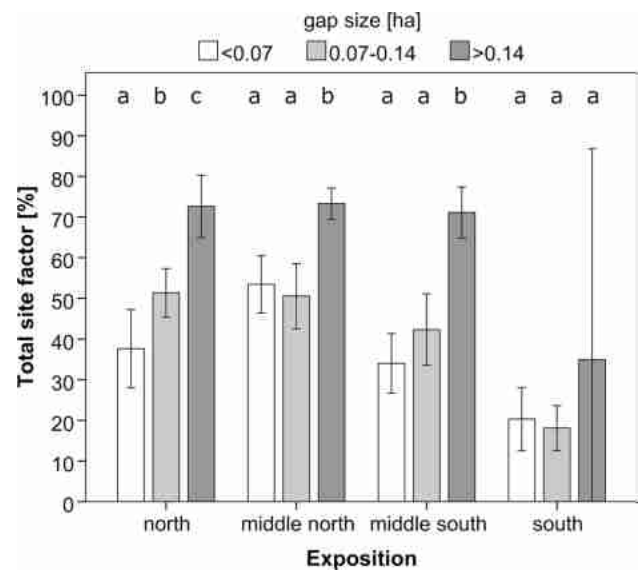

Fig. 2 Average and 95% confidence interval of total site factor (TSF) levels above the vegetation layer systematically measured along north–south transects in 15 artificial canopy openings of varying sizes [< 0.07 ha (white), 0.07–0.14 ha (grey), > 0.14 ha (dark grey)]. Different lower case letters represent statistically significant TSF differences among gap size classes

distributed with highest levels measured around gap centres. Total solar radiation levels (quantified using total site factor TSF) followed the pattern observed for direct solar radiation.

Variation in TSF was greatest in small- (< 0.07 ha) and medium-sized (0.07–0.14) gaps with values along the north–south transect ranging from 6 to 63 and 9 to 65% of open-field conditions, respectively (data not shown). In gaps > 0.14 ha, TSF levels varied between 35 and 75%.

Except in the northern part of the canopy openings, average total solar radiation levels did not significantly differ between gaps < 0.07 and 0.07–0.14 ha in size (Fig. 2). TSF values measured in smaller openings were mainly below 50% of open-field conditions irrespective of location within gap. Significantly higher TSF levels, however, were found in the largest gaps of approximately 0.2 ha. Total solar radiation in larger gaps averaged 70% of open-field conditions across the studied locations with the exception of the southernmost plots.

Photosynthetic performance

Maximum photosynthetic capacity (A_{max}) at a photosynthetic photon flux density (PPFD) of 1500 µmol m^{-2} s^{-1} was slightly positively correlated with TSF ($r = 0.357$,

$p = 0.038$, $N = 35$). Differences in A_{max} between TSF classes were not statistically significant but a trend towards greater A_{max} with increasing TSF was observed (Fig. 3; Table 3). Light compensation points also increased with increasing solar radiation levels (Table 3).

Total height and height growth

Average total height and mean terminal shoot length of the year 2016 of the studied oak seedlings were slightly positively correlated with TSF measured at the terminal bud of each seedling ($r = 0.294$ and 0.487, respectively). Based on the derived generalized linear models, a one per cent increase in TSF resulted in an increase in total height and shoot length of 1.1 and 0.3 cm, respectively (Table 4). Correlation coefficients for the relationship of oak seedling shoot length and ISF as well as DSF ($r = 0.489$ and 0.471, respectively) were comparable to the one for TSF. In contrast, ISF was more strongly correlated with oak seedling height ($r = 0.512$) compared to TSF and DSF ($r = 0.264$).

Despite the positive relationship with TSF in both metrics, total seedling height and shoot length did not significantly differ at TSF levels between 15 and 54% (Fig. 4a, b). In addition, total height and shoot length of the studied oaks substantially decreased at TSF < 15%. Significantly higher averages were, however, found when solar radiation availability exceeded 55 and again 65% (shoot length only) of open-field conditions.
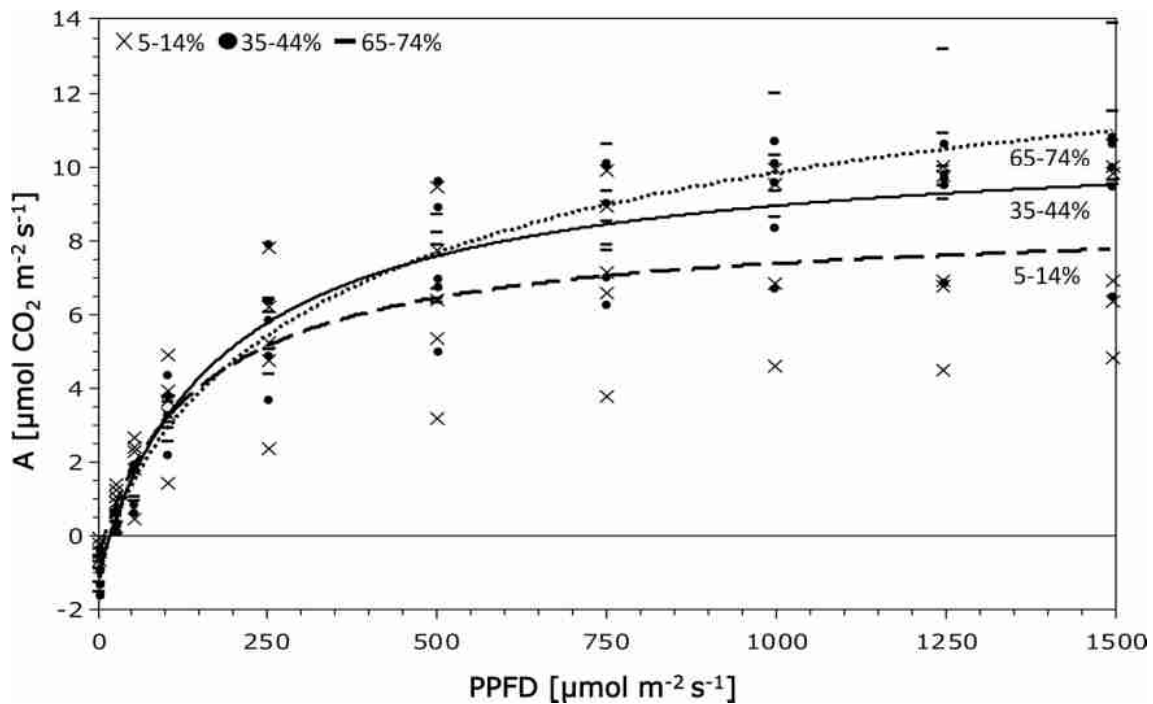
Fig. 3 Modelled light response curves for fully developed leaves of 7-year-old sessile oak seedlings ($N=35$) growing in small canopy openings under varying solar radiation levels quantified using total site factor (TSF, 5–14% dashed line, 35–44% solid line, 65–74% dotted line). Relationships between photosynthetic capacity and photon flux density were found to be very close for all radiation levels; $R^2 = 0.99$

Table 3 Average ($\pm$ standard deviation) maximum photosynthetic capacity (A_{max}, µmol CO_2 m^{-2} s^{-1}) and light compensation point (LCP, µmol PAR m^{-2} s^{-1}) for fully developed leaves of 7-year-old sessile oak seedlings ($N=35$) growing under varying total site factor (TSF, %) levels in canopy openings

TSF	5–14	15–24	25–34	35–44	45–54	55–64	65–74
A_{max}	7.9 ± 2.5	8.8 ± 1.2	8.8 ± 2.8	9.9 ± 1.7	11.0 ± 3.4	9.9 ± 3.5	11.0 ± 1.8
LCP	7.8 ± 4.6	7.3 ± 2.0	9.2 ± 5.6	13.7 ± 5.1	10.8 ± 6.0	13.9 ± 3.5	14.7 ± 1.8

Table 4 Parameter estimates ($\beta, \pm$ standard error) and statistics of generalized linear models for average total height (cm) and shoot length (cm) of the year 2016 of 7-year-old sessile oak seedlings ($N=159$) growing in canopy openings under varying solar radiation levels quantified using total site factor (TSF, %)

Model	β	Wald X^2 value	p value
Height			
Intercept	171.68 ± 18.72	84.14	< 0.0001
TSF	1.09 ± 0.20	28.99	< 0.0001
Shoot length			
Intercept	24.33 ± 3.97	37.51	< 0.0001
TSF	0.3 ± 0.07	19.47	< 0.0001

Competing vegetation and oak dominance

Competing vegetation in study plots consisted mainly of *Rubus* spp. (bramble and raspberry) and individuals of tree species such as European beech, goat willow (*Salix caprea* L.), silver birch (*Betula pendula* Roth), wild cherry (*Prunus avium* L.*),* and European hornbeam. *Rubus* spp. was found on all fenced plots. Early successional tree species were taller than oak at TSF values exceeding 54% of open-field conditions. In contrast, at TSF < 35% only individuals of the shade-tolerant beech and hornbeam were taller than oak. On average, competitors were mostly similar in total height compared to oak. Substantially taller competitors were found at TSF levels above 64% only (Fig. 5). Competition by overtopping understory vegetation and tree species had a detrimental effect on solar radiation availability. Radiation levels above the terminal bud of studied oaks overtopped by competing vegetation averaged only three-fourth of TSF levels measured above the entire vegetation layer. The relative reduction in TSF appeared to increase with increasing
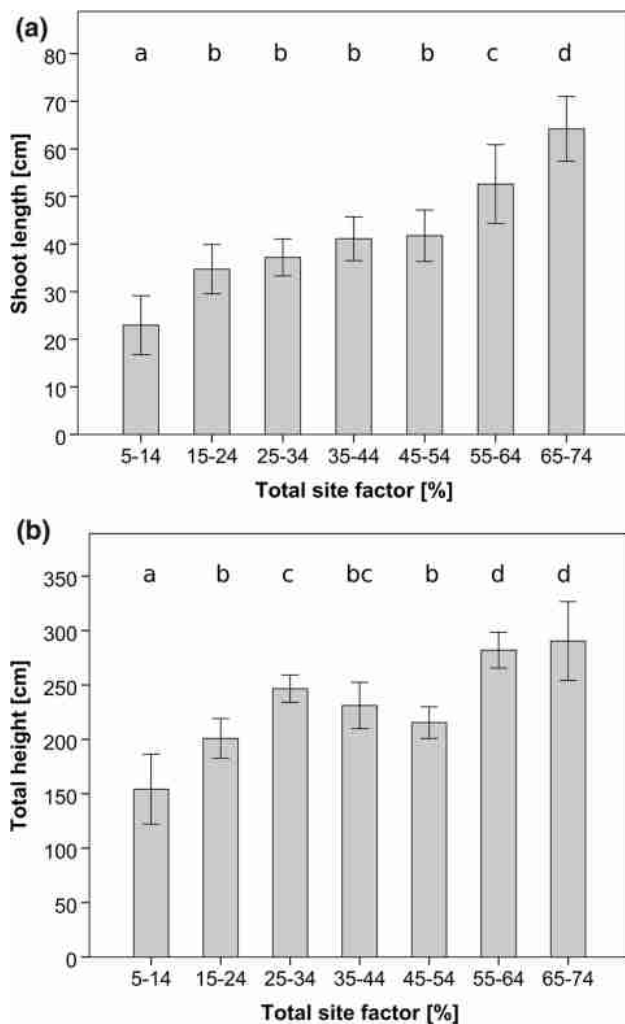
Fig. 4 Length of terminal shoot (**a**) and total height (**b**) of 7-year-old sessile oak seedling growing in small canopy openings under varying solar radiation levels quantified using total site factor (TSF). Bars and whiskers display means and 95% confidence intervals, respectively. Different letters represent statistically significant differences between TSF classes

Fig. 5 Comparison of mean total height of 7-year-old sessile oak seedlings (grey) and competing individuals (white) growing next to each oak seedling as influenced by solar radiation quantified using total site factor (TSF) measured above the vegetation layer. Bars and whiskers display means and 95% confidence intervals, respectively. Different letters represent statistically significant differences between average heights of seedlings and competing vegetation within each TSF class

Discussion

Minimum gap size and optimal gap shape

Findings on the relationship between gaps size and light conditions found in this study were mostly in agreement with similar previous works (e.g. Diaci et al. 2008; Lüpke 2008). TSF levels > 50% of open-field conditions were measured in gaps with a diameter of approximately 45 m from north to south and of at least 0.2 ha in size. Height increment and competitiveness of oak regeneration increased significantly under such light conditions. Because we observed an increase in light availability from south to north within the studied openings, gaps should have a proportionally longer north to south axis as compared to their east–west extent. Similarly, an elliptical gap shape was also recommended by Diaci et al. (2008).

Photosynthetic performance

Variation in and magnitude of photosynthetic capacity (A_{max}) in oak seedlings growing under low and high light conditions as observed in canopy openings of this study were in accordance with previous studies (Terborg 1998; Rodriguez-Calcerrada et al. 2008; Vernay et al. 2016). Similarly, leaf-level light compensation points (LCP) of the studied 7-year-old oak seedlings were comparable to values reported by other authors (Kazda et al. 2004; Ellenberg and Leuschner 2010). Oak LCP values between 10 and 20 μmol

radiation availability, i.e. from 20% reduction on average at TSF < 54% to close to 30 and 40% reduction at TSF > 54% and > 64%, respectively.

Oak dominance, which was determined based on the difference between the tallest oak seedling and the paired tallest individual of a competing species per plot, varied depending on the type of competition examined. Oak seedlings were mostly taller and thus dominant than *Rubus* spp. at TSF > 25% (Fig. 6). In contrast, individuals of accompanying tree species were mostly taller than oaks at TSF levels < 35% and only approximately half the studied plots of 35–64% TSF exhibited oak dominance (Fig. 6). Percentage of plots with oak dominance substantially dropped with TSF levels > 65%.
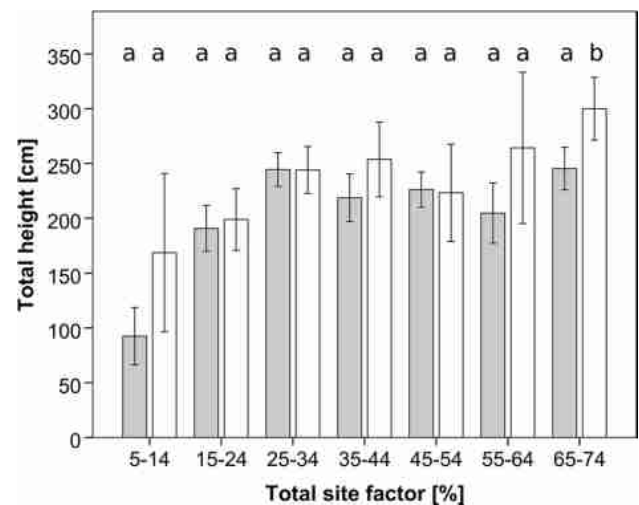
Fig. 6 Number of plots with oak dominance or dominance of competing vegetation by total site factor. Classification was based on the comparison of the tallest oak seedling with the tallest individual of either *Rubus* spp. or accompanying tree species, respectively, of each plot. In addition, average height difference (cm) between the tallest oak seedling and the tallest competitor per plot is provided
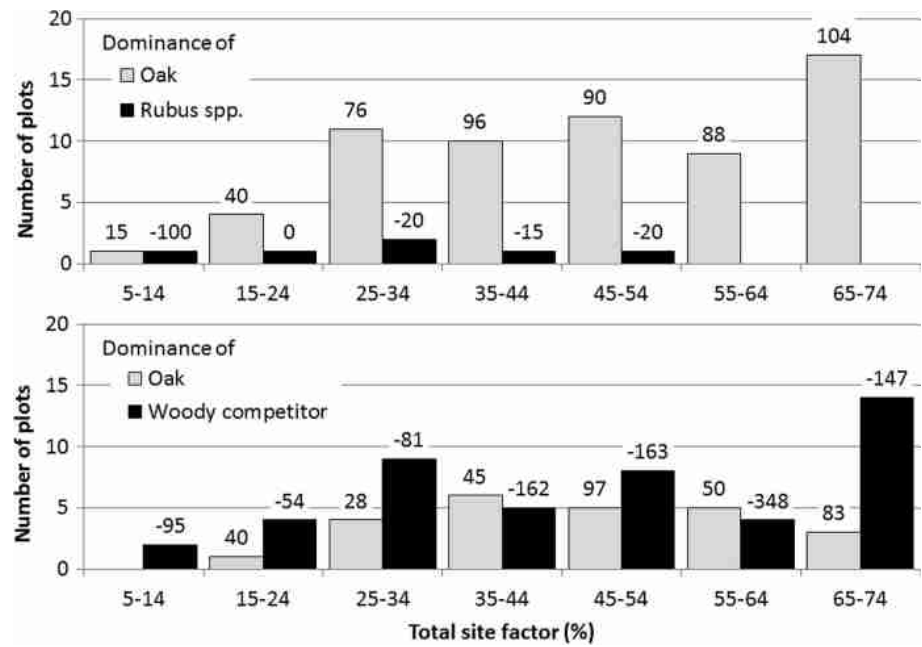
photons m^{-2} s^{-1} as measured here refer to plant species moderately tolerant to shade according to Lüttge and Kluge (2012; see also Niinemets and Valladares 2006). Average A_{max} of oak seedlings growing at lower radiation levels were mostly similar or lower compared to A_{max} values reported in the literature for the more shade-tolerant European beech and European hornbeam (Table 5). However, A_{max} of oak seedlings studied here appeared to increase with increasing light availability at TSF levels > 45% and it surpassed A_{max} of shade-tolerant competitors. Despite this observed trend of increasing A_{max} in oak, shade-intolerant tree species such as *Betula*, *Salix*, and *Prunus* found in larger gaps of this study and thus growing in higher light conditions can exhibit greater A_{max} in comparison with oak (Table 5).

Thus, at all levels of light availability found in gaps, there are companion species that can outperform oaks in terms of photosynthetic capacity.

Total height and height increment

Annual terminal shoot length and total height of studied oak seedling substantially decreased at TSF < 15% but did not differ significantly between studied oak seedling growing at TSF levels between 15 and 54% of open-field conditions. This finding is in agreement with results reported from earlier studies (Lüpke and Hauskeller-Bullerjahn 2004; Brezina and Dobrovolny 2011). This lack of an observed height growth response to increasing light in this range may

Table 5 Leaf-level photosynthetic capacity (A_{max}, μmol CO_2 m^{-2} s^{-1}) measured at specific photosynthetically active radiation levels (PAR, μmol photons m^{-2} s^{-1}) for seedlings of different species varying in shade-tolerance and growing in low (LL) or high light conditions (HL)

Species	Age	Light	A_{max}	PAR	References
Quercus petraea	7	LL	7.9–8.8	1500	This study
		HL	9.9–11.0		
Fagus sylvatica	n.a.	LL	7.9–9.1	800–900	Terborg (1998)
		HL	10.0	800–900	
	2–3	HL	6.0–7.0	~1500	Valladares et al. (2002)
	5–9	HL	7.8	1500	Kazda et al. (2004)
Carpinus betulus	~5	HL	5.0–6.5	1500	Hölscher (2004)
	n.a.	LL	1.7–4.0	1500	Kuehne et al. (2014)
	n.a.	HL	5.7–10.7	1500	
Betula pendula	2	HL	18.0	1000	Oksanen et al. (2005)
	4	HL	12.0	~1350	Oleksyn et al. (1998)
	n.a.	HL	14.5	n.a.	Ellenberg and Leuschner (2010)
Salix caprea	8–10	HL	18.0	1020	Niinemets et al. (2002)
Prunus avium	3	HL	20.0	1700	Centritto et al. (1999)

be explained by a modified resource allocation in oak seedlings. Morphological studies have shown that young oak seedlings allocate disproportionately large amounts of C to belowground biomass at light levels below 50% (Welander and Ottosson 1998; Van Hees 1997). Reduced stem growth was related to substantially higher root/shoot ratios when compared to seedlings growing in more favourable light conditions. Assuming this growth pattern continues and manifests itself over the first several years after germination, the development of a large root system thus might have caused the limited height growth observed in this and other studies.

Contrary to few previous studies, however, TSF levels higher than 50% resulted in further increasing oak shoot length (e.g. Lüpke and Hauskeller-Bullerjahn 1999). The reasons for these contradicting findings are not clear but could be linked to different kinds, and intensities of competition oak seedlings were exposed to in different studies (Brezina and Dobrovilny 2011). Higher total light levels in our small-sized canopy openings strongly correlated with an increased availability of direct solar radiation (Diaci and Thormann 2002). Diaci et al. (2008) and Ligot et al. (2013) were able to show that growth of oak seedlings was specifically responsive to the amount of direct sunlight received. Results of this study on the relationship between seedling attributes and DSF appear not to verify this finding. However, we still found greater growth rates in central and northerly positions within larger gaps of this study likely as a result of higher light availability.

Oak dominance

Light is usually the most growth limiting resource for small trees and seedlings in understories of mature temperate forests with closed canopies (Ellenberg and Leuschner 2010). Increasing understory light levels to foster growth of seedlings and saplings by removing canopy trees, however, improves growing conditions for all understory plants including competing vegetation (Balandier et al. 2012). Forest management therefore aims at carefully manipulating light availability in order to create conditions that favour the desired tree species over others (Röhrig et al. 2006; Wagner et al. 2011).

Depending on the prevailing light conditions, the oaks in canopy openings experienced competition from *Rubus* spp. and shade-tolerant as well as shade-intolerant tree species. Seven years after germination, oak seedlings were mostly taller than *Rubus* spp. Only at radiation levels (TSF) < 25%, *Rubus* spp. appeared to be as competitive as the oak regeneration, i.e. height differences were marginal. However, light levels had to exceed approximately 50% of open-field condition so that height of the tallest oak seedling per plot was always greater than that of adjacent *Rubus* spp. plants. Species of the genus *Rubus* are considered to have a very

high competition potential for tree seedlings (Wagner et al. 2011). Adverse effects of bramble (*Rubus fruticosus* agg.) on oak seedling survival and growth at early stages of shelterwood cuttings in oak-dominated forests have been described in a number of studies (e.g. Harmer et al. 2005; Harmer and Morgan 2007). Besides shading, *Rubus* spp. is known to affect forest regeneration by forming dense thickets that overgrow and eventually press seedlings to the ground under high light and conditions and/or heavy snow (Balandier et al. 2012). At our study site, oak seedlings were able to outgrow and thus establish themselves above the ubiquitous *Rubus* layer if light levels were sufficient. The absence of 'recalcitrant' ground vegetation species (Royo and Carson 2006) at the time of gap creation likely contributed to our finding of oak being mostly dominant over *Rubus* (Ligot et al. 2013; Jensen and Löf 2017). However, and as described recently, successful recruitment of regeneration might not be impacted by *Rubus* cover shortly after canopy opening but may depend on initial tree seedling abundance (Widen et al. 2018). In other studies, a protective effect of *Rubus* spp. against browsing of oak seedlings has been observed (Kelly 2002; Götmark et al. 2011; Jensen et al. 2012). Since the gaps in this study were fenced, this possible interaction between oak seedlings and *Rubus* spp. could not be assessed.

Although direct competition effects were not measured in our study, individuals of accompanying tree species appeared to influence oak growth and dominance to a greater extent than *Rubus* spp. This holds especially true for gap locations with either very low or very high light availability. At lower light levels, individuals of European beech and European hornbeam were taller than oaks confirming findings from several previous studies (Dohrenbusch 1996; Lüpke and Hauskeller-Bullerjahn 2004; Ligot et al. 2013). As a result, one of the two shade-tolerant species constituted the tallest individual seedling on the majority of studied plots with light availability < 35% of open-field conditions. In contrast, early successional species such as willow and birch were substantially taller than oak on plots with very high light availability. Consequently, our findings suggest that at relative radiation levels of close to 50% oak was able to compete with or even outgrow shade-tolerant species while shade-intolerant species were still not competitive enough to dominate the regeneration layer. As a result, about half of the studied plots receiving about half of open-field radiation were dominated by oak, i.e. the tallest woody individual found on a plot was an oak seedling. We found such light conditions only in gaps minimum 0.2 ha in size.

Previous studies reported significantly lower diameter growth in young oaks as a result of weak and moderate competition from early successional tree species (Ammer and Dingel 1997; Wagner and Röker 2000; Petersen et al. 2009). Height growth of studied oaks, however, decreased only with severe competition over a longer time period.

Competition by beech and hornbeam likely imposes stronger growth reduction in oak seedlings as described in earlier studies (Dohrenbusch 1996; Ligot et al. 2013). We therefore argue that conditions found at high light levels in our study are less disadvantageous for oak compared to the ones at low light levels because oak performance was likely less impaired. Tending operations to promote oak survival and growth thus could be delayed in these situations. However, relative reduction in radiation beneath dominant birch and willow trees growing in high light situations in gaps suggest that removal of competing trees is likely necessary within the next few years. A directional shift of the crown centre away from competitors in oak or decreasing annual height increment rates could be early indicators of severe competition by woody neighbours (Wagner and Röker 2000; Rock et al. 2004).

Conclusions and silvicultural implications

This is one of the only few studies documenting successful recruitment of oak in small canopy openings over a moderately long period in managed forests. Over the course of 7 years since the acorn mast in 2009, oak seedlings were able to establish, persist, and often thrive in the fenced forest gaps studied here. Our findings on oak dominance and its light-related assimilation indicate that relative light levels > 50% are most favourable for regeneration of oak stands as the one studied here. Under such light levels, oaks exhibited sufficient competitive strength—especially when compared to the shade-tolerant beech and hornbeam and species of the genus *Rubus*. However, such light levels across the majority of the area in canopy openings were found only in the largest forest gaps of this study. Canopy openings of at least 0.2 ha in size therefore appear necessary to successfully establish natural oak regeneration under the conditions encountered at our research site. Similar recommendations have been given in previous studies (Schütz 1991; Brezina and Dobrovolny 2011, but see Welzenbach 1988; Pisoke and Spieker 1997).

Our findings further corroborate earlier conclusions according to which the mere manipulation of light conditions likely will not result in the long-term survival of regenerated oak, especially when growing in small canopy openings (Lüpke 1998; Ligot et al. 2013). Irrespective of the observed light conditions, similar-sized or taller individuals of accompanying tree species were found close to vigorous oak seedlings. Depending on the prevailing light climate, time since regeneration initiation, and site conditions, individuals of different competing tree species are capable to outgrow, overtop, and eventually suppress neighbouring oaks (Dohrenbusch 1996; Petersen et al. 2009; Ligot et al. 2013). Besides the exclusion of browsing pressure, reduction of interspecific competition by woody species thus appears

to be inevitable to secure a substantial oak component in the regeneration layer in the longer run.

Factors and conditions that either promote or impair oak growth and dominance appear to change over time, i.e. across regeneration and stand development phases (Annighöfer et al. 2015). Thus, our study does not cover a sufficiently long period to provide a reliable assessment of the success or failure of oak regeneration under different conditions of gap size, competition, and light availability. In addition to continuing the monitoring of growth and survival, the influence of competition control on these variables would be important to assess. Also the stability and quality of the young oaks are important variables that should be studied to assess the influence of canopy openings on management goals (Weinreich 2000). At the stand level, vegetation dynamics in areas adjacent to the created gaps should be evaluated to assess their future oak regeneration potential.

References

Ammer C, Dingel C (1997) Untersuchungen über den Einfluss starker Weichlaubholzkonkurrenz auf das Wachstum und die Qualität junger Stieleichen. Forstwiss Centralbl 116:346–358

Annighöfer P, Beckschäfer P, Vor T, Ammer C (2015) Regeneration patterns of European oak species (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) in dependence of environment and neighbourhood. PLoS ONE. https://doi.org/10.1371/journal.pone.0134935

Balandier P, Marquier A, Casella E, Kiewitt A, Coll L, Wehrlen L, Harmer R (2012) Architecture, cover and light interception by bramble (*Rubus fruticosus*): a common understorey weed in temperate forests. Forestry 86:39–46

Bauhus J, Puettmann KJ, Kühne C (2013) Close-to-nature forest management in Europe: Does it support complexity and adaptability of forest ecosystems? In: Messier C, Puettmann KJ, Coates KD (eds) Managing forests as complex adaptive systems: building resilience to the challenge of global change. The Earthscan forest Library, Routledge, pp 187–213

Bazzaz FA, Carlson RW (1982) Photosynthetic acclimation to variability in the light environment of early and late successional plants. Oecologia 54:313–316. https://doi.org/10.1007/BF00379999

Bolte A, Ammer C, Lóf M, Madsen P, Nabuurs GJ, Schall P, Spathelf P, Rock J (2009) Adaptive forest management in central Europe: climate change impacts, strategies and integrative concept. Scand J For Res 24:473–482. https://doi.org/10.1080/02827580903418224

Brezina I, Dobrovolny L (2011) Natural regeneration of sessile oak under different light conditions. J For Sci 57:359–368

Bruciamacchie M, Grandjean G, Jacobee F (1994) Installation de régénérations feuillues dans de petites trouées en peuplement irréguliers. Revue Forestière Francaise 46:639–653

Bundesamt für Kartographie und Geodäsie (BKG) (2016) http://www.geoportal.de. Accessed 10 Nov 2016

Burschel P, Huss J (1997) Grundriss des Waldbaus: ein Leitfaden für Studium und Praxis. Parey, Berlin

Centritto M, Magnani F, Lee HSJ, Jarvis PG (1999) Interactive effects of elevated [CO_2] and drought on cherry (*Prunus avium*) seedlings. II. Photosynthetic capacity and water relations. New Phytol 141:141–153. https://doi.org/10.1046/j.1469-8137.1999.00327.x

Deutscher Wetterdienst (DWD) (2016) www.dwd.de/pub/CDC/observations_germany/climate/multi_annual/mean_81-10/. Accessed 12 Sept 2016

Diaci J (2006) Nature-based silviculture in Slovenia: origins, development and future trends. In: Diaci J, Kotar M, Schuetz JP, Matic S, Piussi P (eds) Nature-based forestry in Central Europe. University Ljubljana, Ljubljana, pp 119–131

Diaci J, Thormann JJ (2002) Ein Vergleich verschiedener Lichtmessmethoden in Buchen-naturwäldern Sloweniens aus verjüngungsökologischer Sicht. Schweiz Z Forstw 153:39–50. https://doi.org/10.3188/szf.2002.0039

Diaci J, Gyoerek N, Gliha J, Nagel TA (2008) Response of *Quercus robur* L. seedlings to north-south asymmetry of light within gaps in floodplain forests of Slovenia. Ann For Sci 65:105. https://doi.org/10.1051/forest:2007077

Dobrowolska D (2008) Effect of stand density on oak regeneration in flood plain forests in Lower Silesia, Poland. Forestry 81:511–523. https://doi.org/10.1093/forestry/cpn025

Dohrenbusch A (1996) Untersuchungen zur natürlichen Verjüngung von Traubeneichen-Hainbuchen-Mischbeständen. Forst und Holz 51:331–339

Ellenberg H (2009) Vegetation ecology of Central Europe. Cambridge University Press, Cambridge

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht, 6. Ausgabe. Eugen Ulmer Verlag, Stuttgart

Frischbier N, Profft I, Arenhövel W (2010) Die Ausweisung klimawandelangepasster Bestandeszieltypen für Thüringen. Forst und Holz 65:28–35

Givnish TJ (1988) Adaptation to sun and shade: a whole-plant perspective. Aust J Plant Physiol 15:63–92

Götmark F, Schott KM, Jensen AM (2011) Factors influencing presence–absence of oak (*Quercus spp.*) seedlings after conservation-oriented partial cutting of high forests in Sweden. Scand J For Res 26:136–145. https://doi.org/10.1080/02827581.2010.536570

Grime JP (1966) Shade avoidance and shade tolerance in flowering plants. In: Bainbridge RG, Evans GC, Rackham O (eds) Light as an ecological factor. Blackwell, Oxford, pp 187–207

Hanewinkel M, Cullmann DA, Schelhaas MJ, Nabuurs GJ, Zimmermann NE (2013) Climate change may cause severe loss in the economic value of European forest land. Nat Clim Change 3:203–207. https://doi.org/10.1038/NCLIMATE1687

Harmer R, Morgan G (2007) Development of *Quercus robur* advance regeneration following canopy reduction in an oak woodland. Forestry 80:137–149. https://doi.org/10.1093/forestry/cpm006

Harmer R, Boswell R, Robertson M (2005) Survival and growth of tree seedlings in relation to changes in the ground flora during natural regeneration of an oak shelterwood. Forestry 78:21–32. https://doi.org/10.1093/forestry/cpi003

Hölscher D (2004) Leaf traits and photosynthetic parameters of saplings and adult trees of co-existing species in a temperate broad-leaved forest. Basic Appl Ecol 5:163–172. https://doi.org/10.1078/1439-1791-00218

IBM Corporation (2016) IBM SPSS statistics version 24. Core system user's guide. Armonk, NY

Jacobee F (2004) Le renouvellement des chênes en futaie irrégulière. Forêt Entrep 155:45–49

Jensen AM, Löf M (2017) Effects of interspecific competition from surrounding vegetation on mortality, growth and stem development in young oaks (*Quercus robur*). For Ecol Manag 392:176–183. https://doi.org/10.1016/j.foreco.2017.03.009

Jensen AM, Götmark F, Löf M (2012) Shrubs protect oak seedlings against ungulate browsing in temperate broadleaved forests of conservation interest: a field experiment. For Ecol Manag 266:187–193. https://doi.org/10.1016/j.foreco.2011.11.022

Kazda M, Wagner C, Pichler M, Hager H (1998) Potentielle Lichtausnützung von *Quercus petraea*, *Fagus sylvatica* und *Acer pseudoplatanus* im Jahr des Voranbaus. Allg Forst Jagdztg 169:157–163

Kazda M, Salzer J, Schmid I, Von Wrangell Ph (2004) Importance of mineral nutrition for photosynthesis and growth of *Quercus petraea*, *Fagus sylvatica* and *Acer pseudoplatanus* planted under Norway Spruce canopy. Plant Soil 264:25–34. https://doi.org/10.1023/B:PLSO.0000047715.95176.63

Kelly DL (2002) The regeneration of *Quercus petraea* (sessile oak) in southwest Ireland: a 25-year experimental study. For Ecol Manag 166:207–226. https://doi.org/10.1016/S0378-1127(01)00670-3

Kuehne C, Nosko P, Horwath T, Bauhus J (2014) A comparative study of physiological and morphological seedling traits associated with shade tolerance in introduced red oak (*Quercus rubra* L.) and native hardwood tree species in southwestern Germany. Tree Physiol 34:184–193. https://doi.org/10.1093/treephys/tpt124

Kühne C, Jacob A, Gräf M (2014) The practice of establishing and tending oak (*Quercus petraea* [Matt.] Liebl., *Q. robur* L.) stands: an interview-based study in the eastern Upper Rhine Plain, Germany. Forstarchiv 85:179–187

Kunz J, Löffler G, Bauhus J (2018) Minor European broadleaved tree species are more drought-tolerant than *Fagus sylvatica* but not more tolerant than *Quercus petraea*. For Ecol Manag 414:15–27. https://doi.org/10.1016/j.foreco.2018.02.016

Kuptz D, Grams TEE, Günter S (2010) Light acclimation of four native tree species in felling gaps within a tropical mountain rainforest. Trees 24:117–127. https://doi.org/10.1007/s00468-009-0385-1

Landeskompetenzzentrum Forst Eberswalde (2009) Waldumbaupotential im Land Brandenburg, Wald im Klimawandel—Risiken und Anpassungsstrategien. Eberswalder Forstliche Schriftenreihe 42:144

Ligot G, Balandier P, Fayolle A, Lejeune P, Claessens H (2013) Height competition between *Quercus petraea* and *Fagus sylvativa* natural regeneration in mixed and uneven-aged stands. For Ecol Manag 304:391–398. https://doi.org/10.1016/j.foreco.2013.05.050

Lüpke BV (1998) Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. For Ecol Manag 106:19–26. https://doi.org/10.1016/S0378-1127(97)00235-1

Lüpke BV (2008) Einfluss unterschiedlicher Hiebsformen auf die Naturverjüngung eines Traubeneichen-Buchen-Mischbestandes. Forstarchiv 79:4–15. https://doi.org/10.2376/0300-4112-79-4

Lüpke BV, Hauskeller-Bullerjahn K (1999) Kahlschlagfreier Waldbau: Wird die Eiche an den Rand gedrängt? Forst und Holz 54:563–568

Lüpke BV, Hauskeller-Bullerjahn K (2004) Beitrag zur Modellierung der Jungwuchsentwicklung am Beispiel von Traubeneichen-Buchen-Mischverjüngungen. Allg Forst Jagdztg 175:61–69

Lüttge U, Kluge M (2012) Botanik—Die einführende Biologie der Pflanzen, 6th edn. Wiley, Weinheim

Newbold AJ, Goldsmith FB (1981) The regeneration of oak and beech: a literature review. Discussion papers in conservation. Univ. College London, London

Niinemets Ü, Valladares F (2006) Tolerance to shade, drought and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecol Monogr 76:521–547. https://doi.org/10.1890/0012-9615(2006)076%5b0521:TTSDAW%5d2.0.CO;2

Niinemets Ü, Aasamaa K, Sõber A, Hartung W (2002) Rate of stomatal opening, shoot hydraulic conductance and photosynthetic characteristics in relation to leaf abscisic acid concentration in six

temperate deciduous trees. Tree Physiol 22:267–276. https://doi.org/10.1093/treephys/22.4.267

Oksanen E, Freiwald V, Prozherina N, Rousi M (2005) Photosynthesis of birch (*Betula pendula*) is sensitive to springtime frost and ozone. Can J For Res 35:703–712. https://doi.org/10.1139/x05-007

Oleksyn J, Karolewski P, Giertych MJ, Zytkowiak R, Reich PB, Tjoelker MG (1998) Primary and secondary host plants differ in leaf-level photosynthetic response to herbivory: evidence from *Alnus* and *Betula* grazed by the Alder Beetle, *Agelastica alni*. New Phytol 140:239–249. https://doi.org/10.1046/j.1469-8137.1998.00270.x

Petersen R, Schüller S, Ammer C (2009) Early growth of planted pedunculate oak (*Quercus petraea*) in response to varying competition by birch (*Betula pendula*) over 8 years. Forstarchiv 80:208–214

Pisoke T, Spiecker H (1997) Eichenwertholz aus ungleichaltrigen Beständen. AFZ - Der Wald 52:208–210

Rock J, Puettmann KJ, Gockel HA, Schulte A (2004) Spatial aspects of the influence of silver birch (*Betula pendula* L.) on growth and quality of young oaks (*Quercus* spp.) in central Germany. Forestry 77:235–247. https://doi.org/10.1093/forestry/77.3.235

Rodríguez-Calcerrada J, Pardos JA, Gil L, Reich PB, Aranda I (2008) Light response in seedlings of a temperate (*Quercus petraea*) and a sub-Mediterranean species (*Quercus pyrenaica*): contrasting ecological strategies as potential of keys to regeneration performance in mixed marginal populations. Plant Ecol 195:273–285. https://doi.org/10.1007/s11258-007-9329-2

Röhrig E, Bartsch N, Bv Lüpke (2006) Waldbau auf ökologischer Grundlage. Eugen Ulmer Verlag, Stuttgart

Royo AA, Carson WP (2006) On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can J For Res 36:1345–1362. https://doi.org/10.1139/x06-025

Runkle JR (1984) Development of woody vegetation in treefall gaps in a beech-sugar maple forest. Ecography 7:157–164. https://doi.org/10.1111/j.1600-0587.1984.tb01116.x

Saha S, Kuehne C, Bauhus J (2017) Lessons learned from oak cluster planting trials in central Europe. Can J For Res 47:139–148. https://doi.org/10.1139/cjfr-2016-0265

Schütz JP (1991) Lässt sich die Eiche in der Kleinlochstellung erziehen? Ein Beitrag zur Mischung von Lichtbaumarten. Deutscher Verband forstlicher Forschungsanstalten, Sektion Ertragskunde

Spellmann H (2001) Bewirtschaftung der Eiche auf der Grundlage waldwachstumskundlicher Untersuchungen in Nordwestdeutschland. Beiträge für Forstwirtschaft und Landschaftsökologie 35:145–152

Terborg O (1998) Die Kohlenstoffassimilation von Rotbuchen und Traubeneichen in einem Mischbestand in der Lüneburger Heide und deren Bedeutung für die interspezifische Konkurrenz. Dissertation, Georg-August-Universität Göttingen

Timal G, Balleux P, Ponette Q (2014) La régénération naturelle des chênes indigènes en Wallonie: état des lieux et expériences réussies. Forêt Wallonne 129:8–18

Valladares F, Niinemets Ü (2008) Shade tolerance, a key plant feature of complex nature and consequences. Ann Rev Ecol Evol Syst 39:237–257. https://doi.org/10.1146/annurev.ecolsys.39.110707.173506

Valladares F, Chico J, Aranda I, Balguer L, Dizengremel P, Manrique E, Dreyer E (2002) The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. Trees 16:395–403. https://doi.org/10.1007/s00468-002-0184-4

Van Cleve J (2012) Natural oak regeneration and vegetation dynamics after group selection harvesting: a case study in southern Germany. Bachelor Thesis. University of Freiburg

Van Hees AFM (1997) Growth and morphology of pedunculate oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) seedlings in relation to shading and drought. Ann For Sci 54:9–18. https://doi.org/10.1051/forest:19970102

Vasconcelos AC (2012) Suitability and Growth of Main Tree Species in Rhineland-Palatinate (Germany) under Climate Change—Integration of Several Assessment Methods. Tagungsband (18) der ForeStClim Final Conference, Liverpool 2012

Vernay A, Balandier P, Guinard L, Améglio T, Malagoli P (2016) Photosynthesis capacity of *Quercus petraea* (Matt.) saplings is affected by *Molinia caerulea* (L.) under high irradiance. For Ecol Manag 376:107–117. https://doi.org/10.1016/j.foreco.2016.05.045

Vilhar U, Roženbergar D, Simončič P, Diaci J (2014) Variation in irradiance, soil features and regeneration patterns in experimental forest canopy gaps. Ann For Sci 72:253–266. https://doi.org/10.1007/s13595-014-0424-y

Wagner S, Röker B (2000) Birkenanflug in Stieleichenkulturen—Untersuchungen zur Dynamik der Konkurrenz über 5 Vegetationsperioden. Forst und Holz 55:18–21

Wagner S, Fischer H, Huth F (2011) Canopy effects on vegetation caused by harvesting and regeneration treatments. Eur J For Res 130:17–40. https://doi.org/10.1007/s10342-010-0378-z

Weinreich A (2000) Qualitätsentwicklung junger Eichen in Bestandeslücken. Dissertation, University of Freiburg

Welander NT, Ottosson B (1998) The influence of shading on growth and morphology in seedling of *Quercus robur* L. and *Fagus sylvatica* L. For Ecol Manag 107:117–126. https://doi.org/10.1016/S0378-1127(97)00326-5

Welzenbach C (1988) Auswirkungen ausgewählter Standortsfaktoren auf die Eichennaturverjüngung in Bestandeslücken. Diplomarbeit, Universität Freiburg

Wetterzentrale (2019): www.wetterzentrale.de. Accessed 20 July 2019

Widen MJ, O'Neil MAP, Dickinson YL, Webster CR (2018) *Rubus* persistence within silvicultural openings and its impact on regeneration: the influence of opening size and advance regeneration. For Ecol Manag 427:162–168. https://doi.org/10.1016/j.foreco.2018.05.049

Ziegenhagen B, Kausch W (1995) Productivity of young shaded oaks (*Quercus robur* L.) as corresponding to shoot morphology and leaf anatomy. For Ecol Manag 72:97–108. https://doi.org/10.1016/0378-1127(94)03482-C

Ziesche TM (2010) Zum ökologischen Gleichgewicht in Eichenwäldern: Der Einfluss struktureller Bestandesfaktoren auf die funktionale Biodiversität. Wissenstransfer in die Praxis. Eberswalder Forstliche Schriftenreihe 44:49–63

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York