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Understory Development in an Oak Forest in Northern Hungary: the Subcanopy Layer

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Abstract – Structural changes in the shrub layer were analysed in a Hungarian oak forest after the oak decline pandemics. This paper focuses on the following questions: (1) which of the woody species tolerated better the forest conditions after oak decline? (2) What are the ecological factors that explain the successful response of woody species to changes in light and thermal conditions? In the monitoring plot, the structural condition of specimens only above 8.0 m was observed. After the appearance of oak decline some *Acer campestre*, *Cornus mas* and *Acer tataricum* specimens appeared that reached between 8.0-13.0 m in height. Significant differences were revealed between top canopy density and foliage cover of the subcanopy and between top canopy density and mean cover of field maple. The findings of the study indicate that the forest responded to oak decline with significant structural rearrangement in the shrub layer and that three woody species compensated for the remarkable foliage loss in the top canopy. These species formed a second crown layer directly below the canopy formed by oaks.

shrub community / woody species / *Acer campestre* L. / cover / dead oaks

Kivonat – A cserjeszint fejlődése Észak-Magyarországon egy tölgyes erdőben: az alsó lombkoronaszint. Egy magyarországi tölgyerdő cserjeszintjének a tölgypusztulás utáni strukturális változásait vizsgáltuk. Ez a dolgozat a következő kérdésekre fókuszál: (1) melyik fásszárú fajok reagáltak jobban a tölgyek pusztulását követően az erdő kondíciójára? (2) Milyen ökológiai tényezők magyarázhatják a fásszárú fajok sikeres válaszát a megváltozott fény- és hőviszonyokra? A monitoring területen a 8,0 m feletti egyedeknek a strukturális kondícióját vizsgáltuk. A tölgypusztulás kezdete után néhány *Acer campestre*, *Cornus mas* és *Acer tataricum* egyed jelent meg elérve a 8,0-13,0 m közötti magasságot. Szignifikáns eltérést találtunk a felső lombkorona denzitása és az alsó lombkorona borítása, illetve a felső lombkorona denzitása és a mezei juhar átlagos lombvetülete között. A kutatásunk megállapításai azt jelzik, hogy az erdő a cserjeszint jelentős strukturális átrendeződésével válaszolt a tölgypusztulásra, és három fásszárú faj pótolta a felső lombkorona jelentős lombveszteségét. Ezek a fajok második lombkoronaszintet hoztak létre közvetlenül a tölgyek alkotta lombkorona alatt.

cserjeközösség / fásszárú fajok / *Acer campestre* L. / borítás / kipusztult tölgyek

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1 INTRODUCTION

Biotic factors such as climate change and extreme weather conditions (Bolte et al. 2010, Kotroczó et al. 2012), pathogens such as root diseases (Jung et al. 2000, Szabó et al. 2007), and insect gradations (Csóka 1998, Bruhn et al. 2000, Moraal – Hilszczanski 2000) and abiotic factors, such as human influence, climate change, fires and air pollution (Mészáros et al. 1993, Signell et al. 2005, Kabrick et al. 2008) lead to a modified functioning of the whole forest ecosystem and may lead to forest decline. Tree decline has heavily affected oak species, and especially *Quercus petraea* Matt. L. (sessile oak) trees in European countries (Freer-Smith – Read 1995, Thomas – Büttner 1998). Oak death has been described as a widespread and complex phenomenon (Klein – Perkins 1987, Bruck – Robarge 1988). An increase in the death of oak forests has been observed in many regions of Hungary since 1978 (Igmándy 1987). In 1976, oak decline began in Slovakia, found its way to former Yugoslavia by 1979, and finally reached Austria in 1984 (Hämmerli – Stadler 1989). Many papers have reported that increased oak mortality is leading to changes in forest dynamics (Moraal – Hilszczanski 2000, Woodall et al. 2005).

Relatively few studies deal with shrub communities and shrub layer dynamics after oak death and the relationship between the tree and shrub layer (Légaré et al. 2002). Shrub dynamics is linked to the ecological functioning of forest ecosystems (McKenzie et al. 2000, Brosofske et al. 2001, Augusto et al. 2003). The shrub layer is affected by light availability when the canopy is closed (Légaré et al. 2002), leading to negative correlations of shrub layer species richness and/or cover with tree basal area (Hutchinson et al. 1999). Shrubs may provide important indications of site quality, overstory regeneration patterns and conservation status (Hutchinson et al. 1999). Tree species diversity had a positive relationship to shrub cover because a diverse overstory generally created more canopy gaps (Gazol – Ibáñez 2009). The tree layer structure strongly influences shrub species cover by altering microsites, resources and environmental conditions (Oliver – Larson 1996, Stone – Wolfe 1996). The variability in below tree layer light availability and canopy openness strongly influence individual performance and community composition of shrub and herb plants in temperate forest (Hughes – Fahey 1991, Goldblum 1997).

Most papers only used changes in structural conditions in the tree layer to monitor the ecological process in the forest community after tree decline (Bussotti – Ferretti 1998, Brown – Allen-Diaz 2009). The studies of shrub species performed have mostly focused on the static population structure (age and size structures); these parameters have been described by a negative exponential model (Tappeiner et al. 1991, Stalter *et al*. 1997). Other studies have focused on the cover and diversity of shrubs (e.g. Kerns – Ohmann 2004, Gracia et al. 2007). In this paper we used frequency, size and cover variables complemented with basal area to obtain a more complete picture of shrub layer dynamics.

The species composition of the canopy layer was stable until 1979 and the healthy *Q. petraea* and *Quercus cerris* L. (Turkey oak) also remained constant in the mixed-species forest stand (*Quercetum petraeae-cerris* Soó 1963) of Síkfőkút. Serious oak decline was first reported in 1979–80 and by 2012, 62.4% of the oaks had died; this decline resulted in an opening of the canopy. The decline affected both forest stands; however it affected sessile oak considerably more. The mortality rate of Turkey oak trunks was lower, only 16% over the last three decades (Kotroczó et al. 2007). The canopy species composition has changed little, only some trees of *Tilia cordata* Mill. and *Carpinus betulus* L. lived as new codominant species on the site. The regeneration of oak species is rather poor and the cover of the herb layer is low. The possible biotic and abiotic factors of oak decline and the effect of decline on the structural condition of the forest community on the Síkfőkút plot have also been studied in many papers (e.g. Jakucs 1985, 1988). Jakucs'results (1988) show that the soil acidification induced by the disappearance of mycorrhizal fungi and the air pollutants that promote water and nutrient absorption, have been evaluated and identified as primary causes of deciduous forests' decline. *Q. petraea* suffered a more drastic decline than *Q. cerris* trees in Hungarian woodlands. Later this theory was bought into question by further research (in particular, drought impact). The results of Mészáros et al. (2011) suggest that magnitude of tree water deficit variation (ΔW) was always smaller in *Q. cerris* than in *Q. petraea*. In contrast, *Q. cerris* trees exhibited larger daytime averages and maxima of sap flow density. Béres et al. (1998) state that the bright – i.e. water filled - outer layer can be considered as the active new xylem. This layer is considerably thicker in the case of *Q. cerris* than in the case of *Q. petraea*. The inner compartment of *Q. petraea* contains a very small amount of water and there is no difference between heartwood and sapwood. On the other hand, *Q. cerris* is clearly different, with higher density heartwood and low density sapwood compartments.

Specifically, we address the following questions: (1) What are the most important structural changes in the forest interior after serious oak decline? (2) What kind of woody species in the understory have the most successful response to oak death? (3) What are the ecological factors that explain the successful response of the woody species to changes in light and thermal conditions? (4) Can the forest make up for the significant losses of leaf canopy by means of new structural foliage formation? (5) Finally, what is the interaction between the woody species of the subcanopy layer?

2 MATERIAL AND METHODS

2.1 Study site

The 27 ha reserve research site is located in the Bükk Mountains of northeast Hungary (47°55' N, 20°46' E) at a distance of 6 km from the city of Eger at an altitude of 320–340 m a.s.l.. The site was established in 1972 by Jakucs (1985) for the long-term study of forest ecosystems. Mean annual temperature is 9.9 °C and mean annual precipitation ranges typically from 500 to 600 mm. The mean annual temperature and precipitation are based on measurements at the meteorological recording tower of the site. Description of the geographic, climatic, soil conditions and vegetation of the forest was undertaken in detail by Jakucs (1985, 1988). The most common forest association in this region is *Quercetum petraeae-cerris* with a dominant canopy of *Q. petraea* and *Q. cerris*. Both oak species are important dominant native deciduous tree species of the Hungarian natural woodlands. It was detected on subcanopy layer of the most sessile oak-Turkey oak stand in Hungary with *Acer campestre* L., *Sorbus torminalis* L. Crantz, *Pyrus pyraster* L. Burgsd, *Ulmus procera* Salisb. and *T. cordata* species. Other codominant tree species of the study site included *Ca. betulus*, *Prunus avium* L. and *T. cordata*. The plot under study is made up of evenly-aged trees, is at least 95–100 years old temperate deciduous forest and has not been harvested for more than 50 years.

2.2 Sampling and data analysis

Conditions in the shrub layer were monitored at regular intervals on a 48 m × 48 m plot at the research site, which was subdivided into 144 permanent subplots, each 4 m × 4 m in size. The investigations were performed during the growing seasons. Monitoring activities started in 1972 and repeated shrub layer inventories took place in 1982, 1988, 1993, 1997, 2002, 2007 and 2012. In 2012 three 10 m × 10 m new fixed plots were selected for vegetation sampling to confirm the detected shrub layer development of the site. Orientation of these extra plots was randomly determined. These plots were subdivided into 16 2.5 m × 2.5 m subplots to determine species occurrence of the understory. Canopy trees were classified as sessile oak and Turkey-oak tree species > 13.0 m in height and ≥ 10.0 cm in diameter at breast height (DBH). Trees were classified as subcanopy trees when between 8.0–13.0 m in height.

In each of the subplots and new plots the following measurements were carried out: species composition, frequency (occurrence % in subplots), species density, height, diameter, basal area and cover of each subcanopy species. The species' density was also determined in plots and the data was extrapolated for one hectare. In stand No. 18 (1982) – 69 (2012) individuals of subcanopy species were sampled in the last decades and then subjected to mean height, mean diameter and mean cover analysis. Plant height was measured with a scaled pole and shoot diameter at 5.0 cm above the soil surface in two directions (if the shape of the shoot of shrub individuals was not regular) with a digital caliper in a field study and the measurement results were averaged.

Within each plot the stand basal area (BA, m^2 ha^{-1}) of subcanopy woody species was calculated from the measured diameters of all subcanopy specimens. Location and percentage cover of the subcanopy trees and high shrubs was also mapped together every 4 to 5 years, beginning in 1972. Many studies included the method of creating a foliage map from the shrubby vegetation (e.g. Jakucs 1985). The foliage map was built in a GIS environment. Based on the digitized map we estimated the foliage area of subcanopy trees and shrub individuals with the Spatial Analysis Tools - Calculate Area function of the GIS. The correlation analysis was used to determine and quantify the connection between stand density and subcanopy layer condition on the monitoring plot from 1982, by using the following structure variables as dependent variables: (1) frequency (2) mean height and diameter (3) mean cover (4) mean and total basal area of subcanopy species. One-way ANOVA with the Tukey's HSD test was used as a post-hoc test if necessary to determine the significant differences among subcanopy species by occurrence frequencies, mean cover and mean basal area. Statistical analysis was performed using PAST statistical software and significant differences for all statistical tests were evaluated at the level of $P \leq 0.05$ or $P \leq 0.01$.

3 RESULTS

Once oak decline had set in, 3 native woody species were identified across the entire study area from 1982 in the new subcanopy layer; *A. campestre* (field maple), *Cornus mas* L. (European cornel) and *Acer tataricum* L. (Tatar maple) were present as subcanopy species in the sample site. In the new plots only some *A. campestre* individuals and single *C. mas* composed this layer. The average number of subcanopy woody specimens per one hectare has varied from 73 to 238 over the past 2 decades. The total top canopy density decreased from 651 to 305 trees ha^{-1}. In contrast, *A. campestre* increased in density (from 56 to 204 specimen's ha^{-1}) and density of *A. tataricum* and *C. mas* did not change in importance (*Figure 1*).

The correlation analysis did show a non-significant association between living oak tree density and occurrence frequency of the subcanopy tree species (r = 0.75, P > 0.05). The species with the highest occurrence in subplots was *A. campestre* with rates of 6.3–25.7% (*Table 1*). A significant relationship between oak tree density and *A. campestre* occurrence frequency (r = 0.77, $P \leq 0.05$) was observed between 1982 and 2012, this relationship was not significant in the cases of *A. tataricum* and *C. mas* (r = 0.21 and 0.47, P > 0.05) between 1982 and 2012 was observed. The one-way ANOVA indicated significant differences among occurrence frequencies of woody species (*Table 2*).

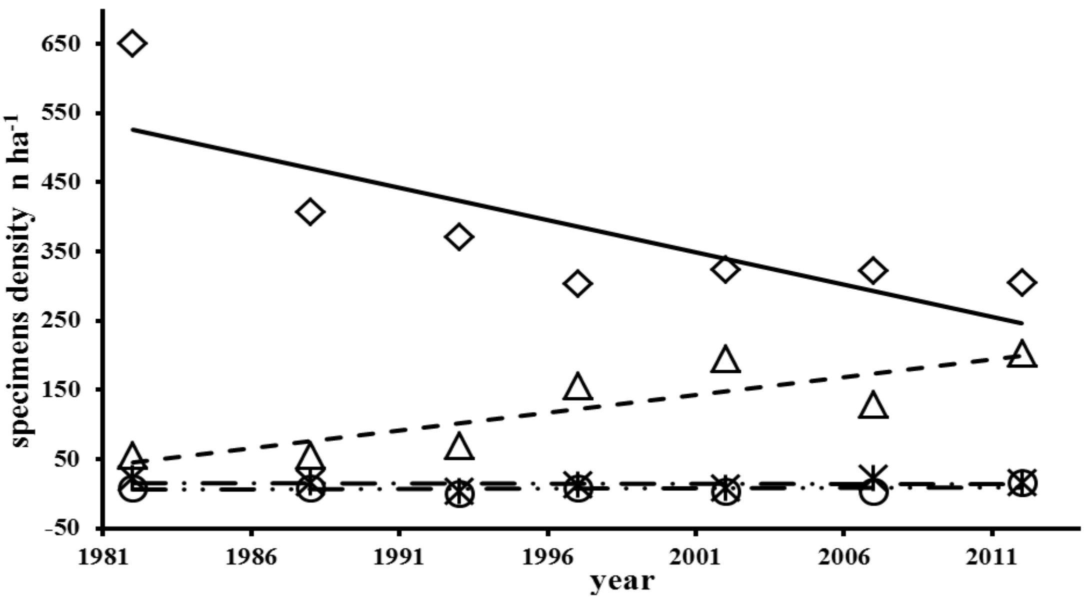

Figure 1. Density trend of oak canopy species and subcanopy woody species for the period from 1982 to 2012 on the monitoring plot.
Notation: ——–, deltoid – living oak trees; – – –, triangle – A. campestre; – · · –, circle – A. tataricum; – · –, asterisk – C. mas

Table 1. Frequency condition of the subcanopy woody species on the monitoring and new plots over the period 1982–2012 (N = 144 subplots; N = 48 subplots)*

subcanopy species	occurrence frequency (%) in subplots							
	1982	1988	1993	1997	2002	2007	2012	2012*
A. campestre								
8–13 m	6.3	6.3	12.5	23.6	25.7	20.1	25.0	27.8
> 13 m	0.0	0.0	2.1	0.7	2.1	13.2	7.6	0.0
A. tataricum								
8–13 m	1.4	1.4	0.0	2.1	2.1	0.7	2.8	0.0
C. mas								
8–13 m	1.4	1.4	0.7	4.2	1.4	3.5	2.8	5.6

*mean frequencies of new plots

Frequency distribution of *A. campestre* and *C. mas* woody species between 1993 and 2012 with height and diameter classes is shown in *Figure 2.* Most stems belonged to the 8.0-10.0 m height and 11.6–16.6 cm diameter classes, which contained almost 75% and 55% of these woody species. The height and diameter frequency distribution of subcanopy species had a corresponding two-peak-pattern in 2012 with a first peak at 901–1000 cm height and 11.6–16.6 cm diameter and a second at 800–900 cm and 8.1–11.5 cm class.

Table 2. Results of one-way ANOVA and Tukey's HSD test (p = significance level, F = variance of the group means) for mean basal area, occurrence frequencies and mean cover of dominant woody species on the monitoring plot. Significant differences are shown in bold

	p / *F* values		
	A. campestre	*A. tataricum*	*C. mas*
Mean basal area			
A. campestre	1	–	–
A. tataricum	**0.0204** / 7.1560	1	–
C. mas	0.0648 / 4.1370	0.3451 / 0.9664	1
Occurrence frequencies			
A. campestre	1	–	–
A. tataricum	**0.0006** / 22.650	1	–
C. mas	**0.0008** / 20.450	0.2730 / 1.3210	1
Mean cover			
A. campestre	1	–	–
A. tataricum	0.8827 / 0.0230	1	–
C. mas	0.3033 / 1.1780	0.4737 / 0.5547	1

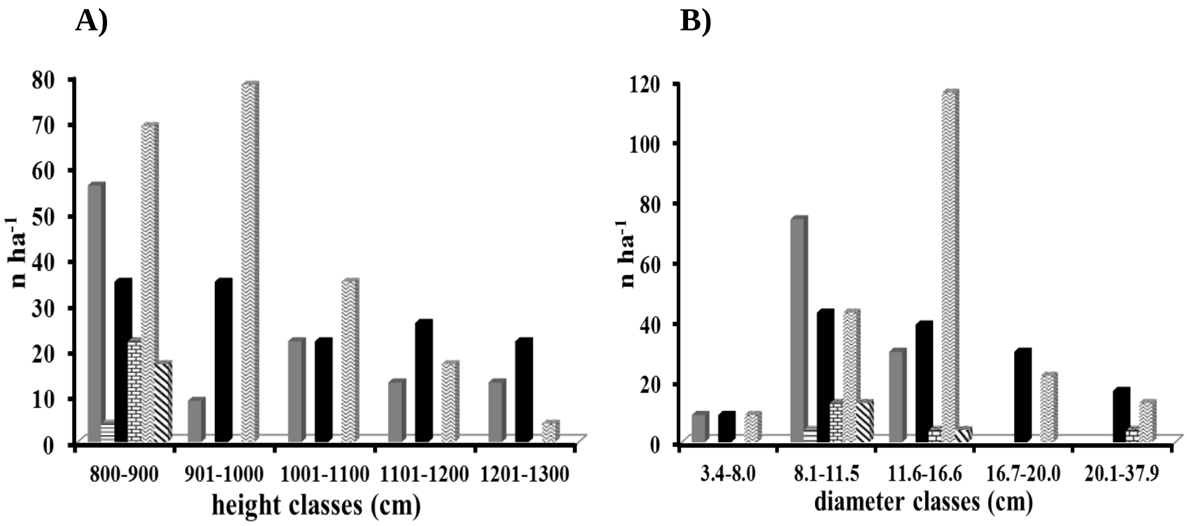

Figure 2. Frequency distribution of A. campestre and C. mas woody species in 1993, 2007 and 2012 considering height (A) and diameter (B) classes on the monitoring plot. Notation: dark gray - A. campestre, 1993; black - A. campestre, 2007; wavy - A. campestre, 2012; ruled - C. mas, 1993; brick - C. mas, 2007; slant line - C. mas, 2012 (N = 499)

Three woody species responded positively to foliage gaps. Box-plots showed the height and diameter changes and distribution of subcanopy species over the period 1982–2012. The median values of *A. campestre* increased considerably, but the minimum and maximum values of height decreased in the last measuring. The *A. tataricum* and *C. mas* boxes did not show unambiguous tendency in height and diameter distribution, but the height decreased considerably between 1982 and 1997. The correlation analysis recorded that after large-scale oak decline, the mean height and shoot diameter of some woody species had increased remarkably but not significantly during the last surveys (height: *A. campestre* $r = 0.78$; *A. tataricum* $r = 0.28$; $P > 0.05$) (diameter: *A. campestre* $r = 0.79$; *A. tataricum* $r = 0.82$; *C. mas* $r = 0.67$; $P > 0.05$). A highly significant relationship between oak tree density and mean height of *C. mas* ($r = 0.99$, $P \leq 0.001$) was confirmed (*Figure 4*).

Stand density and mean and total basal area of subcanopy species were found to have a negative and non-significant relationship (r = 0.43–0.65, P > 0.05). The basal area estimates by woody species show that the total basal area of subcanopy layer varied between 0.33 and 2.75 m^2. The mean basal area of woody species increased continually from 1982 and varied between 0.24^{-2} and 1.84^{-2} m^2 on the monitoring plot. The total basal area of woody species increased after the commencement of oak decline and the greatest values were recorded by maple species in 2012 and by *C. mas* in 2007 (*Table 4*). The ANOVA analysis indicated significant differences among the mean shoot's basal area of maple species (*Table 2*).

We found a negative correlation between top canopy density and total foliage cover of the subcanopy layer (r = 0.95, $P \leq 0.05$). The GIS analysis confirmed that after serious oak death the percentage cover of subcanopy layer increased considerably and was at its maximum in 1997 with 969.9 m^2. Mean cover increment of *A. campestre* negatively correlated to oak tree density (r = 0.85, $P \leq 0.05$). Mean cover of *C. mas* (r = 0.71, P > 0.05) and *A. tataricum* (r = 0.54, P > 0.05) specimens increased, but non-significantly after tree decline. This value increased continually with European cornel individuals, but the mean cover of maple species fluctuated between 11.2 and 18.3 m^2 between 1993 and 2007 (*Table 3*). The ANOVA indicated non-significant differences among mean cover of woody species (*Table 2*).

Table 3. Relationship between oak tree density and mean cover of subcanopy woody species and total foliage cover of subcanopy layer on the monitoring plot over the period 1982–2007

year	oak tree density ($n\ ha^{-1}$)	mean cover (m^2) ± SD.			total foliage cover of subcanopy layer (m^2)
		A. campestre	*A. tataricum*	*C. mas*	
1982	651	4.8 ± 1.2	3.4 ± 0.8	3.6 ± 0.9	81.2
1988	408	7.8 ± 8.8	4.5 ± 4.0	8.5 ± 7.0	150.0
1993	372	11.7 ± 3.4	–	10.4 ± 0.0*	313.8
1997	304	18.3 ± 6.1	11.2 ± 1.6	19.0 ± 2.2	969.9
2002	324	12.0 ± 2.9	18.2 ± 0.0*	27.0 ± 1.9	612.4
2007	323	14.6 ± 2.8	31.7 ± 0.0*	34.8 ± 6.0	671.6

*on the basis of a single individual

Table 4. Relationship between oak tree density and mean and total basal area of subcanopy woody species on the monitoring plot over the period 1982–2012

year	oak tree density ($n\ ha^{-1}$)	mean basal area (m^2) ± SD. / total basal area (m^2)		
		A. campestre	*A. tataricum*	*C. mas*
1982	651	$4.8^{-3} \pm 1.9^{-3}$ / 0.07	$2.5^{-3} \pm 6.0^{-4}$ / 4.9^{-3}	$2.4^{-3} \pm 8.8^{-4}$ / 4.8^{-3}
1988	408	$5.2^{-3} \pm 2.0^{-3}$ / 0.11	$2.3^{-3} \pm 1.1^{-3}$ / 6.1^{-3}	$3.8^{-3} \pm 1.7^{-3}$ / 4.1^{-3}
1993	372	$5.9^{-3} \pm 2.2^{-3}$ / 0.15	–	$4.1^{-3} \pm 0.0$ / 4.1^{-3}*
1997	304	$8.8^{-3} \pm 4.0^{-3}$ / 0.40	$3.8^{-3} \pm 5.6^{-4}$ / 1.1^{-2}	$4.5^{-3} \pm 2.6^{-3}$ / 2.7^{-2}
2002	324	$1.3^{-2} \pm 1.2^{-2}$ / 0.60	$5.6^{-3} \pm 3.0^{-3}$ / 1.7^{-2}	$5.1^{-3} \pm 2.1^{-3}$ / 1.5^{-2}
2007	323	$1.2^{-2} \pm 7.6^{-3}$ / 0.39	$6.1^{-3} \pm 0.0$ / 6.1^{-3}*	$1.0^{-2} \pm 8.7^{-3}$ / 5.1^{-2}
2012	305	$1.8^{-2} \pm 1.8^{-2}$ / 0.87	$7.6^{-3} \pm 5.2^{-3}$ / 3.1^{-2}	$7.4^{-3} \pm 2.3^{-3}$ / 3.0^{-2}

*on the basis of a single individual

4 DISCUSSION

Three types of factors should be examined as possible causes of the shrub layer dynamics observed: (1) Changes in the light and thermal regime resulting from changes in canopy structure, particularly gaps; (2) changes in the species composition and density of canopy trees; and (3) other environmental factors such as changes in forest management or human activities. The last factor can be excluded, because the forest community has not been disturbed by forest management for more than 50 years. The second possible factor is only partially relevant to the study site; a significant proportion of sessile oak trunks ($P \leq 0.01$) died on the site and the percentage foliage cover of the tree layer decreased. Despite this ecological process new and/or invasive species could not establish themselves in the oak forest, because some native species of the understory would respond positively to various sizes of canopy gaps. So our study is in agreement with Dunn (1986) who found that the species composition of the shrub layer to density of dead *Ulmus americana* L. trees was not significant in lowland forests of the USA.

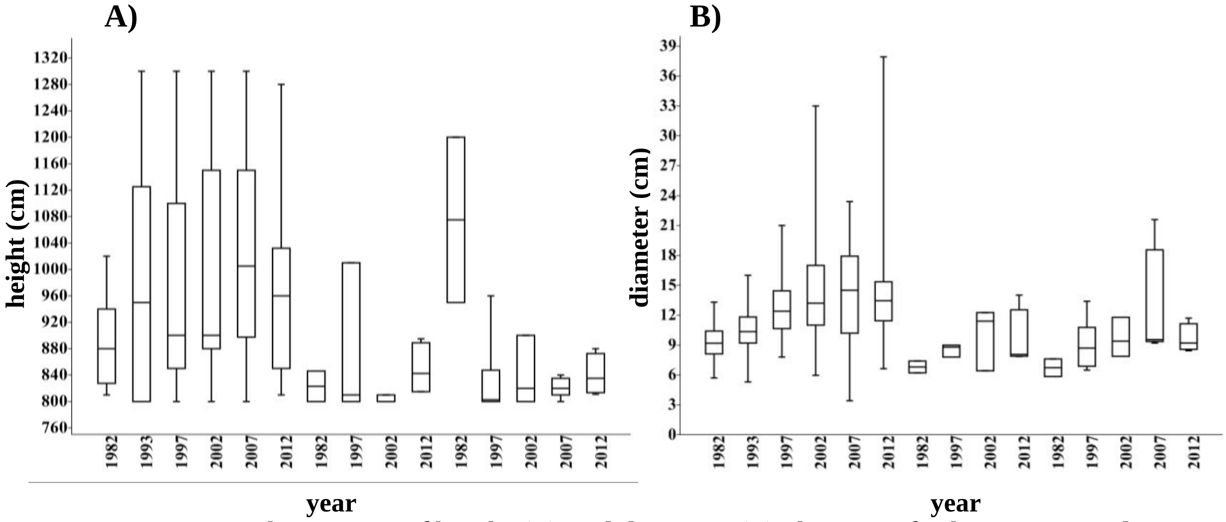

Figure 3. Statistical summary of height (A) and diameter (B) changes of subcanopy woody species (sequentially: A. campestre, A. tataricum and C. mas) on the monitoring plot over the period 1982–2012. Boxes shown are the 25–75% percentile, median, minimum and maximum values (N = 250). Includes only single individual of A. tataricum in 2007 and C. mas in 1993

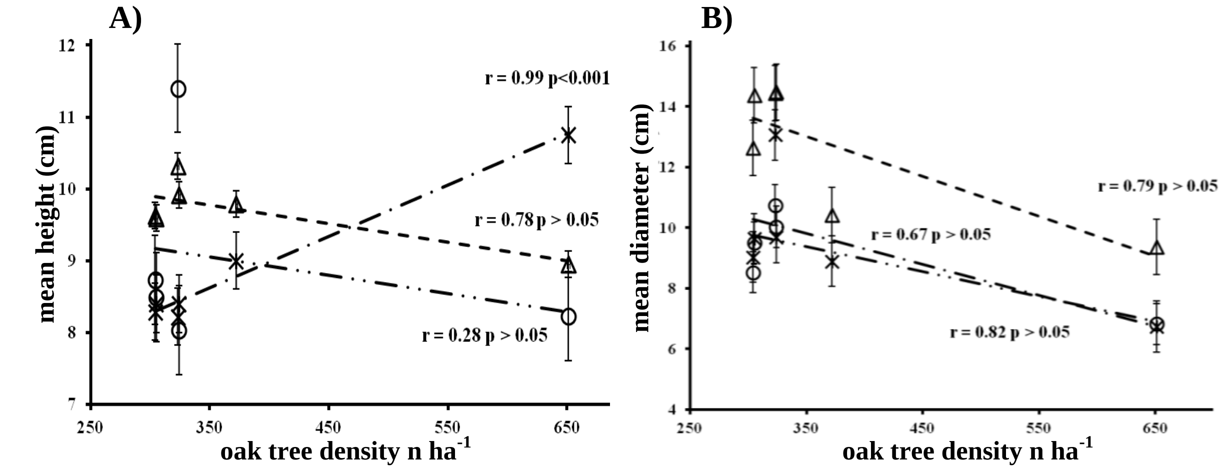

Figure 4. Correlation relationship between oak tree density and average height (A) and diameter (B) ± SE. changes of subcanopy woody species on the monitoring plot over the period 1982–2012 (N = 250).
Notation: – – –, triangle – A. campestre; – · · –, circle – A. tataricum; – · –, asterisk – C. mas

A significant association was not detected between oak canopy density and the density of the subcanopy layer ($P > 0.05$) on the site (*Figure 1*). A non-significant increase in the density of *A. campestre* in the new layer and in the overstory after the oak decline ($P > 0.05$) was recorded, because increasing numbers of *A. campestre* grew out from the subcanopy layer from 1993. This process is coincident with the height increment of the maple specimens (*Figure 4*). The species occurrence frequencies in the subcanopy layer did not change significantly over the past 3 decades. In the USA the total shrub density showed a relationship to dead elm density. The density of shrub layer increased significantly and predictably, when dead elm density was greater than 5 stems/ha (Dunn 1986). Observations from mature *Quercus*-dominated forests throughout the eastern United States suggest that many of these forests are undergoing significant compositional transformation. *Quercus* spp. are being replaced in the understory by species such as *Acer rubrum* L. and *A. saccharum* Marshall, and these mesophytic, relatively shade-tolerant species are likely to become canopy dominants if current trends continue (Shotola et al. 1992, Galbraith – Martin 2005, Nowacki – Abrams 2008). On the other hand, according to Röhrig and Ulrich (1991) *A. campestre* is a relatively drought tolerant species. Oak species cannot successfully compete with these species (McDonald et al. 2002, Zaczek et al. 2002). Our results support these statements, because in Síkfőkút maple specimens showed an increase in size and cover, and a low regeneration potential of oaks due to drought and detected shading effects (*Figure 3, 4, Table 3, 4*). A considerable shifting to the larger height and diameter classes in the subcanopy layer under 15 years has been noted from the monitoring (*Figure 2*). In the canopy gaps these species grew up from the shrub layer into the new foliage layer 8.0–13.0 m in height, below the canopy layer of the sessile oak and Turkey oak species. High drought tolerance of *A. campestre* confirms the results of Kotroczó et al. (2012) in Síkfőkút. The mean leaf-litter production of this species was nearly 110.0 kg ha^{-1} between 1972–76 and was five times higher between 2003–10, these differences are significant ($P = 0.001$).This can be explained by the fact that *A. campestre* formerly occurred in the shrub layer, while presently it forms a part of the canopy-layer, where it has become the second most common tree species, representing 28.2% of the total number of trees in the canopy.

We found a negative correlation between oak tree density and total cover of the subcanopy layer ($P \leq 0.05$). A similar connection between top canopy density and mean cover of the species in the subcanopy was detected (*Table 3*). In 2002 we found an important recidivation in total cover of the subcanopy layer, but the individual density of this layer increased further. The reason being that the mean cover of *A. campestre* individuals decreased by 26.0% compared to 1997. Results from different forest types show that the canopy openings modify light, thermal and moisture conditions (Nakashizuka 1985, Holeksa 2003). After large-scale oak decline, different sized gaps were formed in the foliage of the tree layer in the sample site and the shrub species in these gaps could be increased considerably due to the higher light levels. Concerning trees cover its purported influence on the composition of understory species by through it controlling ecosystem processes such as light transmittance and nutrient cycling (Légaré et al. 2001); we cannot support such a statement with our results. The decreasing total top canopy cover led to changes in the structural condition of the shrub layer, but consistent and directional changes in the shrub species composition has not been reported. The dense tree layer can inhibit regeneration of trees and high shrubs (Tappeiner et al. 1991, Stein 1995, Knowe et al. 1997). At our site, oak decline decreased top canopy cover and led to the notable height growth of three species from the shrub layer; this phenomenon is called the "Oskar"-strategy (Silvertown 1982). The *Acer* species is a genus that displays this characteristic in such circumstances. The results, from a mixed forest stand in France, of Caquet et al. (2010) suggest that the new trees in the gaps at the end of the regeneration phase were dominated by *Fagus sylvatica* L. and *Acer pseudoplatanus* L. Two other species, *A. campestre* and *Acer platanoides* L., are present in high numbers in the seedling bank, but are totally absent at the end of the regeneration phase in the gaps. 3 years later canopy opening seedlings in the gaps displayed significantly greater diameter and height than those under canopy in *Acer* sp. and *F. sylvatica* L. species ($P < 0.001$). All maple and European beech species responded positively and rapidly to canopy openings. Diameter increment was similar across four species, and height increment was greater for *A. platanoides* and for *A. pseudoplatanus* seedlings (Caquet 2010).

Tree decline substantially increases the resources (e.g. light and nutrients) available to other organisms (naturally to shrub species) in the ecosystem. The amount of resources made available depends on the scale of the oak decline (Franklin et al. 1987). At our site 493 specimens of oak trunks died in the last decades so initially this process guaranteed suitable light for the growing of shrub specimens. In the gaps some woody species (especially *A. campestre*) grew quickly, therefore they were the limiting factor for the natural regeneration and growing of other shrub and oak species by restricting the light supply in the forest. Dense cover of two *Acer sp*. and *C. mas* can inhibit regeneration of other trees and shrubs in our site. *Acer* species are considered very important among the hardwoods of Europe and North America, because of their ecological and economic significance (Morselli 1989). These species provide a considerable source of food and foliage cover for wildlife (Morselli 1989).

5 CONCLUSIONS

Our study suggests that (1) the vertical foliage distribution changed in the understory and a new secondary subcanopy layer appeared below the oak canopy layer, 8–13 m in height. (2) *A. campestre* was the most common shade-tolerant woody species in this new layer. Additionaly, some *C. mas* and *A. tataricum* specimens composed the subcanopy layer. (3) The response of these shade and relatively drought tolerant woody species is strong and rapid once oak decline has set in, the so-called "Oskar"-strategy. (4) The total foliage cover of this layer per hectare was substantially higher in 2012 than in 1982; the new layer can makes up for the significant losses of leaf canopy. (5) *A. campestre* has a strong influence on the frequencies of other subcanopy species and on the mean basal area of *A. tataricum*. The study demonstrated that the forest community compensated for the dead oak trees by forming a subcanopy layer. The woody species of this layer responded successfully to the foliage gaps. Archival data from 1982 allowed us to quantify long-term changes in forest structure and to better understand the impacts of a changing top canopy density and foliage cover rate over the past 30 years. Furthermore, understanding understory development and possible interaction between the understory shrub layer and the canopy is critical to achieving forest management goals in the Hungarian oak forest stands, as this knowledge helps explain stand developmental patterns and predict future stand structures. As the decline in the current oak population continues, and with oak seedlings taking so long to reach sufficient height, more *A. campestre* specimens will grow into the canopy which will lead to the formation of mixed oak forest.

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