



Elongated gaps provide a good compromise between abiotic and competitive conditions for sessile oak regeneration



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ABSTRACT

Continuous cover forestry is gaining importance in temperate forests as an alternative to rotation forestry. However, for light-demanding oaks, especially when coexisting with shade-tolerant tree species, the optimal gap size and shape for successful regeneration remain unclear. We therefore examined the effects of four gap types—two sizes (150 and 300 m²) and two shapes (circular and elongated)—on initial sessile oak (*Quercus petraea*) regeneration, abiotic conditions, and competitive vegetation in an oak–hornbeam forest in Hungary. We found that tended oak saplings showed the best growth in the initially brightest and most moist large circular gaps. Growth in large elongated gaps (initially with similar light level but drier soil) and small circular gaps (with similar soil moisture but lower light) was slightly lower. In small elongated gaps, where resources were limited, oak growth was slower but still better than in the closed stand. Survival of tended oak saplings was the highest in large gaps and small circular gaps, with intermediate survival in small elongated gaps. Hornbeam abundance and growth was greater in initially moister circular gaps. In untended quadrats, where competition was present, oak saplings were the most abundant in small elongated gaps. However, their growth was slow. Our results suggest that oak regeneration can be initiated in all 150–300 m² gap types, though tending effort requirements and sapling growth vary. Large circular gaps provide the best abiotic conditions, but if competition is also considered, oak regeneration can be initiated most efficiently (requiring less tending) in elongated gaps. Large elongated gaps allow for higher survival rates and greater growth than small ones, but due to the higher levels of competition, more tending is required. Small elongated gaps may need expansion after a few years to avoid high mortality, but they offer the advantage of continued acorn availability, increasing regeneration chances.

1. Introduction

Oaks (*Quercus* spp.) are among the most valuable hardwood tree species in Central Europe, both from an ecological and economic point of view (Annighöfer et al., 2015; Mölder et al., 2019a; Kohler et al., 2020). Oak forests host a high level of biodiversity and are extremely important for forestry due to the valuable timber of oak species. In the face of climate change, the importance of mixed oak forests is increasing, since oaks are more drought-tolerant and storm-resistant

than some of the other dominant species in Central Europe (e.g., beech—*Fagus sylvatica*) (Kohler et al., 2020; Stimm et al., 2021).

However, a large body of studies has described the failure of natural oak regeneration in many areas of the temperate zone, both in managed and unmanaged forests. This is particularly true in stands where oaks coexist with shade-tolerant tree species such as maple (*Acer* spp.), beech, or hornbeam (*Carpinus betulus*) (Lorimer, 1984; Van Couwenberghe et al., 2013; Böllöni et al., 2021; Dietz et al., 2022). Several theories have been proposed to explain the problem, such as the recent lack of large

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grazing herbivores (Vera, 2000), suppression of low intensity fire (Frellich, 2002), changes in the traditional land use techniques that maintained open stands or transitional habitats (Bobiec et al., 2018; Saniga et al., 2014), the increased browsing effect of overpopulated ungulates (Côté et al., 2004; Zoltán et al., 2024), or the spread of the invasive powdery mildew (Demeter et al., 2021). According to Losseau et al. (2020), the interaction of several elements of the changing climate may also contribute to declining oak regeneration. Scientific research and silvicultural practice must therefore develop solutions to cope with these challenges in order to ensure successful oak regeneration.

The most widely used conventional management system for oak forests is rotation forestry (Larsen and Johnson, 1998; Kohler et al., 2020; Nicolescu et al., 2025), but a growing body of drawbacks associated with its methods has emerged in recent decades. On the one hand, an increasing number of studies show that large cutting areas resulting from rotation forestry are unfavourable for forest biota (de Groot et al., 2016; Elek et al., 2018; Noualhaguet et al., 2023; Brazner et al., 2024). On the other hand, these large harvested areas may significantly amplify the negative effects of climate change, such as heat and drought, due to the lack of the buffering capacity of the stand, which leads to an extreme microclimate (Kovács et al., 2020; Starck et al., 2025). In addition, the use of rotation forestry system results in monodominant stands with a species-poor overstorey layer (Kirby and Watkins, 2015). This is highly unfavourable for biodiversity (Cavard et al., 2011), ecosystem services (Gamfeldt et al., 2013), functioning (Baeten et al., 2019), and stand stability (Jactel et al., 2005).

Sustainable, multifunctional forest management is needed to meet ecological, economic, and protective functions of oak forests, as well as the recreational and cultural needs of society (Pukkala, 2016; Mölder et al., 2019a; European Commission, 2021). Continuous cover forestry that operates with overstorey thinning and small-scale gap-cuttings could be an effective alternative to rotation forestry (Pommerening and Murphy, 2004; Muscolo et al., 2014; Mason et al., 2022). This management system is well developed and supported by a large body of scientific evidence for beech and other shade-tolerant species (Tarp et al., 2000; Vilhar et al., 2015; de Groot et al., 2016), but it is more challenging for light-demanding species such as oaks (Kohler et al., 2020; Patterson et al., 2022; von Lüpke, 1998). Mölder et al. (2019a) emphasize that it is crucial to identify those gap types that are suitable for oak regeneration, while opening the forest canopy as little as possible.

Numerous studies have shown that it is possible to initiate oak regeneration in small gaps (Diaci et al., 2008; Dobrowolska et al., 2022; Ostrogović et al., 2010; Petritan et al., 2025; Tinya et al., 2020). However, the review by Kohler et al. (2020) concludes that these fine-scale regeneration methods are not always successful because the shade-tolerant admixing species (such as beech or hornbeam) outcompete oak in gaps. In order to create suitable conditions for the oak regeneration, it is essential to explore its main drivers.

Both the review of Kohler et al. (2020) and Petritan et al. (2025) state that the most important factors for oak regeneration are light, competition, browsing, and initial seedling abundance. Another key environmental factor may be soil moisture (Götmark et al., 2011; Tinya et al., 2020). However, both light and soil moisture can also promote the herbaceous understorey and the shade-tolerant woody species, which can be strong competitors of oaks. Mölder et al. (2019b) identified competition from shade-tolerant species as a key factor, while Kohler et al. (2020) emphasized a trade-off between light and competition. At low light levels, oak cannot develop properly; at higher light levels, however, it can be outcompeted by other species. They point out that this trade-off is not well understood. According to Diaci et al. (2008) and Modrow et al. (2020), it is not possible to draw robust, general conclusions about adequate light levels because they are influenced by regional and local factors, such as climate or edaphic effects. Moreover,

the environmental demands and the competitive ability of saplings change with age, which also influences the outcome of the trade-off.

In continuous cover forestry, the balance between the optimal environmental conditions and competition can be adjusted by the size and shape of the gaps (Abd Latif and Blackburn, 2010; Garbarino et al., 2012; Vilhar et al., 2015). However, there is a lack of knowledge regarding the exact characteristics of the optimal gap types. Thus, further research is needed to determine the outcomes of available abiotic resources and competition in different gap types (Patterson et al., 2022).

Our study was conducted within the framework of the Pilis Gap Experiment. This is a multi-taxa forest ecology study initiated in 2018 in Central Hungary to examine the impacts of different-sized and shaped gaps on forest site conditions, biodiversity, and regeneration in an oak–hornbeam forest (<https://piliskiserlet.ecolres.hu/en>). The experiment is conducted in a stand with a homogeneous structure and species composition due to the former application of rotation forestry. The four gap types investigated are small circular (SC), small elongated (SE), large circular (LC), and large elongated (LE) gaps. Horváth et al. (2023) already explored the initial microclimatic responses to the different types of gap-cutting, concluding that directly after the interventions, light conditions are mainly influenced by gap size, while soil moisture is driven basically by gap shape, being higher in circular gaps than in elongated ones. They also found that all investigated gap types maintain the cool, humid forest microclimate. The paper by Tinya et al. (2025) described the development of the understorey vegetation in the different gap types during the first five years post-treatment, taking abiotic conditions into account. According to their results, the initial light surplus in large circular gaps disappears after a few years, and the increased soil moisture of circular gaps also decreases as the understorey and shrub layer become dense. Understorey cover increases in all gaps, but its composition depends on gap type. In large circular gaps, bramble (*Rubus fruticosus* agg.) becomes dominant, while in large elongated gaps, graminoid species (*Melica uniflora*, *Carex pilosa*) show a transient increase.

The aim of this paper is to investigate the regeneration success of sessile oak in the differently sized and shaped gaps over a six-year period, taking abiotic conditions and competition into account. We focused on the following aspects of regeneration in the different gap types:

- (1) Light and soil moisture conditions as background factors for regeneration in the sixth post-treatment year;
- (2) Maintenance of the acorn supply;
- (3) The survival rate and growth of oak saplings when competition is excluded through tending, and they are only affected by the abiotic conditions;
- (4) Changes in species richness, abundance, height, and composition of the natural woody regeneration;
- (5) Changes in the abundance and height of oak saplings in the presence of natural competition (in untended quadrats).

Based on these investigations, we tried to explore how the developmental success of oak saplings can be explained by abiotic conditions and competition. We hypothesize that abiotic conditions (light and soil moisture) are initially most favourable for the oak saplings in the large circular gaps. However, when competition is also taken into account, gap types that initially offer more moderate resources (smaller or elongated gaps) are better for oaks during the first few years, due to the lower competitive pressure. Nevertheless, after a few years, small gaps do not provide enough light for the oak saplings without further extension. We also expect that in such homogeneous stands, gap-cutting will increase the diversity of woody species in the regeneration layer and thus potentially contribute to the transformation to mixed forests in the long term.

2. Materials and methods

2.1. Study area

The Pilis Gap Experiment is located on the Hosszú Hill (Pilis Mountains, Transdanubian Range, Hungary, 47°40' N, 18°54' E; Fig. S1a and S1b), at an altitude of 390–460 m, on slightly northeast-facing slopes ($18.2^\circ \pm 14.9^\circ$). The area has a humid continental climate with a mean annual temperature of 9.0–9.5 °C. The mean annual precipitation is 650 mm (Dövényi, 2010). The bedrock of the study area consists of sandstone with loess mixed with limestone (Dövényi, 2010). Luvisols (mainly brown forest soils with clay illuviation) and Rendzic Leptosol are the most common soil types. The soil has a slightly acid pH value of 4.6 ± 0.2 , and its depth varies between 70 and 150 cm with a gentle topographic gradient (Horváth et al., 2023). The study area is covered by Pannonic woods with *Quercus petraea* and *Carpinus betulus* (Natura, 2000 code: 91G0; Council, 1992), which were managed by rotation forestry (regular shelterwood system) in the past (Matthews, 1991). As a result of this management type, the stand prior to the experimental treatments was even-aged (90 years old) and had a uniform structure and species composition. The upper canopy layer was dominated by sessile oak (*Quercus petraea*), with hornbeam (*Carpinus betulus*) forming a secondary canopy layer (Horváth et al., 2023; Table S1). The most common admixing species were Turkey oak (*Quercus cerris*), manna ash (*Fraxinus ornus*), and wild service tree (*Sorbus torminalis*), but none of them exceeded 1% (Table S1). The shrub layer was sparse and consisted mainly of hornbeam and manna ash patches with some admixing shrub species (such as common dogwood—*Cornus sanguinea*, cornel—*Cornus mas*, common hawthorn—*Crataegus monogyna*, and common privet—*Ligustrum vulgare*). After a thinning in 2010, a dense understory of both general and mesic forest species has developed, dominated by *Carex pilosa*, *Melica uniflora*, and *Galium schultesii*. At the establishment of the experimental site, the entire ca. 10 ha study area was fenced against ungulate browsing.

2.2. Experimental design

Gaps were created in February 2019. Five treatments were applied according to a randomised complete block design. They were replicated in six blocks, resulting in a total of 30 sampling plots (Fig. S1c).

The treatments were as follows:

- Control (CO): It is part of the mature closed stand where there has been no intervention.
- Large circular gap (LC): A circular gap of 20 m in diameter (about one tree height). The area is approximately 300 m².
- Small circular gap (SC): A circular gap with a diameter of 14 m and an area of approximately 150 m².
- Large elongated gap (LE): A rectangular gap of 30 m × 10 m in length and width, oriented north-south, with an area of about 300 m².
- Small elongated gap (SE): A rectangular gap measuring 21 m × 7 m in length and width, oriented north-south, with an area of approximately 150 m².

The investigated gap sizes were chosen based on the field experience of practitioners. Circular gaps with a diameter of around one tree height (area of around 300 m²) are often used as a tool for continuous cover forestry in Hungarian oak-dominated stands (Bartha et al., 2014; Appendix A of Horváth et al., 2023). However, foresters found that the increased light levels in these gaps put serious competitive pressure on oak saplings. Some observations suggested that smaller gaps could be more favourable, therefore, a second gap size was employed with an area half that of the 300 m² ones.

Since this study focused exclusively on the effects of the primary gap characteristics (i.e., size and shape), all other gap attributes were

standardized. In particular, elongated gaps were consistently oriented along a north-south axis. This orientation—more common in practice than east-west—has the advantage that, in the northern hemisphere, where most incoming radiation comes from the south, it provides a substantial additional light to saplings in the northern half of the gap despite its narrow width.

Gap dimensions were defined at ground level following the “expanded gap” concept (Runkle, 1982), meaning all trees with trunks within these boundaries were removed. This approach was chosen over “canopy gaps” because canopy openings influence not only the area of the canopy gap itself but also areas extending several meters toward the trunks of the surrounding trees, beneath the canopy. As a result, canopy layer gaps developed irregular shapes and sizes (Fig. S1c). Nevertheless, we confirmed that the intended design—distinct gap shapes and sizes—was maintained, with significant differences in these characteristics among treatments (see Appendix C of Horváth et al., 2023).

2.3. Data collection

2.3.1. Regeneration survey

Compared to closed forests, abiotic conditions (such as the soil moisture, diffuse light, and temperature) change most significantly in the centre of gaps, because it is the farthest from the closed stand (Gray et al., 2002; Ritter et al., 2005). Therefore, we expected the most significant changes in the vegetation to be visible in the middle of the gaps. Consequently, the majority of vegetation samples (herbs, acorns, and natural regeneration under natural competition) were taken from the gap centres. However, we also aimed to explore the best possible growth rates of oak seedlings that they can show under the abiotic conditions provided by the different gap types, in the absence of competition. As direct light, which is also a crucial factor for oak seedlings (Ligot et al., 2013), is the greatest in the northern part of the gaps (Gray et al., 2002; Ritter et al., 2005; Horváth et al., 2023), we examined the growth of tended oak saplings in this area. We assumed that the southern part of the gaps, which is more shaded (Gray et al., 2002; Ritter et al., 2005; Horváth et al., 2023), would provide unfavourable conditions for oaks; therefore, this area was not sampled.

1) Acorn counting

Fallen oak acorns were counted in 2020 (second year after the interventions), which was a mast year. Acorns were counted in one 0.5 m × 0.5 m quadrat in the centre of each gap and control plot (Fig. 1).

2) Survival of tended sessile oak saplings

In the following, we use the term “sapling” to refer to all individuals of woody regeneration less than 5 cm in diameter at breast height. As seedlings were not investigated separately, we included even the smallest individuals under this term, too. The number of living oak saplings (with green leaves or at least living buds) was recorded in four 0.5 m × 0.5 m quadrats in the northern part of each of the 30 plots. The four quadrats were arranged in a square formation, with a 70 cm buffer zone between them (Fig. 1). The saplings belonged predominantly to one cohort, germinating from the acorns of the mast year of 2018 (before the experimental interventions). Counting was done in early fall every year from 2019 to 2024. When the competing saplings of other woody species and bramble became abundant, they were removed, eliminating competition during the vegetation period. This tending ensured a state of no natural competition, allowing for the study of the direct effects of abiotic conditions on survival and growth. Newly established oak saplings (not present in 2019) were also eliminated each year, so the mortality of the originally assessed sapling cohort could be followed.

3) Height growth of individual tended sessile oak saplings

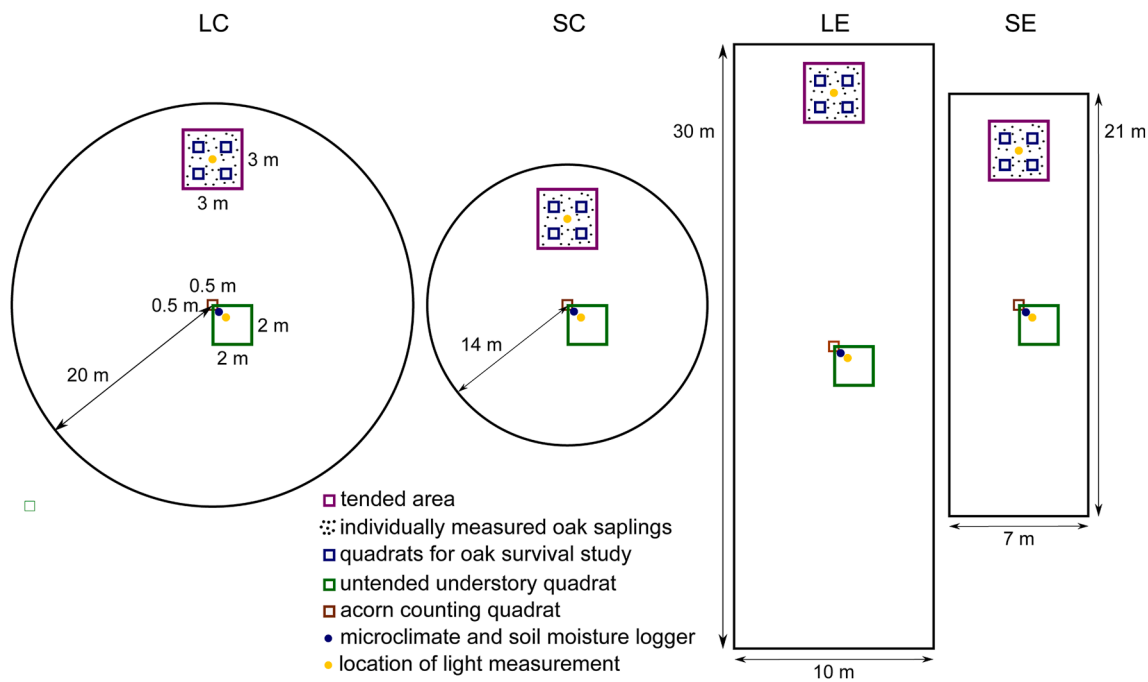


Fig. 1. Sampling design within the different gap types. LC = large circular, SC = small circular, LE = large elongated, SE = small elongated. Design in closed forest control plots follows the design of SC gaps.

In each plot, 30 sessile oak saplings (900 individuals in total) were selected from the natural regeneration for individual height increment measurements. The saplings were even-aged and derived from acorns falling in the mast year 2018. They were selected in the fall of 2020 from the survivors after intensive mortality in the first year, and were located surrounding the quadrats of the survival study in the northern part of the gaps (Fig. 1). Where possible, selected saplings were between 10 and 20 cm tall at the start of the survey (their full range was between 9 and 29 cm) and were spaced at least 40 cm apart. Saplings were marked with tags containing an identification number unique for each individual. The height of the saplings was measured in August–September in 2020 and 2024. Competing vegetation (woody competitors and bramble) was removed when it started to overgrow the oak saplings.

4) Sampling of the natural regeneration in untended quadrats

In the centre of each of the 30 plots, one 2 m × 2 m quadrat was established to sample the understory vegetation (Fig. 1). In addition to estimating the cover of the understory species (Tinya et al., 2025, not shown here), the abundance of woody species was counted in the quadrats before the interventions (in 2018) and in the sixth post-treatment year (2024). The number of individuals was recorded separately for each woody species for four height categories as follows:

(a) 0–20 cm, (b) 20–50 cm, (c) 50–130 cm, (d) >130 cm, but the diameter at breast height is below 5 cm.

In 2024, the height of the tallest individual of each woody species in each quadrat was also measured. The nomenclature of the plant species follows Király (2009).

2.3.2. Light and soil moisture conditions

To estimate light, hemispherical photographs were taken at two points in each plot: (1) above the tended, individually marked saplings in the northern part of the plots, and (2) above the untended quadrats in the gap centres (Fig. 1). A camera (PIXPRO SP360, KODAK) was used, at a height of 1.3 m. Above the tended saplings, the obtained light values were influenced only by the overstory structure (different types of canopy gaps or closed canopy). In the gap centres, due to the lack of tending, the developed shrub layer could shade the camera in some

plots. Therefore, the measured light values here represent the light conditions in the presence of the entire natural vegetation. All photographs were taken at the peak of the growing season (early July), at dusk to reduce any bias due to the capture of the sun disk or the reflection of direct sunlight on the leaves. We calculated the diffuse and direct components of the incoming radiation (indirect and direct site factors, respectively; %) relative to above-canopy light, using the WinSCANOPY 2019 software (Regent Instruments Inc., Canada). Radiation was calculated from May 1 to September 30.

Soil moisture (volumetric water content (VWC)) was measured in the untended quadrats in the gap centre (Fig. 1), by TMS-4 loggers, which continuously collected data from the upper 14 cm soil layer with 15-min logging intervals (TOMST s.r.o., Wild et al., 2019). Soil moisture data were collected throughout the year. Here, we only use data from the vegetation season (May 1st to September 30th).

Both light and soil moisture were measured in each year of the study, but here we present only the results of the sixth year (2024). The first-year light and soil moisture conditions were published in detail by Horváth et al. (2023), while the five-year results were presented by Tinya et al. (2025).

2.4. Data analysis

The number of acorns counted in the 0.5 m × 0.5 m quadrats was extrapolated to 1 m². For the survival analysis of the tended sessile oak saplings, the abundance data of the four 0.5 m × 0.5 m quadrats were pooled in each plot. The percentage survival rate was calculated for each year from 2020 to 2024, compared to the number of saplings in the first year after the interventions (2019).

The four-year height growth of the individually marked tended saplings was calculated as the height of the sapling in 2024 minus its height in 2020. Negative growth values could occur if the shoots of a sapling dried out and it sprouted from the bottom up. Of the original 900 individuals, only 505 survived until 2024, therefore only these were used in the height growth analysis.

In the natural regeneration of the untended 2 m × 2 m quadrats, only three species were sufficiently abundant (more than 20 individuals in total in 2024) for statistical analysis: sessile oak, hornbeam, and

dogwood. For these species, the abundance change was calculated separately for the four size categories, as the difference in the number of individuals between 2024 and 2018.

The maximum development of the three most abundant species (sessile oak, hornbeam, and dogwood) in the different treatments was described by the height of the tallest sapling of the quadrats in 2024. However, due to the low number of quadrats (4 in total) containing dogwood, no statistical analysis was performed for the maximum height of this species.

Linear mixed-effects models were built at the plot level to examine the effect of silvicultural treatments on abiotic conditions and regeneration variables (Zuur et al., 2009). Dependent variables were the relative diffuse and direct light, VWC, the number of acorns, the survival rate of tended saplings, the height growth of the individually marked tended saplings, changes in the species richness of the woody regeneration, regeneration abundance, and height of the tallest saplings in the untended quadrats. Fixed effects were the treatments (four gap types and control), while block was used as a random factor. In the case of the height growth of the individual saplings, plot was also used as a random factor nested within block. In the case of the soil moisture models, monthly averages of the daily means were used as soil moisture data (i.e., five data per year: May, June, July, August, and September), and month was used as a second random factor.

Linear mixed-effects models with Gaussian error distribution were used for the light variables, VWC, height growth of tended saplings, and height of the tallest saplings in the untended quadrats. To meet the normality requirement for the residual distributions, square root transformation was applied for the height growth of tended oak saplings. A generalised linear mixed-effects model with a beta distribution and a logit link function was applied to analyse the survival rate of tended saplings. A Poisson distribution was applied for the number of acorns, changes in species richness of woody regeneration, and regeneration abundance. If the treatment effect was significant ($P < 0.05$), multiple comparisons were performed with user-defined contrasts to find the significantly different treatment types (Bretz et al., 2010).

All analyses were performed with R version 4.4.1 (R Core Team, 2024). General linear mixed-effects models were conducted using the R package “nlme” (Pinheiro et al., 2022), while “glmmTMB” (Brooks et al., 2017) was used for the generalised linear mixed model with a beta

distribution and “lme4” (Bates et al., 2015) was applied to the models with a Poisson distribution. Multiple comparisons were performed using the “multcomp” package (Hothorn et al., 2023). The determination coefficients of the mixed models were calculated using the “MuMIn” package (Bartoň, 2022). For visualization, the “ggplot2” package was used (Wickham, 2016).

3. Results

3.1. Light and soil moisture conditions

In the sixth year after the interventions (2024), the relative diffuse light above the tended saplings was significantly higher than in the closed stand only in the large gaps ($F = 3.350$, $P = 0.030$, $R_c^2 = 0.316$, Fig. 2a). It was highest in the large circular gaps, which were also significantly different from the small circular gaps. In contrast, in the untended understory quadrats, where the vegetation was allowed to grow above the height of the light measurements, in the sixth year after gap creation, relative diffuse light did not differ significantly between treatments ($F = 2.488$, $P = 0.076$, $R_c^2 = 0.256$, Fig. 2b). However, the trend was opposite to that in the tended part: without tending, the mean and median light values in the large gaps were below the values in the small gaps. The results for comparing direct light across the different treatments were similar (Fig. S2).

The soil moisture model for the sixth year after the interventions was also significant ($F = 4.867$, $P = 0.001$, $R_c^2 = 0.626$), VWC was significantly higher in the elongated gaps than in the control, while in the circular gaps it was similar to the control (Fig. 3).

3.2. Acorn supply

In a mast year, two years after the gap creation (2020), the sessile oak acorn supply varied from 0 to 580 acorns·m⁻². Gap centres received a significantly lower number of acorns than the uncut stand ($\text{Chi}^2 = 2,096.9$, $P < 2.2e^{-16}$, $R_c^2 = 0.997$). Among the gap centres, those of small elongated ones received the most acorns, while those of small circular ones received less, and there were almost no acorns in the centre of the large gaps (Fig. 4).

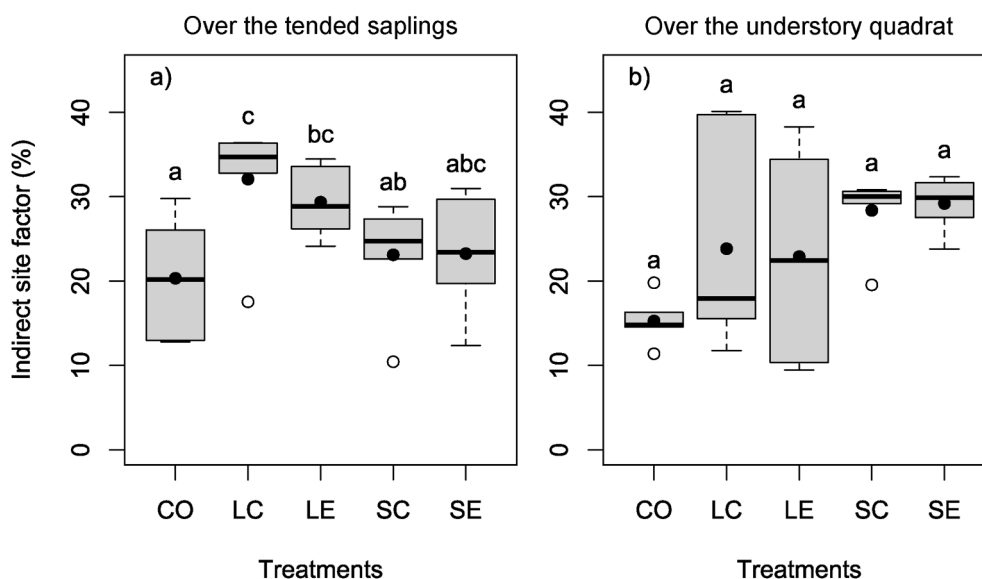


Fig. 2. Boxplots of the relative diffuse light (indirect site factor, %) measured at 1.3 m height (a) over the tended oak saplings and (b) over the untended understory quadrats, in the sixth year after the gap creation (2024). Horizontal lines indicate the median, black dots show the mean, and grey boxes represent the interquartile range. The range without outliers (empty dots) is indicated by whiskers. CO = uncut control. Different letters indicate significant differences at $P < 0.05$ level.

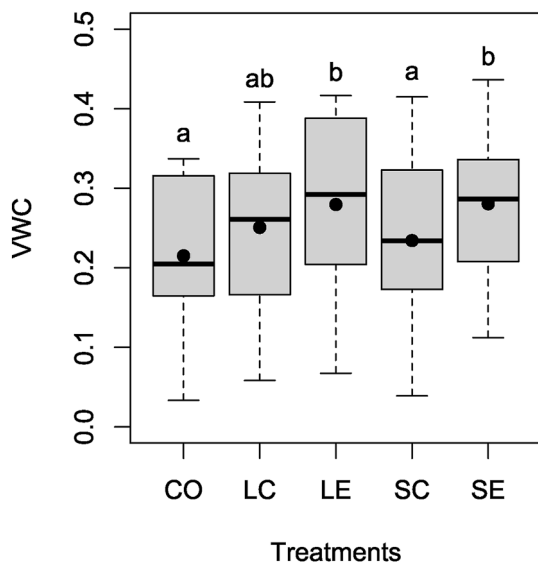


Fig. 3. Boxplot of the soil water content (VWC) in the untended understory quadrats, in the sixth year after the gap creation (2024). Different letters indicate significant differences at $P < 0.05$ level.

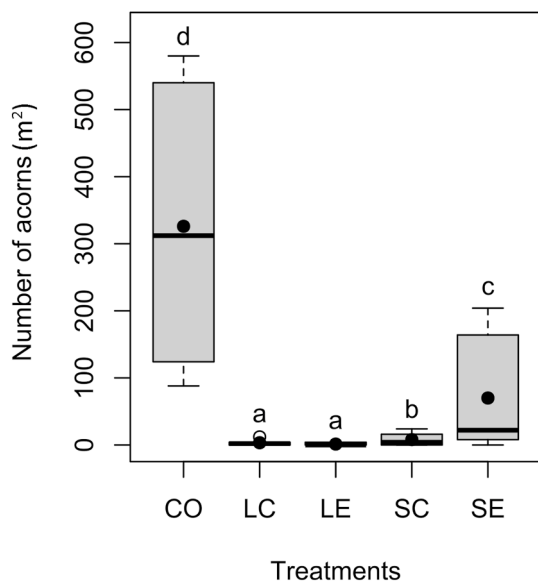


Fig. 4. Boxplot of the treatment effect on the sessile oak (*Quercus petraea*) acorn supply in a mast year two years after the interventions (2020). Different letters indicate significant differences at $P < 0.05$ level.

3.3. Survival and height growth of tended oak saplings

In the first year after the interventions (2019), we counted a total of 10,365 sessile oak saplings in the 30 plots, mainly from the cohort of the mast year just before the gap creation. Their number decreased in all treatments during the first six years (Fig. 5); in the sixth year, only 1,580 saplings were counted. Notably, in the fourth year (2022), the number of saplings in the large gaps and small circular gaps temporarily declined relative to the following years. This decrease can be attributed to the extreme drought that year, which caused several saplings to lose their leaves and appear dead; however, they resprouted in the following year.

Until the third year after germination and gap-cutting (2021), there was no difference in survival between treatments. However, from the fourth year, survival rate in the closed stand became significantly lower than in the gaps. The survival of the saplings was not significantly

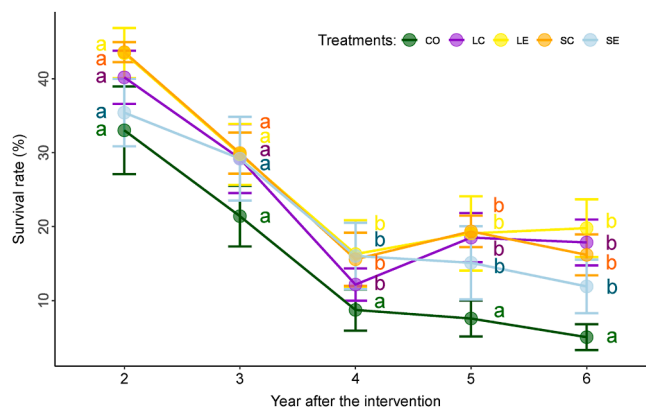


Fig. 5. Percentage survival rate of tended sessile oak (*Quercus petraea*) saplings in the different treatments, compared to the abundance in the first year after the interventions (2019). Different letters indicate significant differences between the treatments within a given year at $P < 0.05$ level.

affected by the gap type, but from the fifth year onwards, there is a trend whereby survival was slightly lower in the SE gaps than in the other gap types (Fig. 5 and Table 1).

In the sixth year after the interventions, the height of the individually measured tended sessile oak saplings ranged from 8 to 94 cm. There was significant difference in height growth among the different treatments ($F = 7.176, P < 0.001, R^2 = 0.406$), with the largest increment in the large circular gaps (Fig. 6). It was intermediate in large elongated and small circular gaps, while it was the lowest among gap types in the small elongated gaps. However, saplings grew significantly better even in this gap type than in the closed control.

3.4. Species richness of the natural regeneration

A total of 12 woody species (8 tree and 3 shrub species) were recorded in the $2\text{ m} \times 2\text{ m}$ quadrats in the centre of the plots during the 7-year long survey from the before-treatment year to the sixth year after interventions (Table S2). Ten species were present in all years, whereas saplings of two additional species occurred only transiently, appearing for 2–3 years in a single plot each before disappearing. Changes in the species richness within the plots were very small (between -1 in a control plot and $+2$ in some small gaps) and therefore did not differ between treatments ($\text{Chi}^2 = 0.742, P = 0.946, R^2 = 0.029$). Most of the species occurred in low abundance, with the exception of sessile oak, hornbeam, and dogwood.

3.5. Abundance and size of the most prevalent competitor species and sessile oak in the untended quadrats

In the case of hornbeam and dogwood, the treatment types differed significantly only in the abundance change of the large saplings ($>130\text{ cm}$ height), while they did not differ in the abundance change of the smaller size categories (Table 2). The number of large hornbeam saplings increased the most in the circular gaps, especially in the SC gap

Table 1

Results of the linear mixed-effects models for sessile oak survival in the different treatments compared to abundance in the first year after the interventions (2019). Values in bold indicate significant treatment effects.

Investigated time interval	Chi ²	P	R ² _c
2019–2020	7.452	0.114	0.423
2019–2021	4.323	0.364	0.254
2019–2022	18.440	0.001	0.559
2019–2023	24.800	0.000	0.665
2019–2024	29.314	0.000	0.755

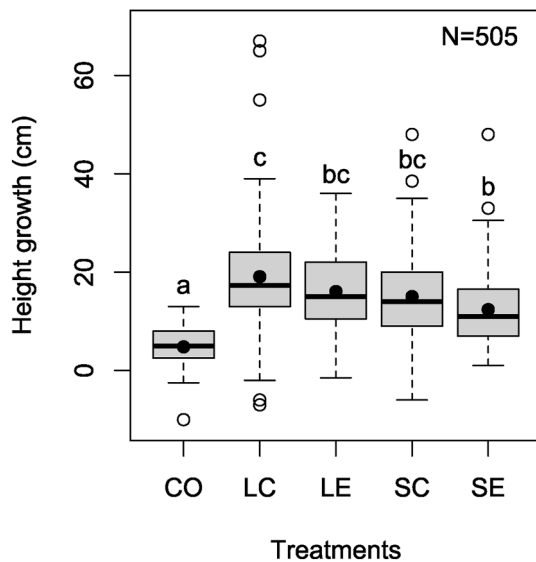


Fig. 6. Boxplot of the four-year height growth of tended sessile oak (*Quercus petraea*) in the different treatments in the study years (2020–2024). Different letters indicate significant differences at $P < 0.05$ level.

(Figs. 7a and S3). Originally, dogwood was only present in some of the large gaps and in one of the control plots. The abundance of large dogwood saplings showed a great increase in the large circular gaps, and an intermediate increase in the large elongated gaps (Figs. 7b and S4). The species was originally absent from small gaps, failing to establish even after interventions.

In the case of changes in the abundance of sessile oak saplings, a significant treatment effect was observed in all size categories (Fig. S5 and Table 2). The abundance of small saplings (less than 20 cm in height) increased the most significantly in the small elongated gaps (Fig. 7c). There was little change in the control and circular gaps, while the number of small saplings decreased in the large elongated gap, partly due to the saplings growing into the larger height categories. The number of oaks in the second and third size categories (20–50 and 50–130 cm, respectively) increased significantly more in all gap types than in the closed stand. The largest increase was observed in the large elongated gaps. Meanwhile, the number of large saplings (over 130 cm tall) only increased in the large circular and elongated gaps. The total abundance of oak saplings (across all size categories) increased the most in the small elongated gaps.

The tallest hornbeam saplings of the 2 m × 2 m untended quadrats were significantly higher in the large circular gaps than in the control, while they were intermediate in the small circular gaps ($F = 4.252$, $P < 0.033$, $R_c^2 = 0.486$, Fig. 8a). They were not significantly higher in the

elongated gaps than in the control. The height of the tallest dogwood saplings was similar in the two large gap types, it was low in the control and they were absent in the small gaps (Fig. 8b). The height of the tallest sessile oak saplings was the largest in the large gaps and intermediate in the small circular gaps ($F = 11.388$, $P < 1e^{-04}$, $R_c^2 = 0.658$, Fig. 8c). In the small elongated gaps, it was not significantly larger than in the control.

4. Discussion

4.1. Environmental conditions of the different gap types

If the shrub layer and bramble are removed by tending, leaving the light conditions solely determined by the overstory, the initial high light availability of the large gaps (Horváth et al., 2023) remains stable even in the sixth year after the interventions. However, in the untended quadrats, the initial high light level of the large gaps at 1.3 m height becomes variable by the sixth year: In some gaps, the light level decreases below that of the closed control (about 10%). This decline in the large gaps was already observed in the fifth year and is caused by the dense shrub layer that has developed (Kohler et al., 2020; Tinya et al., 2025). Meanwhile, in the small gaps, the initially moderately increased light remains relatively stable, as the height of the light measurement (1.3 m) is not overtopped by the regeneration layer, only the lateral ingrowth of the canopy of the adjacent trees results in a slight decrease.

Horváth et al. (2023) found that soil moisture initially increased significantly in circular gaps compared to closed forest control, while the increase in the elongated gaps was moderate and insignificant. This was attributed to reduced root extension of adjacent trees into circular gaps, leading to lower transpiration (Horváth et al., 2023). However, after a few years, this trend reversed, and circular gaps lost their soil moisture surplus (Tinya et al., 2025). Our results show that by year six, the difference between circular and the moister elongated gaps becomes more pronounced. Several studies indicate that, beyond overstory trees, woody regeneration and herbaceous understory reduce soil moisture through increased rainfall interception and transpiration (Balandier et al., 2022; Meijers et al., 2025). Thus, denser vegetation developing in initially moister circular gaps likely creates negative feedback, rapidly restoring moisture levels to those of a closed stand. Based on our results, over time, only elongated gaps retain a soil moisture surplus relative to closed forest.

4.2. Species richness and composition of the natural regeneration

Regardless of gap type, no substantial changes in woody species richness were found in gap centres, despite these areas experiencing the most intense environmental alterations compared to closed stands (Gray et al., 2002; Ritter et al., 2005). Most admixing species occurred at very low abundance. Regeneration diversity and abundance are strongly

Table 2

Results of the generalised linear mixed-effects models for the abundance change of saplings of the three most abundant woody species, separately for four size categories. Fixed effect: treatment types, random effect: block. Size categories: 1: 0–20 cm, 2: 20–50 cm, 3: 50–130 cm, 4: >130 cm, but diameter at breast height <5 cm. Values in bold indicate significant relationships. In these cases, the results of post-hoc tests are shown.

Species	Size categories	Chi ²	p	R _c ²	CO	LC	LE	SC	SE
<i>Carpinus betulus</i>	1	4.199	0.380	0.107					
	2	2.920	0.571	0.153					
	3	1.642	0.801	0.056					
	4	10.607	0.031	0.374	ab	ab	a	b	ab
<i>Cornus sanguinea</i>	1	1.222	0.875	0.038					
	2	1.879	0.758	0.055					
	3	0.617	0.961	0.021					
	4	14.003	0.007	0.350	ab	b	ab	a	a
<i>Quercus petraea</i>	1	228.620	0.000	0.920	c	b	a	bc	d
	2	356.920	0.000	0.993	a	b	d	c	c
	3	8.915	0.000	0.640	a	b	c	c	b
	4	12.858	0.012	0.356	ab	b	ab	ab	a

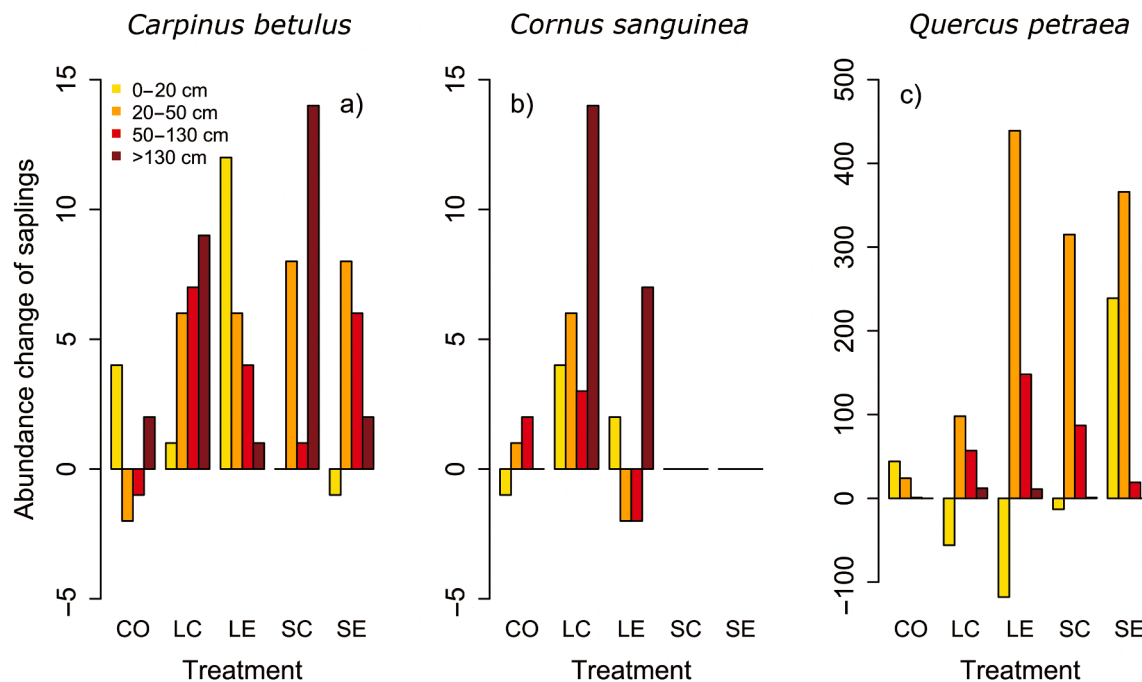


Fig. 7. Abundance change of the saplings of the studied species in the different treatments, between the year before the treatment (2018) and the sixth year after the interventions (2024). (a) hornbeam (*Carpinus betulus*), (b) dogwood (*Cornus sanguinea*), (c) sessile oak (*Quercus petraea*). Columns show the change in the summed number of saplings in the 2 m × 2 m quadrats for the six blocks. Different colours indicate different height categories: yellow: 0–20 cm, orange: 20–50 cm, red: 50–130 cm, maroon: >130 cm, but diameter at breast height <5 cm. The scale of the y-axis is different for sessile oak.

shaped by the overstory composition of both the studied stand and the surrounding forests in the landscape, which is determined by management history (McKenzie et al., 2000; Tinya et al., 2019). Although Sabo et al. (2019) found that gap creation increased regeneration richness in temperate hardwood forests, they studied more species-rich stands. In our case, the surrounding stands were even-aged, homogeneous, and species-poor due to uniform shelterwood management, which limited seed sources for the establishment of new admixing species. The investigated six-year period was also too short for propagule arrival from nearby areas. Additionally, slightly acidic soils of the study area might be unfavourable for admixing species (Dyderski et al., 2025) and may also reduce their response to increased light availability (Modrý et al., 2004; Dobrowolska et al., 2011).

4.3. Regeneration of sessile oak

We found that oak regeneration can be initiated in all 150–300 m² gap types, both circular and elongated. However, growth intensity differs due to variation in abiotic conditions—such as light, soil moisture, and competitive pressure. In addition, abiotic factors also indirectly influence oak regeneration by shaping the abundance and growth of competing species (Annighöfer et al., 2015; Kohler et al., 2020).

4.3.1. Regeneration without competition

During the first three years after gap creation, survival rates of newly established oak saplings did not differ between the gaps and the closed stand. Early survival is mainly driven by acorn size (Annighöfer et al., 2015), but as nutrient reserves are depleted and root system develops—enabling effective water uptake for further development—environmental conditions gain importance, and oak seedlings become increasingly light-demanding (von Lüpke, 1998; Ostrogović et al., 2010; Mölder et al., 2019a). This leads to higher mortality in closed stands from the fourth year onward.

Young oak saplings need a relative light of about 20% for their continuous growth (von Lüpke, 1998; Ligot et al., 2013). This amount of light was provided by all of our gap types, resulting in significantly

better survival and height growth of the tended saplings in all gap types than in the closed stand.

Initially, large circular gaps exhibited the highest levels of both diffuse light and initial soil moisture. While their maxima occurred in gap centres, increased values were also observed in the northern part of the gaps (Horváth et al., 2023), where the tended saplings were located. Therefore, in the case of tending, favourable abiotic conditions of this gap type result in an enhanced height growth of the oak saplings. This supports findings that oaks require larger, and thus brighter gaps than shade-tolerant species (Schumann et al., 2003; Ligot et al., 2013; Tinya et al., 2019; Modrow et al., 2025). Our results are also consistent with Götmarm et al. (2011), who demonstrated the importance of soil moisture for successful oak regeneration.

Large elongated gaps provide similar light conditions but lower initial soil moisture than large circular gaps, while small circular gaps are significantly shadier, but their soil moisture content is similar to that of large circular gaps (Horváth et al., 2023; Tinya et al., 2025). Sapling growth was similar in these two gap types and was slightly lower than in the large circular gaps. It supports the hypothesis of Annighöfer et al. (2015) and the conclusion of Mölder et al. (2019a) that, at higher soil moisture levels, light demands of oak saplings are lower, i.e., light requirement depends on water supply.

When the initial level of both resources is relatively low, as in small elongated gaps, growth is significantly reduced compared to large circular gaps, although it remains significantly higher than in the closed forest. Diaci et al. (2008) also found that oak regeneration can be initiated under limited light conditions, but growth is slower than in larger cutting areas. Nevertheless, conditions of small elongated gaps appear suitable for oak saplings only in the early years; from the fifth year onward, survival rate tends to be slightly lower in small elongated gaps than in other gap types. This is consistent with previous studies stating that light demand of oak saplings increases with age (von Lüpke, 1998; Annighöfer et al., 2015; Petritan et al., 2025).

According to our results, sapling survival under low light levels also depends on soil moisture availability. In small circular gaps, higher initial soil moisture mitigates the effect of low light. Although soil

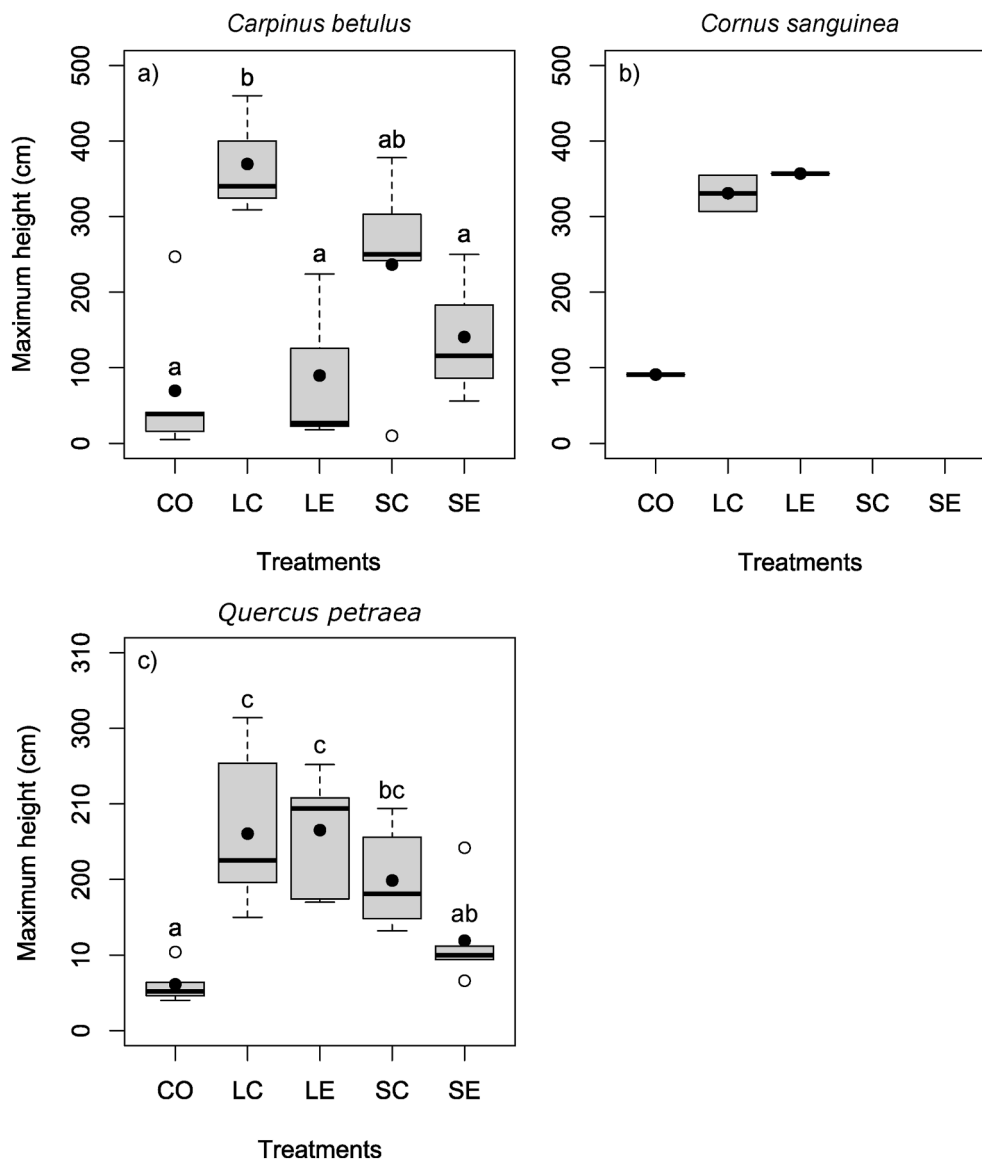


Fig. 8. Boxplots of the maximum sapling height for the three most abundant woody species in the 2 m × 2 m untended understory quadrats in the different treatments. (a) hornbeam (*Carpinus betulus*), (b) dogwood (*Cornus sanguinea*), (c) sessile oak (*Quercus petraea*). Data were collected in the sixth year after the gap creation (2024). Different letters indicate significant differences at $P < 0.05$ level. The scale of the y-axis is different for sessile oak.

moisture surplus of the circular gaps disappears after a few years, its higher initial value may contribute to later survival by supporting the development of more vigorous saplings.

4.3.2. Regeneration under competition

Competition by fast-growing, shade-tolerant species must be considered across all gap types, consistent with previous findings (Tinya et al., 2020; Modrow et al., 2025). Contrary to the statements of Kobe et al. (1995), higher light availability *per se* does not necessarily favour light-demanding species over shade-tolerant ones, as beech and hornbeam can outcompete oak over a wide range of light conditions (from 1% to 60% relative light, Ligot et al., 2013; Dietz et al., 2022). According to Modrý et al. (2004), hornbeam density is positively related to canopy openness, similar to light-demanding species. Modrow et al. (2025) found an increasing photosynthetic capacity and growth of hornbeam with increased light exposure between 1% and 70% relative total light. In contrast, we identified no clear relationship between hornbeam abundance and growth and gap size; instead, hornbeam was more abundant and vigorous in initially moister circular gaps than in drier

elongated ones, highlighting the importance of moisture conditions (Dobrowolska et al., 2022; Thom et al., 2026).

Beyond oak and hornbeam, dogwood was the only woody species initially present in notable abundance in the regeneration layer. It did not colonise new plots, and thus analyses were limited to plots where it was originally present (i.e., in large gaps and control plots). Common dogwood is a tall, fast-growing shrub with strong competitive ability and clonal spread (Kollmann and Grubb, 2001; Deiller et al., 2003). Among our plots, it only expanded within gaps, which is in agreement with Kollmann (1997), stating that it is a light-demanding forest species that typically occurs in gaps and at forest edges. Ellenberg et al. (1992) and Grubb et al. (1996) also emphasize dogwood's light requirements, but report limited information on its soil moisture demands. Our study showed that gaps where a high amount of light is combined with high initial soil moisture (i.e., large circular gaps) promote dogwood's spread, making it a major competitor to oak.

Large circular gaps also favoured bramble, the dominant herbaceous competitor (Tinya et al., 2025), resulting in the strongest overall competitive pressure. Widen et al. (2018) also found that larger gaps support persistent, dense *Rubus* cover, while Walters et al. (2016)

generally found a denser understory and shrub layer in larger gaps. In our study, dense shrub and bramble cover markedly reduced light availability and soil moisture in untended quadrats of large gaps (especially in circular ones) by the sixth year. Consequently, oak abundance declined, though the few saplings that overgrew the competitors exhibited strong growth, indicating that survival and growth can respond differently (Dietz et al., 2022).

In small circular gaps, competitive pressure is comparable to that in large circular gaps. Although in our case dogwood was absent and bramble cover was also slightly lower (Tinya et al., 2025), hornbeam abundance was slightly higher, likely due to the higher initial soil moisture of this gap type. In addition, initial light was significantly lower here (Horváth et al., 2023). Consequently, oak regeneration success was similar to that in large circular gaps, in terms of both abundance and growth. According to these findings, reducing gap size alone does not mitigate the competitive disadvantages of large circular gaps.

In contrast, gap shape proved effective in controlling hornbeam competition. Large elongated gaps initially combine high light with moderately increased soil moisture levels (Horváth et al., 2023; Tinya et al., 2025), allowing oak to remain competitive. Even in initially moist gap centres (Horváth et al., 2023), most of the hornbeam saplings remained small, while the tallest oaks overtopped them. In addition, medium-sized oak saplings (20–50 and 50–130 cm height) were more abundant than in large circular gaps, providing greater regeneration security. The fact that there is a gap type where oak has a relatively good competitive ability contradicts the results of Ligot et al. (2013) for the Ardennes, but according to Mölder et al. (2019a), the outcome of competition depends on climate and site conditions. It may be easier to give oak a competitive advantage in drier, more continental climates (such as those found in Hungary) than in more Atlantic climates. Lower dogwood and bramble abundance in large elongated gaps may further contribute to a better oak performance in this gap type (Tinya et al., 2025). Nicolescu et al. (2025) also recommend the use of elliptical gaps instead of circular ones in mixed oak stands with shade-tolerant competitors, which is in agreement with our findings.

Among gap types, height growth of oak saplings was the lowest in the untended quadrats of small elongated gaps, yet total abundance was the highest here. This likely reflects the reduced resource surplus and thus low competition pressure in this gap type. In the absence of dense vegetation, soil moisture and light level remained stable over time. Regarding the trade-off between light and competition, optimal conditions for oak regeneration may occur at about 20%–30% relative light (Kohler et al., 2020). Above this level, increasing light does not substantially enhance oak growth but continues to favour hornbeam (Modrow et al., 2025). In our study, initially, the recommended 20%–30% relative light level was ensured in small gaps (Tinya et al., 2025), while in the larger gaps, the higher initial light level promoted competition, which ultimately reduced light availability.

Finally, small elongated gaps uniquely ensure acorn dispersal across the entire gap area, including centres. Dietz et al. (2022) emphasize that proximity to parent trees is more critical for abundant regeneration than interspecific competition or light.

4.4. Implications for management

Tending capacity is a key constraint in management planning (Mölder et al., 2019b), alongside sapling growth rate and propagule supply following canopy opening. Our results provide guidance for these decisions.

According to our findings, oak regeneration can be initiated in all 150–300 m² gaps, regardless of their shape. Controlling fast-growing competitors is required in all gap types, but with varying intensity. Initially, large circular gaps offer the most favourable abiotic conditions for oak, but competing vegetation benefits even more than the oak. Therefore, this gap type requires intensive tending to maintain sufficient

sapling density. Although height growth is the highest here, without tending only a few individuals can overtop the competitors.

Where tending capacity is limited, elongated gaps are recommended, as they reduce competitive pressure, resulting in higher oak abundance. Among elongated gaps, larger ones enhance height growth, whereas small elongated gaps maximise sapling density under untended conditions. Although height growth is slower in the smaller gaps, this is less critical under continuous cover forestry, where there is no prescribed time to complete regeneration. Slower growth may also promote root development (Larsen and Johnson, 1998), thereby increasing long-term stability, although this was not assessed here. A limitation is that small elongated gaps provide adequate light conditions only in the early years and may require later expansion to prevent mortality due to shading (Ligot et al., 2013; Lu et al., 2021). Nevertheless, an important advantage of small elongated gaps is continuous acorn input, enabling regeneration even after initial failure. In contrast, other gap types should be opened after many years, over existing seedlings or freshly fallen acorns, and regeneration failure is difficult to compensate.

Increasing light availability in oak-dominated forests through gap creation and expansion benefits both tree regeneration and forest biodiversity, as many oak specialist species are light-demanding (Mölder et al., 2019a). Thus, canopy opening contributes to forest multifunctionality.

However, light demand of oak increases with age (von Lüpke, 1998; Ostrogović et al., 2010; Annighöfer et al., 2015; Petritan et al., 2025), making larger openings necessary over time (ca. 0.1–0.5 or up to 2 ha, Mölder et al., 2019a; Kohler et al., 2020; Modrow et al., 2025; Nicolescu et al., 2025). Thus, even 300 m² large gaps may need to be enlarged over time.

Maintaining a high oak proportion in the overstory (above 80%), as is usual under the rotation forestry, would require an extensive canopy opening at the stand level. However, this would result in a loss of the forest character of the habitat. We therefore recommend accepting a lower oak proportion with a higher share of admixing species. Oak proportion should range between 30% and 60%, with higher values on drier sites and lower on mesic sites, consistent with natural stand composition (Böloni et al., 2021). Increased admixture enhances biodiversity and ecosystem services (Pukkala, 2016) and improves stand stability and productivity (Coll et al., 2018; Zhang et al., 2012). Admixing species also supports oak vitality (Stimm et al., 2021) and climate adaptation (Brang et al., 2014).

Oak-dominated mixed forests managed by continuous cover forestry may also offer economic benefits through reduced tending costs and diversified high-quality timber production (Spiecker, 2006; Knoke, 2009; Csépanyi and Csór, 2017). However, our results indicate that the establishment of admixing species is slow in species-poor stands, even in gaps. Active protection and promotion of these species are therefore required in both the overstory and regeneration layer.

4.5. Limitations and future perspectives

This study did not assess within-gap spatial variation in oak regeneration. However, microsite heterogeneity within the gaps strongly influences abiotic conditions (Ritter et al., 2005; Horváth et al., 2023), species performance, and regeneration success of different woody species (Vilhar et al., 2015; Lu et al., 2021; Patterson et al., 2022). Detailed spatial analyses are therefore needed and are planned for our sites.

Because oak requirements change with age, long-term monitoring of regeneration is also essential. We have shown that small elongated gaps require expansion after a few years, and future work will evaluate the effects of such interventions. Given ongoing climate change and the increasing frequency of extreme weather events, exploring their impacts on oak regeneration is also an important task for the future.

Finally, large ungulates were excluded from this experiment. Their browsing effects should be addressed in future studies, as they may either hinder oak regeneration (Sabo et al., 2019; Zoltán et al., 2024) or,

at moderate population densities, facilitate it by suppressing bramble and other competing species (Harmer et al., 2010; Walters et al., 2016; Szabó et al., 2025).

CRediT authorship contribution statement

Flóra Tinya: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Péter Csépanyi:** Writing – review & editing, Conceptualization. **Margaret Gathoni Gitau:** Writing – review & editing, Investigation, Formal analysis. **Csenge Veronika Horváth:** Writing – review & editing, Investigation. **Bence Kovács:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Csaba Németh:** Writing – review & editing, Investigation, Formal analysis. **Péter Ódor:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2026.100472>.

Data availability

Data are published at the Mendeley Data repository: Tinya et al. (2025), “Data for: Elongated gaps provide a good compromise between abiotic and competitive conditions for sessile oak regeneration”, Mendeley Data, V1: <https://doi.org/10.17632/hs6y47twvb.1>.

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