

Long-term Oak Seedling Dynamics and Regeneration Ability in a Deciduous Forest in Hungary

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Abstract

Long-term structural dynamics and regeneration ability of oak seedlings were not extensively reported in published studies in Central Europe. At the LTER study area 63.0% of adult oak died from 1979-80 in a mixed oak forest, an area covered by a sessile oak-Turkey oak forest (*Quercetum petraeae-cerris*). The research site of the nature reserve is located in the Bükk Mountains of northeastern Hungary. The goals of this study were to determine the conditions of oak seedlings and saplings and the survival of low oaks in studied plots over a 40-year period after the serious oak decline. The oak specimens of the vegetation lower than 1.0 m in height were categorized as low oaks. Over the 40 years of observation, three oak species were continuously observed in the understory, sessile oak (*Quercus petraea* Matt. L.), Turkey oak (*Quercus cerris* L.) and downy oak (*Quercus pubescens* Willd.). The most abundant oak species was sessile oak. Total seedlings and saplings density averaged 12.031 ha⁻¹; sapling numbers for all oaks were low (averaged 336 ha⁻¹). From 1993 to the last measurement there was a poor regeneration rate with only 14 ha⁻¹ oak specimens taller than 0.5 m. The mean height and diameter distribution of low oaks varied between 7.9-25.2 cm and between 1.4-3.7 mm, respectively. The tendency of mean size condition saw a clear-cut decrease from 1972 to 2012. Our results suggest that the seedling regeneration ability is limited and the oak seedlings' structural condition did not affect by oak decline.

Keywords: sessile oak, low understory, density, height, oak decline

Introduction

Despite the comprehensive interest in oak forest dynamics, there has been little long-term monitoring of particular oak forests globally (Chapman et al. 2006, Chapman and McEwan 2016). Though the forest compositional data are abundant, it is not too simple to place findings within the theoretical framework of forest dynamics (Chapman and McEwan 2016). The seedling stage is one of the most vulnerable in the life cycle of arboreal plant species. High mortality rates are caused by many negative ecological factors occurring in the nature (Silvertown and Charlesworth 2001). The survival and persistence of seedlings is of major importance for the maintenance and regeneration of oak specimens and any other species (Beckage and Clark 2003, Harmer et al. 2005). The natural regeneration of oaks (*Quercus* spp.) is a frequent problem at a wide range of locations globally (Lorimer et al. 1994, Ziegenhagen and Kausch 1995, Bobiec et al. 2011). Long-term structural dynamics and regeneration ability of oak seedlings in a temperate deciduous oak forest were not extensively reported in previously published studies in Central Europe (Paluch 2005, Tobisch 2008).

One commonly accepted factor is the suppression and strong competition by the shade-tolerant abundant subcanopy species, particularly lime, hornbeam and beech species (Vera 2000, Paluch 2005). According to Paluch (2005), the shelterwood cutting system (leaving some trees) is the most efficient method of natural oak regeneration in the Białowieża sample plots. The ground flora affects the growth capability and survival of seedlings, and the magnitude of the effect varies with species and the structure and dynamics of forest stands (Harmer et al. 2005). Moreover, growth trend of seedling depends on a number of environmental factors. These factors may be either abiotic as light, water, nutrient availability (Tóth et al. 2011, Juhos and Madarász 2016) and temperature (Aldrich et al. 2005, Fekete et al. 2008, Fekete et al. 2012), or biotic ones as competition, browsing animals (Crow 1992, Harmer 1995), insects and pathogens (Kozłowski 1969, Wargo 1996, Thomas et al. 2002, Haavik et al. 2015). The various natural or human forest disturbances may have effect on forest regeneration. For example, English oak (*Quercus robur* L.) regeneration status was different in three declining forest types in Poland: gaps formed as

a result of bark beetle (*Scolytinae* subfamily) outbreak (Bobiec et al. 2011). Cherrybark oak (*Quercus pagoda* Raf.) forest regeneration may be affected by light availability on their shoot growth and biomass accumulation (Gardiner and Hodges 1998). The foliage gaps influence the tree regeneration in lime-hornbeam forest (*Tilio-Carpinetum* Tracz. 1962) regarding sapling density and composition in Poland (Bobiec 2007).

The woody seedling growth can be impacted by mammalian herbivores directly by them browsing stems, or indirectly by them decreasing the height and survival of seedlings and woody stems (Tilghman 1989). According to Russell et al. (2001) and Kuiters and Slim (2002) over the past 30–40 years in Sweden, moose and deer populations conspicuously increased leading to damage to trees. In this country, many research papers indicate preferences for oak species in ungulate browsing and its impact on regeneration in forests dominated by conifers (Kullberg and Bergström 2001). In England, the conditions in many broadleaved forest stands are unfavourable for natural regeneration, with few good parent trees, well-developed herbaceous layers and high densities of browsing animals (Harmer et al. 1997, Fuller and Gill 2001). The light demands of oak trees might be a key factor, especially in mixed broadleaved woodlands (Vera 2000, Götmark et al. 2005, Oliver et al. 2005). In the understory of mixed-oak forest stands, oak seedling growth and morphology appear to depend on light levels (Gardiner and Hodges 1998). The oak seedlings in eastern deciduous forests (Kellner and Swihart 2016) and beech seedlings stage (Coll et al. 2003, Provendier and Balandier 2008) could have similar problems when competing for light, water and other resources with other vegetation of the understory layer.

Serious oak decline was first reported in 1979–80 in the study site, and by 2012, 62.4% of the oak trees had died during four decades. An increase in the decline of living oaks was observed in many regions in Hungary since 1978 (Igmándy 1987, Kotroczó et al. 2007). The studies on possible biotic and abiotic factors of oak decline and the effect of decline on the structural condition of the mixed oak forest on the Síkfőkút were reported in many papers (Jakucs 1985, Kotroczó et al. 2007, Mészáros et al. 2011). The present study focused on the structural changes of oak seedlings and saplings and the serious problem of oak regeneration in the Síkfőkút forest. The objective of this paper was: (1) to describe the possible long-term effect of canopy tree density on the density, frequency, height and shoot diameter of oak seedlings; (2) to investigate the relation among densities and size variables of oak species in the low understory; (3) to evaluate the natural regeneration potential and growth capability of oak seedlings.

Materials and Methods

Study site

The reserve research site (Síkfőkút Project) is located in the Bükk Mountains (47°552' N, 20°462' E) in the northeast of Hungary at an altitude of 320–340 m a.s.l. and 6 km from the city of Eger. Mean annual temperature is 9.9 °C and mean annual precipitation ranges typically from 500 to 600 mm. Descriptions of the geographic and climatic conditions of the forest were reported in detail by Jakucs (1985). According to the FAO World Reference Base, the soils of the area are Luvisols (Świtoniak et al. 2014). Many descriptions made from the vegetation of the research area. The *Quercetum petraeae-cerris* community tree species structure is presented in the works of Mázsza et al. (2005), Kotroczó et al. (2007) and Fekete et al. (2017); the understory shrub layer is described in works of Misik and Kárász (2010), Misik (2013) and description of the herbaceous layer and the seed bank condition can be found in works of Papp et al. (2006) and Koncz et al. (2010).

Misik et al. (2014) described the dynamics behind the increase in the sizes of woody species and the structure of the new subcanopy layer. Misik et al. (2013) showed the possible responses of parameters of understory shrub layer to changes in stand density in their study. The most common forest association in this region is *Quercetum petraeae-cerris* (sessile oak-Turkey oak forest) made up of sessile oak (*Quercus petraea* Matt. L.) and Turkey oak (*Quercus cerris* L.) species in the canopy layer. Seven dominant native species were identified across the entire studied forest as *Acer campestre* L., *Acer tataricum* L., *Cornus mas* L., *Cornus sanguinea* L., *Crataegus monogyna* Jacq., *Euonymus verrucosus* Scop. and *Ligustrum vulgare* L. in the understory. The plot under study is a temperate deciduous forest constituted of evenly aged trees, at least 100 years old, and was not harvested for more than 50 years.

Sampling

The data were obtained from a 1 ha intensive monitoring site. The site was subdivided into four plots, “A”, “B”, “C” and “D”; all plots are 48 m × 48 m in size. The structural condition of the oak seedlings was monitored on an “A” plot at the research site; the plot was subdivided into 144 4 m × 4 m permanent subplots (Figure 1). The permanent subplots were established in 1972. Repeated shrub inventories took place in 1972, 1979, 1982, 1988, 1993, 1997, 2002, 2007 and finally in 2012. In order to study regeneration dynamics, 40 1 m × 1 m permanent subplots were randomly selected within the four plots. These measurements were carried out annually between 2004 and 2009.

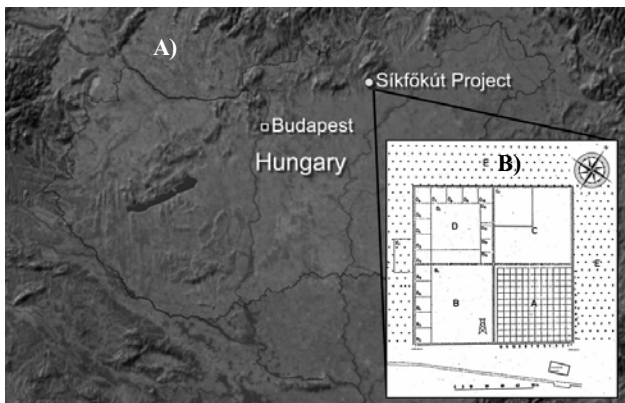


Figure 1. A) Geographical location of the study area in Hungary. B) Study site location with four plots. The 48 m x 48 m "A" plot was subdivided into 144 4 m x 4 m permanent subplots

The woody specimens of the vegetation lower than 1.0 m in height were categorized as low understory. Oak species stems < 50.0 cm in height were inventoried and categorized as oak seedling. Stems > 50.0 cm and ≤ 100.0 cm in height were categorized as oak saplings. The oak seedlings and saplings were ranked into four height categories such as 0-10, 11-25, 26-50 and between 51-100 cm. Due to the low specimen number the height classes over 11 cm were added together to the statistical analysis. The following measurements were carried out for understory oak species in each permanent subplot: species composition, frequency (occurrence % in subplots of the monitoring plot), species density, height and diameter of seedlings and saplings. The oak seedling and sapling density was extrapolated for one hectare. We recorded directly specimen height with a scaled pole and the diameter at a height of 0.05 m above the soil surface with a digital calliper.

Statistical analysis

The experimental data were analysed by linear regression to investigate the possible effects by the structural variables of low oaks (density, occurrence, height, diameter and DHR = diameter-to-height ratio values) on oak canopy density (SPSS Statistics 19, Tulsa, USA). If required, a one-way ANOVA with the Tukey's HSD test was used as a post-hoc test to determine the significant differences among oak seedlings and saplings and years (factors) in density, occurrence, height and diameter (variables). The Pearson's Chi-square test can be used to determine whether there is a significant association between the two or more of the following categorical variables: oak seedling density, height categories, research plots and research time. The test utilised a mosaic plot to examine the relationship between these variables.

The statistical analysis was undertaken using SPSS and significant differences for all statistical tests were evaluated at the level of * $p \leq 0.05$, ** $p \leq 0.01$ and ^{n.s.} $p > 0.05$.

Results

Species composition and density

Oak seedlings and saplings belonging to three oak species (sessile oak, Turkey oak and downy oak (*Quercus pubescens* Willd.)) were identified at the study site. In the understory layer, sessile oak was the most common oak species.

Consequently, the specimen abundance of sessile oak in the low understory was at a mean of 80.2% of oak seedling and sapling density during the four decades. The total oak seedling density demonstrated large-scale fluctuation and varied between 2092 and 228210 pcs. ha⁻¹ over the period of 1972-2012. Seedling density averaged 12.031 pcs. ha⁻¹. Sapling numbers for oak species averaged 336 pcs. per hectare but at a lower density from 1993 to 2012 (Table 1). The results of regression analysis showed that there is a trend that approximated but not reached statistical significance relationship between oak canopy density and oak seedling and sapling density during the monitoring period ($r = 0.50^{n.s.}$; $p > 0.05$) (Table 4). The one-way ANOVA indicated non-significant differences among densities of oak seedling species ($p > 0.05$) (Table 3).

Table 1. Densities (innd.ha⁻¹) of oak canopy, oak saplings, oak seedlings and sessile oak abundance (%) (means ± standard deviation) in the low understory on the monitoring plot

Year	Densities condition (innd.ha ⁻¹) in the low understory				
	Oak canopy	Oak saplings	Sessile oak	Turkey oak + downy oak	Sessile oak abundance (%)
1972	816	1428	10963	1450	88.32
1982	651	846	47354	5229	90.06
1988	408	395	2213	482	82.12
1993	372	0	417	65	86.51
1997	304	0	729	2179	25.07
2002	324	12	1397	131	91.43
2007	323	4	1606	182	89.82
2012	305	0	19248	2600	88.10
mean ± SD		336 ± 536	10491 ± 16313	1540 ± 1784	80.18 ± 22.45

Table 2. Overall occurrence (%) in the 144 subplots of oak seedlings and saplings, of sessile oak and turkey oak (means ± standard deviation) in the low understory

Year	Oak canopy density (innd.ha ⁻¹)	Occurrence (%) in the low understory			
		Oak seedlings and saplings	Sessile oak	Turkey oak	Change of frequency (%)
1972	816	99.31	98.61	34.72	0.00
1982	651	18.75	16.67	3.47	-80.56
1988	408	70.14	63.19	20.83	+51.39
1993	372	22.22	19.44	5.56	-47.92
1997	304	88.89	38.89	77.08	+66.67
2002	324	47.92	40.97	6.94	-40.97
2007	323	47.22	41.67	11.11	-0.70
2012	305	84.03	83.33	29.86	+36.81
mean ± SD		59.81 ± 30.47	50.35 ± 29.19	23.70 ± 24.48	-40.63

Table 3. Details of the one-way ANOVA and Tukey's HSD test (F = variance of the group means, p = significance level) for densities, frequencies and size variables (height and diameter-to-height ratios = DHR) of understory oak species on the monitoring plot. Significant differences are shown in bold

Understory	p / F values	
	Oak seedlings and saplings	Sessile oak
Density		
Oak seedlings and saplings	1	-
Sessile oak	0.86 / 0.03	1
Turkey oak	0.12 / 2.70	0.15 / 2.38
Occurrence		
Oak seedlings and saplings	1	-
Sessile oak	0.54 / 0.40	1
Turkey oak	0.02 / 6.83	0.07 / 3.91
Height		
Oak seedlings and saplings	1	-
Sessile oak	0.96 / 2.20 ³	1
Turkey oak	0.79 / 0.07	0.82 / 0.05
DHR		
Oak seedlings and saplings	1	-
Sessile oak	0.77 / 0.09	1
Turkey oak	0.78 / 0.08	0.57 / 0.34

Occurrence

The seedling and sapling occurrence of sessile oak varied between 16.7% and 98.6%; was at its minimum in 1982 and maximum before the onset of oak decline in the 144 subplots of the monitoring plot. The occurrence of Turkey oak fluctuated between 3.5% and 77.1% over the monitoring period. The occurrence of oak specimens in the low understory displayed high variation over the period. Since 1972, the greatest occurrence recorded was of *Q. petraea* in line with the density condition except for 1997, when *Q. cerris* was measured at its highest value (Table 2). The regression analysis did show a non-significant association between oak canopy density and occurrence of low oak specimens ($r = 0.10^{n.s.}$); non-significant relationship was found between specimens density and occurrence in oak understory ($r = 0.28^{n.s.}$) (Table 4).

A statistically significant difference was recorded between total oak specimen occurrence and Turkey oak specimen occurrence in the understory by ANOVA analysis ($p < 0.05$) (Table 3).

Table 4. Relationship between oak canopy density and structural condition of oak understory species and between oak seedlings and saplings density and occurrence, sizes and DHR of low oaks on the monitoring plot over the period of 1972-2012

Density	p / r values				
	Oak seedlings and saplings				
	Density	Occurrence	Height	Diameter	DHR
Oak canopy	0.20 / 0.50	0.82 / 0.10	0.24 / 0.56	0.10 / 0.72	0.92 / 0.06
Oak seedlings and saplings	1	0.50 / 0.28	0.90 / 0.07	0.96 / 0.03	0.82 / 0.12

Height and diameter

A single sessile oak sapling was recorded with a height of 51.8 cm in 2007. Five years later the highest

oak seedling was 20.0 cm. Over the four decades, the mean height was 19.5 cm among the sessile oak and was about 3.5% lower among the Turkey oak. The mean height distribution of oak seedlings varied between 7.9 ± 2.6 cm and 25.2 ± 15.8 cm. The minimum was evident in the last measurement and the maximum in 1982 (Figure 2). The mean diameter value was 3.1 mm among the sessile oak and about 10.0% thinner among the Turkey oak over the research time. The mean diameter distribution of low oak specimens varied between 1.4 ± 0.5 mm and 3.7 ± 2.4 mm within the period of 1972-2012. It was at its minimum in 2012 and its maximum in 1972. The data shows that mean height and diameter tended to decrease from 1972 to 2012 (Figure 2).

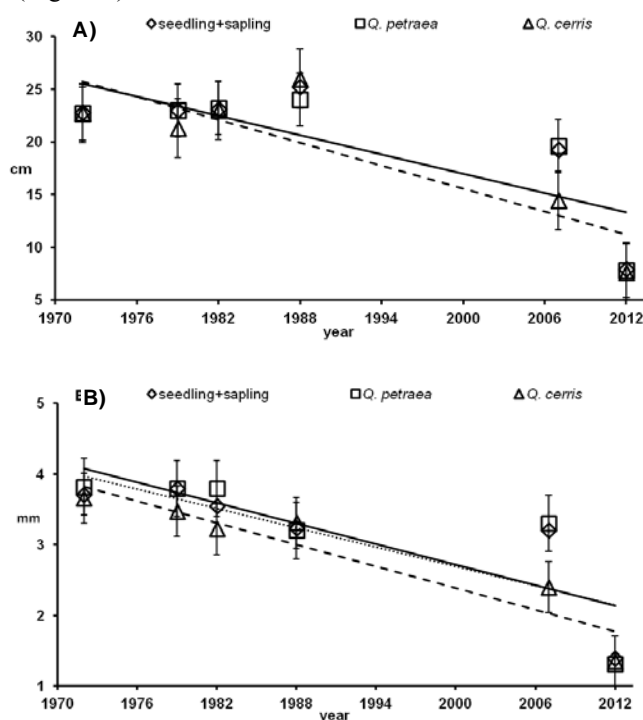


Figure 2. Statistical summary (\pm S.E.) of height (A) and diameter (B) changes of understory oak species (sequentially: oak seedling and sapling, *Q. petraea* and *Q. cerris*) on the monitoring plot over the period of 1972–2012. Notation: seedling and sapling ($R^2 = 0.6111$ and $R^2 = 0.6640$); —, *Q. petraea* ($R^2 = 0.6185$ and $R^2 = 0.6469$); - - -, *Q. cerris* ($R^2 = 0.7218$ and $R^2 = 0.8836$)

Diameter-to-height ratios (DHRs) of low oak specimens changed between 0.13 and 0.18 during four decades. DHR values varied between 0.13 and 0.17 in sessile oak species, and between 0.13 and 0.18 in Turkey oak specimens of low understory. No statistically significant relationship was found between canopy density and mean height, mean diameter and DHR dynamics of oak specimens in the understory and between low oaks density and other structural condition of understory ($p > 0.05$) (Table 4). A non-significant association was

detected among size values of oak species in the understory by ANOVA analysis ($p > 0.05$) (Table 3).

Regeneration ability

The maximum density of *Q. cerris* seedlings was recorded on “C” and “D” plots during the period 2004-2009; the highest density of *Q. petraea* seedlings was on “B” plot. The 99.0% of the low oak specimens belonged to the 0-10 and 11-25 cm height classes. The maximum density of taller oak specimens (> 25 cm) was detected in the first monitoring year with 88 young oaks ha⁻¹ (Table 5). The Pearson’s Chi-square test showed a significant independence of oak seedling densities and plots during the period 2004-2009 ($p \leq 0.01$) (Figure 3).

The Pearson’s Chi-square test showed a significant independence of oak seedling and sapling density and shoot height distribution during the period 2004-2009 ($p \leq 0.01$) (Figure 4). The maximum sessile oak density was recorded in 2004 with 6,450 seedlings and saplings per hectare; its minimum was in 2009 with 194 seedlings ha⁻¹. Turkey oak density per hectare was maximum in 2005 with 10,951 seedlings and saplings, and minimum (1537 specimens) in 2007 (Table 5).

Discussion and Conclusions

The average density of low oaks per hectare varied from 56 in deciduous forests through 333 in mixed-deciduous to 360 in mixed-coniferous forest of Poland according to Bobiec et al. (2011). However, the density was much higher in the mixed-coniferous forest with foliage gaps, ranging between 425 and 1,441 young oak individuals per hectare. The oak density of the low understory layer and the occurrence frequency of low oaks in the Słkřókřt forest stand showed an important fluctuation (Table 1 and 2); only some specimens were observed which were taller than 25.0 cm during the period of 1972-2012. A non-significant relationship was confirmed between number of specimens and occurrence of the low oaks (Table 3). The reason is that the oak seedlings show a clumped distribution in the stand.

The occurrence of low oak specimens was significantly associated with soil condition, vegetation structure, and livestock grazing in the silvopastoral oak woodlands of Greece (Plieninger et al. 2011). Moreover, χ^2 test showed significant relationship ($p \leq 0.05$) between the occurrence frequencies of some dominant shrub spe-

Table 5. Densities of oak species in the low understory in different height categories over the period of 2004-2009

		Densities condition (innd.ha ⁻¹) in the low understory											
years		2004				2005				2006			
Height categories, cm		0-10	11-25	26-50	50<	0-10	11-25	26-50	50<	0-10	11-25	26-50	50<
Sessile oak		5619	781	31	19	738	306	25	19	419	494	19	0
Turkey oak		3131	1925	13	25	8394	2538	0	19	2963	2000	19	6
years		2007				2009							
Height categories, cm		10	11-25	26-50	50<	0-10	11-25	26-50	50<				
Sessile oak		200	338	19	13	56	125	13	0				
Turkey oak		775	756	0	6	4631	1781	25	13				

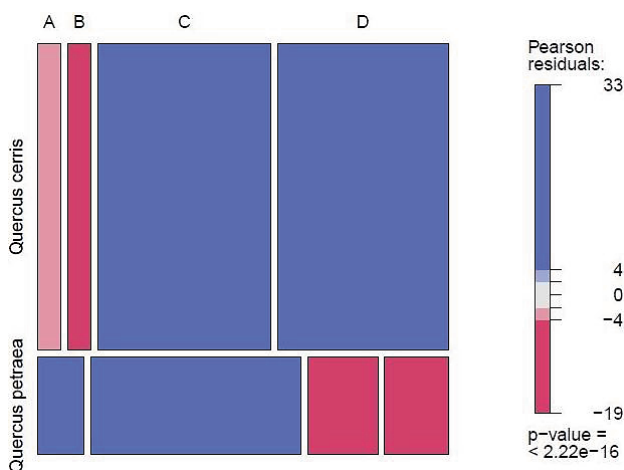


Figure 3. Mosaic plot for the oak seedlings data, showing the marginal model of independence for species densities and plots ($p \leq 0.01$) during the period of 2004-2009 (summary data of years)

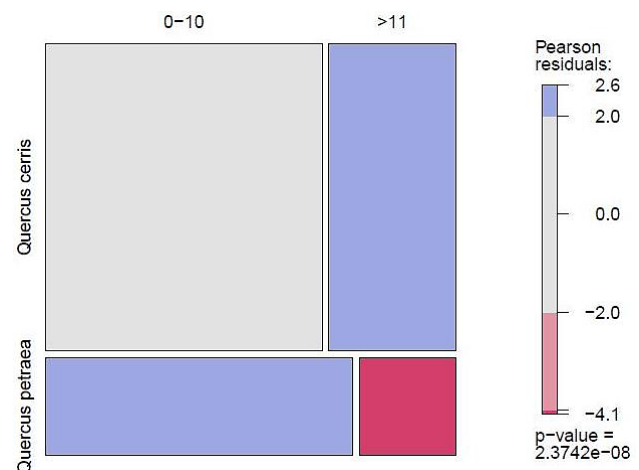


Figure 4. Mosaic plot for the oak seedlings data, showing the marginal model of independence for species densities and shoot height ($p \leq 0.05$) during the period of 2004-2009 (summary data of years)

cies and oak seedling and sapling occurrence (Plieninger et al. 2011). According to Harmer et al. (2005) the distribution of oak, ash and birch seedlings was heterogeneous in an oak shelterwood of England. In our forest stand the oak seedlings showed a randomly distribution with high subplot-level densities on only a few subplots. This statement is especially true in 1982 with 51,737 oak seedling specimens and with 18.8% occurrence. During the four decades low oak specimens were observed in about 60.0% of the 144 subplots.

Most of the low oak specimens taller than 20.0 cm belonged to the vigorous and healthy category, and only a minority was classified as seriously damaged or suppressed (Bobiec et al. 2011). In our sample area, the high rate of low oak specimens belonged to the 0-10 and 11-25 cm height category (Figure 3 and Table 5). Collet et al. (1997) discovered that oak seedling growth ability was related to the level of resource availability. Seedling height was significantly greater in high resource availability than in low or medium resource level. The growth units were always the longest in high treatment and the shortest in low treatment but significant differences were found only for the second flush of 1992, and for the first and second flush one year later. In both monitoring years, average values of growth unit length increased with the flush number.

The results from an oak-hornbeam stand in Hungary reported by Tobisch (2008) suggest that height and diameter growth of sessile and pedunculate oak (*Quercus robur* L.) seedlings significantly decreased with the density, and the diameter-to-height ratios became smaller as the density increased. The same seedling density, the mortality rate was lower but the seedlings were shorter, thinner and the values of DHR were smaller if the distance between stems was lower than that between rows. Our results suggest that mean height and mean diameter of oak seedlings and saplings was decreasing with an accelerating tempo in the last measurements; it was no significant relationship between density tendency and DHR dynamics of oak specimens in the understory layer (Table 4). The shoot height and shoot diameter of oaks were lower by 65.0% and 63.0% compared to the first assessment, respectively (Figure 2). The ecological process is similar to the dominant understory oak species. There is no doubt that there is a multifarious explanation for this process.

The possibility of the natural regeneration of oak canopy species is low. If the rate of oak regeneration in the temperate forest continues at such a low level as revealed by the research (Krasuska and Miścicki 2002, Paluch 2005, Bobiec 2007), it will not be able to sustain the importance of oak. However, foreseeing major species composition shifts in forests, one cannot conclude that oak will disappear from sites. A seedling bank is an

important ecological factor in the regeneration of numerous canopy tree species (Lorimer et al. 1994, George and Bazzaz 2003). Results of Puerta-Piñero et al. (2007) showed that oak or pine microhabitats achieved higher survival rates of *Quercus ilex* L. (Holm oak) seedlings than broom or open areas whilst under oaks in a patchy Mediterranean site; in broom or in open areas, seedling height was lower than under high shrub specimens. Irradiance had significant affect on seedling growth and survival. They recorded that the lower the irradiance, the higher the survival. Maximal growth ability was found at intermediate irradiance, indicating that restrained shade is decisive for oak seedling recruitment. Then again, the findings in the study of Misik et al. (2014) indicate that after the oak decline three woody species, field maple (*A. campestre* L.), Tatar maple (*Acer tataricum* L.) and European cornel (*Cornus mas* L.), formed a subcanopy layer in the foliage gaps directly below the oak canopy. The woody specimens showed an increase in size and foliage cover and a low regeneration availability of oaks due to the detected shading effects by these woody species. According to the opinion of the foresters and the conservation specialist the one reason for poor oak regeneration is the important populations of big game (especially wild boar), which were detected in the Várhegy Forest Reserve, the Bükk Mountains (Horváth 2012) similarly to our site.

The conclusions to be derived from the site are as follows: (1) oak canopy density did not affect the density and other structural condition of oak species in the low understory; (2) A non-significant association was obtained among structural conditions of understory oak species except among occurrence of oak seedlings, saplings and Turkey oak specimens in the period of 1972-2012; (3) The successful regeneration of oak is low, only some oak seedlings reached the 26.0 cm in height and more than 90.0% of these seedlings could not survive their second year of life. Future research is needful to gain a better understanding of the relationship between oak decline and structural condition of the low oak specimens.

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