



On the knowns and unknowns of natural regeneration of silviculturally managed sessile oak (*Quercus petraea* (Matt.) Liebl.) forests—a literature review

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Abstract

• **Key message** This literature review identified the main factors for the success of different silvicultural approaches to regenerate sessile oak naturally and unveiled at the same time important knowledge gaps. Most previous studies were only short-term and restricted to a few factors and single locations. Hence, the findings of these studies are of limited explanatory power and do not allow to develop general, widely applicable management recommendations.

• **Context** Successful natural regeneration of sessile oak (*Quercus petraea* (Matt.) Liebl.) through silvicultural actions depends on a number of biotic, abiotic and management factors and their interactions. However, owing to a limited understanding about the influence of these critical factors, there is great uncertainty about suitable silvicultural approaches for natural oak regeneration, in particular regarding the size of canopy openings and speed of canopy removal.

• **Aims** This study aimed at critically evaluating documented information on natural regeneration of sessile oak. Specifically, we identified (i) the factors that determine the success of approaches for natural regeneration and (ii) evaluated the evidence base associated with different silvicultural approaches.

• **Methods** A comprehensive literature search was done considering relevant peer-reviewed publications of ISI-listed journals as well as non-ISI listed published papers and reports by practitioners. Out of more than 260 collected references, a set of 53 silvicultural ‘core publications’ was identified and analyzed using a catalogue of numeric and categorical evaluation criteria.

• **Results** The most important factors determining regeneration success extracted from the literature were light availability, presence of competing vegetation, initial oak seedling density, browsing of seedlings and intensity of stand tending measures. However, the review revealed also great uncertainty regarding the interactions between these factors and the magnitude of their influence. Most studies were of short duration and restricted to single locations. In only 20% of the experimental studies, the observation period exceeded five years. Total costs of regeneration efforts were quantified and reported in only two studies. This lack of data on the expenses of different approaches to natural oak regeneration appears to be one of the most crucial knowledge deficits revealed in this literature review.

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Contribution of the co-authors

MK has made substantial contributions to the concept of this literature review and the interpretation of results and is the lead author of the manuscript. PP and CK participated in the literature search and interpretation of results and writing. TM supported the literature search and wrote parts of the methods and results sections. JB conceived the study, co-developed the concept and contributed to the interpretation of results and writing.

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• **Conclusion** Natural regeneration of sessile oak may be achieved under a wide range of canopy openings, if competing vegetation and browsing is negligible, seedling density is high and tending to remove competing vegetation is carried out consistently. However, since the silvicultural regeneration success depends on the interactions among these factors, which have often not been adequately considered, we caution against general recommendations for silvicultural systems developed from case studies and call for new long-term studies with comprehensive experimental designs.

Keywords Sessile oak · Light requirements · Competition · Canopy opening · Reproduction method · Silviculture

1 Introduction

Sessile oak (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Q. robur* L.) are among the ecologically and economically most valuable hardwood tree species in Central Europe (Brändle and Brandl 2001; Löf et al. 2016; Mölder et al. 2019a). The two oak species are widely regarded as important components of future mixed-species stands to adapt European forests to climate change (e.g. Frischbier et al. 2010; Jenssen 2009). Since the species are rather drought-tolerant and more storm-resistant compared with other common tree species of the region (Albrecht et al. 2012; Kunz et al. 2018; Schmidt et al. 2010; Zang et al. 2011), their absolute and relative shares in forest cover are expected to increase in Central Europe (Bolte et al. 2009; Hanewinkel et al. 2013).

Oaks form the second most abundant broadleaved tree species group in Germany (Thünen-Institut 2014). However, most oak-dominated forests of the region are of secondary origin, i.e. they stock on sites where European beech (*Fagus sylvatica* L.) forest ecosystems would prevail without human intervention (Ellenberg and Leuschner 2010). In oak forests managed for quality timber, an understorey of shade-tolerant tree species is usually employed to shade the oak stems and thus reduce epicormic sprouting (von Lüpke 1998). A second purpose of this understorey is to inhibit the development of ground vegetation and advance regeneration of shade-tolerant tree species which could be an impediment to the regeneration of oak (Röhrig et al. 2006).

Seedlings of the two oak species are known to be moderately tolerant against shade (Niinemets and Valladares 2006). Admixing the shade-tolerant European beech or common hornbeam (*Carpinus betulus* L.) thus often causes problems when regenerating oak as seedlings of the two former species tend to overgrow and subsequently outcompete oak owing to their greater competitive strength (e.g. Le Duc and Havill 1998; Ligot et al. 2013; von Lüpke and Hauskeller-Bullerjahn 1999). This is particularly relevant for natural regeneration of oak, which is more prominent in *Q. petraea* than in *Q. robur*. Consequently, efforts to regenerate oak stands naturally often fail and there is uncertainty about suitable silvicultural approaches among forest managers (Kuehne et al. 2014a).

Only a small proportion of oak forests in Central Europe is of natural origin. For example, a recent study found that about

90% of a large sample of nearly 300 young oak stands assessed in Central and north-western Germany were established by artificial regeneration such as planting or seeding (Mölder et al. 2019b). Natural regeneration of oak is more common in France and Belgium (e.g. Jacobée 2004; Timal et al. 2014). It is more frequently practised in *Q. petraea* than in *Q. robur* because the former is grown on drier and warmer sites with acidic soils that support less competitive vegetation than at the more fertile and moist sites, where the latter is typically grown (Röhrig et al. 2006). Nevertheless, the two species can also occur in mixture, often without obvious differences in growth rate and timber quality (Collet et al. 2017; von Lüpke 1998). These two temperate European oak species are now being regarded as part of a syngameon which is characterised by hybridisation and introgression among the closely related oak species (Cannon and Petit 2020). While the species retain some level of interfertility, the potential for inter-species gene flow is greatly reduced in comparison to intra-species gene flow, facilitating persistence of each constituent species (Cannon and Petit 2020). Therefore, the two oaks constitute different taxa that occupy partially different ecological niches with a large overlap in soil pH and climatic conditions of sites (Höltken et al. 2012; Neophytou et al. 2010; Reutimann et al. 2020; Leroy et al. 2020).

This review focusses on *Q. petraea*, which occupies, when compared with *Q. robur*, somewhat more acidic and drier soils (Eaton et al. 2016). It is in particular for these site conditions, where natural oak regeneration from seed is comparatively more competitive than on nutrient-rich and moist sites with vigorous ground vegetation, that silvicultural systems based on natural regeneration have been developed.

Despite the issues associated with its implementation in mature *Q. petraea* stands, natural regeneration offers numerous advantages over artificial regeneration through planting. Besides the preservation of autochthonous genetic diversity (Burczyk et al. 2006), successful natural regeneration allows for natural selection from a vast number of individuals and facilitates the formation of undisturbed root systems (Nörr and Baumer 2002). Still, a wider use of natural regeneration appears to be hampered by a number of factors found in mature *Q. petraea* stands. These include an advance regeneration of shade-tolerant woody species, scarcity of heavy acorn crops (so-called mast years), presence of competition from ground

vegetation and the costly requirement to protect seedlings against browsing (von Lüpke 2008; Röhrig et al. 2006; Timal et al. 2014).

While regenerating *Q. petraea* in smaller canopy openings seems to be possible in principle (Dobrowolska 2008; Jacobée 2004; Timal et al. 2014), small-scale reproduction methods such as patch and group selection cuttings have often led to a failure in the long-term establishment of *Q. petraea* seedlings (von Lüpke 2008; Spellmann 2001). Only few studies have reported on efforts to regenerate sessile oak naturally in small patches (Bruciamacchie et al. 1994; Pisko and Spiecker 1997) with some of them mentioning detrimental effects on the quality and stability of young oaks (Keller 1990; Schütz 1991) and others pointing to strong competition by other plants in the ground vegetation (von Lüpke and Hauskeller-Bullerjahn 1999; Schürg 2013). Hence, traditional shelterwood systems with comparatively short regeneration periods at the scale of forest stands are often recommended (e.g. Landesbetrieb Forst 2014) and are currently the prevailing approach used for natural regeneration of sessile oak stands (Kuehne et al. 2014a; von Lüpke 1998).

Shelterwood systems applied in oak forests typically remove all mature oaks (as well as the shade-tolerant understorey) except habitat and veteran trees within a relatively short time period (< 10 years). Such approaches, however, are increasingly criticised particularly by stakeholders from nature conservation agencies and NGOs (e.g. Jedicke and Hakes 2005; Stahl-Streit 2004). To preserve habitat continuity associated with old oaks as a means to conserve and protect species diversity, it has been suggested to manage oak stands according to potentially modified historical silvicultural systems such as coppice with standards (Löf et al. 2016; Mölder et al. 2019a). Such traditional management efforts likely increase stand openness and create transitional habitats that provide suitable oak regeneration niches (cf. Bobiec et al. 2018). Harvest systems with extended cutting cycles that allow for longer stand-level regeneration periods, for example in the form of canopy openings of less than 0.3–0.5 ha (e.g. ML and MU 2018), would be another management approach that allows for the preservation of mature oak stand structures while in theory creating conditions suitable for natural oak regeneration. Such small-scale reproduction methods are often being regarded as more close to nature according to this management paradigm, which derived many of its principles from observation of natural stand dynamics in forests of other species such as European beech (Bauhus et al. 2013). However, uncertainties regarding the success of such small-scale operations remain. In particular, the question of shape and minimum size of canopy openings for establishing a new oak cohort has been repeatedly studied and debated, possibly owing to the lack of robust evidence (e.g. Diaci et al. 2008; Modrow et al. 2020).

In summary, it appears that a number of factors have a critical influence on the success or failure of silvicultural approaches to regenerate *Q. petraea* naturally (e.g. Mölder et al. 2019b; Watt 1919). These factors include prevailing site conditions, microclimate including late frost and light availability, competition by accompanying vegetation and browsing pressure. However, a systematic literature review of these factors across various sites and silvicultural approaches has not been carried out. Based on a comprehensive literature search and the subsequent evaluation of papers deemed meaningful, this study did not aim to derive explicit management recommendations on the silvicultural manipulation of regeneration processes in oak stands but tried to appraise whether there is sufficient scientific evidence that would allow such conclusions. Thus, the supporting objectives were (i) to identify the factors that determine the success of silvicultural approaches to regenerate sessile oak naturally and (ii) to evaluate the evidence base associated with these different silvicultural approaches to establish sessile oak.

Owing to the ecological and economic significance of mature Central European oak woodlands as well as the widespread efforts to preserve such ecosystems, this study focusses on regeneration efforts in silviculturally managed, secondary sessile oak forests where successful natural regeneration is crucial and highly desired and actively pursued. Thus, the term ‘successful oak regeneration’ is defined from a silviculture perspective in the sense that stem density and quality of oak regeneration should be sufficient to form oak-dominated stands with high shares of quality timber.

We therefore did not review literature on issues related to the general regeneration ecology of oaks and how humans may have altered oak regeneration potential at the greater landscape level over centuries as has been done in previous studies (e.g. Bobiec et al. 2018; Reif and Gärtner 2007). Given the greater application of natural regeneration measures due to better prospects of success, this study also focusses on sites where sessile oak is assumed to be the prevailing oak species owing to the species lower resource requirements (Collet et al. 2017). As outlined above, however, owing to the fact that the two species (*Q. petraea* and *Q. robur*) are part of a syngameon (Cannon and Petit 2020) and can also occur in mixtures (e.g. Collet et al. 2017), some results in publications and reports evaluated here may not have been based exclusively on observations of sessile oak. In most studies evaluated here, the oak species were identified based on morphological traits.

2 Methods

2.1 Literature search

The literature search followed a multi-step procedure. First, the literature databases ‘Google Scholar’, ‘Web of Science’,

'Forestry Compendium' and 'Cabdirect' were searched with a fixed set of search terms. These databases and search engines mostly comprise peer-reviewed publications of ISI-listed journals. Search terms used to identify potential documents were entered in English, German and French. However, German and French terms only led to some findings in 'Google Scholar'. The base search query had the following syntax: ('sessile oak' or '*Quercus petraea*') and 'regeneration'.

As the next step, the term 'regeneration' was varied and entered as either 'natural regeneration', 'artificial regeneration', 'planting' or 'sowing'. Additionally, the term 'regeneration' of the above-mentioned base search query was also replaced by 'seedling', 'sapling', 'establishment', 'light', 'shade', 'regeneration ecology', 'silviculture', 'clearcut', 'shelterwood', 'partial harvesting', 'small-scale' or 'gap'. The cut-off date for studies considered was December 31, 2019.

In addition to the online searches, non-ISI-listed published papers as well as reports by practitioners written in German or French were collected by reviewing (i) tables of contents of selected journals from Austria, Belgium, France, Germany, France and Switzerland and (ii) text book contents (Table 1). We focussed on these countries as the natural regeneration of sessile oak has a certain tradition in these Central European countries.

The above-mentioned search terms of the online queries were also applied in the manual search. In addition, reference lists of potential contributions were browsed for theses and dissertations on the topic. Furthermore, unpublished reports on experimental trials and expert opinions were also identified and the authors asked for a copy of the respective documents.

All relevant references were compiled in the reference management and knowledge organisation system CITAVI (Swiss Academic Software GmbH). Publications that did not (fully) meet the search criteria but considered significant background knowledge were also added to the database. All references were classified according to the following descriptors: type of publication (peer-reviewed or not peer-reviewed), origin of information (experiment, expert knowledge or literature review), country, region, location or name of experiment

and oak species. A total of more than 260 references were filed.

2.2 Examination of silvicultural core publications

Out of all the collected references, a set of 53 silvicultural 'core publications' were selected. A core publication was defined as an experimental study or expert review on the natural regeneration of sessile oak under simultaneous consideration of a silvicultural approach for light control (search terms such as 'harvest', 'silvicultural system', 'canopy closure' or 'light'). To specify and classify these silvicultural core publications, a catalogue of numeric and categorical evaluation criteria was developed. Furthermore, these evaluation criteria were assigned to eight major subjects, namely experimental design, initial stand conditions (prior harvest/initiation of regeneration), site conditions, regeneration method, light availability (on forest floor, at regeneration layer), competition, stand tending expenses and regeneration success. The complete list of all evaluation criteria is provided in Annex 1.

The data extracted from these core publications based on the aforementioned evaluation criteria catalogue were entered into a MS Access database. Findings and information of individual studies published in several documents were collected and subsequently compiled as a single database entry. In addition, core publications were further assigned a degree of evidence (scientific reliability) using a rating scheme modified after Binkley and Menyailo (2005) (Fig. 2). All core publications are listed in Table 2 (Annex 2).

3 Results and discussion

3.1 Examination of silvicultural core publications

3.1.1 Type of publication, confidence level and study duration

More than half (28) of the 53 core publications were not peer-reviewed (Fig. 1) and around half of them came from

Table 1 List of Germano- and Francophone journals and text books reviewed for contributions on the natural regeneration of sessile oak. Cut-off date for studies considered: 31 December 2019

| Germanophone journals | Francophone journals and text books |
|--|--|
| <i>AFZ-Der Wald</i> | <i>Forêt entreprise</i> |
| <i>Der Forst- und Holzwirt</i> | <i>Forêt Wallonne/Forêt Nature</i> |
| <i>Forst- und Holz</i> | <i>Revue forestière française</i> |
| <i>Forstarchiv</i> | <i>Annales des Sciences Forestières*</i> |
| <i>Forstw. Centralblatt</i> | <i>Guide silviculture- Chenais atlantique</i> |
| <i>Schweizerische Zeitschrift für Forstwesen</i> | <i>Guide silviculture- Chenais continentales</i> |
| <i>Centralblatt für das gesamte Forstwesen</i> | |

**Annales des Sciences Forestières* already has been an ISI-listed journal when published in French

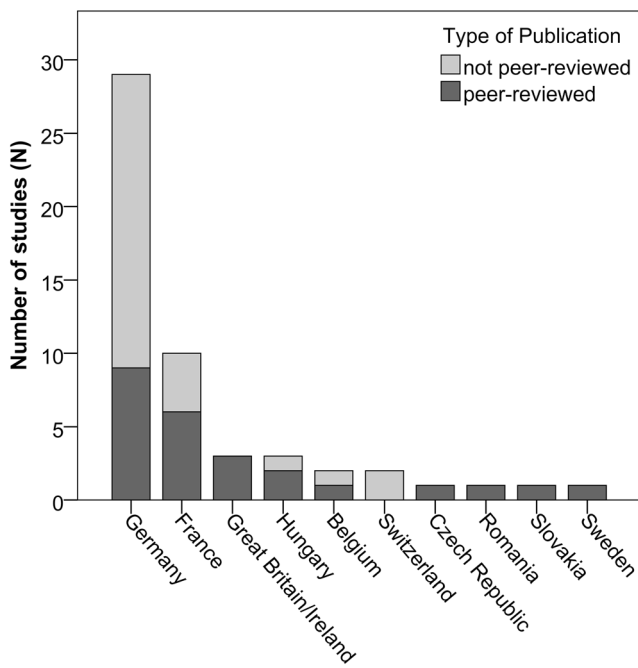


Fig. 1 Number of not peer-reviewed and peer-reviewed core publications about the regeneration of sessile oak by country

Germany with about 70% of these German papers being not peer-reviewed.

Thirty-eight of the 53 core publications were derived from experimental trials, and the 15 remaining papers were classified as documented expert knowledge (summarised findings of surveys and interviews, expert opinions, field excursion reports) or literature review. Following the modified ranking scheme after Binkley and Menyailo (2005), these 15 papers were of the lowest evidence level (Fig. 2; see also the cross table of all core publications in Annex Table 2).

Low or medium evidence (level 5 and 4, respectively) was assigned to 23 publications, while 13 papers were of evidence level 3, i.e. replicated experiments at several sites with no formal a priori plan for extrapolating to the population. Only two papers, namely Götmark et al. (2011) and Ligot (2014), were assigned to the second highest evidence level. Studying up to 25 different experimental sites in uneven-aged forests in southern Sweden, Götmark et al. (2011) examined the effect of canopy cover and competing vegetation on the natural regeneration of sessile and pedunculated oak, but most of the measurements were taken for the latter species. Ligot (2014) studied growth dynamics in mixed young stands of sessile oak and European beech under varying levels of canopy closure at 27 different sites located in the Belgian Ardennes. These two publications of the second highest evidence level studied oak regeneration at a regional level. Not a single paper of the core publications could be assigned to the very strong evidence level 1 (Fig. 2).

Another significant aspect of the experimental design is the study duration. The majority, i.e. about 75% of those 38 core

publications which were based on experiments, collected data over a limited time period of either 1 to 2 or 3 to 5 years, respectively (Annex Table 2). That does mean that oak regeneration was observed from seed fall until the end of the first, second, third or fifth year after establishment. These studies may be regarded as ‘snapshots’ of development of regeneration in a particular year/period of development. Study duration exceeded 5 years only in circa 15% of these experimental studies. The longest study monitored sessile oak regeneration in an Irish national park over 25 years (Kelly 2002). In addition to these experimental studies of varying duration, four papers used a retrospective approach to examine regeneration dynamics over longer periods lasting up to several decades (Bilke 2004; Bruciamacchie et al. 1994; Nutto 1998; Pisoke and Spiecker 1997).

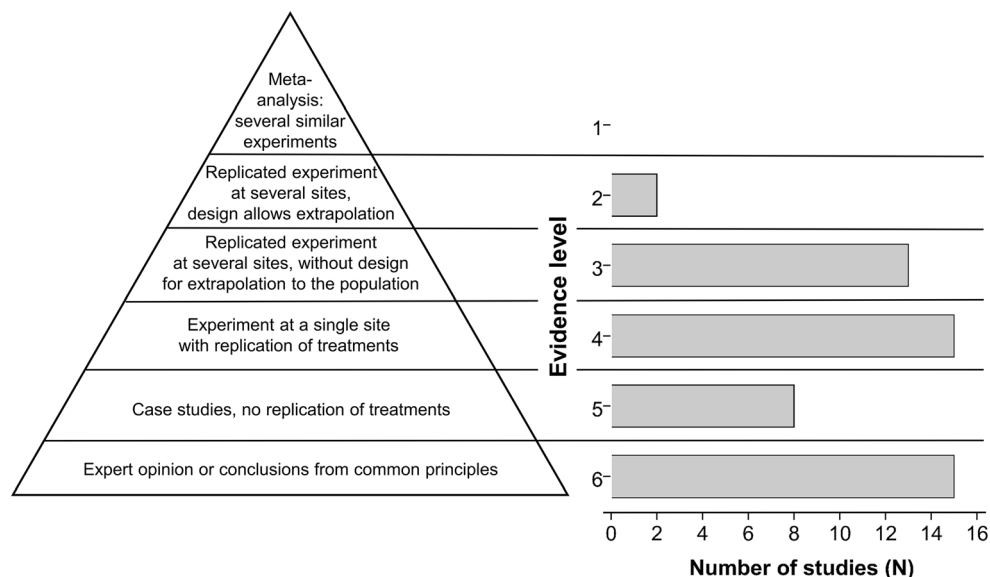
3.1.2 Initial stand conditions

Information on the initial stand conditions prior to or just at the beginning of oak regeneration initiation varied substantially across the studied core publications derived from experimental trials. About three-quarters of these papers lacked qualitative or quantitative data on the condition of the regeneration layer before commencement of canopy opening through removal of understorey and overstorey trees. Important silvicultural indicators such as stand age and basal area per unit area were reported in 52% and 25% of the publications derived from experimental trials, respectively. Only about one fourth of these papers described conditions highly relevant to oak establishment and regeneration success such as canopy closure and/or stocking level. Approximately two-thirds of the experimental studies provided general information on the prevailing site conditions including mean annual temperature and precipitation as well as parent material, while details such as forest floor conditions and base saturation were mentioned in only 40% of the experimental studies.

3.1.3 Silvicultural systems

The majority, namely 45 of the core publications, mentioned the implemented regeneration method and/or the applied type of (regeneration) felling (see the cross table of all core publications in Annex Table 2). Twelve references studied classical shelterwood systems, while 17 papers reported on regeneration success under group selection felling and three under single-tree selection felling. Another eight references compared two or more different types of felling. Five references addressed also the suitability of natural gap dynamics. Specific details on the size of the canopy opening(s) were provided in half of the papers with the majority of these studies analysing artificial canopy gaps of 0.1 to 0.3 ha in size. Other information on the harvest operation(s) associated with the regeneration effort such as the number of harvest entries

Fig. 2 Number of core publications on the natural regeneration of sessile oak by evidence level (from 6 = weak to 1 = very strong) according to a ranking scheme modified after Binkley and Menyailo (2005)



(e.g. removal cuts, gap enlargement fellings), length of regeneration period and shape and exposition of created canopy opening(s) were found in fewer than a quarter of the publications.

3.1.4 Light environment

About two-thirds of the experimental studies described in core publications quantified light availability to young trees (Annex Table 2). The way the topic has been addressed and discussed in these papers suggests that many authors perceived light availability as the most decisive factor for the success of regeneration. However, measurement details necessary to derive minimum light requirements for oak seedlings and saplings from the experimental findings have been rarely presented. Only 35% of these publications reported at what height above ground or above the regeneration layer or in relation to oak height light measurements were taken. This is of particular significance in case that oak regeneration is overgrown and suppressed by other vegetation, and measured light levels, thus, do not represent light availability for the cohort of oak seedlings or saplings. The relationship between light availability and height growth of oak was assessed in 50% of the experimental studies described in core publications (Annex Table 2).

3.1.5 Oak regeneration

Oak regeneration density and height was quantified in ca. half of the experimental studies. Average initial oak seedling density 1 to 2 years after seed fall varied greatly between 1500 and 230,000 individuals ha^{-1} among studies. Only 15% of the experimental studies provided data on the quality of the young

oaks, i.e. stem form and branching pattern. Browsing was considered in half of the experimental studies by protective measures or quantifying the intensity of browsing.

3.1.6 Competing vegetation

Aspects that describe and quantify interspecific competition within the regeneration layer were reported in most of the core publications. For example, naturally regenerated individuals of accompanying woody species were mentioned in three-quarters of the evaluated papers. In addition, 75% of all references also listed the most abundant competing tree species such as *Fagus sylvatica*, *Carpinus betulus* and *Betula pendula*. However, only 25% of the publications based on experimental trials quantified density, height and/or diameter of tree species other than oak, and only three studies (Hager 1994; Ligot et al. 2013; von Lüpke and Hauskeller-Bullerjahn 2004) reported shoot lengths of woody competitors. Less than a fifth of these references provided information on predominant species, height and/or cover of the competing ground vegetation.

3.1.7 Tending and protection measures

Owing to the initially slow aboveground growth of young oak seedlings, control of competing vegetation is often crucial for oak survival (Collet et al. 1996; Röhrig et al. 2006). Surprisingly, details on the expenses and/or the kind and intensity of tending measures such as cleaning, liberation and weeding were reported only in a fifth of the experimental core publications. Total costs of regeneration efforts were quantified and reported in only two papers (Nebout 2009; Rößler et al. 2019).

3.2 Evaluation and synopsis of published findings

As previously mentioned (Section 3.1.3), core publications commented not only on the suitability of traditional shelterwood cutting but also on smaller-scale regeneration methods such as group selection felling, single-tree selection felling or oak regeneration through natural gap dynamics. The comparatively large number of publications that reported on and recommended small-scale regeneration approaches (> 20 references) may be misleading for the following reasons: (i) there appears to be a generally greater research interest in the suitability of less-proven small-scale reproduction methods as an alternative to conventional shelterwoods and (ii) the experimental design of the majority of these studies on regeneration in small canopy openings did not include larger canopy openings as a reference. Correspondingly, the authors of the majority of core studies which addressed the question of minimum size of canopy openings for successful oak regeneration argued that gaps between 0.1 and 0.3 ha in size would be sufficient, whereas a minimum canopy opening size of 0.5 ha or larger was suggested in four core publications (Fig. 3).

Although 90% of the experimental studies mentioned the studied types of regeneration felling, 40% of them did not provide management recommendations with regard to suitable types of regeneration felling. The term ‘regeneration period’ was generally defined as (i) the number of years required or (ii) the timeframe available to successfully establish a new oak cohort no longer in need of protection against browsing. Summarising these two definitions, seven of the 13 studies that commented on the regeneration period suggested a time span of 5 years. The other core publications advocated longer regeneration periods greater than or equal to 15 years.

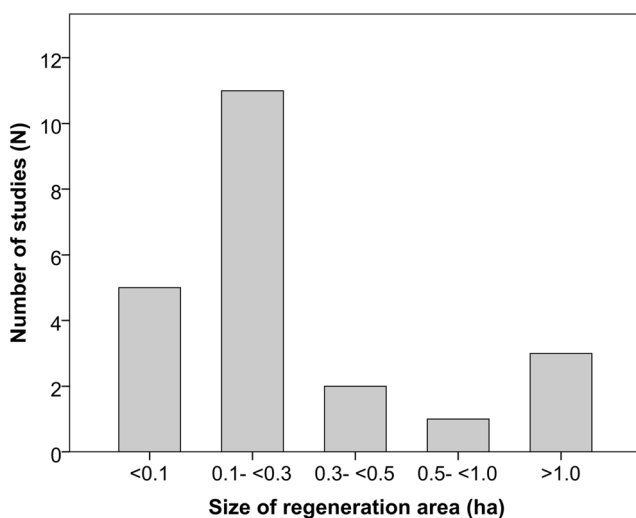


Fig. 3 Frequency (*N*) of the minimum gap size required for successful oak regeneration as suggested in the analysed core publications

3.2.1 Identification of factors crucial for regeneration success

Based on the 53 core publications examined, Fig. 4 shows the number of references by biotic or abiotic factors, identified as important for the success of forest management activities to regenerate sessile oak stands. The five most frequently mentioned and thus the most influential key factors were light availability (30 references), competing vegetation (25 references), browsing (14 references), initial oak seedling density (12) and tending effort or investment (11 references). Site quality was mentioned in six references as an important factor. This number of publications appears to be rather low, but the majority of studies were limited to a single or only very few different site types, respectively. Only five studies systematically integrated site quality into the experimental design (Annighöfer et al. 2015; Bilke 2004; Götmark et al. 2011; Ligot 2014; Mölder et al. 2019b). Thus, we cannot draw general conclusions about the effect of site conditions based on the available literature.

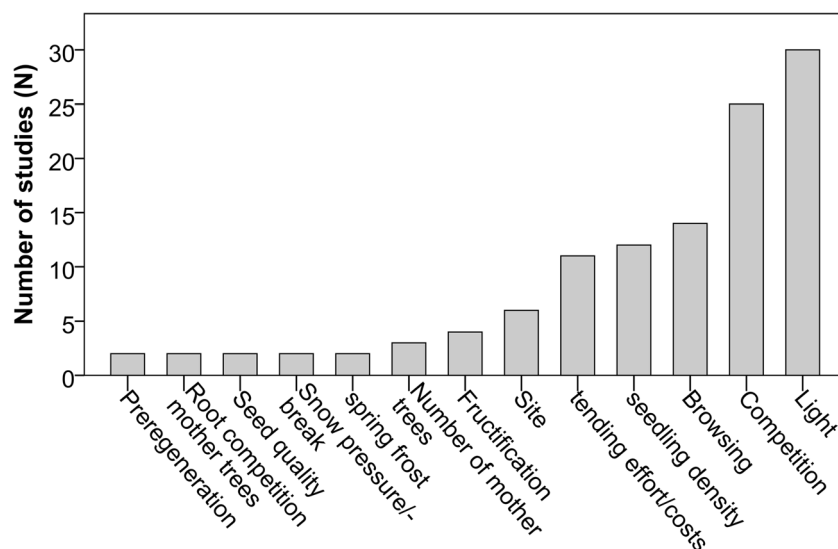
Not a single study examined in this review has analysed the aforementioned five most important factors simultaneously in a systematic approach. Almost two-thirds of the experimental studies evaluated only one or two key factors, while three factors were addressed at the same time in seven publications, respectively. Only two studies (Annighöfer et al. 2015; Brezina and Dobrovolny 2011) considered four key factors (s. a. Annex Table 2).

3.2.2 Key factors light availability and competing vegetation

Given their overall significance, the two correlated key factors light availability and competing vegetation are further discussed in greater detail in the following section which also considers additional literature on the topic other than the reviewed 53 core publications.

The adjustment of light conditions to achieve the desired tree regeneration is a central aspect of silvicultural systems (Diaci et al. 2008; Röhrig et al. 2006). In addition to the direct effects of light on young trees, indirect influences such as the effect on the establishment and development of competing vegetation are also very important (Annighöfer et al. 2019; Wagner et al. 2011). Higher light levels, as found in larger canopy openings, may create growing conditions that favour other ground flora species over the one desired by management. If desired seedlings are overgrown by competitors as a result of altered growth dynamics within the regeneration layer, they can be exposed to light levels less favourable compared with the ones that prevail in smaller openings without vigorous competition (e.g. Wagner 1999). For example, young sessile oak saplings on a sandy site in northwest Germany appeared to be less sensitive to low overstorey light levels than to reductions in lateral light availability caused by the direct neighbourhood vegetation (Annighöfer et al. 2019).

Fig. 4 Frequency (N) of the main factors influencing oak regeneration mentioned in the analysed literature (core publications; multiple assignments of factors per study were possible)



There are only few studies in which reduction in light levels for oak regeneration through vegetation of competing species has been quantified (e.g. Kuehne et al. 2005; Modrow et al. 2020). Light levels measured directly above the terminal bud of 7-year-old oaks which were overtopped by competing vegetation were on average 25% lower than above the competing vegetation. The relative reduction in light levels appeared to increase with increasing radiation availability (Modrow et al. 2020). More often, however, light levels below the canopy and above the ground vegetation are too low for the longer-term survival of oak seedlings and saplings (e.g. Kelly 2002). At low light levels < 25% of open-field light, oak seedlings can be disadvantaged against more shade-tolerant tree species and/or vigorous ground vegetation, which grow comparatively better at lower light levels (Ligot et al. 2013; von Lüpke and Hauskeller-Bullerjahn 2004; Modrow et al. 2020). Consequently, a close monitoring of growth dynamics as well as competition control measures appears to be essential management aspects to regenerate oak stands successfully (cf. Ligot et al. 2013; von Lüpke 1998).

3.3 Light requirements of sessile oak regeneration

Light requirements of young deciduous woody plants usually increase with increasing plant size (Givnish 1988; Messier et al. 1999; Valladares and Niinemets 2008). To create conditions that favour desired species over others by means of silvicultural activities, managers thus need to be aware of the dynamics in (i) minimum light requirements to assure survival of the desired species with time and (ii) light levels of maximum growth (light saturation) to prevent conditions that potentially favour competing and more light-demanding species over the desired one (Fig. 5). Consequently, the silvicultural manipulation of the canopy should preferably result in light

levels within the range defined by these lower and upper species-specific thresholds.

As it is depicted in Fig. 5, the few studies that evaluated the relationship between light availability and growth of oaks, in most cases, did not analyse the entire light range between possible compensation points and light saturation levels. Moreover, most of the few studies that considered a comparatively large range of light levels did not run over a sufficiently long period of time to capture the dynamic light requirements in the ontogeny of young oaks. The importance of long-term studies, however, becomes evident in the findings of Schütz (1991) who studied oak pole stands 40 years after their establishment in forest gaps with an average size of 0.15ha. At this age, oak survival was only marginal at a distance of 5–10 m from the forest edge in these small canopy openings. This finding questions the general recommendations of small-scale reproduction methods in oak stands provided in some of the core studies following short-term assessments (cf. Fig. 3).

3.4 Shade tolerance of sessile oak regeneration

Comparative studies on the shade tolerance of young oaks and accompanying tree species have documented the higher light requirements of oak for continuous survival and growth compared with European beech and common hornbeam (e.g. Kazda et al. 2004; Kuehne et al. 2014b; Le Duc and Havill 1998; Terborg 1998). According to von Lüpke (1998) and 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 Ligot et al. 2013; Newbold and Goldsmith 1981). In fact, oak seedlings appear to be fairly shade-tolerant throughout the first 2 years after germination (e.g. Valladares et al. 2002), which is partly attributable to the comparatively large amount of

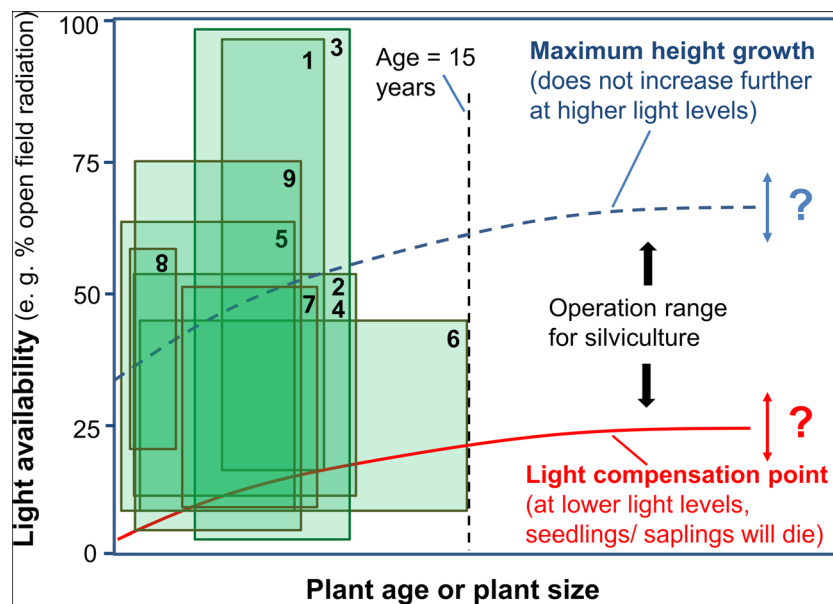


Fig. 5 Conceptual illustration of the optimal range of light availability levels to promote regeneration of desired tree species in forest understories. The range of light levels and ontogenetic development covered in different studies on sessile oak regeneration is depicted in the form of boxes that span the observation gradients; the dashed vertical line serves as a reference for tree age representing a time period of 15 years after regeneration initiation. 1 = Brezina and Dobrovolny (2011); 2 = Hauskeller-Bullerjahn (1997); 3 = von Lüpke (1998); 4 = von Lüpke and Hauskeller-Bullerjahn (1999); 5 = von Lüpke and Hauskeller-Bullerjahn (2004); 6 = Ligot et al. (2013); 7 = Annighöfer et al. (2019); 8 = Jaloviar et al. (2014); 9 = Modrow et al. (2020). Light

levels ought to be greater than the light compensation point of the desired species to prevent seedling mortality. Light availability should also not exceed levels associated with maximum growth rates (light saturation) of the desired species to prevent conditions that potentially favour competing, more light-demanding species over the desired one. The light levels depicting maximum height growth and light compensation point follow measurements of authors 5, 6 and 9. As indicated by the question marks at the right end of the curves, the precise light levels for these two curves at every age/size of oak plants, which also depends on other stresses (water, nutrients, pathogens, herbivory), are not known and are also not decisive for this conceptual figure

available resources stored in acorn (Grime 1966; Reif and Gärtner 2007; Ziegenhagen and Kausch 1995). Average light compensation points between 2 and 5% and approximately 10% of open-field light conditions were reported for European beech and sessile oak seedlings, respectively (Ligot et al. 2013). Oak mildew, which occurs more likely in larger canopy openings than in closed canopy stands (Marçais and Desprez-Loustau 2014), appears to further reduce shade tolerance in young oaks (Dillen et al. 2017; Rackham 2003).

3.5 Height growth and biomass allocation in relation to light availability

Early height growth of sessile oak peaks at relative light levels of 20 to 40% of open-field conditions (von Lüpke 1998; Shaw 1974, in Reif and Gärtner 2007). Similarly, maximum height growth of 1.5 to 3 m tall sessile oak trees was reported between 25 and 30% relative light, whereas height growth of similar-sized European beech saplings peaked at relative light levels of 20% (Ligot et al. 2013). Other studies, however, found in 4–7-year-old naturally regenerated sessile oak a further increase in terminal shoot length with light availability exceeding relative levels of 40% (e.g. Brezina and Dobrovolny 2011; Modrow et al. 2020). The reasons for these contradicting findings are

not clear but could be linked to different ranges of light levels investigated.

Owing to the apparent light saturation of height growth, height increment by itself is not a reliable indicator of oak seedling vigour and fitness. Given the observed continuous increase in the number of branches and nodes with increasing light availability (Collet et al. 1998; Igboanugo 1990; Nicolini et al. 2000), crown development and branching appears to be a better or suitable additional indicator. Also, pedunculate oak seedlings growing in shady conditions at relative light levels of 33% exhibited greater shoot lengths but lower total biomass and root–shoot ratios than oaks growing in full light (Ammer 2003; Jarvis 1964). The root–shoot ratio of young oaks (tap root system) is usually significantly higher compared with European beech (heart-shaped root system) seedlings of the same age (e.g. Welander and Ottosson 1998). The more pronounced allocation of C to the root system in oak species has been interpreted as an adaptation mechanism to better withstand drought and fire events (Larsen and Johnson 1998) and potentially also browsing (Bideau et al. 2016). This allocation pattern also explains—at least in part—why oak seedlings, despite their higher photosynthetic capacities, exhibit inferior aboveground growth

rates when compared with seedlings of more shade-tolerant accompanying species (e.g. Kuehne et al. 2014b; Valladares et al. 2002). At the same time, the root–shoot ratio in oaks is more profoundly reduced with decreasing light availability than for example in European beech (e.g. Ammer 2003; Welander and Ottosson 1998). A smaller root system likely reduces tolerance against environmental stressors and disturbances such as drought and browsing. For example, a combined effect of shading and browsing had a greater negative effect on biomass accumulation in oak seedlings than in accompanying species including European beech (Harmer 1999).

3.6 Competitiveness of oak regeneration

The aforementioned light levels of 20–40% of open-field conditions do not necessarily warrant general dominance of oak regeneration over individuals of accompanying species. For example, at 30% of full light, height increment of oaks was reduced on average by 24% as a result of competition by other species (Hauskeller-Bullerjahn 1997). However, Hauskeller-Bullerjahn (1997) still suggested relative light levels of 20 to 30% as an optimal trade-off between reduced oak height increment, limited competition from accompanying species and a favourable qualitative development of young oaks.

Comparative height growth is an important indicator of the competitiveness of species in mixed communities. Regarding the displayed height increment differences when compared with more shade-tolerant tree species, sessile oak appears to be inferior in height growth over a wide range of the studied light availability (Fig. 6). However, height increment differences between sessile oak and European beech diminish and eventually vanish with increasing light intensity (Ligot et al. 2013; von Lüpke and Hauskeller-Bullerjahn 2004). These findings indicate that successful natural regeneration of oak requires associated silvicultural measures to control competition by accompanying species at least under the site conditions of the reviewed studies (cf. Gayer 1874; Mölder et al. 2017; Vanselow 1960).

When mixed with European beech, higher light availability seems to reduce the risk of sessile oak being overgrown. For example, no oak seedling taller than 50 cm was found in a mature mixed sessile oak–European beech stand at the foothills of the Black Forest, Germany managed by group selection harvest for about 25 years (Schürg 2013). Instead, relative abundance of the two more shade-tolerant tree species (*F. sylvatica* and *Acer pseudoplatanus*) grew continually with increasing total plant height (Schürg 2013).

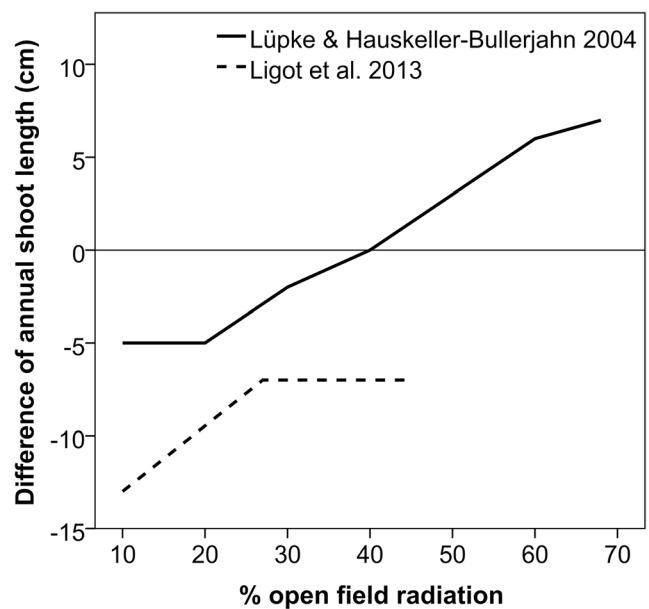


Fig. 6 Average differences in height increment between sessile oak and European beech across varying relative light levels. The first data point series (solid line) depicts modelled height increment values of planted 4- to 6-year-old seedlings growing in a forest stand located close to Göttingen, Lower Saxony, Germany (von Lüpke and Hauskeller-Bullerjahn 2004). The second data point series (dashed line) depicts height increment of circa 1.5 m tall, naturally regenerated seedlings as predicted by height growth models developed from data collected in numerous forest stands of the Belgian Ardennes (Ligot et al. 2013)

In addition to competing woody species, ‘recalcitrant’ ground vegetation species (Royo and Carson 2006) such as bracken (*Pteridium aquilinum* (L.) Kuhn) and bramble (*Rubus fruticosus* L. agg.) can have strong adverse effects on oak regeneration growth and survival (e.g. Harmer et al. 2005; Harmer and Morgan 2007; Humphrey and Swaine 1997a; Laurent et al. 2017a). 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 heavy snow.

A large majority of the reviewed core publications of this study did not report on the properties of the understorey vegetation layer found at the time of regeneration initiation. Given the apparent significance of pre-existing ground vegetation, in particular that of shrub and tree species, on the regeneration success as outlined in some publications (Euler et al. 2017; Rumpf 2011), this lack of information seems to be a crucial shortcoming.

The competitive potential of accompanying vegetation is likely also determined by prevailing site conditions and not only light availability. Sessile oak is known to cope better with acidic soils and low water availability compared with many accompanying species which thus exhibit reduced competitive potential under such conditions (Annighöfer et al. 2015; Kunz et al. 2018). However, there has been no systematic assessment of

the influence of site quality on the competitiveness of sessile oak in relation to typical companion species. More studies that systematically examine the interaction between light availability, site properties and competition and their effect on oak survival and growth are necessary (Laurent et al. 2017b).

4 Conclusions

This literature review focussed on important aspects associated with the process of naturally regenerating sessile oak. Our review clearly revealed surprisingly large knowledge gaps that would have to be filled for evidence-based silvicultural recommendations for successful natural regeneration of sessile oak. The essential conclusions of this study are as follows:

- 1 Despite many studies on different aspects of natural regeneration of sessile oak, the evidence base on the influence of silvicultural manipulation on the regeneration success is not solid. Most of the existing publications are of low or moderate evidence, i.e. short-term experiments at a single site or mere expert opinions. Comprehensive, systematic experimental trials are missing, and owing to the lack of reliable studies, a meta-analysis appears currently not feasible.
- 2 Although the majority of existing publications on the suitability of different types of regeneration felling studied group selection felling systems and recommended that canopy openings between 0.1 and 0.3 ha in size would be sufficient to naturally regenerate sessile oak, this finding is of limited validity because the experimental designs of these studies did not include larger canopy openings for comparison.
- 3 Regenerating oak naturally in small canopy openings seems to be possible in principle as already shown by nineteenth-century silviculture in the Spessart Mountains (Mölder et al. 2017). However, owing to the short duration of most studies, this conclusion is only in part based on sufficient evidence and, thus, needs to be reassessed in future medium- to long-term studies. It is advisable to follow the development of regeneration as long as competing vegetation can have a significantly adverse effect on oak establishment and survival (i.e. height of oak regeneration between 2 and 3 m), which coincides with the period in which early tending measures are applied. Almost all of the reviewed references did not meet this requirement.
- 4 The most important factors for regeneration success identified here comprise light availability, competition by accompanying woody and ground vegetation species, browsing, initial oak seedling density and stand tending measures. However, not a single publication studied these factors simultaneously in a comprehensive experimental approach. Therefore, any general conclusions regarding the suitability of different types of regeneration felling have to be viewed with great caution.
- 5 Early stand tending efforts as well as overall management costs associated with the successful establishment of a new oak cohort have been rarely quantified in regeneration experiments. This is surprising because (a) vegetation control can be a very effective measure to ensure oak survival and growth, (b) it can make up a large proportion of the costs of establishing regeneration, and (c) the degree of canopy opening associated with different silvicultural systems has a direct influence on the development of competing vegetation. Based on the information currently available from the literature, a comparison of the costs associated with different reproduction methods is not possible. This lack of data on the expenses of different approaches to natural regeneration appears to be one of the most crucial knowledge deficits revealed in this study.
- 6 Because the majority of reviewed studies were limited to a single location, extrapolating the findings of existing studies to the population of *Q. petraea* stands across different site types is not recommended.
- 7 Here, we did not compare natural regeneration with planting. The advantages of the former are mainly the greater potential for genetic selection from a much higher number of individuals and the higher probability of undistorted root systems. The costs are not necessarily lower owing to the longer period in which competitive vegetation needs to be controlled. However, where some of the above identified factors crucial for success of natural regeneration cannot be controlled or where there is great uncertainty about their development and impact (e.g. seedling density, competing vegetation, ungulate browsing), planting of oaks should be considered.

5 Recommendations

It is important to acknowledge the current knowledge deficits regarding the natural regeneration of sessile oak, one of Central Europe's most important deciduous tree species. The debates about right or wrong and more or less suitable silvicultural approaches might benefit from the appreciation that solutions established in one locality or region may not be

transferable to another because of different influences or importance (e.g. costs) of the different factors.

For the same reason, locally successful silvicultural approaches to establish sessile oak should not be hastily or inconsiderately replaced with alternative, insufficiently studied approaches. Management recommendations for methods employing small canopy openings should be carefully scrutinised as they lack a solid scientific foundation. The current conflict regarding timber harvest and reproduction methods in old oak forest stands centres mainly on concerns about habitat continuity. Thus, it appears advisable to clearly and deliberately separate and distinguish between management efforts to preserve valuable structural elements such as habitat trees and those required to establish oak regeneration in sufficiently large canopy openings, for example by spatial separation at the stand and landscape level. The retention of a sufficient number of habitat and legacy trees is a way to integrate both management goals (cf. Borrass et al. 2017; Mölder et al. 2019a). In addition, coordinated forest planning efforts at the landscape level can help to provide habitats for rare and endangered oak specialist species in need of larger-scale contiguous areas of old oak forest. This could include significantly extended production periods in forest patches or entire stands, i.e. the extension of final harvest operations over a prolonged period.

Systematic long-term experimental trials on the natural regeneration of sessile oak are needed to derive reliable management recommendations. These experiments should (i) include canopy openings of varying sizes (e.g. 0.1–1 ha), (ii) be replicated at different locations of varying site conditions, (iii) consider browsing as an important factor, (iv) quantify early stand tending expenses in a comparative manner and (v) run for extended periods (\pm 15 years) to include later phases of the stand initiation stage. Since these experiments will be quite expensive to conduct, it is recommended that they best be implemented and accompanied by networks of research institutions following common designs and protocols.

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Data availability Data will be made available on request.

Compliance with ethical standards

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

Annexes

Annex 1: Catalogue of reference examination criteria

Experimental design and documentation: metadata

- Author(s) and citation
- Type of publication (peer-reviewed journal, non-referred literature, unpublished)
- Potential for extrapolation of findings (yes/no)
- Replication of treatment(s) (yes/no, single site, several sites)
- Consideration of spatial heterogeneity within treatment(s)
- Initiation of study (year, age of regeneration/seedlings)
- Duration of study
- Country
- Region
- GPS coordinates

Initial stand and site conditions

- Silvicultural system: high forest, coppice with standards, coppice forest
- Oak species: *Quercus petraea*, *Q. robur*, *Q. pubescens*
- Stand age
- Stand height
- Yield class (absolute)
- Diameter (at breast height) distribution
- Canopy closure or stocking level (including homogeneity of stocking)
- Admixed tree species (species, proportion, mixture type)
- Existing (species, height)
- Potentially natural regeneration
- Parent material, bedrock
- Humus type
- Soil chemical and physical properties
- Climate data (mean annual temperature and precipitation)
- Ground vegetation and shrub layer composition and vigour

Reproduction method

- Type of (regeneration) felling:
- Clearcut or group selection harvest: size of harvested area, shape and general exposition of canopy opening, gap factor (opening diameter/stand height)
- Shelterwood cutting: time of seed/establishment cut (also in relation to acorn crop year), number of removal cuts and (absolute) basal area removal per

entry, time until final removal cut, change of diameter distribution over time

- Disruption of orderly course of action (yes/no/cause)
- Retention of seed/habitat/legacy trees (number of individuals or basal area per unit area)
- Acorn production in mast year (heavy or moderate crop, absolute quantities)
- Site preparation measures (e.g. removal of competing vegetation, logging debris) including top soil manipulation (manual or mechanical)

Light conditions

- Indirect: stocking level, canopy closure (quantitative, qualitative)
- Light measurements: sensors, hemispherical photographs
- Time of measurements (year, age/height of regeneration)
- Height above forest floor or regeneration layer of measurements
- Position of measurements within canopy opening
- Determination of relationship between light availability and oak regeneration
- Height increment (total height)
- Root–shoot ratio

Oak regeneration

- Type of regeneration: natural regeneration from seeds, vegetative (re)sprouting, regeneration by artificial seeding or planting
- Number of acorns per unit area
- Origin of planting material or seeds
- Planting material specifics (age and/or height)
- Browsing protection (fence, grow-tubes), duration and time (also in relation to age of regeneration) of protection measure
- Other damaging agents (mice, pest insects, oak mildew) and protective measures
- Recorded oak regeneration characteristics and properties including time of measurement(s) and monitoring/sampling design:
 - Total height and length of terminal shoot
 - Root collar or breast height diameter
 - Tree density (number of seedlings per are unit)
 - Root system parameters (soil penetration, tap root development)
 - Browsing intensity
 - Oak quality (stem form, crown type, percentage of quality tree)

Competing vegetation

- Accompanying tree and shrub species
- Type of regeneration for woody species other than oak: natural regeneration from seeds, vegetative (re)sprouting, regeneration by artificial seeding or planting
- Competitive woody vegetation characteristics and properties including time of measurement(s) and monitoring/sampling design:
 - Total height and length of terminal shoot
 - Root collar or breast height diameter
 - Tree density (number of seedlings per are unit)
 - Root system (soil penetration, tap root development)
 - Browsing intensity
 - Growth indicators in relation to oak regeneration (e.g. proportion, mixture type, dominance)
 - Species of competing ground vegetation
- Recorded information on ground vegetation including time of measurement(s) and monitoring/sampling design:
 - Average or maximum height
 - Cover (percentage of total area)
 - Dynamics along edges of managed (regenerated) stand area

Expenses

- Costs of sowing/planting and refilling/replanting
- Early stand tending efforts (yes/no/not documented)
- Type of tending measure (manual, mechanical)
- Tending intensity (selective, extensive, schematic, total duration and periodicity)
- Tending expenses per unit area
- Browsing protection expenses per unit area
- Costs of other protective measures per unit area
- Total costs of regeneration effort per unit area
- Measures and expenses of monitoring and survey

Concluding remarks

Conclusions on

- Silvicultural system
- Type of regeneration
- Size of regeneration area
- Regeneration period
- Additional silvicultural implications
- Criteria of success/failure
- Research needs

Annex 2

Table 2 Cross table of all core publications comprising the main important criteria and factors that can be assigned to these publications

| Reference | Peer-reviewed | Country | Evidence level | Study type | Study duration [years] | Type of regeneration felling | Light availability quantified | Light to height growth relationship | Total cost of regeneration efforts | Minimum gap size suggested [ha] | Number of main success factors gradually considered |
|--|---------------|---------|----------------|------------------|------------------------|------------------------------|-------------------------------|-------------------------------------|------------------------------------|---------------------------------|---|
| Annighöfer et al. (2015) | Yes | GER | 3 | Experiment | 3 | SW | Yes | No | | | 4 |
| Annighöfer et al. (2019) | Yes | GER | 4 | Experiment | 1 | SW | Yes | Yes | | | 2 |
| Baudry (2013); *Baudry et al. (2013) | No | BEL | 3 | Experiment | 4 | SW | Yes | Yes | | | 2 |
| Bilke (2004) | No | GER | 3 | Experiment | n.a. | GSF | No | No | | <0.3 | 3 |
| Bonneau (1996) | Yes | FRA | 4 | Experiment | 9 | | No | No | | | 0 |
| Brezina and Dobrovlny (2011) | Yes | CZE | 3 | Experiment | 4 | SW, GSF, CC | Yes | Yes | | <0.3 | 4 |
| Bruciamacchie et al. (1994) | No | FRA | 4 | Experiment | n.a. | GSF | No | No | | <0.3 | 2 |
| Chara and Colin (1999) | Yes | FRA | 4 | Experiment | 2 | SW | No | No | | | 0 |
| Dohrenbusch (1996) | No | GER | 4 | Experiment | 8 | SW, CC | Yes | Yes | | | 2 |
| Euler (2016); *Euler et al. (2017); Freise et al. (2017) | No | GER | 4 | Experiment | 1 | GSF | Yes | Yes | | 0.2–0.3 | 3 |
| Fischer and West (1991) | No | GER | 6 | Expert knowledge | | SW | | | | | 0 |
| Götmark et al. (2011); *Götmark (2007) | Yes | SWE | 2 | Experiment | 7 | SW | Yes | Yes | | | 2 |
| Hager (1994) | No | GER | 4 | Experiment | 1 | GSF | Yes | Yes | | | 3 |
| Hauskeller-Bullerjahn (1997); *Hauskeller-Bullerjahn et al. (2000) | No | GER | 3 | Experiment | 5 | SW | Yes | Yes | | | 2 |
| Heuer et al. (2006) | No | GER | 3 | Experiment | 4 | SW, GSF | Yes | Yes | | 0.1 | 1 |
| Humphrey and Swaine (1997a) | Yes | GBR | 3 | Experiment | 3 | nG | Yes | No | | 0.5–1.0 | 1 |
| Humphrey and Swaine (1997b) | Yes | GBR | 4 | Experiment | 2 | nG | No | No | | | 2 |
| Jaloviari et al. (2014) | Yes | SLO | 4 | Experiment | 1 | SW | Yes | Yes | | | 2 |
| Karius (2004) | No | GER | 6 | Expert knowledge | | SW, CC | | | | | 0 |
| Keller (1990); *Schütz (1991) | No | SUI | 3 | Experiment | 1 | GSF | No | No | | <0.3 | 2 |
| Kelly (2002) | Yes | IRL | 4 | Experiment | 25 | GSF | Yes | No | | <0.1 | 3 |
| Kollár (2017) | Yes | HUN | 3 | Experiment | 2 | GSF | Yes | Yes | | | 2 |
| Kuehne et al. (2014a) | Yes | GER | 6 | Expert knowledge | | SSF, nG, SW, CC | Yes | Yes | | Min. 1.0 | 0 |
| Laurent (2016); *Laurent et al. (2017a), Laurent et al. (2017b) | Yes | FRA | 4 | Experiment | 1 | | Yes | Yes | | | 2 |
| Ligot (2014); *Ligot et al. (2014a); Ligot et al. (2014b); Ligot et al. (2013) | Yes | BEL | 2 | Experiment | 5 | SSF | Yes | Yes | | 0.05 | 3 |
| von Lüpke (1998); *von Lüpke & Hauskeller-Bullerjahn (1999) | Yes | GER | 3 | Experiment | 8 | SW, GSF, CC | Yes | Yes | | >0.3 | 2 |
| von Lüpke (2008) | Yes | GER | 5 | Experiment | 13 | GSF, CC | Yes | Yes | | >0.25 | 2 |
| Mechler and Lieber (2000) | No | GER | 6 | Expert knowledge | | SW | Yes | Yes | | <0.3 | 0 |
| Modrow (2016); *Modrow & Pyttel (2019); Modrow et al. (2020) | Yes | GER | 4 | Experiment | 1 | GSF | Yes | Yes | | >0.2 | 3 |

Table 2 (continued)

| Reference | Peer-reviewed | Country | Evidence level | Study type | Study duration [years] | Type of regeneration felling | Light availability quantified | Light to height growth relationship | Total cost of regeneration efforts | Minimum gap size suggested [ha] | Number of main success factors gradually considered |
|--------------------------------|---------------|---------|----------------|-------------------|------------------------|------------------------------|-------------------------------|-------------------------------------|------------------------------------|---------------------------------|---|
| Mölder et al. (2017) | Yes | GER | 6 | Literature review | | GSF | | | | Depending on management goals | 0 |
| Mölder et al. (2019a) | Yes | GER | 6 | Literature review | | | | | | | 0 |
| Mölder et al. (2019b) | Yes | GER | 3 | Experiment | 2 | | | | | | 3 |
| Nebout (2009) | No | FRA | 6 | Expert knowledge | | | Yes | No | | Depending on management goals | 0 |
| Nicolini et al. (2000) | Yes | FRA | 5 | Experiment | 5 | SW | | | 2500–3600 | | 1 |
| Nutto (1998); *Nutto (2000) | No | GER | 5 | Experiment | n.a. | nG | Yes | Yes | | | 1 |
| Petrinan et al. (2013) | Yes | ROU | 5 | Experiment | 1 | GSF | No | No | <0.3 | | 2 |
| Pisoke and Spiecker (1997) | No | GER | 5 | Experiment | n.a. | nG | No | No | | | 0 |
| proQueucus (2010) | No | SUI | 6 | Expert knowledge | | GSF | No | No | | Min. 1.0 | 0 |
| proQueucus (2013) | No | FRA | 6 | Expert knowledge | | | | | | | 0 |
| Rößler et al. (2019) | No | GER | 5 | Experiment | 1 | SW, GSF | | | | | 2 |
| Rumpf (2011) | No | GER | 6 | Expert knowledge | | SW | Yes | Yes | 14,000 | Min. 1.0 | 0 |
| Sanchez and Auquièrre (2015) | No | FRA | 6 | Expert knowledge | | | | | | 0.3–0.5 | 0 |
| Scheeder (1989) | No | GER | 6 | Expert knowledge | | GSF | | | | 0.1–1.0 | 0 |
| Schürg (2013) | No | GER | 4 | Experiment | 1 | SSF | Yes | No | | | 2 |
| Spellmann (2001) | No | GER | 5 | Experiment | 5 | | No | No | | | 2 |
| Stahl-Streit (2004) | No | GER | 6 | Expert knowledge | | SSF | | | | | 0 |
| Tinya et al. (2019) | Yes | HUN | 3 | Experiment | 1 | SW | Yes | No | | | 2 |
| Tobisch (2009) | No | HUN | 4 | Experiment | 4 | GSF | Yes | Yes | | | 2 |
| van Cleve (2012) | No | GER | 5 | Experiment | 2 | GSF | Yes | No | | | 2 |
| van Couwenberghe et al. (2010) | Yes | FRA | 3 | Experiment | 1 | nG | No | No | | | 2 |
| van Couwenberghe et al. (2013) | Yes | FRA | 4 | Experiment | 4 | GSF | Yes | Yes | | | 2 |
| Wilhelm and Rieger (2013) | No | GER | 6 | Expert knowledge | | GSF | | | | <0.3 | 0 |
| Wilhelm et al. (2019) | No | GER | 6 | Expert knowledge | | GSF | | | | <0.1 | 0 |

Type of regeneration felling: SW = shelterwood, GSF = group selection felling, SSF = single-tree selection felling, nG = natural gap, CC = clearcut
n.a. not available

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