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RESEARCH PAPER

Seedling development and regeneration success after 10 years following group selection harvesting in a sessile oak (*Quercus petraea* [Mattuschka] Liebl.) stand

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Abstract

• ***Key message*** **This study showed that regeneration success (presence of oaks ≥ 150 cm in total height) in artificial canopy openings of a mature mixed sessile oak stand was mainly driven by initial oak seedling density.**

• ***Context*** Small-scale harvesting methods as practiced in close-to-nature forestry may disadvantage the regeneration of more light-demanding tree species including sessile oak (*Quercus petraea* [Mattuschka] Liebl.) and thus cause regeneration failure. However, owing to the short-term nature of many previous studies, regeneration success of sessile oak could not be properly ascertained.

• ***Aims*** This study examined oak seedling development over a time period of ten growing seasons in canopy openings of 0.05 to 0.2 ha in size created through group selection harvesting in a mature mixed sessile oak forest in southwestern Germany. We tried to answer the following research questions: (i) how do initial stand conditions relate to and interact with oak seedling density and seedling height growth, and (ii) what are the driving factors of regeneration success under the encountered site conditions.

• ***Methods*** We evaluated the influence of solar radiation, *Rubus* spp. cover, initial oak seedling density, and competition from other tree species on change in density and height of oak seedlings, as well as overall regeneration success (oak seedlings ≥ 150 cm in height).

• ***Results*** Regeneration success increased with initial oak seedling density and solar radiation levels and decreased with early *Rubus* spp. cover. Density and maximum height of oak seedlings was negatively related with competition of other woody species.

• ***Conclusion*** Results of our longer-term study demonstrate that forest management activities to regenerate sessile oak naturally are only successful in stands (i) without advance regeneration of other woody species and without established, recalcitrant ground vegetation, (ii) with a sufficiently high initial oak seedling density in larger patches following mast years, and (iii) where periodic

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monitoring and control of competing woody individuals can be ensured. Our findings further corroborate the view that natural regeneration of sessile oak in small-scale canopy openings is possible in principle.

Keywords Natural regeneration · Forest gap · Canopy opening · Interspecific competition · *Rubus* spp. · Seedling density · Close-to-nature forest management

1 Introduction

Sessile oak (*Quercus petraea* [Mattuschka] Liebl.) is one of the economically and ecologically most valuable hardwood tree species in Central Europe (Brändle and Brandl 2001; Leuschner and Ellenberg 2017). In the context of climate change, the importance, i.e., absolute and relative share in forest cover of sessile oak, are expected to increase in Central Europe (Bolte et al. 2009; Hanewinkel et al. 2013) as the species is relatively storm-resistant (Schmidt et al. 2010) and rather drought-tolerant (Kunz et al. 2018) in comparison with other more common tree species of the region. Across Europe, the close-to-nature forest management (CTFM) paradigm (Diaci 2006) has been advocated as an approach for managing forests to cope with future climate change (Brang et al. 2014). As part of the widespread implementation of the CTFM paradigm in central Europe, forest managers aim at regenerating forests naturally where the dominant tree species are suitable. This is commonly done by applying reproduction methods that avoid the creation of large canopy openings. Small-scale harvesting methods as practiced in CTFM, however, may disadvantage the regeneration of more light-demanding tree species such as sessile oak (Bauhus et al. 2013). Moreover, there is large uncertainty regarding the suitability of small-scale reproduction methods in sessile oak stands which arises from the lack of a holistic understanding of interdependent factors determining regeneration success (Kohler et al. 2015).

Regeneration outcomes using small-scale reproduction methods such as patch and group selection cuttings in oak stands have been rather variable as documented in previous studies (Spellmann 2001; Lüpke 2008
). Competition from woody species and ground vegetation appears to be of great significance for the mid- and long-term establishment of oak and therefore has been identified as one of the main reasons for regeneration failure (Annighöfer et al. 2015; Mölder et al. 2019). Shade tolerant tree species such as European beech (*Fagus sylvatica* L.) or European hornbeam (*Carpinus betulus* L.) can outgrow and eventually outcompete oak regeneration if light levels are unfavorable over a longer time period (Lüpke and Hauskeller-Bullerjahn 1999; Valladares et al. 2002; Ligot et al. 2013). Patch and group selection cuttings do not create light conditions as found after larger-scale shelterwood harvest (Lüpke 1998). However, based on few 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 principle.

Consequently, the silvicultural manipulation of light conditions is of major importance to promote survival and growth of oak seedlings (Röhrig et al. 2006; Diaci et al. 2008). According to Röhrig et al. (2006), following germination 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 to become and remain a dominant component of the tree regeneration layer (Lüpke and Hauskeller-Bullerjahn 2004). In a recent study, for example, sessile oak seedlings performed best at light conditions around 50% of open field levels (Modrow et al. 2020). On plots within gaps exhibiting such conditions, oak was able in many cases to outgrow more shade-tolerant competitors and thus maintain or gain height dominance. Light levels > 50% of open field conditions, however, were only found in canopy openings of at least 0.2 ha in size. However, since light conditions near the ground are highly dynamic following gap formation (Brokaw and Busing 2000; Diaci et al. 2012), one source of uncertainty regarding the conclusions about canopy openings and light levels required for successful oak regeneration has been the short duration of many previous studies.

The aim of this study was therefore to examine the long-term development of sessile oak seedlings in small-scale canopy openings created through group selection harvesting in a mature mixed sessile oak forest after a heavy acorn mast. We evaluated the influence of solar radiation, *Rubus* spp. cover, initial oak seedling density, and competition from other tree species on density and height of oak seedlings and regeneration success defined as presence of oak seedling ≥ 150 cm in height. Using data from a time period spanning ten growing season since regeneration initiation, we tried to answer the following research questions: (i) how do initial stand conditions relate to and interact with oak seedling density and seedling height growth and (ii) what are the driving factors of regeneration success under the encountered site conditions.

2 Material and methods

2.1 Study site

The study site is located in 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). The main soil type is a pelosol with a loamy to silty structure which developed from the prevailing gypsum Keuper. The soils have a moderate water holding capacity (available field capacity is between 50 and 90%) and are characterized by a medium to very high (lower soil horizons) cation exchange capacity (BKG 2016). The potentially natural forest community is mapped as a Luzulo-Fagetum, i.e., European beech forest with individual admixed sessile oak trees (Leuschner and Ellenberg 2017).

The study site is dominated by approximately 160-year-old, 30-m tall sessile oak trees with an under- and midstory of mainly European beech and some hornbeam. Previously managed as coppice with standards, high forest management at the study site started around the beginning of the last century. Total stand basal area prior to gap creation was 22 m^2 ha^{-1} with 80% oak and 20% beech. Site index was estimated from tree height and age using 30 and 35 m of top oak and beech height, respectively, expected at a reference age of 100 years, corresponding with a mean annual increment of 8 and 9 m^3 ha^{-1}, respectively (Landesforstverwaltung Baden-Württemberg 1993). Judging from these site indices, the study site classifies as highly productive with a competitive growth potential of oak in relation to the usually more dominating beech. 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, canopy openings of varying size were created by group selection harvesting in winter 2010/2011 (Van Cleve 2012). The average distance between margins of neighboring canopy gaps (edge to edge) was approximately 30 m (min 15 m, max 100 m). Ground vegetation was sparse before gaps were created. In 2013 and 2017, low-intensity control of competing vigorous and dominant individuals of mostly fast-growing early-successional tree species in the form of snapping or pollarding was carried out. To prevent browsing, all gaps were fenced in early spring 2011. Fences were removed in 2018.

2.2 Data collection

Margins of the artificially created forest canopy openings were defined by the position of bordering trees and their crown extension towards the gap center (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 14 openings studied here varied between 0.05 and 0.2 ha (Van Cleve 2012; Table 1).

Regeneration dynamics were monitored on permanent, square sample plots 1 m^2 in size and systematically established around the center of each studied opening. Sample plots were placed on either side of a north-south transect that ideally split the gap into two equal halves (Fig. 1; Van Cleve 2012). Tree seedling regeneration growing on the permanent sample plots was inventoried at the end of the growing season in 2010, 2012, 2013, 2014, 2015, and 2019. Numbers of individuals per tree species and total height of the five tallest individuals (if present) of each species were recorded per plot. A comprehensive ground vegetation inventory was conducted in summer 2011 with cover (proportion of plot area) and average height recorded for each species including herbs, grasses, ferns, rasp- and blackberry (*Rubus* spp., i.e., *R. idaeus* and *R. fruticosus*), and mosses. A similar inventory was done in 2015, but, given its dominance, only cover and height of *Rubus* spp. was recorded.

Solar radiation was quantified by evaluating individual hemispherical photographs taken directly above the terminal bud of the tallest oak seedling per plot in 2011. Hemispherical photographs were taken with a Canon EOS Digital Rebel XSi reflex camera (Canon, Ota, Tokyo, Japan) equipped with a Sigma 4.5-mm fisheye lens (Sigma, Rödermark, Germany). Using the software WinSCANOPY (Régent Instruments Canada Inc.), direct site factor (DSF), indirect site factor (ISF), and total site factor (TSF) were estimated from each photo. TSF is the relative amount of incident diffuse radiation plus the incident direct radiation 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, while DSF is the percentage of direct PPFD under open-field conditions and ISF is the percentage of indirect PPFD under open-field conditions.

2.3 Explanatory variables

Given the various response variables (see below), a wide array of explanatory variables initially deemed potentially influential was considered. Some of these variables represent and quantify similar factors affecting oak seedling development and thus can be combined and classified into distinct groups including light availability, (initial) oak seedling occurrence and density, as well as competition from (i) seedlings of tree species other than oak and (ii) ground vegetation. We hypothesized that irrespective of the examined response variable, influential predictors would be found in all of these groups.

Table 1 Canopy gap and expanded gap area (m^2), orientation and length of the longest gap transect, and length of the longest north-south transect (m) within canopy gap areas created through group selection harvesting

Area (m^2)		Orientation	Length (m)		TSF (%)	Number of plots
Canopy gap	Expanded gap	longest transect	Longest transect	North-south transect		
484	962	NW-SE	29	23	33 (26–44)	8
504	1175	NE-SW	49	17	50 (26–58)	6
549	953	NE-SW	37	24	48 (41–52)	4
552	921	NE-SW	39	18	49 (39–58)	8
575	1131	NW-SE	40	31	46 (31–56)	8
657	1174	E-W	49	15	36 (25–48)	4
688	1546	N-S	38	32	48 (31–57)	8
705	1277	NW-SE	41	32	38 (27–45)	8
747	1383	NE-SW	37	27	35 (18–51)	8
756	1433	NE-SW	45	28	52 (46–58)	4
932	1540	NE-SW	54	31	57 (43–64)	8
1224	1652	NW-SE	56	38	56 (36–67)	8
1649	2474	NW-SE	74	47	62 (58–65)	8
2143	3127	NE-SW	85	38	56 (6–68)	8

Initial solar radiation is reported as mean (min-max) total site factor (TSF) that was determined on a different number of 1 m^2 plots within canopy openings

Explanatory variables representing canopy openness included size of canopy gap (SIZE, m^2), size of expanded canopy gap (EXPSIZE, m^2), and length of longest north-south transect within canopy gap ($LENGTH_{NS}$, m). Initial growing conditions following gap creating were captured by the variables expressing proportion of plots with oak seedlings in 2010 ($PROP_{2010}$_OAK), proportion of plots with at least ten oak seedlings in 2010 ($PROP10_{2010}$_OAK), proportion of plots with at least 20 oak seedlings in 2010 ($PROP20_{2010}$_OAK), and mean initial seedling density across all plots in 2010 ($meanN_{2010}$_OAK, # m^{-2}). To better capture spatial variability of initial oak seedling density, we further calculated what we termed average opening-level oak seedling density in 2010 ($meanDEN_{2010}$_OAK = $PROP_{2010}$_OAK

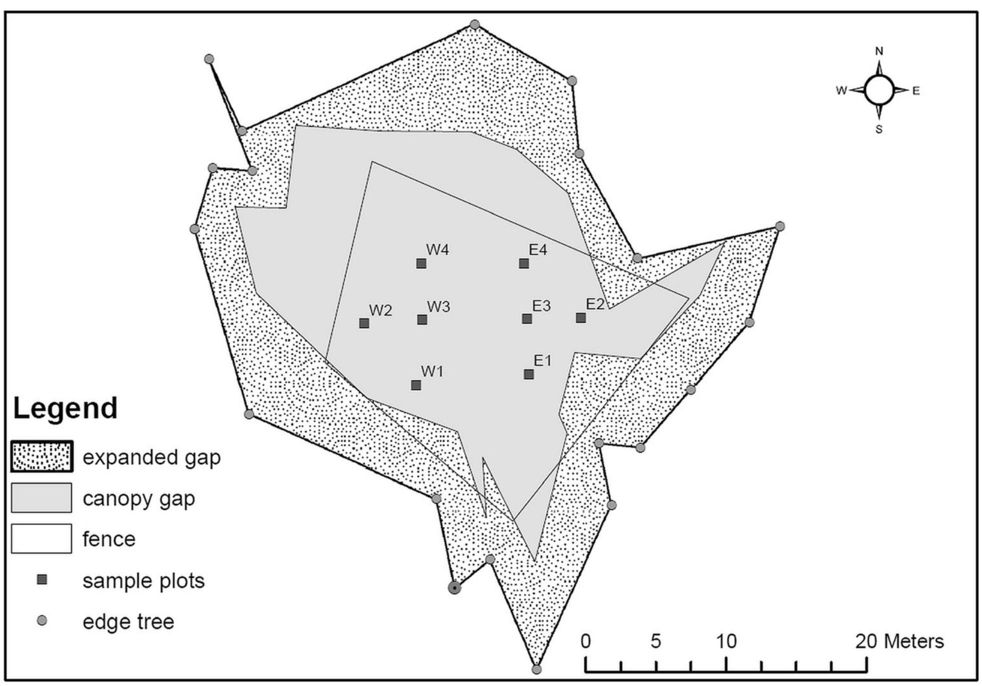

Fig. 1 Example of sample plot layout within individual canopy opening

* $meanN_{2010}$_OAK). Plot-level explanatory variables considered in this analysis included DSF (%), ISF (%), TSF (%), distance to southern canopy edge ($DIST_S$, m), initial oak seedling density in 2010 (N_{2010}_OAK, # m^{-2}), oak seedling density in 2015 (N_{2015}_OAK, # m^{-2}), *Rubus* spp. cover (proportion of plot area) in 2011 (COV_{2011}_RUBUS) and 2015 (COV_{2015}_RUBUS), mean *Rubus* spp. cover of 2011 and 2015 (meanCOV_RUBUS = (COV_{2011}_RUBUS+ COV_{2015}_RUBUS)/2), as well as number of individuals of late-successional tree species in 2010 (N_{2010}_LATE) and number of individuals of early- and late-successional tree species in 2012 (N_{2012}_EARLY, N_{2012}_LATE) and 2015 (N_{2015}_EARLY, N_{2015}_LATE). The variables N_{2015}_EARLY and N_{2015}_LATE were adjusted for potential height differences between oak and individuals of other tree species, i.e., only competitors at least as tall as the smallest of the potentially five tallest oak seedlings of a plot were considered. Similar adjustments were not made for 2010 and 2012 because (i) major height differences between oak and individuals of other tree species were not observed initially and (ii) no tending measures had taken place prior to 2013. We further accounted for competitor height by calculating the sum of heights of early- or late-successional species seedlings per plot, respectively, measured for total height in 2010 ($sumHT_{2010}$_LATE), 2012 ($sumHT_{2012}$_EARLY, $sumHT_{2012}$_LATE), and 2015 ($sumHT_{2015}$_EARLY, $sumHT_{2015}$_LATE). As outlined above, $sumHT_{2015}$_EARLY and $sumHT_{2015}$_LATE were also adjusted for potential height differences between oak and individuals of other tree species. Shading by dominant saplings of early-successional species growing outside the monitored plots was recorded in 2019 ($SHADE_{2019}$). Finally, we used seedling age (AGE, years) as an explanatory variable in models evaluating change in oak seedling attributes over time.

2.4 Response variables

Plot-level COV_$RUBUS_{2011}$ and COV_$RUBUS_{2015}$, oak seedling density (N_OAK), maximum (HT_{MAX}_OAK) and average maximum height of the five tallest oak seedlings of a plot (meanHT_{MAX}_OAK), as well as presence of oaks ≥ 150 cm in total height in 2015 ($PRES_{2015}$_OAK_{150}) and 2019 ($PRES_{2019}$_OAK_{150}) were evaluated in this study. We used a threshold of 150 cm of total seedling height for $PRES_{2015}$_OAK_{150} and $PRES_{2019}$_OAK_{150} because the terminal bud of seedlings of this size is no longer considered of being at risk to be browsed by roe deer. Finally, presence of oak ≥ 300 cm in total height in 2019 ($PRES_{2019}$_OAK_{300}) was also examined in a separate model. A summary of all response and explanatory variables is provided in Table 2.

2.5 Data analysis

We used nonlinear mixed effects modeling (NLME), the function nlme of the package nlme (Pinheiro et al. 2018), and the programming software R (version 3.5.1, R CoreTeam 2018) to study and model potentially influential effects on the examined response variables. Owing to their binary (0/1) or proportional structure (0–1), $PRES_{2015}$_OAK_{150}, $PRES_{2019}$_OAK_{150}, COV_{2011}_RUBUS, and COV_{2015}_RUBUS were modeled by means of a logistic function of the following form:

$$Y = \left(\frac{1}{1 + exp(-(X\beta))}\right) \quad (1)$$

where Y is the response variable and $X\beta$ is the model-specific explanatory variable design matrix with the associated estimated fixed and random parameters (linear predictor function, i.e., linear combination of coefficients (including an intercept) and explanatory variables, Zuur et al. 2009). In contrast, N_OAK, HT_{MAX}_OAK, and meanHT_{MAX}_OAK were modeled with an exponential function of the following form:

$$Y = exp(X\beta) \quad (2)$$

with all variables defined above. The N_OAK analysis was limited to the years 2012, 2013, 2014, 2015, and 2019 because N_{2010}_OAK was used as an explanatory variable.

Canopy opening and canopy opening nested within inventory year were treated as random in the logistic regression and exponential models, respectively, to account for spatial and temporal correlation. Starting with a null model containing an intercept only, explanatory variables were added in a stepwise fashion and retained in the model based on plausibility, significance, and effect on prediction accuracy evaluated using Akaike's information criterion (AIC) and area under the curve (AUC) for the binary response variables, as well as mean absolute bias (MAB, absolute value of observed—predicted) and root mean square error (RMSE) for the proportional and continuous response variables. Because model development aimed at and thus was driven by optimizing model performance, explanatory variables were transformed where appropriate to maximize prediction accuracy. We tested for potential multicollinearity among explanatory variables of a model using the variance inflation factor (VIF), which was quantified using the corvif function in R (Zuur et al. 2009). Variance structures to account for variance heterogeneity (R function varPower, Zuur et al. 2009) were incorporated in the final N_OAK, HT_{MAX}_OAK, and meanHT_{MAX}_OAK models, and residuals of all models were checked for fit and concurrence with model assumptions.

Table 2 Tabular summary of all response and explanatory variables for plots with oak seedlings in 2010

Acronym	Description	Data level	Mean	SD	Min	Max
COV_{2011}_RUBUS	Cover (proportion of plot area) of *Rubus* spp. in 2011	Plot	0.09	0.18	0	0.80
COV_{2015}_RUBUS	Cover (proportion of plot area) of *Rubus* spp. in 2015	Plot	0.48	0.37	0	1
N_OAK	Oak seedling density (# m^{-2})	Plot	13.67	22.14	0	178
$meanHT_{MAX}$_OAK	Average maximum oak seedling height (cm)	Seedling	98.40	81.16	5	550
HT_{MAX}_OAK	Maximum oak seedling height (cm)	Seedling	126.26	100.51	7	550
$PRES_{2015}$_OAK_{150}	Presence of oak seedlings ≥ 150 cm in height 2015	Plot	0.50	0.50	0	1
$PRES_{2019}$_OAK_{150}	Presence of oak seedlings ≥ 150 cm in height 2019	Plot	0.47	0.50	0	1
$PRES_{2019}$_OAK_{300}	Presence of oak seedlings ≥ 300 cm in height 2019	Plot	0.24	0.43	0	1
SIZE	Size of canopy gap (m^2)	Opening	864.75	470.31	483.63	2143.12
EXPSIZE	Size of expanded canopy gap (m^2)	Opening	1490.42	596.25	921.2	3126.83
$LENGTH_{NS}$	Length of longest north-south transect (m)	Opening	29.48	8.62	15	47.30
$PROP_{2010}$_OAK	Proportion of plots with oak seedlings 2010	Opening	0.86	0.19	0.38	1
$PROP10_{2010}$_OAK	Proportion of plots with > = 10 oak seedlings 2010	Opening	0.55	0.30	0.12	1
$PROP20_{2010}$_OAK	Proportion of plots with > = 20 oak seedlings 2010	Opening	0.39	0.27	0	0.75
$meanN_{2010}$_OAK	Average oak seedling density 2010 (# m^{-2})	Opening	25.31	16.55	3.38	51.50
DEN_{2010}_OAK	$PROP_{2010}$_OAK * $meanN_{2010}$_OAK (# m^{-2})	Opening	23.71	16.65	1.94	49.12
DSF	Direct site factor (%)	Plot	47.48	13.48	4.23	68.44
ISF	Indirect site factor (%)	Plot	48.34	8.15	18.99	66.56
TSF	Total site factor (%)	Plot	47.59	12.37	6.15	67.24
$DIST_S$	Distance to southern canopy edge (m)	Plot	14.24	9.62	0	48.70
N_{2010}_OAK	Oak seedling density 2010 (# m^{-2})	Plot	27.79	35.99	1	178
N_{2015}_OAK	Oak seedling density 2015 (# m^{-2})	Plot	7.95	10.94	0	55
N_{2010}_LATE	Density of late-successional tree species seedlings 2010 (# m^{-2})	Plot	1.10	2.25	0	13
$sumHT_{2010}$_LATE	Sum of height measurements, late-successional tree species 2010 (cm)	Plot	18.03	32.01	0	130
N_{2012}_EARLY	Density of early-successional tree species seedlings 2012 (# m^{-2})	Plot	0.24	0.78	0	4
$sumHT_{2012}$_EARLY	Sum of height measurements, early-successional tree species 2012 (cm)	Plot	28.00	105.35	0	729
N_{2012}_LATE	Density of late-successional tree species seedlings 2012 (# m^{-2})	Plot	1.03	2.32	0	15
$sumHT_{2012}$_LATE	Sum of height measurements, late-successional tree species 2012 (cm)	Plot	47.46	83.8	0	289
N_{2015}_EARLY	Density of early-successional tree species seedlings 2015 (# m^{-2})	Plot	0.17	0.59	0	3
$sumHT_{2015}$_EARLY	Sum of height measurements, early-successional tree species 2015 (cm)	Plot	37.33	182.75	0	1300
N_{2015}_LATE	Density of late-successional tree species seedlings 2015 (# m^{-2})	Plot	0.53	1.15	0	5
$sumHT_{2015}$_LATE	Sum of height measurements, late-successional tree species 2015 (cm)	Plot	91.21	220.32	0	1066
$SHADE_{2019}$	Shading by dominant saplings growing outside the monitored plots 2019	Plot	0.10	0.31	0	1
AGE	Seedling age (years)	Seedling	4.2	2.49	1	10

3 Results

3.1 Light conditions and competing woody and ground vegetation

With very few exceptions (shading by advance regeneration of shade-tolerant tree species), DSF, ISF, and TSF values measured in 2011 varied between 25 and 70% of open-field conditions.

Plot-level seedling density of woody species other than oak in 2010 averaged 1.25 (0–13) individuals m^{-2} with a mean height of 22 cm (0–80) and consisted mainly of beech and hornbeam. In 2012, 1 year before the first tending operation of low intensity that sparsely removed individual woody competitors, average seedling density of other woody species remained at 1.25 (0–15) seedlings m^{-2} with plot-level maximum total height of these individuals averaging 98 cm (19–293). In addition to the still dominant beech and hornbeam, goat willow (*Salix caprea* L.) and European ash (*Fraxinus excelsior* L.) were observed in 2012. Density and maximum height of individuals of competing tree species averaged 0.9 (0–7) and 0.4 (0–6) trees m^{-2} as well as 222 (35–525) and 175

(20–420) cm in 2015 and 2019, respectively. In addition, dominant and very vigorous sweet cherry (*Prunus avium* L.) trees were observed in many canopy openings in 2019.

The initially species-rich ground vegetation layer was soon dominated by *Rubus* spp. In 2011, individuals of *Rubus* spp. were found in all gaps and on about half of all studied permanent sample plots, averaging 0.33 in cover and 40 cm in mean height on these plots. In 2015, almost 90% of plots had *Rubus* spp. which averaged 0.55 in cover and reached a mean average height of 110 cm. $PROP_{2010}$_OAK, N_{2010}_OAK, and N_{2010}_LATE had a significantly negative and $DIST_S$ a significantly positive effect on COV_{2011}_RUBUS (Table 1). None of these four explanatory variables were found to be a significant driver of COV_{2015}_RUBUS which significantly decreased with N_{2015}_OAK and $sumHT_{2012}$_LATE (Table 3).

3.2 Oak seedling density

Seventy-eight of the 98 permanent plots had oak seedlings at the end of the vegetation period of 2010. The initial oak seedling density averaged 24 (0–178) individuals m^{-2}. All following results relate to plots with oak seedlings in 2010.

Approximately three quarters of the plots with oak seedlings in 2010 still carried oak seedlings in 2015. The proportion of plots with oak further decreased in 2019 with about half of the initial oak seedling plots still having oaks. Oak seedling density on plots with oaks averaged 10 (1–55) and 5 (1–15) m^{-2} in 2015 and 2019, respectively. With one exception, plots with oak in 2019 were found in all canopy openings.

N_OAK significantly decreased with AGE, COV_{2011}_RUBUS, COV_{2015}_RUBUS as well as $sumHT_{2015}$_LATE and significantly increased with N_{2010}_OAK and DSF (Table 4).

3.3 Oak seedling height

Average HT_{MAX}_OAK on plots with oak seedlings increased from 81 cm (24–163) in 2012 to 176 cm (44–310) in 2015 and to 302 cm (40–550) in 2019. AGE, N_{2010}_OAK, and ISF had a significantly positive effect on $meanHT_{MAX}$_OAK and HT_{MAX}_OAK, while both response variables significantly decreased with increasing COV_{2011}_RUBUS, N_{2012}_EARLY, and N_{2015}_LATE (Table 5, Fig. 2). A significantly negative effect on $meanHT_{MAX}$_OAK was also found for COV_{2015}_RUBUS (Table 5).

3.4 Regeneration success

The number of plots with oak seedlings ≥ 150 cm in total height slightly decreased between 2015 and 2019 from 39 to 37. Seven plots with oaks ≥ 150 cm in total height in 2015 had no such oaks in 2019. Nineteen plots exhibited oaks ≥ 300 cm in total height in 2019. $PRES_{2015}$_OAK_{150} (data not shown) and $PRES_{2019}$_OAK_{150} significantly increased with N_{2010}_OAK and ISF and significantly decreased with COV_{2015}_RUBUS (Table 6, Fig. 3). The loss of oaks ≥ 150 cm in total height from 2015 to 2019 was driven by N_{2015}_OAK and COV_{2015}_RUBUS but not ISF or any other measure of canopy openness (data not shown). In contrast, ISF was a significant driver of $PRES_{2019}$_OAK_{300} as well as COV_{2015}_RUBUS (Table 6). There was no significantly negative effect of individuals of other tree species on oak regeneration success.

4 Discussion

This study evaluated changes in oak seedling density and height as well as overall regeneration success following group selection harvesting in the winter of 2010/2011 to establish a new oak cohort within artificial canopy openings. Our longer-term analysis showed that initial plot-level oak seedling density in 2010 and early occurrence of *Rubus* spp. in 2011 were significant variables explaining presence of oak ≥ 150 cm in total height in 2015 and 2019. In addition, change in overall plot-level oak seedling density over time as well as average height of the five tallest oak seedlings per plot and plot-level maximum oak seedling height were also driven by initial oak seedling density and *Rubus* spp. cover in 2011, pointing to the great importance of initial conditions. Because early *Rubus* spp. cover was significantly influenced by oak seedling density at the plot-level as well as at the canopy opening-level (percentage of plots with oak seedlings in 2010), we argue that initial number of oak seedlings per unit area is most influential for the successful establishment of oak regeneration.

This finding regarding the importance of initial oak seedling density on the regeneration success in managed sessile oak stands is in accordance with other studies and reviews (e.g., Kohler et al. 2015). The most plausible causal explanation is that a high oak seedling density prevents or delays establishment of competing ground flora and woody species. Our findings show that the development of *Rubus* cover was at least retarded by high oak seedling density following opening up the closed tree canopy of the studied mature oak stand. This likely also applies to individuals of early-successional tree species including *Salix* spp. and *Betula* spp. Large numbers of oak seedlings per unit area might also better suppress individuals of more shade-tolerant late-successional species such as beech and hornbeam. Likewise, another study in southern Germany showed that where abundance of oak regeneration was high, European beech regeneration was of low density and vice versa (Annighöfer et al. 2015). This indicates that in addition to resource gradients (niche partitioning), the temporal and spatial stochastic influences on seed dispersal and establishment (chance events) (Brokaw and Busing

Table 3 Parameter estimates (± standard error, SE) and statistics of nonlinear mixed models for *Rubus* spp. cover in 2011 (COV_{2011}_RUBUS) and 2015 (COV_{2015}_RUBUS) observed on permanent sample plots in fenced canopy openings created through group selection harvesting in winter 2009/2010

Variable	COV_{2011}_RUBUS Estimate	SE	*t* value	*p* value	COV_{2015}_RUBUS Estimate	SE	*t* value	*p* value
Intercept	− 3.6516	0.8879	− 4.1126	< 0.0001	0.9328	0.2942	3.1711	0.0021
ln($PROP_{2010}$_OAK)	− 1.9149	0.6404	− 2.9902	0.0037				
ln(N_{2010}_OAK+ 0.1)	− 0.3494	0.101	− 3.4605	0.0009				
N_{2010}_LATE	− 0.2347	0.1129	− 2.0794	0.0408				
ln($DIST_S$ + 0.1)	0.6081	0.2526	2.4075	0.0184				
sqrt(N_{2015}_OAK)					− 0.4185	0.104	− 4.0248	0.0001
sumHT_{2012}_LATE					− 0.0039	0.0016	− 2.3806	0.0196

2000) play an important role for the establishment of oaks and other woody species in gaps of secondary forests of sessile oak (cf. Van Couwenberghe et al. 2013). We further argue that our finding after which *Rubus* spp. cover in 2011 was negatively influenced by initial oak seedling density supports the proposition by Widen et al. (2018) that (persistent) patches of *Rubus* spp. may be better conceptualized as a symptom rather than a driver of inadequate regeneration during the early stages of stand development.

Irrespective of the kind of competing vegetation, intraspecific competition prevails in patches of high oak seedling density and hence more likely results in an oak tree to emerge as the dominant individual from that patch at the end of the highly dynamic early stand initiation phase. Moreover, as intraspecific competition among oak seedlings will often be of lower intensity than interspecific competition (e.g., Saha et al. 2014), more oaks are likely to survive in spots of high oak seedling densities over the first years after regeneration initiation. The significance of initially high plant densities for successful regeneration appears to also hold true for pedunculated

Table 4 Parameter estimates (± standard error, SE) and statistics of the nonlinear mixed model for oak seedling density (N_OAK) observed on permanent sample plots with oak seedlings in 2010 in fenced canopy openings created through group selection harvesting

Variable	Estimate	SE	*t* value	*p* value
Intercept	0.9945	0.2326	4.2754	< 0.0001
AGE	− 0.2180	0.0240	− 9.0903	< 0.0001
ln(N_{2010}_OAK)	0.7595	0.0261	29.1546	< 0.0001
COV_{2011}_RUBUS	− 1.8440	0.4698	− 3.9250	0.0001
COV_{2015}_RUBUS	− 0.8872	0.0872	− 10.1781	< 0.0001
sumHT_{2015}_ LATE	− 0.0003	0.0001	− 2.0674	0.0395
DSF	0.0116	0.0032	3.6096	0.0004

oak (*Quercus robur* L.) plantations as recently reported by Wallraf and Wagner (2019).

Species of the genus *Rubus* are known to be almost ubiquitous and to compete strongly with tree seedlings not just in oak but almost all types of forest stands with open canopies (Wagner et al. 2011). *Rubus* spp. was hardly found at our study site prior to gap creation, yet its cover in 2011 had an adverse effect on all examined oak seedling attributes as well as overall regeneration success. *Rubus* spp. swiftly established and rapidly spread after gap creation and thus was found in all openings already during the first post-harvest growing season. Occurrence, cover, and height of *Rubus* spp. further increased over time and eventually suppressed and outcompeted most other ground vegetation. The significantly negative impact of *Rubus* spp. on oak regeneration attributes found here are in agreement with findings from similar studies (e.g., Harmer et al. 2005; Harmer and Morgan 2007). Besides shading, *Rubus* spp. is also known to affect forest regeneration by forming dense thickets that overgrow and eventually press seedlings to the ground under high light conditions and/or heavy or wet snow (Balandier et al. 2012). Consequently, the absence of competitive ground vegetation which includes *Rubus* spp. was found to be beneficial in a comprehensive study evaluating success factors for oak regeneration (Mölder et al. 2019).

In other studies, a protective effect of *Rubus* spp. against browsing of oak seedlings has been observed (e.g., Kelly 2002; Jensen et al. 2012). Since gaps in this study were fenced, this possible interaction between oak seedlings and *Rubus* spp. could not be assessed. However, we observed ample but heavily browsed oak regeneration in the proximity of the majority of the studied openings, i.e., beneath overstory trees at the gap border. Consequently, owing to widespread detrimental browsing pressure by ungulates (e.g., Ammer 1996), protecting young oak cohorts remains an important management measure in Europe to avoid regeneration failure (Lüpke 1998; Leonardsson et al. 2015). This appears to hold

Table 5 Parameter estimates (± standard error, SE) and statistics of nonlinear mixed models for average height of the five tallest oak seedlings ($meanHT_{MAX}$_OAK) as well as maximum oak seedling height (HT_{MAX}_OAK) measured on permanent sample plots in fenced canopy openings created through group selection harvesting in winter 2009/2010

Variable	$meanHT_{MAX}$_OAK				HT_{MAX}_OAK			
	Estimate	SE	*t* value	*p* value	Estimate	SE	*t* value	*p* value
Intercept	2.4099	0.1136	21.2103	< 0.0001	2.6273	0.1488	17.6585	< 0.0001
ln(AGE)	1.0886	0.0311	34.9991	< 0.0001	1.1636	0.0356	32.6704	< 0.0001
ln(N_{2010}_OAK)	0.1387	0.0099	13.9662	< 0.0001	0.0838	0.0137	6.0993	< 0.0001
COV_{2011}_RUBUS	− 0.4282	0.0774	− 5.5313	< 0.0001	− 0.8418	0.1427	− 5.9005	< 0.0001
COV_{2015}_RUBUS	− 0.1178	0.0305	− 3.8688	0.0001				
N_{2012}_EARLY	− 0.0967	0.0132	− 7.3397	< 0.0001	− 0.0724	0.0245	− 2.9593	0.0033
N_{2015}_LATE^2	− 0.0077	0.0022	− 3.4155	0.0007	− 0.0081	0.0041	− 1.9837	0.0482
ISF	0.0054	0.0020	2.6156	0.0090	0.0070	0.0026	2.6531	0.0084

especially true for small-scale regeneration efforts (Kühne et al. 2014).

Our analyses showed that higher light levels corresponded with higher oak seedling density, improved oak height growth, and enhanced regeneration success but also increased *Rubus* spp. cover. Improved solar radiation as a result of overstory disturbances thus not only promoted individuals of the targeted tree species but all other forest vegetation as well (e.g., Royo and Carson 2006). The adequate manipulation of forest canopy openness to create light conditions that favor oak over other species is therefore a major silvicultural challenge (Diaci et al. 2008; Brězina and Dobrovolny 2011; Annighöfer et al. 2015). Our findings suggest that light levels at the higher end of the solar radiation range found in the canopy openings studied here (Table 1) are more favorable for oak growth and establishment. This is in accordance with a previous study at the same site, which found that oak dominance within gaps was more likely at TSF levels > 50% of open-field conditions (Modrow et al. 2020).

Apparently, direct solar radiation is more important and thus more beneficial for oak growth and establishment than indirect sunlight (Diaci et al. 2008; Ligot et al. 2013). Although our findings on the relative importance of the direct and indirect site factor seem not to corroborate this, we do not think that the results of our case study offer reliable and meaningful insights on the matter (see also Modrow et al. 2020). Instead, a more comprehensive evaluation with a wider variation in site and stand conditions is needed to address this research issue (Modrow and Pyttel 2019).

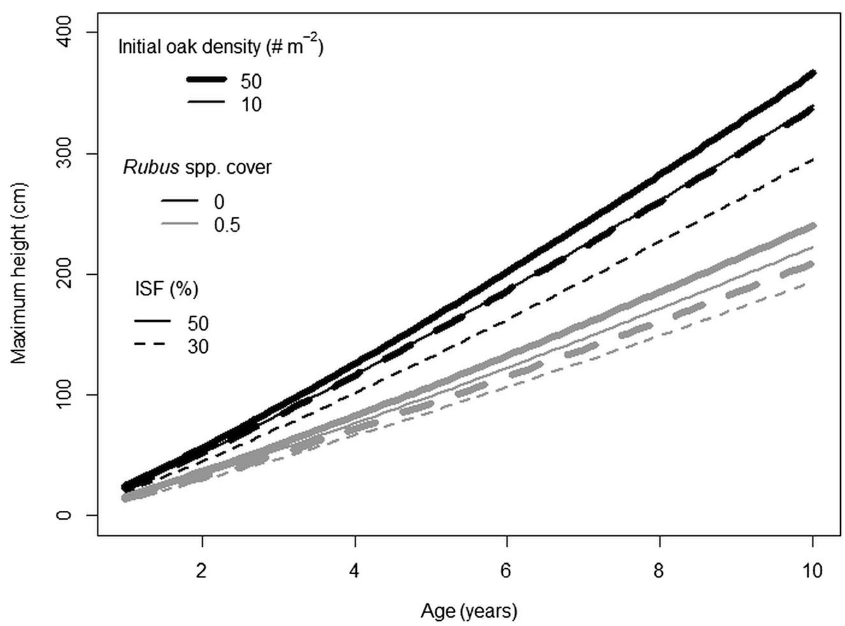

Fig. 2 Modeled maximum oak seedling height over seedling age and as influenced by initial oak seedling density in 2010, *Rubus* spp. cover (proportion of sample plot area) in 2011, and indirect site factor (ISF) on permanent sample plots in fenced canopy openings created through group selection harvesting. Note that density of early-successional species in 2012 (N_{2012}_EARLY) as well as late-successional species in 2015 (N_{2015}_LATE) were set to their means of 0.25 and 0.525 seedlings m^{-2}, respectively

Table 6 Parameter estimates (± standard error, SE) and statistics of nonlinear mixed models for presence of oak seedlings with a total height ≥ 150 cm ($PRES_{2019}\_OAK_{150}$) or 300 cm in 2019 ($PRES_{2019}\_OAK_{300}$) observed on permanent sample plots with oak seedlings in 2010 in fenced canopy openings created through group selection harvesting

Variable	$PRES_{2019}\_OAK_{150}$				$PRES_{2019}\_OAK_{300}$			
	Estimate	SE	*t* value	*p* value	Estimate	SE	*t* value	*p* value
Intercept	− 15.1745	5.1463	− 2.9486	0.0045	− 2.4281	1.5788	− 1.5379	0.1292
$\ln(N_{2010}\_OAK)$	4.9011	1.4985	3.2706	0.0018				
COV_{2015}_RUBUS	− 18.798	5.4507	− 3.4488	0.0010	− 15.497	5.7522	− 2.6941	0.0091
ISF^2	0.0045	0.0016	2.8231	0.0064	0.0018	0.0008	2.2707	0.0267

Although woody competitors of species other than oak were initially snapped and later pollarded during tending operations, they still had a negative influence on the examined oak seedling variables. Potential explanations include (i) time of first tending operation, i.e., the initial tending was conducted in 2013 at a time were individuals of early-successional species in particular had already overtopped oak seedlings, and (ii) tending intensity, i.e., only selected individuals of competing woody species were treated. Early successional tree species also have the potential to rapidly resprout and thus may swiftly regain their competitive advantage. Furthermore, only vigorous and dominant, i.e., prominent seedlings of fast-growing early-successional tree species, were removed in 2013 because individuals of late-successional tree species were mostly fully embedded in the oak seedling matrix and thus neither easily visible nor overtopping.

European oak species including sessile oak, however, are not just highly susceptible to shade from above but also to lateral shading. This might explain why plot-level density of late-successional woody competitors as well as sum of heights of late-successional species seedlings was significant explanatory variables in the derived models explaining oak density and maximum oak height. Interestingly, while density of early-successional species seedlings in 2011 was a significant driver for mean and maximum oak seedling height, it was not found to be influential on oak seedling density. In contrast, density of late-successional species seedlings in 2015 was significantly associated with all three of the aforementioned response variables. This could reflect the lower competitive strength of early- compared with late-successional species (e.g., Saha et al. 2014). In addition, oak seedling density appeared to be less sensitive to shading compared with oak seedling height which in turn has been shown to be less sensitive to shading than oak diameter growth (Ammer and Dingel 1997; Petersen et al. 2009). Since negative competition effects on oak seedling density and height were still found in our study despite the periodic removal of competitors of other woody species, the tending efforts at our study site were presumably much more beneficial than could be assumed based on the mere modeling results (cf. Ligot et al. 2013). The lack

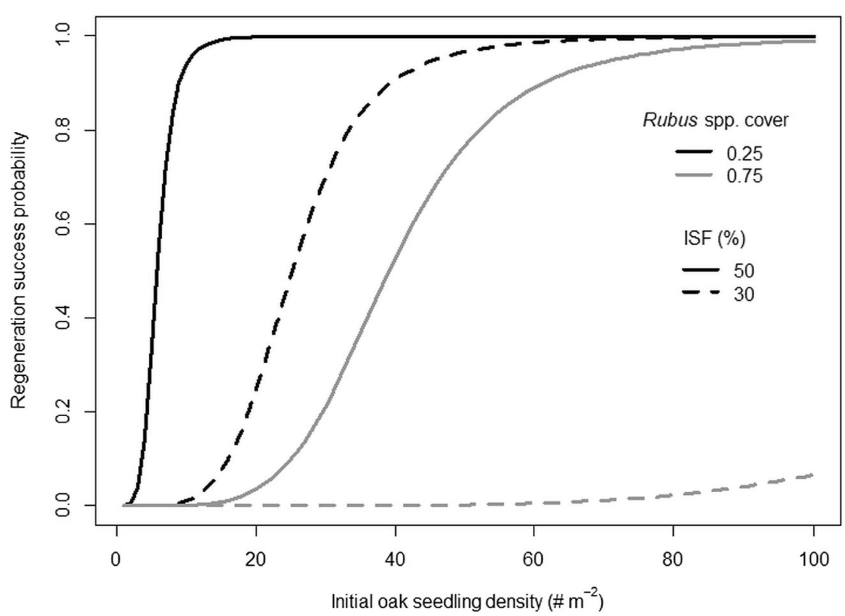

Fig. 3 Probability of regeneration success (oak seedlings ≥ 150 cm in total height in 2019) for permanent plots in artificial canopy gaps created through group selection harvesting in the winter 2010/2011 as influenced by initial oak seedling density, *Rubus* spp. cover (proportion of sample plot) in 2015, and indirect site factor (ISF)

of significantly negative effects of woody competitors on oak regeneration success seems to support this view.

The finding that the presence of oaks ≥ 150 cm in height in 2019 was significantly associated with initial seedling density in 2010 whereas the presence of oak saplings ≥ 300 cm in height in 2019 was not could indicate two potential pathways to regeneration success. Firstly, high initial seedling density retards establishment of severe interspecific competition but leads to intense intraspecific competition which reduces height growth and thus delays development of individual, surviving oak seedlings. Secondly, independent of initial seedling density, sufficiently high light levels may allow oak seedlings to outgrow potential competitors, *Rubus* spp., and individuals of shade-tolerant, late-successional tree species in particular (Modrow et al. 2020).

5 Conclusions and silvicultural implications

To our knowledge, this is the first scientific study that followed oak regeneration success in small-scale canopy openings over a longer period of ten growing seasons. Although this is only a case study conducted at one particular site with very limited potential for generalization, our results contribute to verify widely held perceptions and views among forest practitioners. According to these views, natural regeneration of (sessile) oak, irrespective of the silvicultural approach, will only be successful in stands (i) without advance regeneration of other woody species and without established, recalcitrant ground vegetation (Lüpke 1998), (ii) with a sufficiently high initial oak seedling density in larger patches (Kohler et al. 2015), and (iii) where successive control measures against competing woody specimen can be ensured (Mölder et al. 2019). At the same time, our findings do not conflict with the standpoint that natural regeneration of sessile oak in small-scale canopy openings is possible in principle (Bruciamacchie et al. 1994; Jacobee 2004; Timal et al. 2014). Openings of at least 0.2 ha in size, however, appear necessary at least under the conditions of our study site given the higher and thus more favorable initial light conditions on the ground (Modrow et al. 2020). It resides with forest managers or owners, respectively, to decide whether (i) the rather spotty oak regeneration pattern in the canopy openings as observed here will lead to a sufficiently high future oak proportion and (ii) the resulting potentially modified species composition will provide the goods and services required in the mid- and long-term management objectives. Given proper management, i.e., intensified hunting efforts and careful removal of border trees to enlarge canopy openings, browsed seedlings found outside of the initially fenced in studied openings could add to the present young oak tree bank already established within created gaps. The vigorous, dominant cherry trees found in many canopy openings offer an additional promising management option at the site studied here.

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Data availability The datasets generated are available from the corresponding author on reasonable request.

Compliance with ethical standards

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

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