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Initial regeneration success of tree species after different forestry treatments in a sessile oak-hornbeam forest

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ABSTRACT

Ecological, economic, and social demands triggered a shift in the management of temperate deciduous forests from rotation forestry system towards more nature-based forest management techniques such as continuous cover forestry. However, there is insufficient knowledge on the regeneration success of different tree species—especially oaks—within this management system. Through a systematic experiment, we compared the regeneration processes of a sessile oak-hornbeam forest after gap-cutting (as an element of continuous cover forestry system) to regeneration after clear-cutting, preparation cutting, and in retention tree groups (treatments of rotation forestry system). A managed, closed, mature forest was used as control. Several different aspects of the regeneration were studied: (1) seed supply of sessile oak—*Quercus petraea* (Matt.) Liebl., (2) species number and abundance of the natural regeneration, (3) survival and growth of individual saplings of five tree species (sessile and Turkey oak—*Quercus cerris* L., hornbeam—*Carpinus betulus* L., beech—*Fagus sylvatica* L., and common ash—*Fraxinus excelsior* L.). The number of acorns was high in closed forest, intermediate in preparation cutting and retention tree group, low in gaps, and zero in clear-cutting. Four years after the interventions, there was no detectable treatment effect on the species number of regeneration. Survival increased in every treatment compared to control, but there was no significant difference in this measure between the differently treated sites. Height growth was highest in the gaps and clear-cuts, intermediate in preparation cuts, and lowest in retention tree groups and controls. Species with different seed dispersal mechanisms responded differently to treatments: oaks were dispersal-limited in the gaps and clear-cuts, while anemochorous species (e.g., hornbeam and manna ash) were present in every treatment. The survival and growth pattern of the particular species proved to be similar, but the intensity of the response differed: shade-tolerants (hornbeam, beech, and ash) showed better survival than oaks in most treatments, and their height growth was larger. According to our results, oak regeneration establishes successfully in oak-hornbeam forests not only in the case of rotation forestry, but also during continuous cover forestry (gap-cutting). The survival and growth of the saplings are similar in cutting areas and gaps, but keeping in mind other considerations (such as preserving forest continuity, balanced site conditions, and forest biodiversity), continuous cover forestry should be preferred.

1. Introduction

Forest management is an elementary driver of forest biodiversity (Lindenmayer and Franklin 2002, Paillet et al. 2010) and regeneration (Phillips and Shure 1990, Huggard and Vyse 2002, Man et al. 2009). In the last decades, an on-going shift has been observed in temperate deciduous forests from rotation forestry system towards a more nature-based forest management that has been triggered by conservational, economic, and social demands (Matthews 1991, von Lüpke 1998, Pommerening and Murphy 2004, Gustafsson et al. 2012). From ecological perspective, the main disadvantage of the most widely used even-aged rotation forestry system is the temporal discontinuity of the forest environment (Bengtsson et al. 2000, Uhía and Briones 2002, Fenton et al. 2003). Regeneration in cutting areas also comes up with some

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difficulties: because of the harsh environmental conditions (e.g., higher solar irradiance, extreme temperature fluctuations, higher wind speed, low air humidity, extreme plant surface temperature that can deplete photosynthesis and injure plant tissues, increased exposure to frost damage), regeneration is often unsuccessful (Keenan and Kimmins 1993, Man and Lieffers 1997, Fleming et al. 1998, Kellner and Swihart 2016). In the case of clear-cutting, artificial regeneration and competition control are necessary, which need large human effort and cost (Dey et al. 2008). These problems can be mitigated by applying uniform shelterwood system instead of clear-cutting (Matthews 1991, Brose 2011). It is based on natural regeneration but does not solve the problem of temporal discontinuity if a final cut is applied. Clear-cuts and the final cuts of uniform shelterwood system can be combined with retention tree groups that ameliorate the negative effects of the cutting areas on biodiversity and regeneration (Lindenmayer et al. 2012). However, there is a lot of uncertainty regarding their buffering capacity: the success depends on the given forest type, the level of retention, and the investigated organism groups (Gustafsson et al. 2012, Fedrowitz et al. 2014).

Continuous cover forestry offers uneven-aged stands as an alternative to rotation forestry systems (Möller 1922, von Gadow et al. 2002, Pommerening and Murphy 2004, Diaci 2006, Schütz et al. 2012, Pro Silva 2019). In continuous cover forestry system, the formation of smaller gaps instead of large cutting areas keeps the continuity of the canopy cover and of the forest environment at stand scale. Within the stand, this forestry system maintains heterogeneous stand structure, variable and balanced age- and diameter-distribution, while higher tree species diversity, essential structural elements and microhabitats can also be preserved (Pommerening and Murphy 2004, Diaci 2006). As a result, it can be more favorable for forest biodiversity (Alder et al. 2018, Elek et al. 2018, Tinya et al. 2019a), may provide more ecosystem services (Pukkala 2016), and supports more the multifunctionality of the forests (Peura et al. 2018). It also has substantial benefits from the regeneration viewpoint, for example, the saplings are not exposed to extreme microclimatic conditions as in cutting areas (Keenan and Kimmins 1993). Mimicking the natural stand dynamic, continuous cover forestry can better build upon natural regeneration, which can be a possible option for sustainable forest management (Emborg 1998, Modrý et al. 2004). By lower investments for tending, and by harvesting large, valuable trees, continuous cover forestry can be also economically beneficial (Knoke 2009, Diaci and Firm 2011, Csépányi and Csór 2017). Providing for the natural regeneration of the dominant tree species is an elementary condition for the successful application of continuous cover forestry. Concerning this issue, a huge amount of forestry experiences has been accumulated (e.g., Möller, 1922, Leibundgut 1986, Sturm 1993, Diaci 2006, Schütz 2011); however, both the management practice and the base research still suffer from some uncertainties. Thus, it is essential to compare the regeneration processes of continuous cover forestry and rotation forestry under similar circumstances, but such comparative experiments are rather rare (Huggard and Vyse 2002, Mason et al. 2004, Looney et al. 2017), especially concerning of oak forests (Phillips and Shure 1990).

The regeneration (establishment, survival, and growth) of various deciduous tree species of the temperate region to the particular forestry treatments is different. There is substantial evidence concerning the regeneration of European beech (*Fagus sylvatica* L.) (Standovár and Kenderes 2003, Mountford et al. 2006, Feldmann et al. 2018). It is well known that it can successfully regenerate in old-growth stands characterized by fine-scale gap dynamics (Emborg 1998, Mihók et al. 2005, Feldmann et al. 2018) and that irregular shelterwood and group selection systems can be applied effectively in beech-dominated managed forests (Mountford et al. 2006, Nocentini 2009, Csépányi and Csór 2017). Much less information is available about the regeneration of admixing tree species within various forestry systems, although they are also instrumental in forest regeneration (Modrý et al. 2004). Even the shade-tolerant species differ in their tolerance of shade and in their response to the developed gaps (Canham 1989, Modrý et al. 2004, Barna and Bosela 2015). Emborg (1998) stated that regeneration of common ash (*Fraxinus excelsior* L.) is similarly strongly shade-tolerant as beech, while, according to Beck et al. (2016), common ash is light-demanding in its mature stage. Hornbeam (*Carpinus betulus* L.) is also considered a shade-tolerant species (Modrý et al. 2004, Tinya et al. 2009), however, the occurrence of its saplings within a stand is related to the light pattern (Tinya and Ódor 2016). Even less is known about the regeneration of oaks (*Quercus* spp.) in gaps; although, oaks are among the most important tree species in temperate deciduous forests, both from ecological and economical perspectives (McShea and Healy 2002, EEA 2007). Nowadays, regeneration of oaks is a crucial issue in forest management. Both in North America and Europe, it is often observed that in unmanaged oak forests, shade-tolerant species regenerate instead of oaks (Feist et al. 2004, Petritan et al. 2013, Saniga et al. 2014). In North America, it is mainly maple species (*Acer* spp.) (Abrams et al. 1997, Feist et al. 2004). In Western Europe and the Carpathian Mountains, beech became dominant over sessile oak—*Quercus petraea* (Matt.) Liebl. (Rohner et al. 2012, Petritan et al. 2013). In the lowland oak forests of Poland and in the oak-hornbeam forests of Hungary, hornbeam is the main species in the regeneration layer (Brzeziecki et al. 2016, Standovár et al. 2017). Similarly, the retreat of oaks is also observable in the natural regeneration of managed oak stands (Van Couwenberghe et al. 2013, Kollár 2018).

Oaks are considered to be light-demanding species that need large open areas to regenerate (Thomas and Packham 2007, Bobiec et al. 2011). Historically, these open areas are related to large-scale natural disturbances or human land-use. In North America, fire is considered the main driver (Cowell et al. 2010, Nemens et al. 2018). In Europe, open landscapes were maintained by large herbivores (according to the wood-pasture concept of Vera 2000) or by traditional human land-use (Bobiec et al. 2011, Saniga et al. 2014). Based on the "oakscape" concept of Bobiec et al. (2018), many recent oak-dominated stands regenerated in various kinds of open and transitional habitats (e.g., meadows, fallowed croplands, wood pastures, etc.), which were more abundant in the past at the landscape-scale. However, nowadays landscape mosaics are more fixed and segregated, and from the management perspective, oak regeneration should be located in the current forest areas.

There are evidences of successful regeneration of oaks and other shade-intolerant species in gaps (von Lüpke 1998, Diaci et al. 2008, Varga 2013, Csiszár et al. 2014, Schütz et al. 2016). Some studies suggest that oak can regenerate in gaps if the saplings of shade-tolerant species are controlled (von Lüpke 1998, Van Couwenberghe et al. 2013). According to Bobiec (2007) and Thomas and Packham (2007), regeneration of oaks can be successful in gaps in special ephemeral circumstances (e.g., spots of exposed mineral material, inaccessibility to browsers) or by means of proper forest site conditions and under an open canopy layer. According to Kellner and Swihart (2016), it depends on complex agents such as the intensity of disturbances, abiotic factors, herbivore pressure, competition, or weather conditions.

The numerous, above-mentioned knowledge gaps lead us to implement a study, which investigates the regeneration of sessile oak-hornbeam forests, after different forestry treatments, in a uniform, experimental framework. We compared the effects of the typical treatments of the rotation forestry system (preparation cutting, clear-cutting, and retention tree group) and the impacts of a widely used element of the continuous cover forestry system (gap-cutting). In Hungary, the sessile oak-hornbeam stands are typically managed in even-aged uniform shelterwood system, where the regeneration felling is usually divided into two or three steps. The preparation cutting and the seeding cutting generally happen in one step, when the mature trees has cropped well. This cutting removes approximately the 30% of the growing stock. After a couple of years, it is followed by the secondary cutting, and later by the final cutting. Many times, these last two operations are carried out in one step, as well, when the seedlings are

25–40 cm high. Normally, the whole series of operations takes only 3–10 years. Because of the shortness of this period, in the current experiment, the complete process could be modelled by a clear-cutting (cutting all the trees in one step). Thus, this treatment of the experiment represents the final cutting of the uniform shelterwood system.

The aim of this study was to investigate the effect of these treatments on the regeneration (establishment, survival, and growth) of different tree species. Our main focus was on the regeneration and growth of sessile oak, as the major tree species of sessile oak-hornbeam forests, both from silvicultural and conservational perspectives, but we also evaluated the response of some admixing tree species. To get the most comprehensive picture, several different variables related to regeneration were studied: (1) seed supply of sessile oak, (2) species number and abundance of natural regeneration (trees and shrubs), (3) survival and growth of individual saplings. Here, we show the four-year results of our experiment.

2. Materials and methods

2.1. Study area

The study area was located in the Pilis Mountains (47°40′N, 18°54′E), the north-eastern ridge of the Transdanubian Range, Hungary (Fig. 1a). Concerning the site conditions, stand structure, composition, and prevalent management practices, the investigated stand represents the managed sessile oak-hornbeam forests (in Natura 2000: Pannonic woods with *Quercus petraea* and *Carpinus betulus,* code: 91G0, Council 1992; EEA, 2007). It is placed on north-facing, moderate slopes (7.0–10.6°), at 370–450 m a.s.l. The average annual mean temperature is 9.0–9.5 °C, while the mean annual precipitation is 600–650 mm (Dövényi 2010). The limestone and sandstone bedrock is mixed with loess. The main soil types are slightly acidic Luvisol (lessivage brown forest soil) and Rendzic Leptosol, the pH of the top 20 cm layer varies between 4.2 and 5.3 (Kovács et al. 2018). The stand was managed by shelterwood forestry system (Matthews 1991), which resulted in an even-aged stand (it was 80 years old at the beginning of the experiment) with uniform structure and species composition. Sessile oak dominates the upper canopy layer, while hornbeam forms a secondary canopy layer. Manna ash—*Fraxinus ornus* L., beech, Turkey oak—*Quercus cerris* L., and wild cherry—*Cerasus avium* (L.) Moench also appear as subordinate species. The shrub layer is scarce, and the understory layer consists of general and mesic forest species; the dominant herbs are *Carex pilosa* Scop. and *Melica uniflora* L.

2.2. Experimental design

The current work is a part of the Pilis Forestry Systems Experiment (Effect of forestry, 2019), which investigates the effects of different forestry treatments on forest site, regeneration, understory vegetation, various animal groups, and ecosystem functions. The experiment was carried out with the help of a randomized complete block design, with six replicates, using the following silvicultural treatments (Fig. 1b):

1. control (C): closed-canopy stand, without harvesting;
2. clear-cutting (CC): a circular clear-cut (diameter: 80 m), surrounded by closed stand;
3. gap-cutting (G): an artificial circular gap in the closed stand (diameter: 20 m, approximately one tree height/gap diameter ratio);
4. preparation cutting (P): 30% of the dominant trees (based on the basal area) was removed in a spatially even arrangement, and the whole secondary canopy and shrub layer were felled (diameter: 80 m),
5. retention tree group (R): within the clear-cuts, a circular group of trees was retained (diameter 20 m, 8–12 individuals).

The selected size and implementation of the treatments mimicked the general forest management practices in Hungary. Within the uniform shelterwood system, the maximal size of the cutting (regeneration) areas is 5 ha in protected montane/submontane native forests (Anonymous 1996). Because of practical and conservational reasons, the size of our experimental clear-cut is smaller, only 0.5 ha. However, we assume that the larger cutting areas of the uniform shelterwood system have similar or more extreme microclimate and site conditions compared to closed stand. In Hungary, the paradigm shift towards continuous cover forestry started two decades ago (Frank 2000, Varga 2013). The introduction of the different methods of continuous cover forestry happened mainly in beech-dominated mixed forest. In sessile oak-hornbeam forests, forest managers use many different procedures in the framework of continuous cover forestry, a generally accepted methodology is still missing. In the first attempts, the applied gap size varies between 0.5 and 1.5 tree height/gap diameter ratio (Bartha et al. 2014). The experimental interventions were carried out in the winter of 2014–2015.

The microclimate of the plots have been intensively studied and

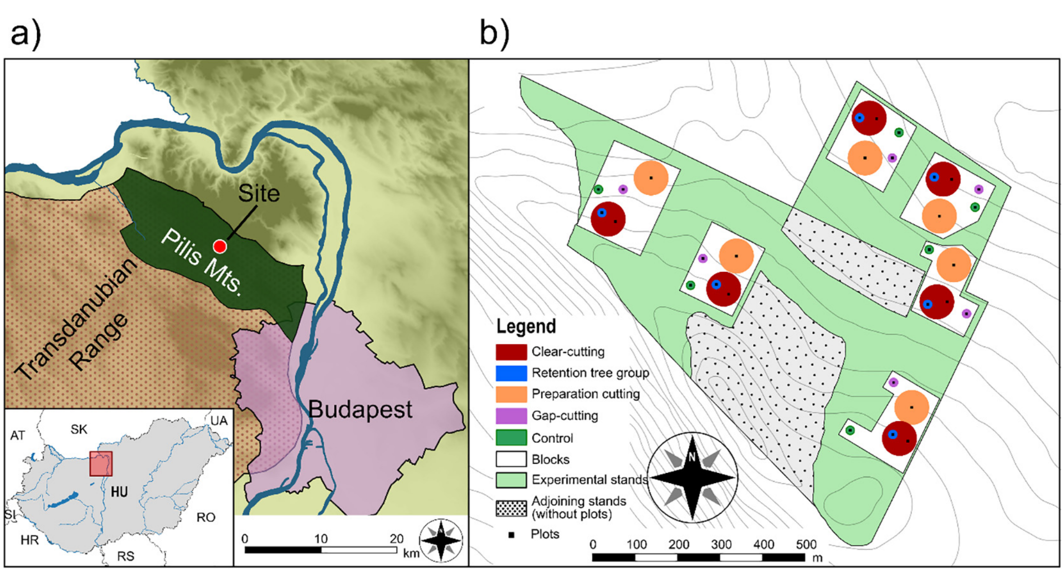

Fig. 1. The study area of the Pilis Forestry Systems Experiment. (a) Site location in the Pilis Mountains (Transdanubian Range, Northern Hungary). (b) Experimental design showing the five treatments replicated within six blocks.

described in details by Kovács et al., 2018, 2020). Microclimate measurements were taken next to the localities of the regeneration surveys. The various treatments resulted in significantly different microclimatic conditions (Kovács et al. 2018), and these initial circumstances did not change substantially during the first few years (Kovács et al., 2020). Clear-cuts were characterized by extreme light conditions, high temperature, intermediate soil moisture, and large daily variances of the microclimatic variables. In gaps, light was intermediate, soil moisture was high, but the air humidity and temperature remained balanced. In preparation cuts, light and soil temperature increased moderately; soil moisture did not change compared to the closed stand. Retention tree groups received a slightly increased amount of irradiance. The soil was warmer than in the closed forest, and the soil moisture was low (Kovács et al., 2018, 2020). Based on our measurements, in 2018, mean relative diffuse light was 61% in clear-cuts, 20% in gaps, 15% in preparation cuts, and 12% in retention tree groups, while in the closed control sites it was 2% (Tinya unpubl.).

2.3. Data collection

The five treatment types in the six replicates resulted in altogether 30 plots. In every plot, a 6 m × 6 m study area has been fenced to exclude the effects of game species (such as browsing, trampling, and rooting). All surveys of the current work have been carried out within the fenced area. The data collection for all studied variables was performed in the first (2015) and the fourth year (2018) after the interventions.

Three different aspects of the regeneration have been studied: (1) acorn production of sessile oak, (2) species number and abundance of natural regeneration, (3) survival and individual growth of planted and naturally regenerated saplings.

(1) The acorn production was examined by counting the fallen sessile oak acorns on one square meter within the fence. In order to reduce seed predation, poultry netting was also mounted to the fence from the ground up to 0.5 m (mesh size: approx. 1 cm). In both years, one sampling was carried out in October.
(2) Natural regeneration was investigated in one 2 × 2 m^2 quadrate per plot. The number of saplings was counted separately for every woody species (trees and shrubs) in four size categories: (I) 0–20 cm height, (II) 20–50 cm, (III) 50–130 cm, (IV) height > 130 cm, diameter at breast height < 5 cm. Sampling was carried out in summer, both in 2015 and 2018.
(3) The survival and the individual growth of regeneration was measured for planted saplings to obtain standardized initial stage and sample size for comparing the treatments. Five species were planted: sessile oak, as the dominant species of the investigated forest type and hornbeam, which constitutes the secondary canopy layer. Turkey oak and beech were the main species of the adjacent forest types around the region of the oak-hornbeam forests (beech forests, usually at higher elevations, and Turkey oak-sessile oak forests, typically at lower elevations). Both of them can occur as admixing species in sessile oak-hornbeam stands. Finally, a further admixing species of mesic forests, the common ash, was also planted. Five individuals of each species were planted in every plot (25 individuals per plot, 150 saplings per species, altogether 750 individuals) in the spring of 2014. In the spring of 2015, the dead saplings were substituted with new ones. The saplings were arranged in a 70 cm grid in a randomized order. Height and leaf area were measured at the end of both summers (2015 and 2018). For each sapling, a typical leaf was scanned with a portable laser leaf-area meter (CID-202, CID Bio-Science, USA), and its area was multiplied by the leaf number to get an estimated total leaf area. All leaves were counted for smaller saplings, while the leaf number was estimated for larger ones (by the multiplication of the counted leaf number of some branches).

To examine the natural survival and growth of the regeneration independent of the effects of planting stress, we also measured the naturally regenerated saplings present within the fences. Height and leaf area measurements followed the same methodology as in the case planted saplings. Among this natural regeneration, three species were abundant enough for statistical analysis: sessile oak, hornbeam, and manna ash. Since their growth pattern in the different treatments proved to be very similar to that of planted ones, they are interpreted only in the Appendix of the current paper.

Because the small seedlings of manna ash and common ash (*Fraxinus ornus* L. and *F. excelsior* L.) could hardly be distinguished, all naturally regenerated ashes were identified as manna ash.

All the used data are available in dataset (Tinya et al., 2019b).

2.4. Data analysis

To investigate the effect of the forestry treatments on the different variables of the regeneration, general and generalized linear mixed-effects models were applied. Treatment was used as fixed factor, and block was captured as random factor. The details of the models were different for the studied regeneration variables:

(1) For the number of acorns, two distinct models have been created for 2015 and 2018 due to the obvious year effect caused by masting in 2018. Generalized linear mixed-effect models with Poisson error structure were performed for these variables.

(2) Species number and abundance of the natural regeneration followed Poisson distribution as well, thus generalized linear mixed-effects models were used for these variables also. Similar to acorn production models, separate models were built for 2015 and 2018. For the abundance analyses, three species were found adequately abundant for the modelling procedure: sessile oak, hornbeam, and manna ash. Wild fruit tree and shrub species (wild cherry, common dogwood—*Cornus sanguinea* L., common hawthorn—*Crataegus monogyna* Jacq., European crab apple—*Malus sylvestris* (L.) Mill., blackthorn—*Prunus spinosa* L., dog rose—*Rosa canina* L., and wild service tree—*Sorbus torminalis* (L.) Crantz) were merged as endozoochorous species group and analyzed together. Separate models were built for the four size categories of each species and the species group.

(3) In the case of the individual saplings, survival and height growth were analyzed. For the survival analysis of the planted saplings, the 495 individuals which were alive in the spring of 2015 (from the original 750) were used. Saplings that had died in the first year of planting, before or during the interventions, were excluded from the calculations. Among the naturally regenerated saplings, altogether 125 individuals could be analyzed from the three species. Generalized linear mixed-effects models were used with logit link function (binomial distribution), and predicted survival rates were calculated for each species. In the case of sessile oak survival, the Bayesian model was applied to handle quasi-complete separation.

Into the growth analyses, we included all available individuals (both the original and the replanted ones). The effect of substituting of dead saplings was tested as a random factor, but it was not significant. Therefore we excluded this variable from the final models.

Only those individuals which survived between the summer of 2015 and 2018 were analyzed—altogether 423 specimens in the case of planted saplings, and 107 individuals in the case of natural saplings. The dependent variable was the three-year increment in height and leaf area between 2015 and 2018. General linear mixed-effects models could be applied; however, in most cases (except the height growth of hornbeam and beech), natural logarithm transformation of the growth data was necessary to reach the normal residual distribution.

For all performed models, multiple comparisons were done with user-defined contrasts to find the significant differences between treatments.

All analyses were carried out with R version 3.5.1 (R Development

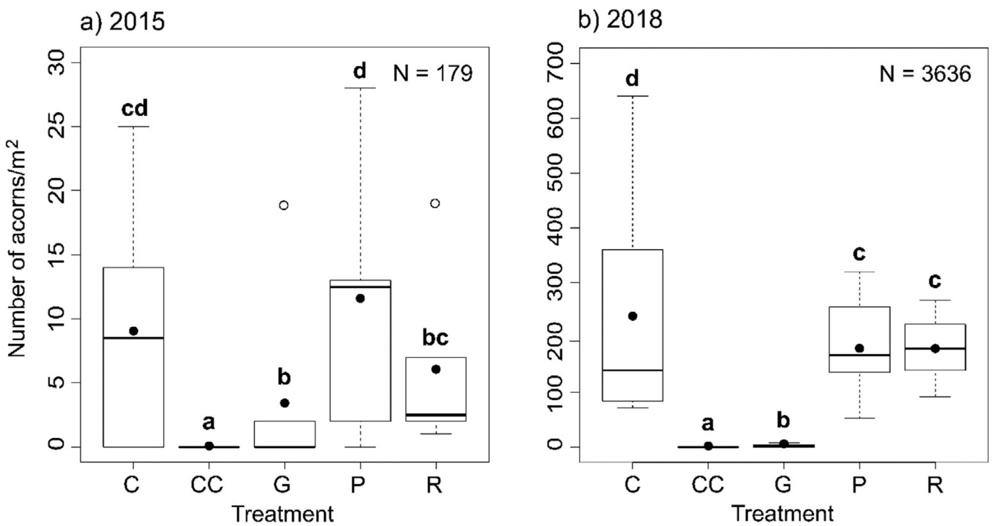

Fig. 2. Boxplot of sessile oak—*Quercus petraea* (Matt.) Liebl. acorn density in the different treatments, a) in the first year and b) in the fourth year after the interventions. Treatments: C = control, CC = clear-cutting, G = gap-cutting, P = preparation cutting, R = retention tree group. 2018 was a masting year, thus the scales of the y axes are different. Black dots represent the mean values. Dissimilar letters mean significant differences between the treatments at $P < 0.05$ level.

Core Team 2018). General linear mixed-effects modelling was conducted by the R package "nlme" (Pinheiro et al. 2013), while "lme4" was used for the generalized linear mixed models, and "blme" packages were used in the case of sessile oak survival (Bates et al. 2015, Chung et al. 2013). Multiple comparisons were calculated by the "multcomp" package (Hothorn et al. 2015).

3. Results

3.1. Seed supply of sessile oak

The density of sessile oak acorns ranged from 0 to 28 pieces/m^2 in the non-masting year (2015, Fig. 2.a) and from 0 to 640 pieces/m^2 in the masting year (2018, Fig. 2.b). There was a significant difference between the treatments in the number of acorns in both years (2015: $Chi^2 = 83.002$, $P < 0.001$; 2018: $Chi^2 = 3512.400$, $P < 0.001$). In the non-masting year, most of the acorns were accumulated in the preparation cuts and in the control sites (11.33 ± 9.99 and 9.33 ± 9.54 pieces/m^2, respectively), the acorn number was intermediate in the retention tree groups and in the gaps, and no acorn was found in the clear-cuts (Fig. 2. a). In the studied masting year, significantly the highest acorn number was recorded in the control closed forest sites (239.33 ± 223.68 pieces/m^2). There was an intermediate amount of seeds in the preparation cuts and retention tree groups (also very high number: 183.33 ± 94.57 and 180.67 ± 66.67 pieces/m^2, respectively). There were only a few acorns in the middle of the gaps (2.66 ± 3.27 pieces/m^2), and no acorns in the clear-cuttings (Fig. 2.b).

3.2. Species number and abundance of natural regeneration

In the first year after the interventions, the total species number of woody species was 11, while in the fourth year it was 14. Number of species in the 2 m × 2 m understory quadrates ranged from 1 to 5 in both years. There was no significant difference between the treatments in either year (2015: $Chi^2 = 0.836$, $P = 0.934$; 2018: $Chi^2 = 4.794$, $P = 0.309$).

Altogether 501 and 960 saplings were recorded in 2015 and 2018, respectively. Treatment effect on the abundance of saplings was analyzed in separate models for the three species (sessile oak, hornbeam, manna ash) and for the species group of endozoochorous species, for the four size categories (Fig. 3, Appendix Table A1). In 2015, significant differences were found between the treatments in two cases: the number of size I hornbeam saplings was significantly higher in every treated site than in the control, and it was the highest in the gaps ($Chi^2 = 127.720$, $P < 0.001$, Appendix Table A1; Fig. 3b, left plot). Endozoochorous saplings of size II did not occur in the gaps; their number was intermediate in the controls, clear-cuts, and preparation cuts, and significantly the highest in the retention tree groups ($Chi^2 = 10.494$, $P = 0.033$, Appendix Table A1; Fig. 3d, left plot). Large (size IV) saplings of any species did not occur anywhere.

In 2018, significant treatment effect was detectable for all species (Appendix Table A1; Fig. 3, right column). In the case of sessile oak, the number of small saplings (size I) was the highest in the controls, intermediate in the retention tree groups and preparation cuts, and low in the clear-cuts and gaps ($Chi^2 = 749.800$, $P < 0.001$, Appendix Table A1; Fig. 3.a, right plot). Total number of size I sessile oaks was extremely high (5 4 5), because 2016 was a masting year.

The number of hornbeam saplings differed significantly between the treatments in every size category (Appendix Table A1; Fig. 3.b, right plot). Size I saplings were most abundant in the retention tree groups, while size II saplings were most abundant in the preparation cuts. The number of size III saplings was the largest in the clear-cuts and gaps, and that of size IV ones was the highest in the gaps. Their abundance in the control was always low.

For the manna ash saplings of size I, the treatment effect also became significant: they were more abundant in the retention tree groups than in the other treatments ($Chi^2 = 21.503$, $P < 0.001$, Appendix Table A1; Fig. 3.c, right plot).

In the case of endozoochorous species, similar to the first year, only the size II saplings showed a significant response to the treatments; their number was still the highest in the retention tree groups ($Chi^2 = 10.519$, $P = 0.033$, Appendix Table A1; Fig. 3.d, right plot).

In the controls no large (size IV) saplings were found from any species, even in the fourth year after the interventions, while in the clear-cuts and gaps, all species reached the fourth size category for this time (Appendix Table A1; Fig. 3, right column). The hornbeam and the endozoochorous species, in particular, reached a considerable relative abundance in these treatments.

3.3. Survival and growth of individual saplings

Considering the survival rates of the planted tree species, all species showed a significant response to the treatments, except common ash (Fig. 4). Survival was usually low in the closed forest controls, while the interventions increased the survival rate. In the case of sessile oak, survival was significantly better only in the gaps than in the control ($Chi^2 = 11.830P = 0.019$, Fig. 4.a). In the case of Turkey oak, it was higher in all treated sites ($Chi^2 = 48.111$, $P < 0.001$, Fig. 4.b). Survival of hornbeam was the highest in the gaps, and it was also significantly higher in the clear-cuts than in the control ($Chi^2 = 17.078$,

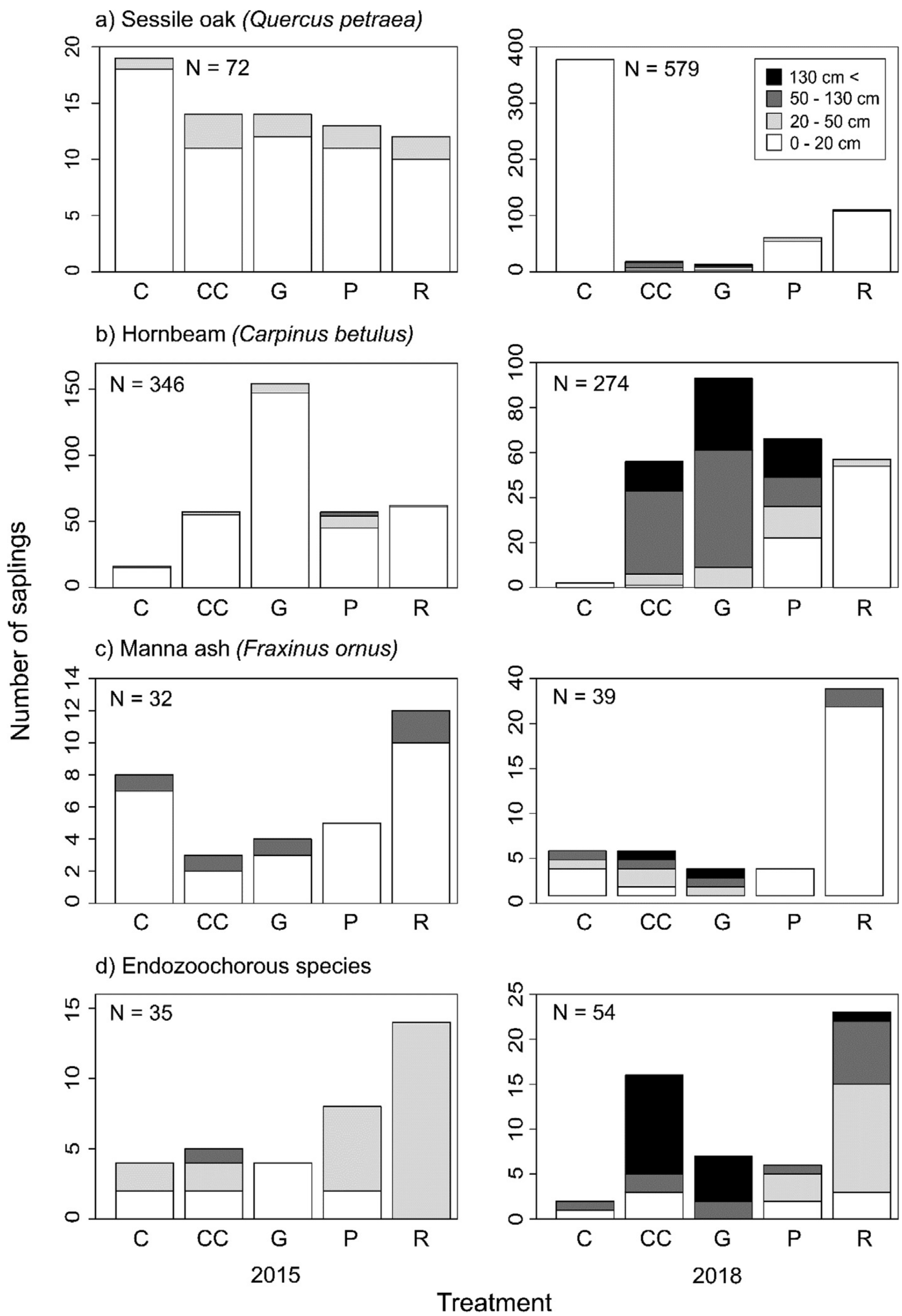

Fig. 3. Abundance of the saplings of the investigated species and species group in the different treatments, in the first year (2015, left column) and in the fourth year (2018, right column) after the interventions. Columns show summarized number of saplings in the 2 × 2 m^2 quadrates for the six blocks. Different colors mean different size categories. Treatments: C = control, CC = clear-cutting, G = gap-cutting, P = preparation cutting, R = retention tree group. The scales of y axes are different.

P = 0.002, Fig. 4.c). Beech survival was the best in the gaps, clear-cuts, and preparation cuts (Chi^2 = 12.859, P = 0.012, Fig. 4.d). Common ash survived well in all treatments, including the control sites (Chi^2 = 2.129, P = 0.712, Fig. 4.e).

The survival of the investigated naturally regenerated saplings was better than that of the planted ones (Appendix Fig. B1). Sessile oak survived better in all treated sites than in the control, while the survival of hornbeam and manna ash was high in every treatment, including the closed forest control.

The treatments also had a significant effect on the growth of the planted saplings for all species. Here, we demonstrate only the height growth models (Fig. 5). The leaf-area analyses presented quite similar results (Appendix Fig. B2). The growth of sessile and Turkey oak was most intensive in the clear-cuts and gaps (F = 10.742, P < 0.001 and F = 83.820, P < 0.001, respectively, Fig. 5a and b). Turkey oak showed a weak increment in the preparation cuts, but sessile oak did not. Their mortality in the control sites was so high that their growth could not be analyzed. Hornbeam and beech grew best in the gaps and clear-cuts, but here, contrary to oaks, the mean values were slightly (but not significantly) higher in the gaps than in the clear-cuts (F = 46.855, P < 0.001 and F = 22.294, P < 0.001, respectively, Fig. 5.c and d). Their growth in the preparation cuts was intermediate. Common ash showed an extreme intensive increment in the gaps (295.64 ± 78.25 cm), and its growth was intermediate but substantial

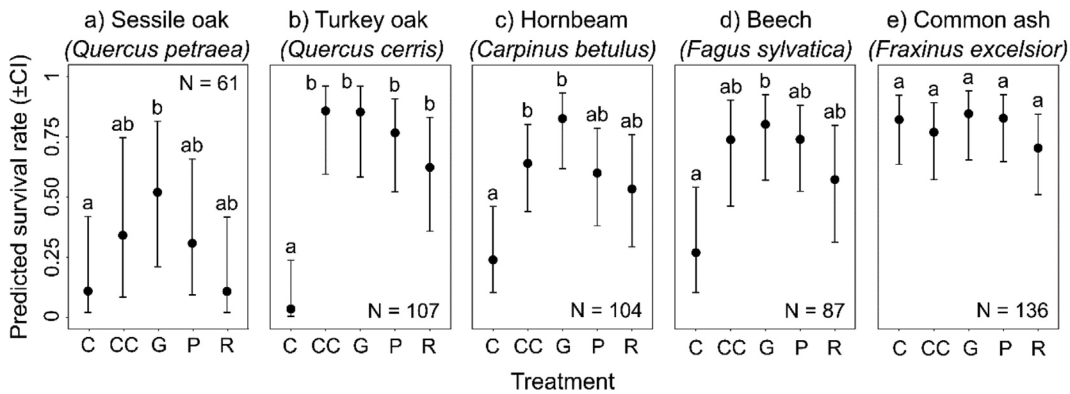

Fig. 4. Predicted survival rate (means and 95% confidence intervals) of the five planted tree species in the different treatments, based on their survival between the first and the fourth year. Treatments: C = control, CC = clear-cutting, G = gap-cutting, P = preparation cutting, R = retention tree group. Dissimilar letters mean significant differences between the treatments at $P < 0.05$ level.

in the clear-cuts ($F = 61.892$, $P < 0.001$, Fig. 5.e). None of the planted species could grow in the retention tree groups and controls.

The growth pattern of the investigated naturally regenerated (sessile oak, hornbeam, and manna ash) saplings in the different treatments was similar to those of the planted ones (Appendix Fig. B3).

4. Discussion

4.1. Regeneration of different species

The differential response to the treatments between the species was primarily related to their seed dispersal mechanisms. Species with large, heavy seeds (oaks) were hardly able to get to the internal area of the clear-cuts and to center of gaps, while seeds of anemochorous species (hornbeam and manna ash) were present even in the clear-cut areas. After the seeds reached the sites, the treatments influenced the establishment of seedlings and the growth of the plants—but in the general responses, the particular species proved to be more similar. Only the intensity of the response differed between light-demanding and shade-tolerant ones: shade-tolerants (hornbeam, beech, and ash) showed better survival than oaks in most treatments, and their height growth was, especially, larger than that of oaks.

There are some contradictions in the literature about the competition of light-demanding and shade-tolerant tree species. The question is that in the natural regeneration, with the increase of the cutting areas, whether light-demanding species outcompete the shade-tolerant ones or vice versa (McClure and Lee 1993 vs. Ligot et al. 2013; Reuling et al. 2019). Similarly to Ligot et al. (2013) and Reuling et al. (2019), we found that in oak-hornbeam forests, where both shade-tolerant and intolerant species are present, shade-tolerant species (primarily hornbeam) have a competitive advantage over sessile oak (larger abundance, better survival, and growth) even in sites of high light availability such as gaps with 20%, and clear-cut areas with about 60% relative diffuse light. This means that if sessile oak is the target species of management, it must be helped by restraining the growth of the hornbeams independent of the applied forestry system, which is in congruence with the field experiences of foresters and has also been emphasized by other experts investigating either sessile oak forests in Europe (von Lüpke 1998) or other oak forest types in North America (Brose 2011). However, the establishment of homogeneous, monodominant oak stands should not be the aim of an ecologically sustainable forest management. The oak-dominated upper canopy layer of sessile oak-hornbeam forests managed by rotation forestry systems is a result of human impact (Haraszthy 2014). Based on the survey of current near-natural forests (Halamová and Saniga 2006) and on historical sources (Bartha and Oroszi 2004), natural sessile oak forests are characterized by a mixed tree species composition. Admixing tree species not only make a substantial contribution to forest biodiversity and stability (Jactel et al. 2005, Cavard et al. 2011, Király et al. 2013) but also positively affect the stem straightness of oak trees (Jensen and Löf 2017). However, the latter study suggests that interspecific competition also decreases the survival of the oak regeneration, thus it is necessary to find a balance between these trade-offs.

Endozoochorous species were most abundant in the retention tree groups, but larger saplings (higher than 50 cm) occurred mainly in the clear-cuts and gaps. Grünewald et al. (2010) stated that at local spatial scales, the structure of the habitat does not influence the dispersal behavior of the mammals. Thus, we can suppose that the abundance of the endozoochorous saplings in the different treatments mainly depends on the environmental conditions, not on dispersal. Most of these wild fruits are species of forest edges and shrublands. The relatively dry and warm soil and air conditions of the retention tree group as well as the relatively high cover of bare soil and the low herbaceous cover make this treatment favorable for the establishment of endozoochorous arboreal species. However, their height growth was most successful in those treatments where soil moisture was the highest—in the clear-cuts and gaps (Kovács et al., 2018, 2020).

4.2. Effect of the different treatments on regeneration

4.2.1. Closed forest control

Despite the continuous seed availability, closed forests (our control sites) do not ensure proper conditions for regeneration, presumably due to low light availability and modest soil moisture (Kovács et al., 2018, 2020). Survival of the species was low (except common ash), and height growth during the first four years after the interventions was almost zero for every species. After masting years, the abundance of sessile oak seedlings is extremely high, but these seedlings are unable to survive and grow without the opening of the canopy.

4.2.2. General effects of the applied treatments

Compared to the closed forest, the applied treatments did not increase the species number of the regeneration layer significantly. The most common admixing tree and shrub species of the area were also present in the control sites, while rare species could not establish during such a short time. Only in the clear-cuts and retention tree groups appeared some new woody species; mainly species of forest edges such as common hawthorn, dog rose, or European crab apple and pioneer species such as goat willow—*Salix caprea.* Reuling et al. (2019) also found—in northern hardwood forests—that various sized gap-cuttings did not change the diversity of the regeneration.

Survival of the saplings increased in every treatment compared to control, but there was no significant difference in this measure between the differently treated sites. However, height growth was significantly

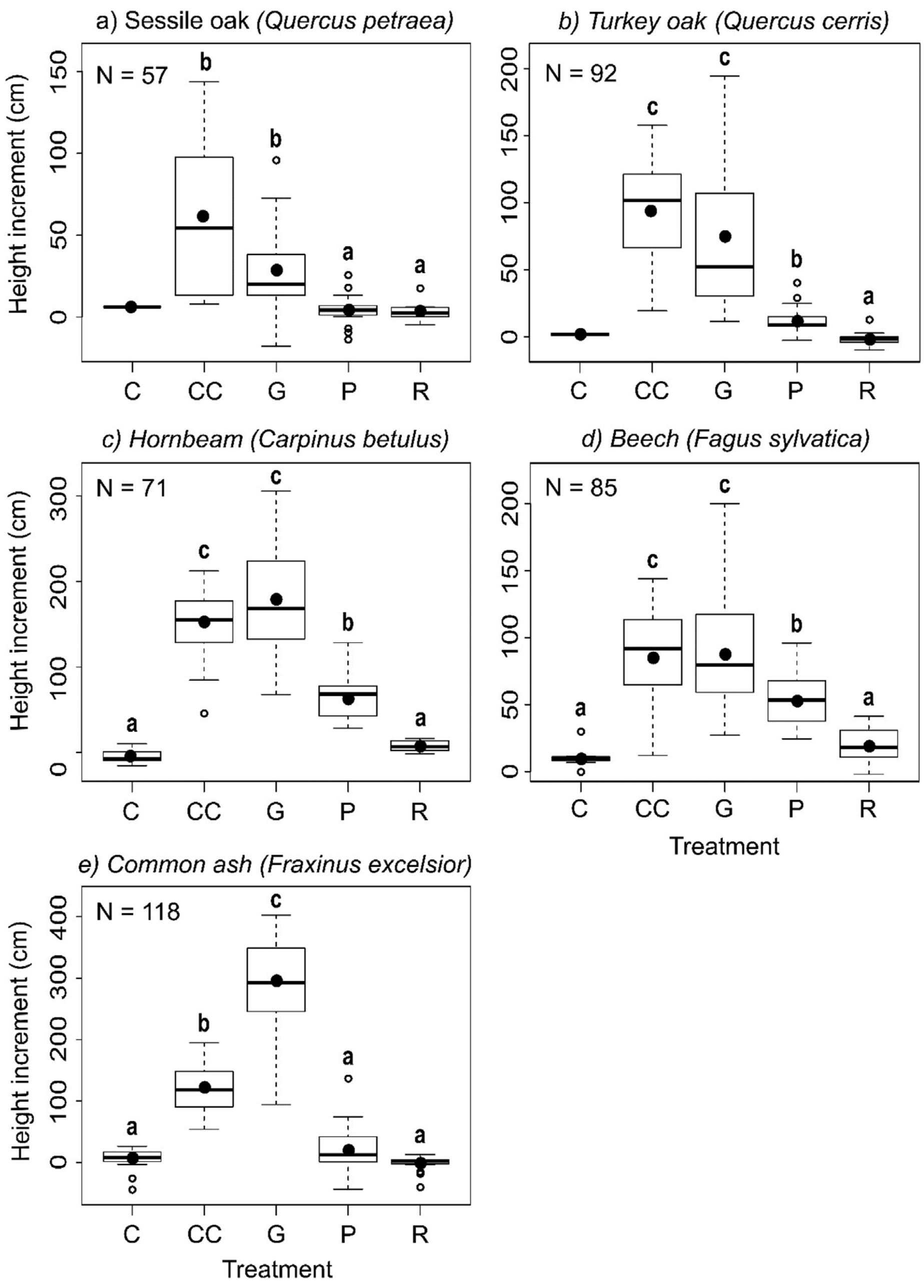

Fig. 5. Boxplot of height growth of the planted tree saplings, between the first and the fourth year, in the different treatments (C = control, CC = clear-cutting, G = gap-cutting, P = preparation cutting, R = retention tree group). The scales of y axes are different; black dots represent the mean values. Dissimilar letters mean significant differences between the treatments at $P < 0.05$ level. In the case of sessile oak and Turkey oak, control was not included into the models, because there were no enough saplings for the analysis.

higher only in preparation cuts, gaps, and clear-cuts, and there were significant differences between them. These results are in agreement with the findings of Sevillano et al. (2016), who stated that the survival of oak and beech do not differ between light conditions from 28 to 100% of the full light (which are similar values to our treated sites), while the growth of sapling depends on the light conditions. Besides light, other components of the microclimate may also drive the differences of the regeneration responses to the various treatments. Hence, next we discuss the specificities of the regeneration in the different treatments separately.

4.2.3. *Clear-cutting and gap-cutting*

In general, regeneration proved to be most successful in the clear-cuts and gaps. However, the establishment of oaks in these treatments was strongly dispersal-limited. In clear-cuts, newly fallen acorns were completely absent, while there was a low but significantly higher number of acorns in the center of the gaps. We can suppose that the outer parts of the gaps get even more acorns from the adjacent trees (Csiszár et al. 2014). Kollmann and Schill (1996) found that acorns can be dispersed to 10–20 m by mice, while for larger distances (several hundred meters) acorns are carried only by Eurasian jay (*Garrulus glandarius* L.). Mice transport the seeds to unmown grasslands also, while jays preferred mown sites. Since the center of the clear-cut sites were further than 20 m from the adjacent trees, and their vegetation was dense, these factors could also have contributed to the differences between the seed supply of the two treatment types. Based on other Hungarian studies, we can suppose that in this region the effect of jays is limited in acorn dispersal: Ádám et al. (2013) and Tinya et al. (2019c) found that sessile oak regeneration is strongly related to the presence of mother trees. This suggests that felling should be carried out the year after a masting to ensure there are enough acorns on the sites. However, this measure is advisable for other forestry systems also as, for example, Brose (2011) suggested for shelterwood management. An alternative solution could be the retention of mother trees for seeding, both in smaller gaps and larger cutting areas.

Abundance of large saplings (higher than 50 cm) in the natural regeneration and the growth of the individual saplings were the largest, and similar, in clear-cuts and gaps. However, while the initial increment of the saplings was intensive in the clear-cuts, the dense understory vegetation established in this treatment (Tinya et al. 2019a) might suppress the tree regeneration in a few years. Brose (2011) found that in clear-cuts, three years after the felling, light decreased substantially because of the upgrowing vegetation. Moreover, he stated that only certain species are able to utilize the extra amount of light of the clear-cuts as compared to the gaps. Based on our results, most of the species did not grow better in the clear-cuts (with over 60% diffuse light) than in the gaps (with ca. 20% diffuse light). Only the leaf area increment of Turkey oak was an exception, but it was not connected to a height increment, thus from the forestry aspect, it was not an advantage. For the regeneration, a further difficulty can be the harsh microclimatic conditions in the clear-cuts (e.g., higher maximum air and soil temperature, lower soil temperature and air humidity minimum, Kovács et al., 2018, 2020). Years with extraordinary weather events (e.g., severe drought) may have a more severe negative effect on regeneration in clear-cuts than in less intensive treatments (Kellner and Swihart 2016). Successful regeneration in large cutting areas under the above-mentioned circumstances may need extra human interventions (weed control, site preparation, etc.), which can be unprofitable from the financial perspective, harmful for biodiversity, and adverse for subsequent stand development (Fleming et al. 1998, Man et al. 2009, Brose 2011).

Gap-cutting resulted in similar intensive height growth, without the discussed disadvantages of the clear-cuts. Light increment in the gaps also proved to be enough for the regeneration, while other aspects of the microclimate remained more balanced (Kovács et al., 2018, 2020). Though the mean height growth of the species did not differ between clear-cuts and gaps, in the case of shade-tolerant species (hornbeam, beech, and common ash), maximal increment of the saplings was observable in gaps, while growth of sessile oak was the largest in the clear-cuts. This suggests that in the gaps, oaks must be helped by controlling the shade-tolerants. Dominance relations of shade-tolerants vs. oaks can be influenced by the applied gap size and shape (Montgomery et al. 2013, Poznanovic et al. 2014). However, as mentioned while discussing the species, the results are contradictory and depend on the local site conditions and species composition (Diaci et al. 2008, Diaci and Firm 2011), thus further investigation on the effects of gap size on regeneration in sessile oak-hornbeam forests is needed.

4.2.4. Preparation cutting

In preparation cuts, the success of regeneration was moderate, which corresponds to the intermediate microclimatic conditions (primarily light and soil moisture conditions, Kovács et al., 2018, 2020). Its advantage over clear-cuts and gaps was the large number of acorns present. However, Brose (2011) emphasized that even in uniform shelterwood system, preparation cutting should be done in years when there is an adequate density of oak seedlings. For most species, we found an intermediate survival rate between the control and the clear-cuts/gaps, which is in agreement with the result of Brose (2011) for oaks. In general, height growth of the saplings was weak. Brose (2011) stated that in preparation cuts, the larger proportion of diffuse light can help the oak regeneration against competitor species; however, we found that even preparation cut facilitated the growth of the shade-tolerant species over oaks. Growth of hornbeam and beech was significantly larger than in the closed stand, and in the case of hornbeam, some individuals of the natural regeneration reached size categories above 50 cm.

Contrary to this, oaks and common ash could not grow in the preparation cut sites. Under the shelterwood system, oak saplings are expected to grow in height only after the following steps of the cutting (Brose 2011, Holzmueller et al. 2014). According to Kellner and Swihart (2016), the shelterwood system may support a more stable regeneration compared to clear-cutting due to its buffering capacity against extreme weather conditions. However, gap-cutting also ensures these balanced conditions, and besides, it has some advantages compared to the uniform preparation cutting: It maintains long-term forest continuity, and by creating a more complex stand structure, it provides buffered, but heterogeneous microsite conditions for the forest biota.

4.2.5. Retention tree group

The aim of the retention tree groups is not to help the regeneration, but to ensure the continuity of the forest structure and composition and thus preserve the legacies of the forest biodiversity and functions (Gustafsson et al. 2012, Lindenmayer et al. 2012, Šavrak et al. 2019, Tinya et al. 2019a). Retained trees often attenuate the survival and growth of the regeneration (Gradowski et al. 2008, Lennie et al. 2009). In our study, survival in the retention tree groups was not significantly weaker than in other treated sites. Compared to clear-cuts and gaps, the moderate light and the drier soil and air resulted in a sparser understory vegetation (Kovács et al., 2018; Tinya et al., 2019a; Kovács et al., 2020). At the same time, soil temperature was higher than in the closed stand (Kovács et al., 2018, 2020). This dry, warm, open soil surface, without a considerable competition, favored the establishment of some small-seeded woody species of forest edges and xerothermic forests. This is in agreement with Modrý et al. (2004), who stated that beside higher direct light, the increased competition can result in a lower density of woody species. However, in our retention tree groups, the lack of sufficient soil moisture precluded the growth of the saplings. Among the natural regeneration, only some endozoochorous shrub species and some manna ash could reach the larger size categories. The height growth of the individually-measured saplings was always close to zero (similar to the closed control). Thus, retention tree groups are not the localities of successful stand regeneration, however, in some ways they can still contribute to it, for example via seed scattering—presumably even to the surrounding clear-cut areas, retention tree groups can ensure some seed supply. Moreover, they provide habitat for some admixing tree and shrub species, which are not the typical species of closed humid forests, thereby increasing forest biodiversity.

5. Conclusions

This study evaluated the initial success of regeneration, four years after the interventions. Because of the shortness of this period we cannot draw inferences about the whole process of forest regeneration; to evaluate the long-term responses, the data collection is continuing. According to our results, oak regeneration establishes successfully in oak-hornbeam forests not only in the case of rotation forestry, but also during continuous cover forestry (gap-cutting). The survival and growth of the saplings are similar in cutting areas and gaps, but keeping in mind other considerations (such as preserving forest continuity, balanced site conditions, and forest biodiversity), continuous cover forestry should be preferred. To exploit the advantages of rotation forestry as well, it can also be retained, at landscape scale, among the applied systems.

Both in case of clear-cutting and gap-cutting, timing seems to be crucial: felling should be carried out in the first subsequent year after a masting to ensure there are enough acorns on the sites. If management's priority is to regenerate sessile oak, shade-tolerant competitor species (primarily hornbeam) must be restrained. This is valid for all investigated kinds of management because hornbeam has a more intensive dispersal rate, a better survival rate, and better growth in comparison to sessile oak. However, the issue is especially relevant in the case of gap-cutting, because the shaded environment of gaps serves better the shade-tolerant species than oaks. Completely homogeneous sessile oak-hornbeam stands cannot be achieved by continuous cover forestry, and neither should it be the aim since mixed stands are more resilient to abiotic and biotic disturbances and converge better to natural forests.

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.

CRediT authorship contribution statement

Flóra Tinya: Conceptualization, Methodology, Investigation, Visualization, Funding acquisition. **Bence Kovács:** Conceptualization, Methodology, Formal analysis, Investigation, Visualization. **Réka Aszalós:** Investigation. **Bence Tóth:** Investigation. **Péter Csépányi:** Conceptualization, Methodology, Resources. **Csaba Németh:** Investigation. **Péter Ódor:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Supervision, Project administration, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117810.

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