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Regeneration success of sessile oak under different gap cuttings in an oak-hornbeam forest

MSc THESIS

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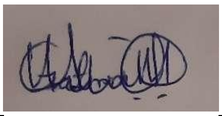

Signature of Student

Dedication

To you, dear researcher, may your quest for knowledge be fulfilled.

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List of Abbreviations

IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
TEEB	The Economics of Ecosystem and Biodiversity
FAO	Food and Agriculture Organization
RFM	Rotation Forestry Management
CCF	Continuous Cover Forestry
CO	Control
LC	Large Circular
LE	Large Elongated
SC	Small Circular
SE	Small Elongated
LAI	Leaf Area Index
USA	United States of America
EV	Exposure Value
LiDAR	Light Detection and Ranging
DSF	Direct Site Factor
ISF	Indirect Site Factor
SWC	Soil Water Content
GLMM	Generalized Linear Mixed Model

Abstract

There is a shift in the European region towards a more inclusive forestry management system encompassing ecosystem services while improving the biodiversity status and reversing forest degradation besides timber production. One of the ways forest management authorities are trying to achieve this is nature-based forest management that mimics the natural stand dynamics. Among the temperate nature-based management techniques is the creation of forest openings. Gap creation in forests is advantageous for light-demanding species such as *Quercus petraea* and results in the regeneration success of saplings established in the gaps. Conducted in northern Hungary, this study investigates the regeneration success of naturally occurring *Quercus petraea* saplings in artificially created canopy gaps ranging between 0.015 ha to 0.03 ha. The study utilised four canopy opening types (large circular, large elongated, small circular and small elongated gaps), hereafter referred to as treatments and one control site, forming five plots with six replicates. The effect of the treatments was studied on the acorn supply, the height growth, survival and abundance of *Quercus petraea* saplings.

Additionally, several environmental variables of the treatments were investigated (soil moisture, light, understory herbs and perennial forbs) to see how they affected the regeneration of the *Quercus petraea* saplings. The study compared the pre-treatment conditions with the short-term conditions after treatment. Independent and dependent variables were measured on plots established at the centre and the northern part of each of the 30 plots.

The results revealed that gap cuttings significantly affected the acorn supply, the height increment and the abundance of the *Quercus petraea* saplings. However, initial survival was driven by other factors independent of the gap type. Abiotic conditions (light and soil moisture) proved the most favourable for oak regeneration in the large circular gaps. However, these circumstances also promoted the competing vegetation (perennial forbs and some woody species such as *Carpinus betulus* and *Cornus sanguinea*). Large elongated and small circular gaps offered only slightly lower resources (light and soil moisture), with lower competition. Thus, in these gap types, more oak saplings could reach the larger size categories, with a slightly smaller but considerable growth. The height increment of oak saplings was the weakest in small elongated gaps, but it also ensured their survival, while acorn production was the highest in this gap type. Our findings imply that oaks can be regenerated in small-scaled gaps. However, the competing perennial species must be controlled for successful regeneration in sites with suitable abiotic factors (soil moisture and light), or regeneration should be favoured using smaller or narrower gaps.

1. Introduction

1.1 Background of the study

Forests are important ecosystems because they are vital in biodiversity conservation, habitat provision, supply of raw materials, recreation, climate regulation, and soil erosion control. Forests worldwide have been exploited mostly for timber and wood products. Consequently, this has led to a decline in the natural forests. The increasing human population has also led to deforestation for establishing settlements and other infrastructure to support livelihoods. Forest biodiversity is determined by the number of individual species in the forests and by the genetic, structural, and functional diversity (Muys et al., 2022). European forests comprise diverse ecosystems ranging from coniferous-dominated boreal forests to temperate deciduous and Mediterranean forests (Muys et al., 2022). Species diversity is declining significantly in all these forest types, with very few remaining pristine forests. Major threats to biodiversity are the land use changes over time; for forests, it is the widespread use of conventional forest management (IPBES 2018, Felipe-Lucia et al., 2020). Most European forests are utilized for timber similar to forests in other continents. To this end, it is important that forest management systems not only focus on wood production but on other aspects of forests, such as biodiversity conservation and preserving ecosystem functions and services (Forest Europe, 2020). In the past decades, there has been increased emphasis on multifunctional forest management (Peura et al., 2018). More diverse forests offer many ecosystem services in addition to their numerous species. The Economics of Ecosystem and Biodiversity report (TEEB, 2010) highlights the significance of the ecosystem service cascade in which biodiversity forms the basis for other ecosystem services. Hence, increasing the biological diversity increases the monetary and non-monetary benefits of forests to humans. For instance, biological diversity enables timber production through the development of suitable tree species along with mycorrhizal fungi that increase tree productivity.

In Hungary, forests cover about 20% of the territorial area. Of this, nearly 60% constitutes the native tree species such as sessile oak (*Quercus petraea*), pedunculate oak (*Quercus robur*, beech (*Fagus sylvatica*) and hornbeam ((*Carpinus betulus*). The remaining 40% is dominated by plantations of exotic tree species, mainly black locust (*Robinia pseudoacacia*) and poplars (*Populus spp*). National Agrarian Centre, 2022). The government owns nearly 60% of the forests, while the remaining percentage is owned by individuals and companies (National Agrarian Centre, 2022). National laws regulate forest management, and government authorities supervise forests (Jáger et al., 2015).

Previous research concentrated on oaks' photosynthetic activity and growth in experimental conditions (Vernay et al., 2016). Nevertheless, studies and publications dealing with oak regeneration in forests with competition from other species are rare (Diaci et al., 2008; Dobrowolska et al., 2008; Březina et al., 2011). Implementing continuous cover forestry enables regeneration of trees in natural conditions, which helps prevent the clearing of huge areas in forests hence maintaining the physiological characteristic of forests (Pommerening & Murphy, 2004). In implementing continuous cover forestry in Hungary, the Pilis Gap Experiment was introduced to study how the various gap types influence regeneration. This study is conducted under the framework of the Pilis Gap Experiment.

1.2 Aim of the research

1.2.1 The aims of the Pilis Gap Experiment

The Pilis Gap Experiment was started in 2018 as a collaboration between the Institute of Ecology and Botany, Centre for Ecological Research and Pilis Park Forestry Ltd. It is located in an oak–hornbeam forest that was 90 years old at the start of the study. The experiment aims at investigating what type of canopy gaps should be created to make sure that there is simultaneous forest regeneration, forest microclimate preservation, and biodiversity preservation. The experiment investigates the effects of gap size (whether large or small), gap shapes (circular or elongated) and the procedure of gap creation. One method is creating gaps in one step, and the other is creating the gaps in two steps (extended gaps) by first creating small, elongated gaps and, after some years expanding them to large circular gaps. The gaps created are compared to closed forest controls with no treatments. Microclimate, soil and litter conditions are investigated in each treatment. As biodiversity indicators, understory vegetation, enchytraeid worms, carabid beetles, spiders, dipterans and soil microbiome are investigated in the experiment.

1.2.2 The aims of the thesis

This thesis aims to compare the regeneration of the different tree species under different gap treatments. The study focuses mainly on the regeneration success of *Quercus petraea*, a dominant canopy-forming species in the oak–hornbeam forests. The regeneration success is evaluated based on acorn production, seedling survival, and the individual *Quercus petraea* saplings growth. The number of species and abundance of natural regeneration are also studied to understand regeneration success better. The environmental variables affecting regeneration are also studied: the incident light, soil moisture content, and abundance of the understory herbs and forbs. The "extended" gaps of the experiment have not been enlarged yet (they are still in the stage of small elongate gaps); thus, in the current thesis, these gaps are not studied.

1.2.3 Specific objectives

1. To examine how the various sized and shaped gaps affect the environmental variables (light, soil moisture and understory vegetation);
2. To study the acorn supply in the different gap types;
3. To investigate the survival and growth rates of individual sessile oak saplings in the different gap-cuttings;
4. To investigate the species richness and natural regeneration abundance in different gap types

1.2.4 Hypothesis

In this research, we hypothesise that

1. The larger gaps will have a greater effect on the environmental variables. Based on the initial results published by Horváth et al. (2023), the gap size is expected to mainly influence the light, while the gap shape will influence soil water content. We suppose that both gap size and shape will influence the understory cover.
2. Gaps will receive less acorns than the closed part of the stand, especially the large circular gaps.
3. The seedling survival and growth rates of individual *Quercus petraea* saplings will be greater in the larger gaps, especially in the large circular ones.
4. In the fourth year after gap creation, species richness of the regeneration will have only a moderate response to the various gap-cuttings. However, it will slightly increase in all gaps. The abundance of regeneration is expected to increase in the gaps, but the different species will respond differently to the conditions of the various gap types.

2. Literature review

2.1 Disturbance regimes of temperate forests

A disturbance is an occurrence that affects the ecosystems, habitats, or individuals at a given time, including environmental changes and destructive events, regardless of whether they are considered normal for a particular system (White & Pickett, 1985). Disturbance regimes refer to the accumulative impacts of disturbances occurring in a given area over a specified period, often characterised by intensity, frequency, regularity and duration (Turner, 2010). Forests are dynamic ecosystems shaped by natural and anthropogenic disturbances that operate spatially and temporarily on different scales (Lorimer & Halpin, 2014).

The role of natural disturbances in shaping ecosystems is now broadly recognised in ecology (Muscolo et al., 2014). When researching the stand structure, tree species composition and distribution of natural forests, disturbance regimes play a crucial role in determining which trees will appear in the forest canopy (Feldmann et al., 2018). The need to conserve forest biodiversity and increase ecosystem services offered by forests has consequently increased the need for management to understand and mimic natural disturbance regimes (Thom & Seidl, 2015). Natural disturbances in temperate forests occur in the form of infrequent large-scale disturbances including wind, snow and ice and more frequent fine-scale gap dynamics which arises from the death of individual or groups of trees establishing small gaps in the canopy (Standovár & Kenderes, 2003; Aszalós et al., 2022). Both small-scale and large-scale disturbances create forest openings that improve reproduction and regeneration (Muscolo et al., 2014). Researchers in the recent past have discussed natural disturbances with inconclusive thoughts on their impacts on ecosystem management (Thom & Seidl, 2015).

Besides natural disturbances, using forests for timber production has also influenced the structure and composition of many European forests (Sommerfeld et al., 2018). Natural disturbance regimes changed significantly between 1986 and 2016; however, the disturbance size varied across countries (Senf & Seidl, 2021). In their research, Kulakowski et al. (2017) found that countries with small-scale forest management practices showed smaller disturbance size and intensity even though they experienced large-scale disturbances. Because of the complex link between natural disturbance regimes and anthropogenic disturbances, characterising the disturbance in Europe calls for a holistic approach combining natural and anthropogenic regimes (Senf & Seidl, 2021). Europe needs more quantitative information on disturbance regimes, including human and natural disturbances (Senf & Seidl, 2021). Even though some previous studies describe the disturbance regimes over time, they focus on natural disturbances and ignore anthropogenic ones (Senf et al., 2018; Nagel et al., 2017; Aszalós et al., 2022).

2.2 Canopy gaps in forests

Gaps can be created by natural and anthropogenic disturbances that interfere with the dynamics of species populations (Naaf & Wulf, 2007). Canopy gaps resulting from natural or human causes are a crucial part of the development of forest ecosystems (Holík et al., 2018).

2.2.1 Gap microclimate

Over the past two decades, due to increasing anthropogenic climate change and its impact on ecosystems, environmental scientists and other researchers are interested in microclimate trying to incorporate the results into climate-dependent models (Bramer et al., 2018; Kovács et al., 2020). Forest management practices that cause clearing some parts of the forest result in new microclimate conditions that differ from others (Chen & Franklin, 1997). Fine-scaled gaps create a heterogeneous abiotic environment at stand level.

In gaps, there is increased solar radiation (Denslow, 1987; Abd Latif & Blackburn, 2010), and the light intensity depends strongly on the size of the gaps, with larger gaps receiving higher amounts of radiation (Brown, 1993; Horváth et al., 2023). Increasing solar radiation within the gaps increases air temperature, which heats the soil (Malcolm et al., 2001; Abd Latif & Blackburn, 2010). Furthermore, creating gaps also decreases relative humidity (Abd Latif & Blackburn, 2010; Kovács et al., 2020). The impact of gap openings on soil moisture content was observed in temperate forests by Malcolm et al. (2001), Gálhidy et al. (2006) and Kovács et al. (2020), indicating that soil moisture content was higher in the gaps than in the surrounding areas. The increase could have been because of reduced transpiration in the gaps and increased rainfall penetrating directly into the soil without interception by the forest canopy (Zhu et al., 2014). Nevertheless, the magnitude of the changes in these abiotic factors is dependent on such gap characteristics as gap size and gap shape and are much less drastic than changes in larger cutting areas (Muscolo et al., 2014; Horváth et al., 2023). Microclimatic conditions in the gaps also lead to changes in soil chemical composition due to the effect of the change in soil microbial biomass (Denslow, 1987).

2.2.2 Biodiversity in gaps

Combining different gap shapes and sizes creates a conducive environment for many plant species that thrive under different environmental conditions (Hubbell, 1999). Creating gaps in formerly closed stands of forests increases soil water content that may enhance seed germination for understory species (Canham et al., 1990). The increased light enhances photosynthetic activity, increasing plant biomass (Kuijper et al., 2009; Tinya et al., 2020; Han et al., 2020). Besides, gaps also influence the plant species composition, as they create a new environment for herbs and woody plants to start new regeneration by removing well-established competing species (Yamamoto, 1999; Tinya et al., 2020). De Groot et al. (2016) also discovered that selective logging increased the abundance of graminoids and herb species in southwestern Slovenia. Research by Whitmore (1989) suggests that in larger gaps, light-demanding species can develop better under conditions that do not favour the growth of climax saplings of the dominant forest trees.

Some studies have proved that small gaps improve microbial diversity (Yang et al., 2017; Wang et al., 2021). Research by Boros et al. (2019) revealed that enchytraeid worm communities are better preserved in gaps than in larger cutting areas due to the buffered conditions. Additionally, a study by Šebek et al. (2015) revealed that opening up forests led to distinct communities and increased species number of butterflies, vascular plants, saproxylic and floricolous beetles within the gaps.

2.2.3 Regeneration in gaps

Gaps are key contributors to determining temperate forests' regeneration (Sapkota et al., 2009). Microclimate conditions have various effects on the regeneration: For beech and other shade-tolerant species, it is favourable (Kenderes et al., 2008; Hobi et al., 2015; Feldmann et al., 2018); nevertheless, in oaks, it is more complex. Various studies indicate that gap sizes are key to regeneration success (Holladay et al., 2006; Webster & Lorimer, 2005). Furthermore, the gap dynamic theory implies that the gap size influences solar radiation, consequently affecting the composition and growth of the regenerating species (Dietze & Clark, 2008). Nevertheless, researchers have varying views about the relationship between gap size and regeneration (Arévalo & Fernández, 2007; Fajardo & de Graaf, 2004).

2.3 Characteristics of oak species

2.3.1 Importance and ecology of oaks

Oak species have great relevance in European forests, both from an ecological and economic point of view (Kuehne et al., 2020). The two major oak species are pedunculate oak (*Quercus robur*) and sessile oak (*Quercus petraea*), which have wider ecological extents that are suitable for their growth (Annighöfer et al., 2015). Oaks have large acorns, hence in the first years, they can grow in the shade due to the nutrient reserves of the acorns, but later they are light-demanding (Von Lüpke, 1998; Kohler et al., 2020). To this end, their regeneration depends on their habitats' openness through natural or anthropogenic interventions (Bobiec et al., 2018).

Researching pristine forests helps understand natural forests' dynamics (Schütz et al., 2016). However, there are very few natural forest reserves in Europe, making up about 3% of Europe's total forest area (FAO, 2020). Pristine oak forests are especially rare. Thus, there are considerable knowledge gaps regarding the natural dynamics of oak species. What is experienced is that on sites where shade-tolerant admixing species such as European beech thrive well, oaks compete for survival. Nevertheless, oaks compete naturally and establish their ecological niche in areas with extreme conditions (Bauhus et al., 2017). Studies on the climate change impact on the area of sessile oak forests predict a slight decline, but the decline is lesser than for beech (Illés & Móricz, 2022).

2.3.2 Oak regeneration and its problems

Regeneration of oaks in Europe and North America has been problematic recently, and the species has yet to regenerate well naturally (Shaw, 1968). Oak-dominated forests in many parts of the world are declining due to poor regeneration (Dey et al., 2019), a disheartening phenomenon given their ecological and economic importance. Acorn production in oaks varies between years, with individual trees producing acorns synchronously (Koenig et al., 2013). In mast-seeding years, there is a production of a high density of acorns, while in non-masting years, the number of acorns is low. The variation has been explained previously by Sork et al. (1993) and Koenig et al. (1994b), who state that the differences in acorn production not only depend on the optimal abiotic factors for reproduction but also on evolutionary strategies aimed at switching tree resources between producing acorns and performing other functions in different years. Even in masting years, most of the acorns fail to germinate (Ovington & Macrae, 1960), which can be attributed to factors such as infestation by insects (weevil *Curculio glandium*) pre- and post-dispersal (Bąk et al., 2017) and pathogenic fungi and summer drought (Bobiec et al., 2018).

There is conflicting information on the regeneration capacity of oaks in competitive environments (Kelly, 2002). Oak regeneration faces a major challenge from competing with other woody species and herbaceous vegetation (Mölder et al., 2019). In conditions of low light, less light-demanding species can eventually outcompete the oaks (Ligot et al., 2013). In unmanaged oak forests in Europe and North America, shade-tolerant species have been observed to regenerate and survive, unlike oaks (Van Couwenberghe et al., 2013; Stimm et al., 2021). For instance, beech dominated the regeneration in the Carpathian Mountains instead of sessile oak (Petritan et al., 2013).

Various researchers have come up with possible reasons for the failure of oak regeneration. Vera (2000) states that the decline is due to the lack of large herbivores that maintained open woodlands favourable for oak regeneration in historical times. Bobiec et al. (2018) and Saniga et al. (2014) explain the weak oak regeneration with changes in land use. Other researchers have attributed the regeneration failure to the seedbed characteristic, such as litter availability (Kuiters & Slim, 2003; Perea et al., 2013). In North America, most oak-dominated forests exist partially due to past forest fires; therefore, this relationship led to the suggestion that oaks survive better than other tree species where there are periodic fires (Nowacki & Abram, 2008; McEwan et., 2011; Johnson et al., 2019).

Besides, a disturbing trend in Europe is that oaks are becoming the most preferred forage by ungulates in temperate forests (Petersson et al., 2019). Additionally, in denser ecosystems that lack shrubs for ungulates to browse on, oaks are occasionally browsed by ungulates dwindling the regeneration further (Bobiec et al., 2018; Dobrowolska, 2020).

2.3.3 Regeneration success of oaks in gaps

There have been reports of regeneration successes of sessile oaks in gaps in various countries. Research by Diaci et al. (2008) in Slovenia revealed that pedunculate oaks could regenerate in small gaps of 0.03-0.05 hectares. In his research, Von Lüpke (1998) concluded that sessile oak regeneration can happen in small gaps with diameters of at least 17-20 metres; however, in these gaps, the oaks need to be protected from browsing animals. It was noted that hornbeam is a better admixing species in the regeneration as compared to beech as it does not grow into the crowns of oaks as it matures, and it also provides ground litter; nevertheless, it has a higher nutrient demand (Von Lüpke, 1998). Kohler et al. (2020) found that the regeneration success of sessile oak depends on the sapling number at the start of the regeneration and the silvicultural treatments applied to the saplings. The silvicultural treatments affect the microclimate conditions and are crucial to the regeneration success (Kohler et al., 2020). A study by Modrow et al. in 2020 revealed that the regeneration of oaks is successful under light conditions of around half of the light in open fields. Furthermore, their research concluded that sessile oak saplings could thrive in fenced forest gaps.

2.4 Forest management practices in Europe

2.4.1 Rotation forestry management

The European forests cover is roughly 227 million hectares accounting for 35% of the continental land area (Forest Europe, 2020). Most of these forests are 20 to 80 years old even-aged stands, with only a quarter of the forests considered uneven-aged (Mason et al., 2022). Most European countries are implementing forest management practices closer to nature to some extent (Forest Europe, 2020). Nevertheless, the even-aged structure of most forests indicates that the common practice was and still is rotation forestry management (RFM) (Aszalós et al., 2022; Mason et al., 2022). In rotational forestry, trees are removed from a stand, resulting in age-aged regeneration and homogeneous stands (Matthews, 1989). Conventional management practices mainly focus on producing timber and other ecosystem services of forests as a by-product (Biber et al., 2015). The exploitation of forests for timber harvesting has faced much criticism as the use of RFM deteriorates the ecosystem service provision capabilities of forests (Puettmann et al., 2015).

2.4.2 Shifting from rotation forestry management

Alternative forest management practices focus on having more diverse forests in species composition, forest structure, and stand ages (Puettmann et al., 2015). European countries have been implementing alternative methods to RFM for the past 100 years (Schütz et al., 2012). Because forests are of major economic importance in Europe, studies have been conducted on the effectiveness of the various forest management practices for economic and ecological services (Mason et al., 2022). Temperate oak stands in Central Europe were greatly influenced and managed using centuries-old management practices (Kirby & Watkins, 2015). These management practices, such as pannage (releasing pigs in a forest to feed on the seeds and vegetation), wooded pastures, and coppicing (cutting down trees to allow shoots to sprout from the trunk), promoted the growth of oaks and, in most areas, led to decreasing numbers of European beech (Bobiec et al., 2018). Among the alternatives is continuous cover forestry (CCF), implemented using more nature-based silviculture practices (Brang et al., 2014).

2.4.3 Continuous cover forestry

Continuous cover forestry (CCF) aims to regenerate forests where natural conditions are favourable for the dominant species (Kuehne et al., 2020) and is mainly characterised by harvesting specific individual trees or a group of trees. The created small canopy openings cause minimal interference with the continuous cover of the forest (Pommerening & Murphy, 2004; Gustafsson et al., 2020; Kuehne et al., 2020; Mason et al., 2022). It is the main forestry management model in some European countries, for example in Germany and Slovenia, and some countries use the system in combination with other management practices (Gustafsson et al., 2020). The spatial scale of the CCF intervention is much smaller than that of rotational forestry; however, the time between interventions at the same stand is more frequent (5-8 years). Many countries in Central Europe aim at using CCF to convert even-aged pure forest stands to uneven-aged stands of mixed species (Bürgi & Schuler, 2003). Due to the different timing of harvesting individual trees or groups of trees, CCF results in uneven-aged stands (Schütz et al., 2012). Additionally, CCF results in a more heterogeneous stand structure and diverse tree species because admixing species or habitat trees, such as veteran trees and dead or living microhabitat-bearing trees, can be better preserved with small-scale interventions. In sessile oak–hornbeam forests, foresters use various procedures under continuous cover forestry without a commonly accepted method (Tinya et al., 2020). In continuous cover forestry, it is challenging to regenerate the light-demanding oak species within gaps; however, there is evidence that even oaks can be regenerated by gap-cuttings (Von Lüpke, 1998; Diaci et al., 2008; Kuehne et al., 2020; Tinya et al., 2020).

3. Materials and methods

3.1 Study area

This study was conducted in the Pilis mountains in the Transdanubian range of Hungary (47°40′N, 18°54′E, Figure 1). The study site is located in the northern region of Hungary and is under the management of Pilis Park Forestry Ltd. The area experiences an average annual temperature of between 9.0 and 9.5 °C with 630mm average annual precipitation (Dövényi, 2010). The study site is located near the Pilisszántó village, on the north-facing slopes of Hosszú-hill, at 370–450m above sea level, with a slope gradient of 7.0°–10.6°. It lies on limestone and sandstone bedrock (Dövényi, 2010). The soil mainly comprises acidic luvisol and rendzic leptosol with a pH between 4.2 and 5.3 (Kovács et al., 2020). Due to the management through the shelterwood forestry system, the forest is even-aged (90 years) with low tree species numbers and an even structure. The forest is dominated by sessile oak in the upper canopy and hornbeam is the second layer. Other species appearing in a significant number include Turkey oak (*Quercus cerris*), wild cherry (*Prunus avium*), and European beech. The study site contains some areas that are dominated by rock outcrops. The area has a scarce shrub layer, and the herbaceous understory mainly consists of hairy sedge (*Carex pilosa*) and wood melick ((*Melica uniflora*). The 9-ha site used for this study was fenced to minimise herbivory by ungulates.

3.2 Experimental design

At the beginning of the experiment, in 2018, the pre-treatment conditions of the site were assessed. In February 2019, some trees were felled to create the gaps. Five treatments were applied following a randomised complete block design and replicated across six blocks, resulting in 30 sampling plots (Figure 1). The blocks are numbered 1 to 6.

The five treatments are as follows:

a) Control (CO): consisting of mature closed stands free from intervention.
b) Large circular gap (LC): A circular gap 20 m in diameter. The area is approximately 300 m^2.
c) Large elongated gap (LE): A rectangular gap with 30 m × 10 m length and width dimensions, oriented north-south, with an area of approximately 300 m^2.
d) Small circular gap (SC): A gap of 14 m in diameter with an area of approximately 150 m^2.

e) Small elongated gap (SE): A rectangular gap with 21 m × 7 m length and width dimensions, oriented north-south, with an area of approximately 150 m^2.

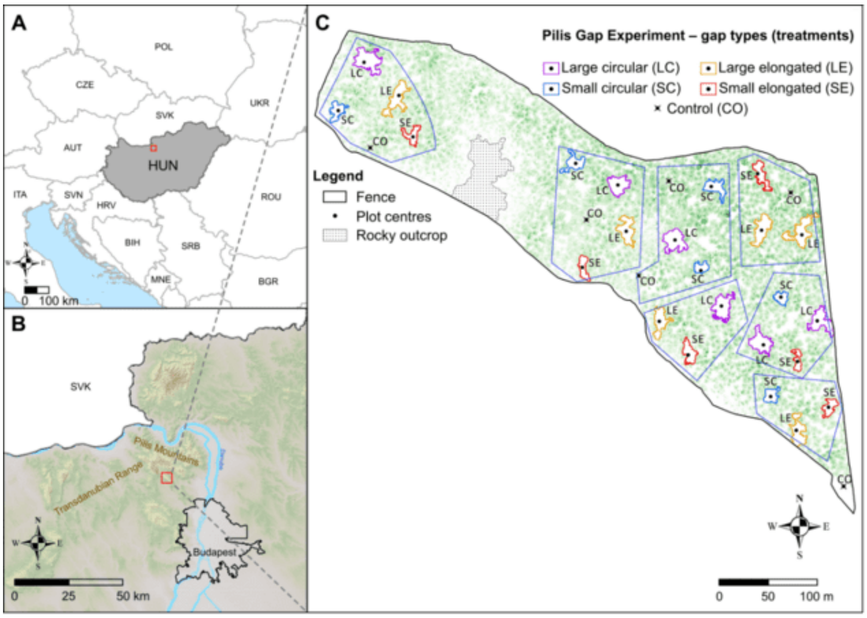

Figure 1. Location of the study area. (A) the study area location in Hungary, (B) the study site in the Pilis Mountains; (C) the experiment site consisting of six blocks with the five treatments.

3.3 Data collection

All procedures for data collection and data records before 2022 were retrieved from the raw data records of the Pilis Gap Experiment. The 2018 data was used as the pre-treatment data, while the 2022 data was the after-treatment data where the respective data was used. For the acorn counting, 2020 was used to study the after-treatment effect. The individual growth rate monitoring started in 2020 when the individual saplings were selected and marked. The survival rate used 2019 as the starting year because it followed the 2018 acorn mast year. This thesis's author contributed to the collection of the light, understory cover, oak survival, abundance and height measurement data for 2022. Other participants of the Pilis Gap experiment collected the soil water content and acorn data.

3.3.1 Light estimation

In 2018, light estimations were conducted using LAI-2000 Plant Canopy Analyser (LI-COR Inc., Lincoln, USA), at the northern part of the plots (above the individually marked saplings where the intensively growing understory and shrubs were removed), at 1.3 meters height from the soil surface. For light estimation in 2022, hemispherical photographs were captured at the same points using WinSCANOPY System (Regent Instruments Inc., Québec, Canada) with a KODAK PIXPRO SP360 camera. All photographs were taken in June of 2022, between 4 pm and 7 pm, when the light intensity was lower, to reduce reflection. At each point, two photographs were taken, one with an exposure value (EV) of -0.3 and the other of -0.7. The one with better quality was used to analyse the two images acquired.

3.3.2 Measurement of soil water content

In 2018, the soil moisture content was measured using FieldScout TDR 350 probe equipped with 7.5 cm steel rods (Spectrum Technologies Inc, Aurola, Illinois, USA). Measurements were conducted once in the top 7.5cm of the soil, at the centre of each plot in each month for June and August. In 2022, TMS-4 loggers (TOMST s.r.o., Praha, CZ) with 15-minute logging intervals were used. The equipment conducted continuous soil moisture measurements daily in 8 to 14 cm of the upper soil layer, at the centre of each gap between May and September 2022.

3.3.3 Sampling of the understory herbs and natural regeneration

This study used the abundance of understory herbs as independent environmental variables for the sessile oak regeneration. In each of the 30 plots, one quadrat of 2 m × 2 m was established where the understory vegetation was sampled. The quadrats were located at the centre of the plots. The understory was surveyed twice in both 2018 and 2022 (April and June). Only a few spring herbs were documented in April, whose leaves retracted for summer. All the herbaceous plant species and the saplings of woody species below 50 cm in height in the quadrats were identified. The identification key for vascular plants by Király (2009) was used to identify vegetation in the field. Then the percentage vegetation cover in the quadrats was estimated for each species separately. with the maximum possible percentage being 100% if the investigated element covered the quadrat completely. However, the total cover in a quadrat could be greater than 100% due to multiple overlapping layers of the understory vegetation. The next step involved the estimation of the abundance of woody vegetation in the quadrats. The saplings were divided into four height categories as follows:

a) 0-20 cm
b) 20-50 cm
c) 50-130 cm
d) >130 cm

The number of individuals in each woody species was counted for each size category. The most abundant woody species were used for analysis.

3.3.4 Acorn counting

Fallen sessile oak acorns were counted in 2018 (before the treatments) and 2020 (2^{nd} year after the treatments). Both years were masting years, with a huge number of seeds. Acorns were counted in the plot centres; quadrat size was 1 m × 1 m in 2018, while in 2020, counting was done in 0.5 m × 0.5 m quadrats, and values were extrapolated for $1m^2$.

3.3.5 Oak survival study

In each of the 30 plots, four 50 cm × 50 cm quadrats were placed in the northern part of the plot. The number of oak saplings present for each height category was recorded here. Counting was carried out since 2019, yearly in early autumn. When the competing vegetation (saplings of other woody species and *Rubus fruticosus agg.*) became dense it was eliminated from the quadrats to allow investigation of the direct effect of abiotic conditions on survival. Newly established saplings (not present in 2019) were eliminated every year to follow up on the mortality of the originally counted seedling group.

3.3.6 Height measurement of individual sessile oak saplings

In each plot, 30 sessile oak saplings (900 individuals) were selected from the regeneration used in the individual height increment measurements. Saplings were even-aged (presumably from acorns falling in the masting year 2018). They were chosen and marked in the autumn of 2020, out of the survivors after the first-year intensive mortality. The saplings were located in the northern part of the gaps which receives the most direct light. Where possible, the marked saplings were between 10 and 20 cm in height at the start of the survey and were at least 40 cm apart. Saplings were marked with tags containing an identification number for each individual. The height of the oak saplings has been measured between August and October every year since 2020.

3.4 Data analysis

3.4.1 Light calculation from hemispherical photographs

The device used for the pre-treatment measurement only recorded relative diffuse light (DIFN, diffuse non-interceptance), which in practice is similar to the indirect site factor (ISF) estimated by the hemispherical photography (Appendix 3). However, the measurement method was different, resulting in different values. Simultaneous measurements were conducted with the LAI-2000 Plant Canopy Analyzer and the hemispherical photography system in 2020, and based on these data, a correction function was calculated and applied to the 2018 data to make the data compatible.

The photographs taken in 2022 were analysed using WinSCANOPY 2019 software. Relative light was calculated for the growing season. The timeframe between 01st May and 30th September represented that. The software automatically analysed the photographs by classifying each image's pixels as either sky or vegetation based on brightness (called thresholding). However, in some images, where the leaves are too bright, they could be mistaken for the sky, or when the sky is too dark, it could be mistaken for leaves. In such cases, the photo was edited manually for proper classification. For each image, the software calculated the light variables: the direct site factor (DSF), indirect site factor (ISF), total site factor (TSF), and canopy openness. Openness was calculated as the whole part of the sky where the leaves did not obstruct the sky. The direct site factor is the proportion of direct radiation below the canopy to the direct radiation above the canopy. The indirect site factor (ISF) is the proportion of diffuse light below to the diffuse light above the canopy (in percentage). The total site factor (TSF) is the proportion of the total diffuse and direct light above the canopy to the total diffuse and direct light below the canopy. Foreign objects (non-vegetation) captured in the photographs were masked before analysis. For statistical analysis, diffuse and direct light was used for 2022, and diffuse light for 2018.

3.4.2 Soil moisture calculation

The soil water content (SWC) was expressed as the soil moisture percentage in sampling points. For 2018, two data (June and August) were used. The monthly averages were calculated from the measurements taken for each month. In 2022, the calculations were done for five months (May, June, July, August and September). The mean monthly values were calculated from the daily averages for each plot, giving a total of 150 data points (5 treatments × 6 blocks × 5 months).

3.4.3 Herb cover calculation and perennial forb cover calculation

The total herb cover for all the plots was calculated by adding values of the cover for all herb species for each plot. This calculation resulted in 30 data points (5 treatments × 6 blocks). Since the herb cover combined the less competitive graminoid and annual forb species and the more competitive perennial forbs, the perennial forb cover was also calculated separately using the procedure detailed above.

3.4.4 Survival rate calculation

The survival rate was calculated by comparing the number of sessile oak saplings in each plot in 2022 with those in the same plot in 2019 (number of oaks in 2019/number of oaks in 2022, multiplied by 100).

3.4.5 Growth rate calculation for oak saplings

The growth rate was obtained by calculating the height increment between 2020 and 2022 for those individually marked saplings alive in 2022.

3.4.6 Abundance of the natural regeneration

From the naturally growing woody species, three (*Quercus petraea, Carpinus betulus* and *Cornus sanguinea*) were selected whose values were sufficient for analysis. The abundance change between 2018 and 2022 was used as a dependent variable in the models for each species and size category separately.

3.4.7 Statistical analysis and visualisation

The data analysis used R version 4.2.2 (R Core Team, 2022). The effects of the treatments on the various environmental and regeneration variables were studied using general and generalised linear mixed-effect models. The data distribution was checked statistically using the Kolmogorov-Smirnov Normality Tests. Where the dependent variable did not follow a normal distribution, logarithmic or square root transformations were performed to approximate normal distribution (St-Pierre et al., 2018). For the variables that followed (at least in a transformed form), a normal distribution, linear mixed effect model was used (herb cover, perennial forbs cover, survival rate, acorn supply, light, and soil water content). Generalised linear mixed effect models were used for the variables with Poisson distribution (sapling growth, sapling abundance). In the analysis, “treatment” was the fixed factor with five levels, and "block" was the random factor. However, in the soil water content analysis, where "month" could also influence the moisture content, it was also set as an additional random factor. The linear mixed effect models were constructed using the "nlme" package (Pinheiro, 2017), while the generalised linear mixed effect models used the "lme4" package (Bates et al., 2015). The treatment effect was tested using the “Anova” function in the “car” package (Fox & Weisberg, 2019). Where treatments were significant, multiple comparisons were carried out using user defined contrasts with the “glht” function in the “multcomp” package (Hothorn et al., 2016). The models’ goodness of fit was investigated using the “r.squaredGLMM” function (Bartoń, 2022). The models' residuals were checked for normality using (quantile-quantile plots). The variance homogeneity was checked using residuals and standardised residuals plots against fitted values plots. The study used an alpha level of 0.05 for all the statistical tests.

4. Results

4.1 Effect of the different sized and shaped gaps on environmental variables (light, soil moisture, herbaceous understory vegetation)

4.1.1 Light

Before the treatments, the relative diffuse light in the closed stand was 20.52% ± 1.18%. In 2022, the canopy openness of the closed stand was 10.37% ± 1.29%. The direct site factor (DSF) was 10.66% ± 1.05% and was almost equal to the total site factor (TSF) with 11.33% ± 1.00%. The Indirect Site Factor (ISF, diffuse light) was 15.83% ± 2.43%.

Before the interventions, diffuse light did not differ significantly in the northern part of the treated plots and control (Figure 2a). Four years following the interventions, the treatments showed significant effects on both the indirect and direct light (ISF: $Chi^2 = 31.57$, $p < 2.342e\text{-}06$, $R^2C = 0.5212$ and DSF: $Chi^2 = 134.29$, $p < 2.2e\text{-}06$, $R^2C = 0.8224$). The indirect light increased in 87.5% of the gaps between 0.5% and 21%. The large circular gap received 31.60% ± 2.99%, and the large elongated gap received 30.93% ± 0.75% (Figure 2b). The smaller gaps received 25.91% ± 1.90% and 22.65% ± 2.52% for small elongated and small circular, respectively. A similar trend occurred for the direct light (Figure 2c): the large gaps received 47.22% ± 3.38% in the large circular and 37.19% ± 1.88% in the large elongated. The small gaps received intermediate light (small circular: 29.32% ± 1.69%, small elongated: 28.72% ± 2.81%).

According to these results, light measurements on places where the understory was restricted (above the measured saplings, in the northern part of the plots) indicated that the highest amount of light was recorded in the large gaps. Within the same size gaps, the shape did not influence the amount of light in the small gaps (SC=SE). However, when the light was measured where the understory, shrubs and regeneration were growing freely (at the centre) then the trend was different. In several plots, the understory grew over the height of the light measurement, and thus, the direct light decreased in all the gaps such that it did not significantly differ from the closed stand.

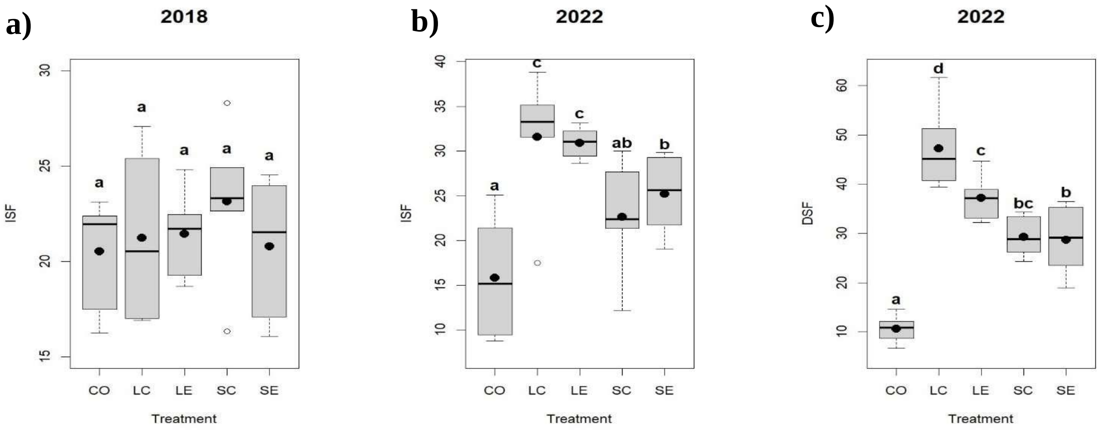

Figure 2. Treatment effects on light. (a) pre-treatment Indirect Site Factor (ISF); (b) effect of the treatments on ISF; (c) effect of the treatments on Direct Site Factor (DSF) in 2022, respectively. In these boxplots, grey boxes show the interquartile range, the black dot shows the mean, and the thick black lines represent the median. The whiskers represent the range without outliers. The treatment types are CO = Control, LC = Large Circular, LE = Large Elongated, SC = Small Circular and SE = Small Elongated. Lowercase letters above whiskers indicate significance testing in pairwise comparisons (ANOVA- test alpha level 0.05). The y-axis scales for the three diagrams are different.

4.1.2 Soil moisture

The monthly values of soil water content in 2018 (Table 1) were lower in June and August of 2018 compared to the same months in 2022 (Table 2). For instance, in August, all treatments recorded soil moisture content of more than 7% in all treatments in 2022 than in 2018.

Table 1. Soil water content in the 2018 vegetation season

SWC (%) 2018	June	August	Treatment Average
CO	10.37	4.66	7.51
LC	9.26	4.28	6.77
LE	9.36	4.15	6.75
SC	9.54	5.07	7.3
SE	9.1	4.61	6.85
Monthly mean	9.53	4.55	
Standard deviation	0.44	0.32	

Table 2. Soil water content in the 2022 vegetation season

SWC (%) 2022	May	June	July	August	September	Treatment Average
CO	27.79	17.86	11.44	12.44	15.46	16.99
LC	33.76	29.12	15.72	14.59	19.12	22.44
LE	32.26	27.39	12.39	12.81	17.40	20.42
SC	28.46	23.88	13.74	13.80	16.47	19.26
SE	35.36	26.75	14.99	15.20	18.13	22.08
Monthly mean	31.52	24.99	13.77	13.77	17.31	
Standard deviation	2.95	3.94	1.61	1.04	1.27	

In 2018, the soil water content did not differ between the "treatments" (Chi^2 = 1.9418, p = 0.7465, R^2C = 0.8794) (Figure 3a). Four years after the interventions, the SWC in the control and the gaps varied slightly, with significantly higher values in the large circular gaps than in the control (Figure 3b). The results of the model revealed that the treatments significantly affected the soil water content in the year 2022 (Chi^2 = 9.7837, p = 0.0442, R^2C = 0.5484).

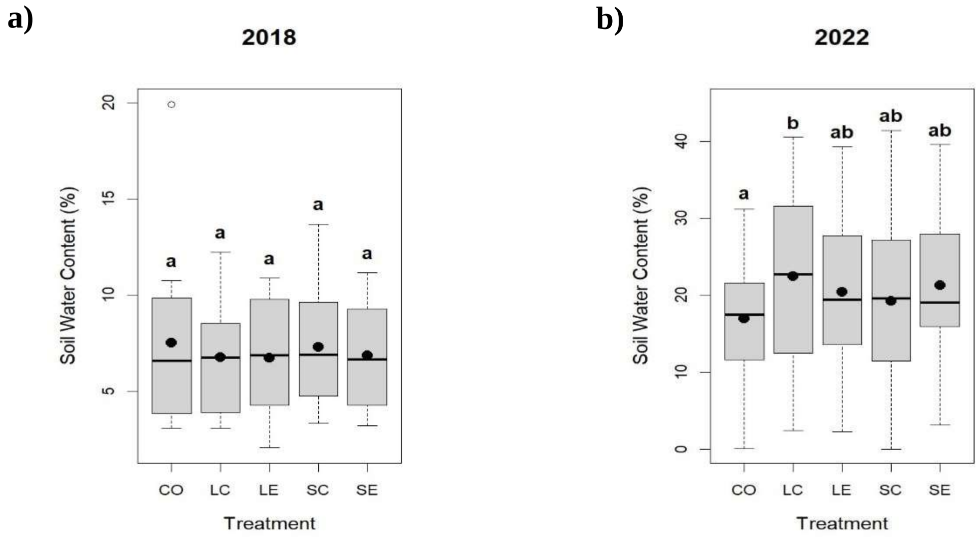

Figure 3. Treatment effects on soil water content in 2018 (a) and 2022 (b). For legends, see Figure 2.

4.1.3 Understory vegetation

In this study, 55 species were recorded in the understory layer (Appendix 1). The species included saplings of woody species, perennial and annual forbs and graminoids. The most frequent species were *Quercus petraea* (the woody species which is the main subject of the study) and *Melica uniflora*, a graminoid (grass) appearing in all the studied plots. *Carex pilosa*, a graminoid (sedge) species, was the third most frequent. The most frequent perennial forbs were *Galium schultesii*, *Stellaria holostea*, *Rubus fruticosus agg.*, *Melittis melissophyllum* and *Viola reichenbachiana*. *Carpinus betulus,* a woody species which forms the secondary canopy layer in the mature forest of the study area, was also present in the top ten frequent species (Figure 4). *Rubus fruticosus agg.,* was present in 60% of the plots; nevertheless, it had a total cover of 22.26%. Of the ten most abundant species, five of them were perennial forbs (Figure 5). The perennial forb cover increased by approximately 56% between 2018 and 2022.

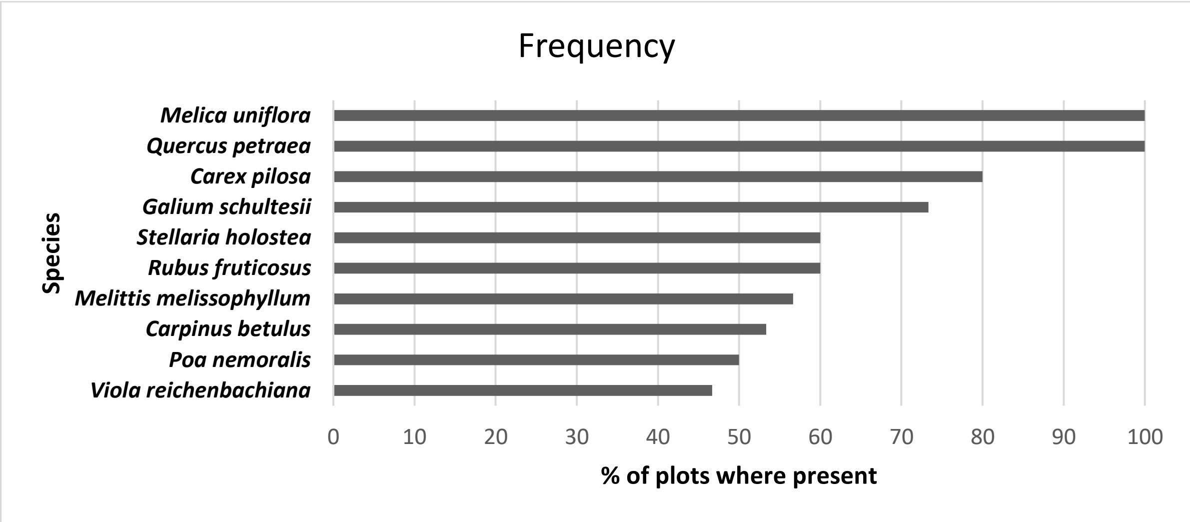

Figure 4. Most frequent species in the 30 understory quadrats of 2m × 2m in 2022.

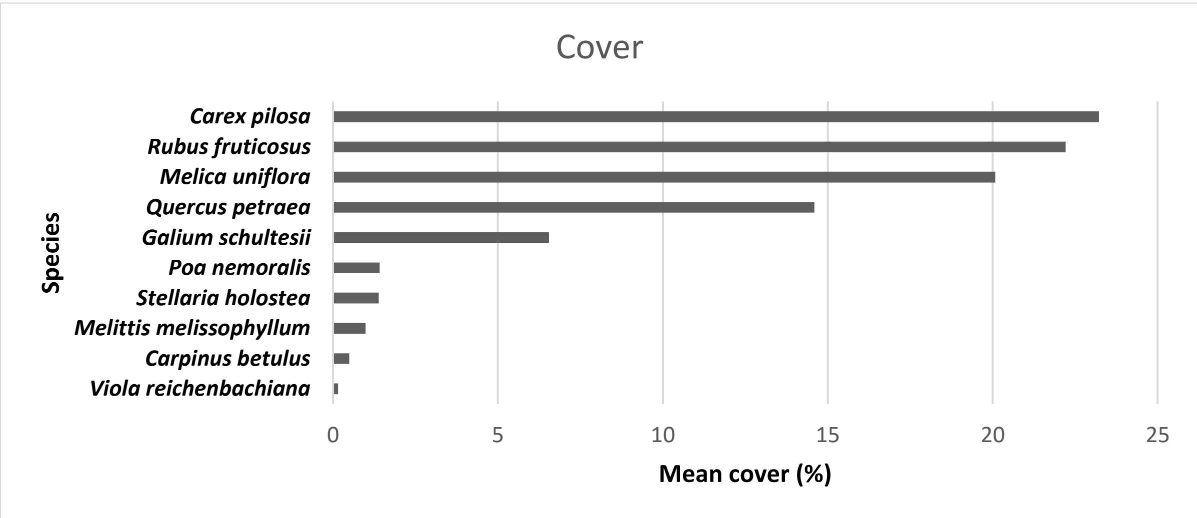

Figure 5. Mean relative cover of the most abundant species in the 30 understory quadrats of 2m × 2m in 2022.

There was no difference in the herb cover in the “treatments” in 2018 ($Chi^2 = 4.2118$, $p = 0.3781$, $R^2C = 0.3512$) (Figure 6a). The models also revealed the treatments' significant on the herb cover in 2022 ($Chi^2 = 20.162$, $p = 0.0046$, $R^2C = 0.4163$) (Figure 6b). It was highest in the elongated gaps, moderate in the circular gaps and lowest in the closed stand (Figure 6b).

There was no difference for perennial forb cover in the "treatments" in 2018 ($Chi^2 = 5.5966$, $p = 0.2314$, $R^2C = 0.3209$) (Figure 6c). The models show that the treatments affected the perennial forb cover ($Chi^2 = 23.988$, $p = 8.034e\text{-}05$, $R^2C = 0.5929$) (Figure 6d). The perennial forb cover was highest in the larger gaps, moderate in the smaller gaps and lowest in the closed stand (Figure 6d).

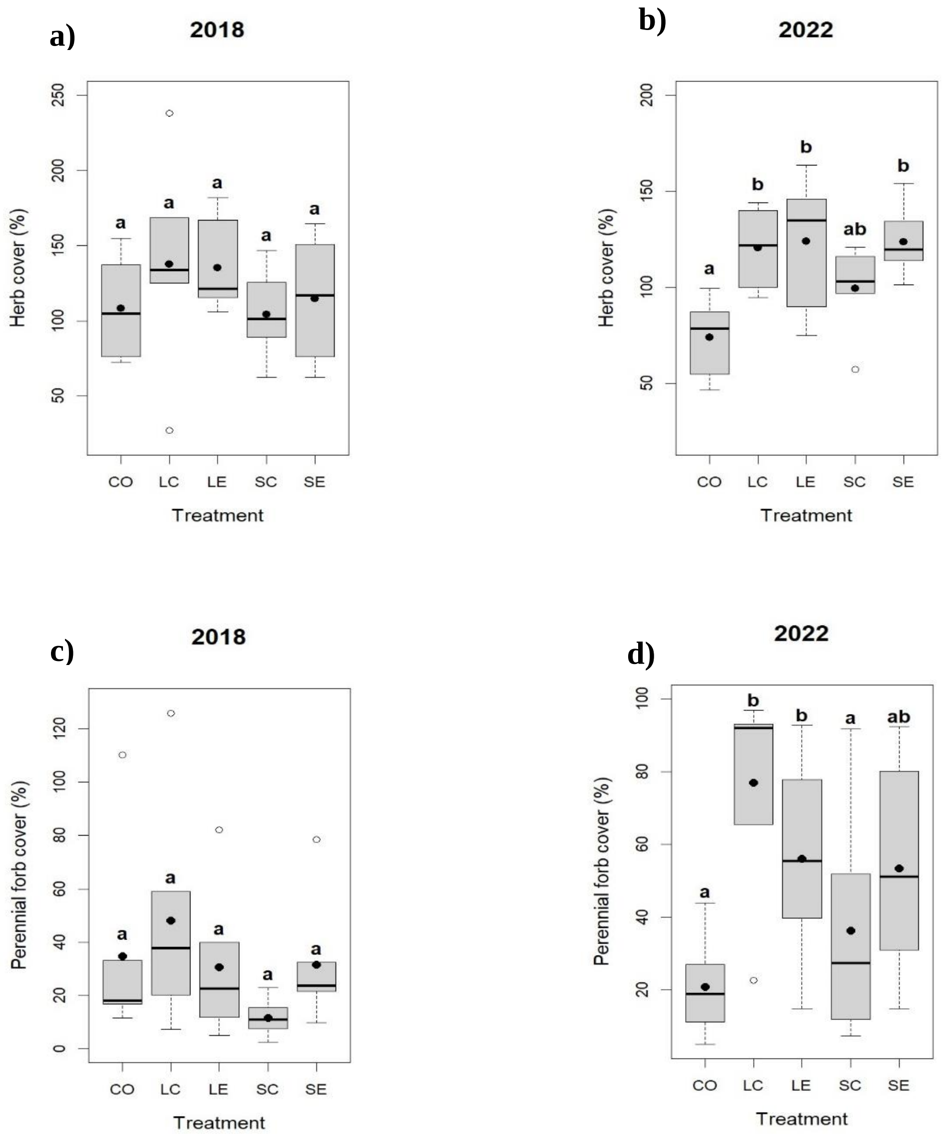

Figure 6. Treatment effects on vegetation cover in 2018 and 2022. For herbs (a, b) and for perennial forbs (c, d). For legends, see Figure 2.

4.2 Acorn supply in the different gap types

The sessile oak acorn supply varied from 68 to 608 acorns/m^2 in the pre-treatment mast year (2018) and 0 to 580 acorns/m^2 in the mast year after treatment (2020). Though weak, there was a variation in the acorn supply in "treatments" before the interventions ($Chi^2 = 16.193$, $p = 0.0027$, $R^2C = 0.4971$), as shown in Figure 8a. However, the effects intensified after the interventions, where almost all treatments significantly differed from each other apart from the large gaps ($Chi^2 = 2096.9$, $p < 2.2e-16$, $R^2C = 0.9969$) (Figure 8b). Before the interventions, acorns accumulated in higher densities in the control and small circular plots 462.67 ± 40.64 pieces/m^2 and 449.33 ± 98.32 pieces/m^2. The acorns accumulated moderately in the large circular and elongated and small elongated gaps.

After the intervention, the number of acorns in the closed stand remained high (326.00 ± 83.35 pieces/m^2) while it decreased substantially in the gaps, especially the larger ones: the large elongated and circular gaps received 1.33 ± 0.84pieces/m^2 and 3.33± 1.90 pieces/m^2, respectively. The small circular gaps also received a few acorns (8 ± 4.13 pieces/m^2). Among the gaps, only the small elongated ones received a relatively high number of acorns after gap creation (70 ± 36.67 pieces/m^2) (Figure 8b).

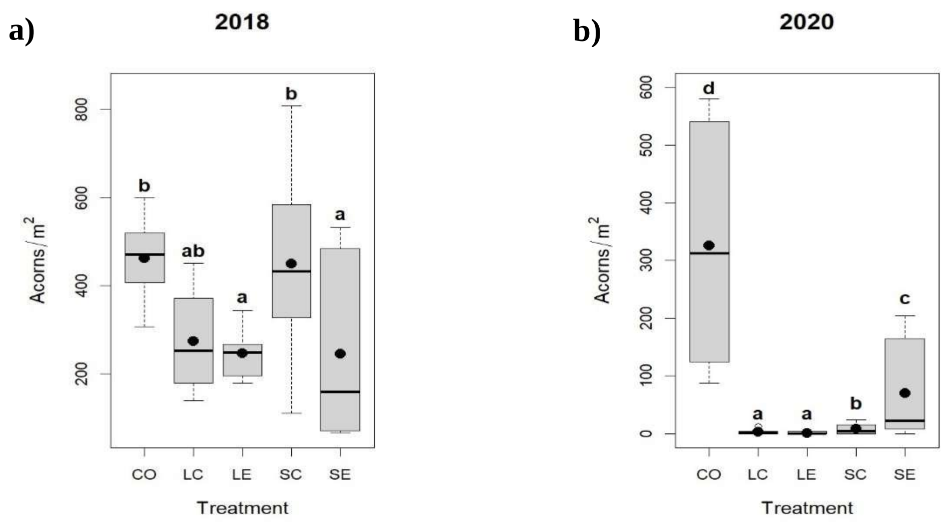

Figure 7. Treatment effect on the acorn supply in 2018 (a) and 2020 (b). For legends, see Figure 2.

4.3 Seedling survival of sessile oak and the growth rate of individual oak saplings under different gap-cuttings

4.3.1 Seedling survival of sessile oak

In 2019, there were 900 individually marked saplings combined for all treatments, while in 2022, there were 644 saplings. There was an average of 43 ± 0.59 seedlings in the 0.5 m x 0.5 m quadrats for 2019. For 2022, the saplings number decreased; the average was 13 ± 0.27 saplings per quadrat. The survival rate was generally low for all the treatments, with only 16.67% of quadrats recording a survival rate of more than 50%. The models' results revealed that the treatments did not affect the three-year survival rate ($Chi^2 = 4.9617$, $p = 0.2912$, $R^2C = 0.3377$), but some trends are observable (Figure 8a). The highest mortality was found in the closed stand, where the survival rate was 17.45% ± 5.59%. Survival was also low in the large circular gap (24.28% ± 4.24%). The survival rate in the small circular, small, and large elongated gaps was almost similar, with averages of 31.12% ± 7.17%, 32.04 ± 8.93 and 32.47 ± 9.19, respectively.

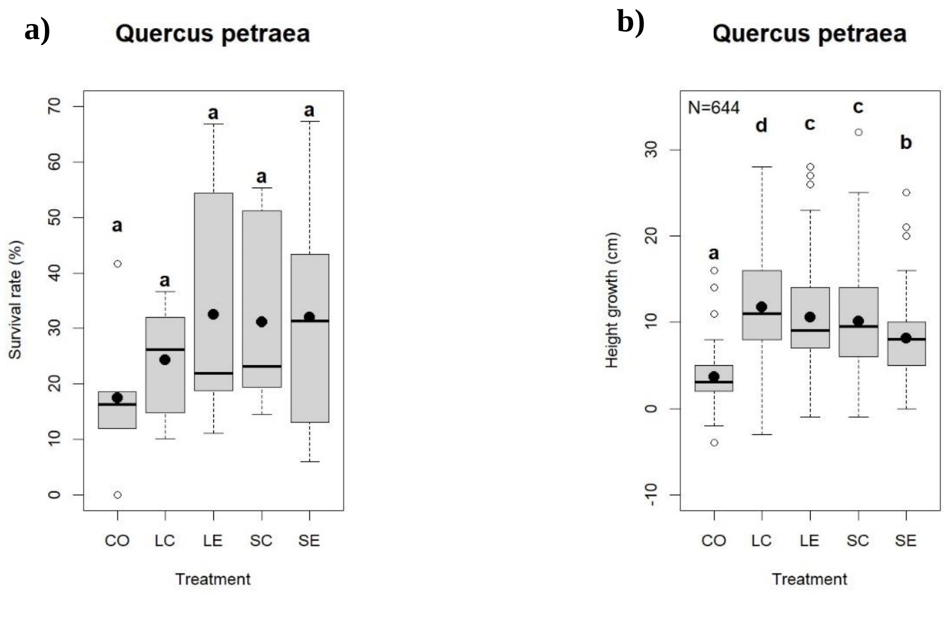

Figure 8. Treatment effect on *Quercus petraea* survival rate (a) and growth (b). For legends, see Figure 2.

4.3.2 Individual growth rate of sessile oak saplings

The models revealed that the treatments affected the growth of the sessile oak saplings significantly, even during two years ($Chi^2 = 292.62$, $p < 2.2e\text{-}16$, $R^2C = 0.4629$) (Figure 8b). In the surviving individually marked *Quercus petraea* saplings, 98.87% had a height increase of 1-32cm in all the gaps. The highest growth was recorded in the large circular and elongated gaps with an average of 11.78cm ± 2.29cm and 10.59cm ± 2.35cm, respectively, while the least growth was recorded in the closed stand (3.39cm ± 1.18cm). The largest negative differences in growth rate were recorded if the individual sapling had a secondary shoot in the previous year, which later died. The circular gaps showed a better growth rate in the same-sized gaps (growth in the large circular gap was higher than large elongated, and small circular growth was higher than small elongated). However, the shape differences were more pronounced in the small gaps.

4.4 Species richness and abundance of natural regeneration in different gap types

Before the treatments, in 2018, eight woody species were present in the understory vegetation in the plots (Figure 9). The species are *Quercus petraea, Carpinus betulus,* common dogwood (*Cornus sanguinea*), wild cherry (*Prunus avium*), field maple (*Acer campestre*), common hawthorn (*Crataegus monogyna*), manna ash (*Fraxinus ornus*) and *Quercus cerris*. In 2022, the species remained the same (Figure 10). The number of woody species in the plots did not change considerably with the interventions: pre-treatment, it varied between 1 and 4; after treatment, the number ranged between 1 and 5. However, the sum of all saplings increased from 780 pre-treatment to 3147 after the treatment. Hence, the total sapling abundance was four times more in 2022 than in the pre-treatment.

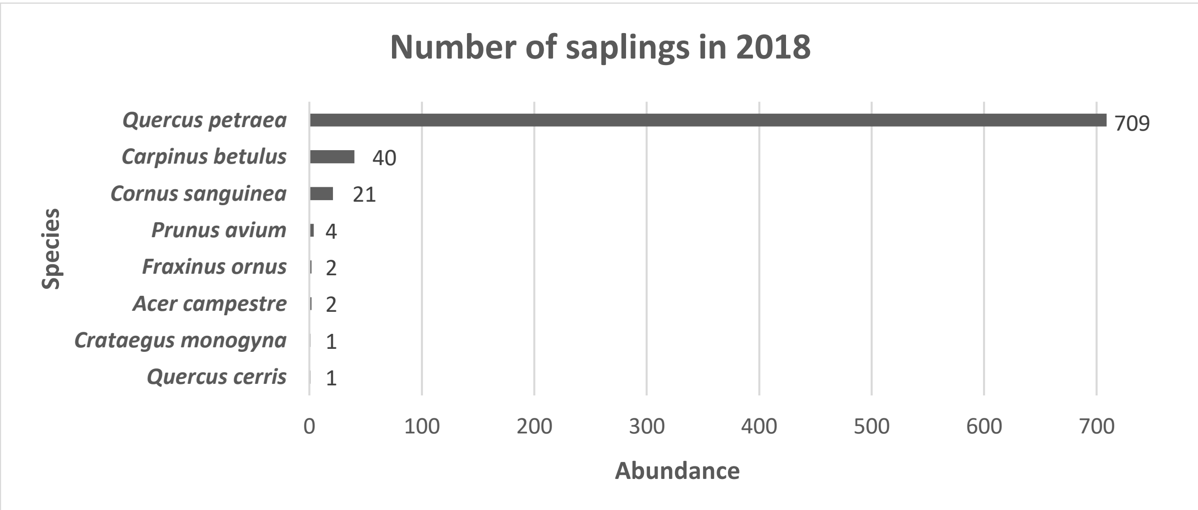

Figure 9. Total number of saplings for the most abundant woody species in 30 understory quadrats of 2m × 2m in 2018.

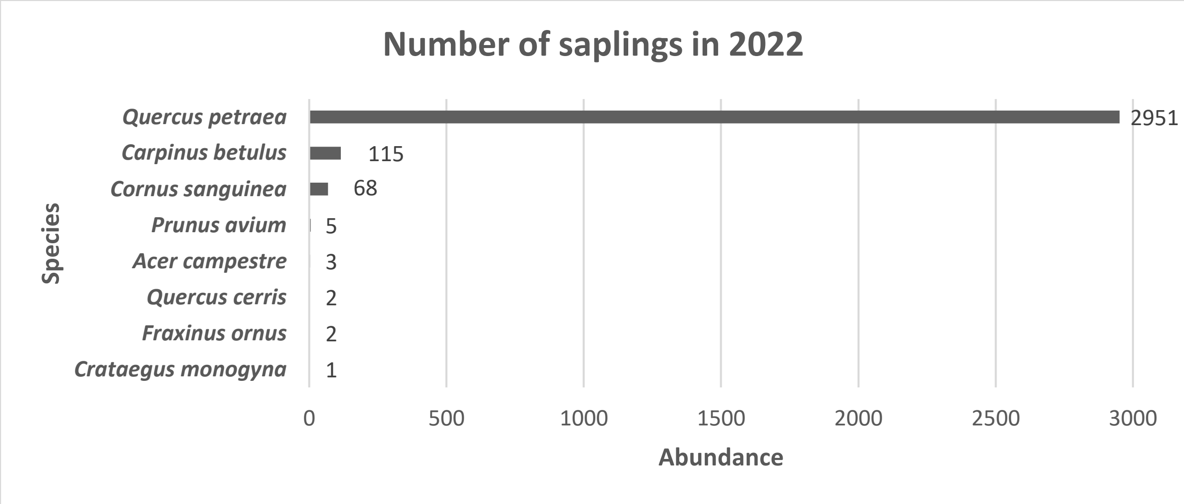

Figure 10. Total number of saplings of the most abundant woody species in 30 understory quadrats of 2m × 2m in 2022.

The three species with the highest abundance (highest number of saplings) in the natural regeneration were *Quercus petr*aea, *Carpinus betulus* and *Cornus sanguinea*; therefore, these species were used for further individual analyses. In 2018, all sessile oak and hornbeam recorded most of their saplings in the shorter size categories I and II (Table 3). In 2022, saplings were also recorded in the larger categories III and IV (Table 4).

Table 3. Number of saplings of the most abundant woody species in each size category in 2018. The treatment types are CO = Control, LC = Large Circular, LE = Large Elongated, SC = Small Circular and SE = Small Elongated. Size I = 0-20cm, Size II = 20-50cm, Size III = 50-130cm and Size IV =>130cm.

2018	***Quercus petraea***					***Carpinus betulus***					***Cornus sanguinea***				
	I	**II**	**III**	**IV**	**sum**	**I**	**II**	**III**	**IV**	**sum**	**I**	**II**	**III**	**IV**	**sum**
CO	178	5	0	0	**183**	6	7	2	0	**15**	2	1	0	0	**3**
LC	74	6	0	0	**80**	3	2	0	0	**5**	0	3	7	0	**10**
LE	189	10	0	0	**199**	0	1	0	0	**1**	0	3	5	0	**8**
SC	139	4	0	0	**143**	6	1	4	0	**11**	0	0	0	0	**0**
SE	97	7	0	0	**104**	6	0	2	0	**8**	0	0	0	0	**0**

Table 4. Distribution of the most abundant woody species in each size category in 2022. For legends, see table 3

2022	***Quercus petraea***					***Carpinus betulus***					***Cornus sanguinea***				
	I	**II**	**III**	**IV**	**sum**	**I**	**II**	**III**	**IV**	**sum**	**I**	**II**	**III**	**IV**	**sum**
CO	476	79	1	0	**556**	8	6	1	2	**17**	0	2	1	0	**3**
LC	31	138	67	8	**244**	5	5	7	7	**24**	1	4	16	30	**51**
LE	117	498	107	1	**723**	17	4	2	1	**24**	0	2	5	7	**14**
SC	197	437	66	1	**701**	6	6	5	8	**25**	0	0	0	0	**0**
SE	385	332	10	0	**727**	12	6	5	2	**25**	0	0	0	0	**0**

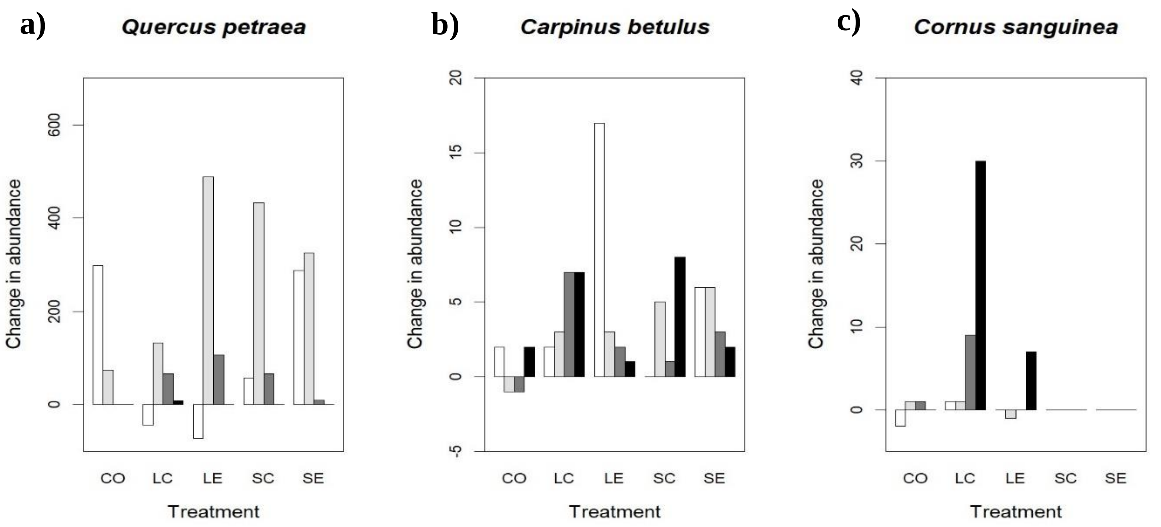

Figure 11. The abundance change of the most abundant woody species between 2018 and 2022, (a) *Quercus petraea*, (b) *Carpinus betulus*, (c) *Cornus sanguinea*. Size I = 0-20cm, Size II = 20-50cm, Size III = 50-130cm and Size IV >130cm. The three figures have different y-axis scales

The treatments significantly affected the abundance change for *Quercus petraea* in all size categories except size IV (Figure 11a). As there was a masting year in the investigated period (2020), there was a considerable number of new saplings in the size I category for the closed stand and the small elongated gap. The large gaps recorded a decrease in the abundance of sessile oaks in size I (Figure 11a). The amount of size II saplings increased in all treatments but to a significantly different degree; the largest increase was in the large elongated and small circular gap (Figure 11a). For the third size category, the sessile oak sapling abundance increased the most in the large elongated and intermediately in the circular gaps. Very few saplings reached the largest size category (size IV); they were somewhat though not significantly, abundant in the large circular gaps (Figure 12d).

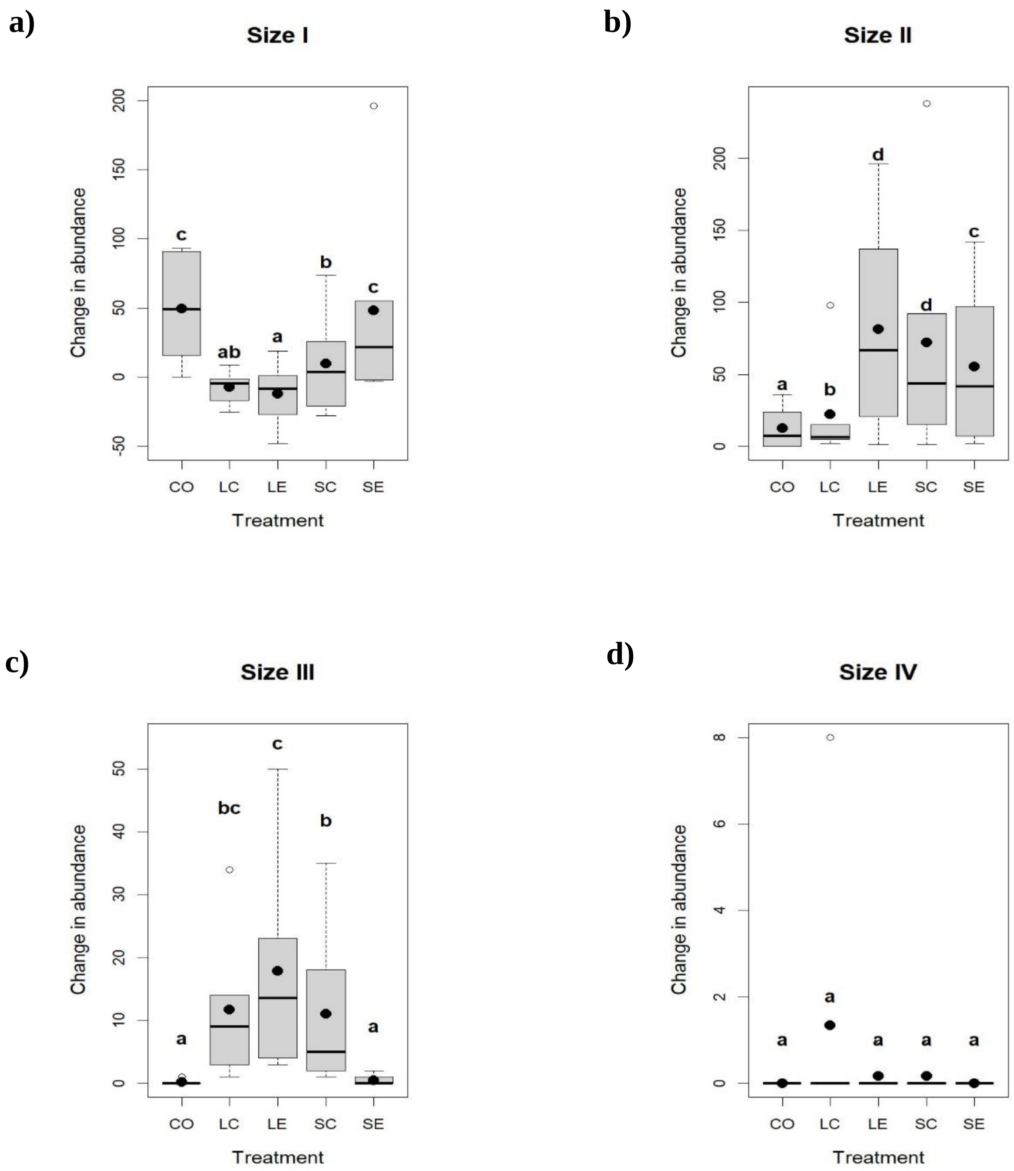

Figure 12. Treatment effects on the abundance change of *Quercus petraea*. The four figures have different y-axis scales. The small letters (a to d) represent the pairwise comparison significance differences (ANOVA-test, alpha level = 0.05).

For *Carpinus betulus*, the result of linear mixed effect models indicates that the treatments had no significant effect on the abundance change for any size category (Figures 13a-d). However, some trends could be observed (Figure 11b): Hornbeam abundance showed a more intensive increment in the gaps than in the control (Figure 11b). Several new saplings were recorded in the first size category in the elongated gaps, but only a few reached larger categories in this gap type. The circular gaps had the highest increase in larger hornbeams (size categories III and IV).

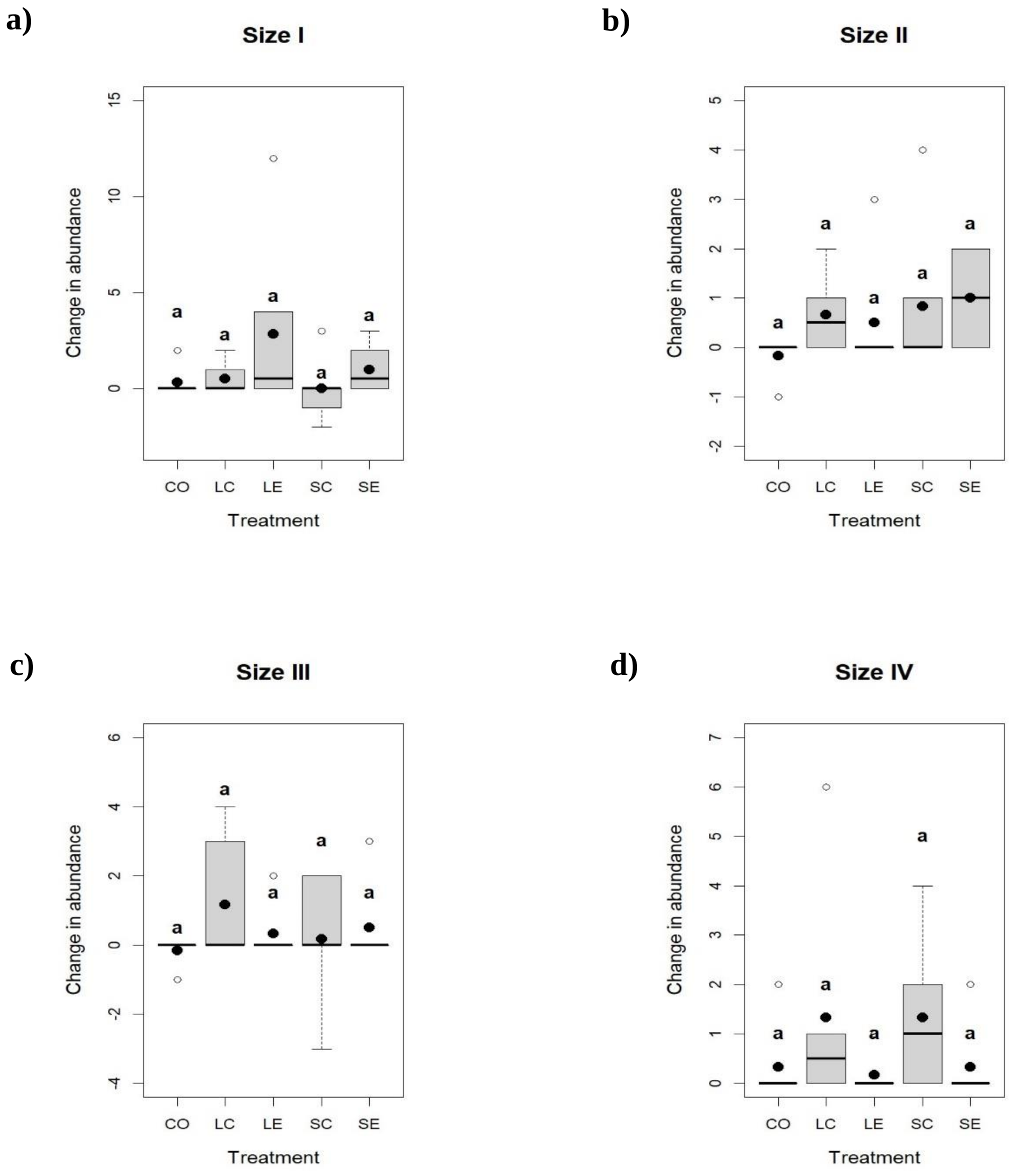

Figure 13. Treatment effects on *Carpinus betulus* abundance change. For legends, see Figure 12.

The treatments had no significant effects on the abundance change for *Cornus sanguinea*, except in the fourth size category ($Chi^2 = 41.405$, $p = 2.215e\text{-}08$, $R^2C = 0.6503$) (Figures 14a-d). There was no considerable change in abundance for *Cornus sanguinea* in the control, small circular and small-elongated treatments. However, the abundance slightly increased in the large gaps, especially in the large circular, and most individuals reached the largest size category.

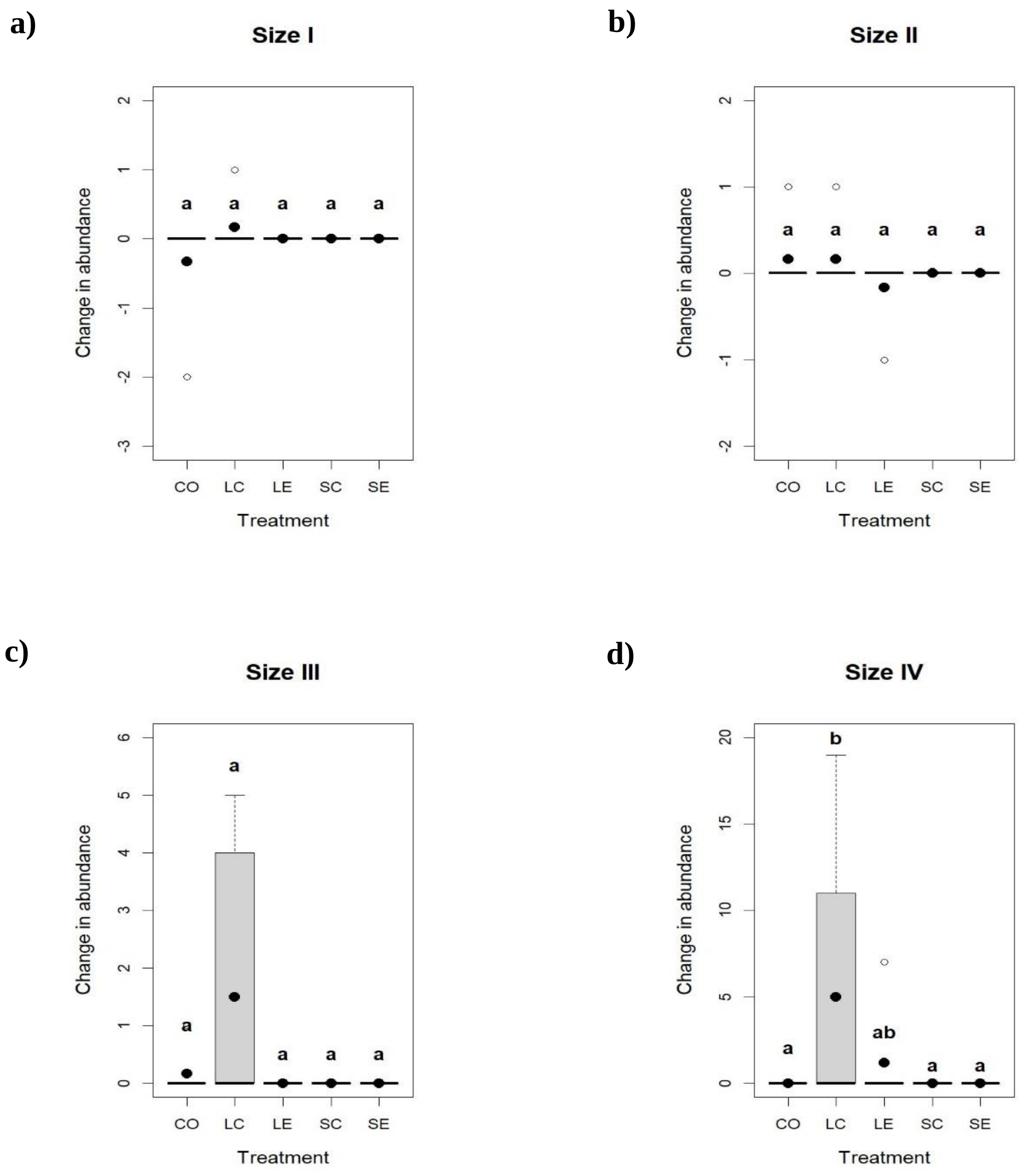

Figure 14. Treatment effects on *Cornus sanguinea* abundance change. For legends, see Figure 12.

5. Discussion

This study investigated the short-term effects of the various sized and shaped gaps on the regeneration of sessile oak and other woody species. As hypothesised, the success of oak regeneration was different in the different gap types; both the size and shape of the gaps affect certain regeneration variables. The light and soil moisture content increased after gap creation, increasing the growth and abundance of the sessile oaks and perennial forbs.

The closed stand recorded the lowest abundance of understory herbs and natural regeneration. Furthermore, in these plots, the survival and growth rate for the sessile oak was the lowest. Due to the low herb cover in the closed stand, the regeneration was almost not exposed to competition. However, the low availability of light could explain the sessile oaks' low survival rate in the closed stand despite the huge number of acorns. The observation above is in line with the findings of Von Lüpke (1998) that even in light levels of $<10\%$, survival with slow growth is still possible in the short term between four and six years. Despite having large acorns that allow the start of the regeneration in closed forests, saplings require ample light for growth and survival after the nutrient reserves in the cotyledons are exhausted (Johnson et al., 2019).

5.1. Influence of gap size and shape on the abiotic environment and understory vegetation

5.1.2 Light

Previous research in temperate forests revealed that gap creation influenced the irradiance where light intensity increased with increasing gap size (Gagnon et al., 2004; Gálhidy et al., 2006; Heithecker & Halpern, 2006; Vilhar et al., 2015; Diaci et al., 2020). Our results align with the findings of these studies. The pre- and post-treatment comparisons revealed that solar radiation increased in all gap types. The larger gaps received the most light (47% and 37% direct light in the large circular and elongated gap respectively), similar to the observations of Gray et al. (2002). The differences between the treatments were visible for both diffuse and direct light. Direct light was higher than diffuse light in all treatments, and a greater variation between the treatments was observed in the direct light. The above findings agrees with the observation of Gray et al. (2002) that mainly the direct light determines the light differences in the gaps. These findings can be attributed to the larger gaps being more open.

The gap shape basically did not influence the amount of light. This observation contradicts the finding of Muscolo et al. (2014) that narrower gaps receive lower light than circular gaps. The only exception in our study was the direct light in the large gaps. Studying the spatial pattern of light in the same gaps in the first year after the interventions, Horváth et al. (2023) found that direct and diffuse light have robust, but different spatial pattern: Direct light has a strong north-south gradient, especially in the circular gaps, being the highest at the northern part. Contrary to this, diffuse light has a concentric pattern, and is the highest in the centre of the gaps. They stated that light is basically determined by gap size and not gap shape, however, the northern part of the large circular gaps receives an extremely high amount of direct light. Our findings align with the discovery that at the northern part of the gaps, diffuse light is independent of gap shape, while direct light is more in large circular gaps compared to the large elongated ones.

Light in the small gaps was significantly lower than in the large gaps, but was still sufficient for developing the saplings. For the height increment of *Quercus petraea* saplings, more than 20% relative light is required (Von Lüpke, 1998; Mölder et al., 2019; Kohler et al., 2020). These previous studies suggest that the direct light in our small (150 m^2) gaps was enough for regeneration (around 29% in the small circular and elongated gaps). Additionally, our findings are similar to those of Tobisch (2010), that light and soil moisture in small gaps (15m diameter) is sufficient to support oak saplings' continual but slow development.

5.1.3 Soil moisture

Soil moisture content was homogeneous pre-treatment. The treatment effect for the soil water content was significantly different in all the treatments one year after gap creation (Horváth et al., 2023); however, for the fourth year, the difference almost disappeared (soil moisture was significantly higher only in the large circular gap than in the closed stand). Since the first-year differences in the soil water content between the various gap types could affect the regeneration patterns observed in the fourth year, the first year's results are also discussed as an explanatory variable.

The large circular gap recorded the highest moisture (5.84% more than the closed stand). The longer distance of the surrounding stand could explain the initial high soil moisture content difference. Nevertheless, in 2022, the developed dense vegetation in the gaps took up much water from the soil, reducing the soil water content difference between the large circular and other gaps.

Although the large elongated gap received similar light as the large circular gap, soil water content increment was less intensive in this gap type. Unlike light, soil water content is mainly influenced by the gap shape (Horváth et al., 2023). In the first year after the gaps creation, soil moisture in small circular gaps was higher than in large elongated ones, while in small elongated gaps, it was significantly lower. For the fourth year, these differences disappeared and the large elongated and the two small gap types recorded almost similar soil moisture content. As mentioned above, it can be explained by the water uptake of the developed vegetation.

5.1.4 Herbaceous understory vegetation

The analysis of the total herb cover revealed that it was not a good explanatory variable for regeneration. Perennial forbs are more competitive species than graminoids and annual forbs, and had considerable abundance in the plots. Hence, the perennial herb cover is used to explain the regeneration trends. The perennial forb cover increased with increasing gap size. Before the gap creation, the mean perennial forb cover in the "treatments" was also relatively high but increased considerably after the treatments (56% total increase).

The optimal light and soil moisture conditions in the large circular gaps promoted the growth of perennial forbs. One of the most competitive and abundant perennials was *Rubus fruticosus agg.*, thriving in this gap type, and thus becoming a competitor for *Quercus petraea.* According to previous studies, *Rubus fruticosus agg*. is a light-flexible clonal plant that can produce an intensive horizontal growth besides optimal abiotic conditions (Gálhidy et al., 2006; Klimešová and de Bello, 2009). Since – in a low abundance – it was widely present in the forest stand before the interventions, after gap creation, it started an intensive vegetative development, especially in the large circular gaps rich in light and soil moisture.

The large elongated gaps had a perennial forb cover almost as high as the large circular gaps. Since these gaps had high light and only slightly lower soil moisture content than large circular gaps, understory vegetation sprouted intensively here. The small circular gaps had the least cover of the understory herbs and perennial forbs; neither the herb nor the perennial forb cover were significantly higher here than in the closed stand. We assume that the considerably lower light conditions than in small circular gaps caused the lower cover.

Competition from herbaceous vegetation is a significant aspect of establishing oaks and is one of the major causes of regeneration failure (Annighöfer et al., 2015). According to our results, in the gaps where the availability of both abiotic resources is high (e.g. in large circular gaps), both herbs and, more so, perennials are abundant. Where the amount of light is high and soil water content is moderate (e.g. in large elongated gaps), the herb and perennial forb cover is only slightly lower. However, the herb cover remains moderate if soil moisture is high and light is considerably lower than in the large circular gaps (e.g., in small circular gaps). Thus, there was intensive competition for the regeneration in the large gaps, and a more moderate one in the smaller gaps.

5.2. Effects of gap size on sessile oak acorn supply

The quality and quantity of seed production is an essential determinant of establishment and survival of plants. In cases where trees are exploited for commercial purposes, producing abundant seeds reduces the restoration costs as it favours natural regeneration (Fischer et al., 2016). Additionally, regenerating forests naturally from the locally fallen seeds is ecologically better: propagules are local; hence they are better adapted to the conditions. Furthermore, using local seeds ensures that no new sub-species of the given tree are introduced. In this study, the difference in the supply of acorns in the gaps was mainly influenced by the distance between the centre of the plots and the surrounding mature sessile oak trees. The above statement explains the low numbers of acorns in the large gaps after the gap creation.

The small circular gaps received the highest number of acorns among the gaps in the pre-treatment year. However, in the masting year after the treatment, the number was quite low compared to the closed stand. The low acorn number is presumed to be due to the distance to the mature *Quercus petraea* trees, which caused few acorns to reach the centre of the gaps. However, the number of acorns was significantly higher here than in the large gaps.

After the large elongated gaps, small elongated gaps received the lowest acorns in the 2018 masting year. Nevertheless, in 2020, this gap type received the highest number of acorns among the gaps. Because the surrounding mature trees are closer to the centre of the gap, the acorn number is significantly higher in this gap type than in the others but lower than in the closed stand. Suppose one wants to use the acorns falling in the gaps for regeneration; this is the best gap type because the heavy *Quercus petraea* acorns can disperse only to such small distances, characteristic of this gap type (Tobisch, 2010).

5.3 Seedling survival and sapling growth rate in different gaps

5.3.2 Survival rate

Though the treatments did not affect the survival rate of *Quercus petraea*, it was somewhat (though not significantly) better in all the gaps compared to the closed stand. Contrary to our expectations, the survival rate of individually marked saplings was not the highest in the large circular gap (where abiotic conditions are the most optimal). This gap type recorded the lowest survival rate among the gaps (24%), proving to be only slightly (7%) better than the closed stand. The low survival rate can be attributed to the high competition from the understory vegetation. The finding aligns with the results of Denslow et al. (1998) that continued growth of established and emerging herbs and shrubs prevents light from reaching seedlings.

Investigation of the dead saplings during the study showed that most of the dead saplings had no roots. Therefore, it is supposed that small rodents could have eaten some of the saplings' roots. Additionally, self-thinning among the saplings could have reduced their number. Hence, the survival of young saplings is driven by other factors independent of the treatment.

5.3.3 Growth

The height increment of a tree species is a significant aspect in terms of competition for survival, with taller saplings being able to outcompete shorter ones (Stimm et al., 2021). The height growth for the *Quercus petraea* was higher in the gaps than in the closed stand, and each gap differed significantly from one another apart from the large elongated and small circular gaps, which were the same. This finding concurs with the discovery of Sevillano et al. (2016) that light availability affects the growth of oaks but not their survival.

Generally, the height growth of *Quercus petraea* proved to be the best in the large circular gap. Most seedling growth in temperate forests is mainly restricted by the amount of light (Lambers & Clark, 2003). Since large circular gaps received the highest light, and especially the direct light was prominently high at the northern part of these gaps (diffuse light was 32%, direct radiation was 47%), these conditions facilitated the growth of the *Quercus petraea* saplings in this gap type. It concurs with the findings of Diaci et al. (2008) and Ligot et al. (2013) that oak growth is better in conditions of higher direct sunlight. Investigating the height growth of *Quercus petraea* saplings in forestry gaps of the Pilis Mountains, Csépányi et al. (2021) also found that growth is the best at 30-50% direct light, i.e. at similar light conditions to our large gaps. Despite the relatively low survival and abundance of *Quercus petraea* in large circular gaps, saplings that grew above the competing vegetation recorded the highest growth rate, which can be attributed to the optimal direct sunlight.

The growth of the individually measured *Quercus petraea* saplings was similar in large elongated and small circular gaps: it was lower than in the large circular gaps, but still considerably high. In large elongated gaps, diffuse light was similarly high as in the large circular gaps, direct light was slightly lower, but still optimal and the soil moisture was intermediate in the first years (Horváth et al., 2023). In the small circular gaps, soil moisture was optimally high, and light was intermediate, but still acceptable (Horváth et al., 2023).

Accordingly, it seems that light and soil moisture have a complex effect on the height growth of the saplings: if one of these resources is in optimal, and the other in an intermediate amount, the growth response is moderate.

The growth rate in the small elongated gap (where neither the amount of light nor the soil moisture is optimal) was low; hence very few saplings reached a height above 50cm. The low growth rate can be explained by the earlier findings of Von Lüpke (1998) that in the first years, survival is possible with slow growth in low-light conditions

5.4. Variation in species richness and abundance with gap type during natural regeneration

The large circular gap has the best light and soil moisture conditions. However, increasing the light and soil moisture in the understory to improve the survival and growth of desired saplings favours the growth of all other vegetation, including competing species (Balandier et al., 2012). Due to the strong competition from perennial forbs and the saplings of other woody species, *Quercus petraea* could not utilise the advantages of the abiotic conditions of the large circular gaps (high direct radiation, lower precipitation interception by the leaves and reduced root concurrence of the mature stand). Hence, this treatment had a very low abundance of oak individuals.

The abundance increment of *Quercus petraea* was the highest in the large elongated gaps for the second and third size categories. This gap type received very few acorns in both masting years, which explains the decreasing abundance of the size I category of saplings. Nevertheless, these gaps had lower competing vegetation (*Carpinus betulus, Cornus sanguinea*), enabling the abundance of *Quercus petraea.* Additionally, the high survival rate ensured the high abundance despite having few acorns.

In the small circular gaps, the abundance increment of *Quercus petraea* was also quite high for the size II and III categories—a similar amount of *Quercus petraea* saplings reached the third category as in the large circular gap, due to many acorns pre-treatment and the environmental conditions (high soil moisture content and intermediate light). Nevertheless, size III abundance increment in the small circular gap was less than in the large elongated gaps which due to lower light conditions in the smaller gaps. The size II oaks also increased considerably, which was different for the large circular gaps and can be explained by the lower competition pressure compared to the large gaps. However, since the number of newly fallen acorns declined with the gap creation, size I saplings only increased slightly. Also, the saplings growing into size II were replaced by a few new saplings or, in some cases, none. The high initial abundance of the size I and II saplings could have hindered the establishment of the herbs, perennial forbs and other woody species in this gap, aligning with the findings of Kuehne et al. (2020) that greater oak sapling abundance delays the establishment of other competing vegetation.

The small elongated gaps recorded the highest increment in the number of size I (2022 total abundance is four times more than in 2018) and a considerably high increase in size II (third highest increase after the large elongated and small circular gaps) of *Quercus petraea* saplings. The high number of acorns in both masting years is assumed to cause the high number of size I and II *Quercus petraea* saplings. However, due to the less optimal abiotic conditions in small elongated gaps (low light and soil moisture), very few saplings could reach the third, and almost none the fourth size category. The low abundance in third and fourth size categories is in accordance with the low height increment values of the individually measured saplings in this gap type.

Though the abundance increment was low for the *Carpinus betulus* saplings, the large elongated gaps recorded the highest increase. This can be explained by the relatively high soil moisture content in this gap type. As *Carpinus betulus* is a shade-tolerant species of mesic forests, its development seems to be more driven by soil moisture than light (Tinya et al. 2009). The abundance increment was mainly in the size I saplings indicating that the conditions here favoured new sapling establishment. However, the abundance increment was not significant.

The abundance increment for *Cornus sanguinea* was observable mainly in the large gaps, especially in the large circular gaps. *Cornus sanguinea* is a clonal species developing well on a vegetative way from the roots (Klimešová and de Bello, 2009). Sapkota et al. (2009) found that both seed availability and sprouting capabilities influence the density of the species in gaps. According to our findings, the favourable abiotic conditions of the large circular gaps promoted the intensive development of new shoots.

6. Conclusions and implications for management

This study evaluated the short-term regeneration success of sessile oaks after gap creation. Because of the short duration of the observation (2 to 4 years), we cannot draw conclusions regarding the entire process of forest regeneration. Nevertheless, the initial response is useful because it is a determinant phase for regeneration. Continued data collection is recommended to evaluate the long-term effects of the different gap types. Based on our results, oaks regenerate better in the gaps than in the closed stand. The large circular gaps recorded the highest growth increment indicating that the complex abiotic conditions (light, soil moisture) here were most favourable for growth. Nevertheless, conditions of this gap type also favoured the development of other competing vegetation (perennial forbs, such as *Rubus fruticosus agg*., and some woody species, such as *Carpinus betulus and Cornus sanguinea*). Therefore, if oaks were to be regenerated here, it would require constant pruning and weeding to remove unwanted species leading the forest managers to incur more costs.

Competitive perennial forbs seem to prefer those places where both the amount of light and the availability of soil moisture are high (i.e. large circular gaps). The growth of *Carpinus betulus* seems to be driven by the soil moisture (growing the best in the circular gaps), while *Cornus sanguinea* is mainly affected by the light (growing the best in the large gaps). Therefore, large elongated and small circular gaps are better sites for oak regeneration: the abiotic conditions are slightly lower than in large circular gaps but still ensure a proper height increment, with lower competition with the herbs and other woody species.

Small elongated gaps are less favourable for oak regeneration since they do not ensure enough light and soil moisture for the intensive growth of the oak saplings. However, this gap type also has several advantages: the acorn supply after the gap creation remains good, contrary to the larger (or the same-sized) circular gaps. The slightly increased light ensures a similar survival for the saplings as the large elongated and small circular gaps, with a lower competition pressure. As oaks are relatively shade-tolerant in their first years and allocate more to the growth of their root system, they can survive and strengthen even in moderate light conditions of small elongated gaps. It is hypothesised that extending the small elongated gaps to large circular gaps after several years will result in an intensive growth of the survived saplings, as these larger, strengthened saplings will better utilise the received extra light and soil moisture than the small saplings of gaps immediately created as large circular. Besides, several-year-old saplings of extended gaps will have some competitive odds against the herbs and other woody species established only after the gap extension. This hypothesis will be tested in the Pilis Gap Experiment in the next years.

To achieve the best regeneration of *Quercus petraea*, a balance between favourable abiotic conditions and competition can be set by choosing the proper gap size, shape and timing of gap creation and extensions, always considering the local forest site conditions and the initial understory species composition.

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APPENDICES

Appendix 1: List of the understory species.

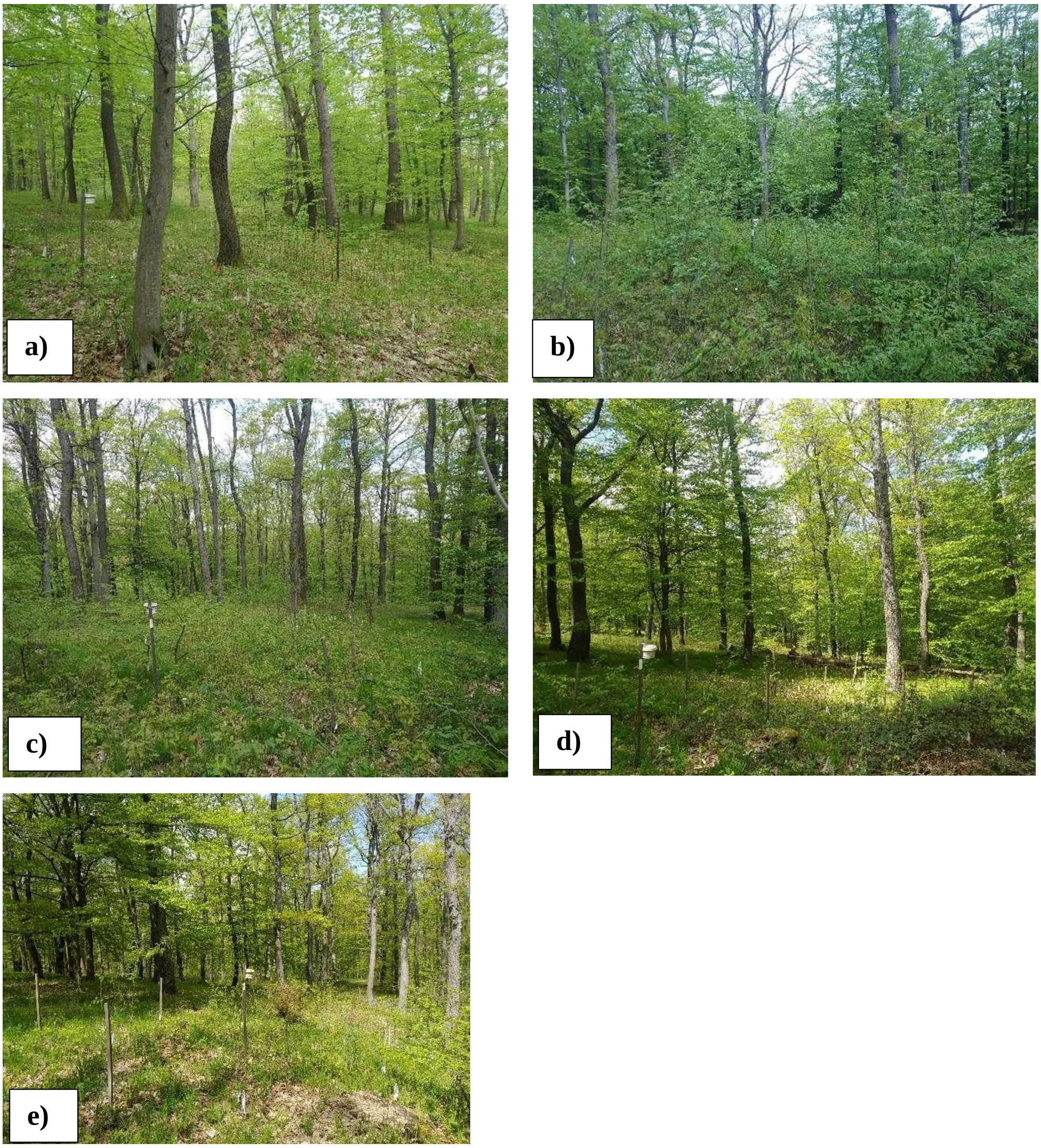
Functional groups: WD = Woody, PF = Perennial Forb, GR = Graminoid, AF = Annual Forb.

Species	Functional Group	Frequency (%)	Mean cover (%)
Acer campestre	WD	10.00	0.0235
Ajuga reptans	PF	13.33	0.0508
Athyrium filix-femina	PF	3.33	0.0521
Brachypodium pinnatum	GR	10.00	0.5606
Bromus benekenii	GR	3.33	0.0391
Cardamine bulbifera	PF	33.33	1.3845
Carex pilosa	GR	80.00	23.2177
Carpinus betulus	WD	53.33	0.4902
Cephalanthera longifolia	PF	3.33	0.0130
Convallaria majalis	PF	13.33	0.5345
Cornus sanguinea	WD	13.33	0.0508
Dactylis polygama	GR	3.33	0.0026
Euphorbia amygdaloides	PF	26.67	0.2386
Fragaria vesca	PF	36.67	0.8656
Fraxinus ornus	WD	3.33	0.0026
Galium aparine	AF	16.67	0.0939
Galium odoratum	PF	10.00	0.3976
Galium schultesii	PF	73.33	6.5497
Hieracium sabaudum	PF	6.67	0.0091
Hypericum hirsutum	PF	6.67	0.0287
Hypericum perforatum	PF	3.33	0.0391
Impatiens parviflora	AF	16.67	1.2306
Lathyrus niger	PF	3.33	0.0065
Lathyrus vernus	PF	30.00	0.2597
Ligustrum vulgare	WD	3.33	0.0391
Luzula luzuloides	GR	3.33	0.0026
Lysimachia punctata	PF	3.33	0.1564
Melampyrum nemorosum	AF	6.67	0.0078
Melampyrum pratense	AF	3.33	0.0078
Melica uniflora	GR	100.00	20.0759
Melittis melissophyllum	PF	56.67	0.9842
Moehringia trinervia	AF	10.00	0.0042
Mycelis muralis	PF	3.33	0.0104
Parietaria officinalis	PF	3.33	0.2868
Poa nemoralis	GR	50.00	1.4105
Polygonatum multiflorum	PF	10.00	0.3911
Prunus avium	WD	6.67	0.0104
Quercus cerris	WD	3.33	0.0078
Quercus petraea	WD	100.00	14.5968

Species	Functional Group	Frequency (%)	Mean cover (%)
Ranunculus ficaria	PF	10.00	0.8630
Rubus fruticosus agg.	PF	60.00	22.2139
Rumex sanguineus	PF	3.33	0.0782
Scrophularia nodosa	PF	6.67	0.0196
Stachys sylvatica	PF	6.67	0.8474
Stellaria holostea	PF	60.00	1.3847
Stellaria media	AF	3.33	0.0052
Symphytum tuberosum	PF	3.33	0.0026
Tanacetum corymbosum	PF	6.67	0.0078
Urtica dioica	PF	3.33	0.1304
Veratrum nigrum	PF	6.67	0.1043
Veronica chamaedrys	PF	10.00	0.0065
Veronica officinalis	PF	3.33	0.0013
Vicia sepium	PF	3.33	0.0391
Viola alba	PF	6.67	0.0130
Viola reichenbachiana	PF	46.67	0.1499

Appendix 2: Photos of the treatments in the fourth year after treatment intervention.

The treatments are a) control, b) large circular, c) large elongated, d) small circular, c) small elongated gaps. (photos taken by Flóra Tinya)



Appendix 3: Hemispherical photographs of the treatments taken at the northern part of the plots.

The treatments are a) control, b) large circular, c) large elongated, d) small circular, c) small elongated gaps. (photos taken by Flóra Tinya)