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LONG-TERM DYNAMICS OF SUBCANOPY LAYER AS NEW LAYER IN AN OAK FOREST OF HUNGARY

Tamás MISIK[*], Imre KÁRÁSZ

Department of Environmental Sciences and Landscape Ecology, Eszterházy Károly Catholic University, Hungary
*Corresponding author: misiktom@gmail.com

ABSTRACT

Structural dynamics of the shrub layer were analysed in a Hungarian oak forest after the serious oak decline pandemics. Vertical foliage distribution changed in the understory and a new subcanopy layer appeared below the oak canopy in the last decades. This paper focuses on the following questions: (1) how have the new foliage layer developed after oak decline? (2) Which woody species are the most frequent in this layer? (3) How have the mean sizes of these species changed? The forest association in the monitoring site is *Quercetum petraeae-cerridis* with *Quercus petraea* Matt. L. (sessile oak) and *Quercus cerris* L. (Turkey oak). The site was subdivided into 144 permanent subplots. Woody individuals were classified as subcanopy trees between 8.0–13.0 m in height. Measured structural parameters were carried out in the period 1982-2017. Three woody species, *Acer campestre* L. (field maple), *Acer tataricum* L. (Tatar maple) and *Cornus mas* L. (European cornel) played a key role in the new layer and their height was between 8.0–13.0 m or higher than 13.0 m. The density of species in this layer increased considerably between 1982 and 2002. The most frequent woody species was *A. campestre*. The mean height, diameter and mean cover of the dominant woody species increased significantly after the decreasing oak density. Our results suggest that the mixed oak forest responded to oak decline with significant structural rearrangement in the shrubs and three woody species compensated for the remarkable foliage loss in the canopy. These species formed a new subcanopy layer.

Keywords: *Shrub community, Oak decline, New foliage layer, Acer campestre, Dominant woody species.*

INTRODUCTION

Oak decline has been described as a widespread and complex phenomenon worldwide in many countries (Tomiczek, 1993; Sonesson and Drobyshev, 2010). Various abiotic (air pollution, nitrogen eutrophication, soil chemical stress, climatic extreme events, site conditions) and biotic factors (insect defoliation, borer attack, infection by pathogenic fungi, microorganisms) have been related to the serious oak decline in the world (Thomas *et al*., 2002). An increase in the death of oak trees has been observed in many regions of Hungary since 1978 (Igmándy *et al*., 1986). In the Síkfőkút forest stand species composition of the canopy was stable until 1979 and the healthy *Quercus petraea* Matt. L. (sessile oak) and *Quercus cerris* L. (Turkey oak) also remained constant. Oak decline was first reported in 1979–80 and by 2017, 62.9% of the oak trees had died in the mixed-species oak forest stand (*Quercetum petraeae-cerris* Soó 1963). This means that the oak trees density decreased from 816 living trunks to 651 trunks in the first decade. The oak decay continued at a variable rate in the following decades, from 651 - through 408 trees in 1988 and 372 trees five years later - to 303 healthy trunks by 2017. Tree decline resulted in an opening of the canopy. Many papers have reported that oak mortality is key factor influencing the structure and dynamics of forest community (Moraal and Hilszczanski, 2000; Woodall *et al*., 2005).

Relatively few studies deal with shrub layer dynamics after oak death and the possible relation between trees and shrubs (Légaré *et al.,* 2002). Understory and overstory relationships are complex but are dominated by the canopy layer condition and structure (Burrascano *et al*., 2011; Burton *et al*., 2011; Cutini *et al*., 2015). Shrub layers of forest ecosystems change dynamically and respond sensitively to the environmental changes (Chipman and Johnson, 2002; Rees and Juday, 2002). They are strongly related to the composition and structure of the overstory (Klinka *et al.,* 1996; Palik and Engstrom, 1999). The shrub community is affected by light availability when the canopy is closed (Légaré *et al*., 2002), leading to negative correlations of shrub species richness and/or cover with the increase of tree basal area (Hutchinson *et al*., 1999). Shrub species play a major role in the cycles of some essential nutrients, including the dynamics of carbon,nitrogen and potassium (Gilliam, 2007). The shrub layers are directly contributes to forest biodiversity (Kerns and Ohmann, 2004; Čermák *et al.,* 2008), including compositional and structural diversity, enhancing the aesthetics of forest ecosystems and helping to protect watersheds from erosion (Alaback and Herman, 1988; Halpern and Spies, 1995; Muir *et al.,* 2002). The consequences of serious oak decline cause notable changes in the light and stand thermal conditions of forest community which led to structural changes of the shrub layer (Chapman *et al.,* 2006).

Misik *et al*. (2014) described the dynamics behind the increase in the sizes of some woody species and the structure of the new subcanopy layer below the oak canopy. This paper focuses on the following questions: (1) how have the new foliage layer developed after oak decline? (2) Which woody species are the most frequent in this layer? (3) Finally, how have the mean sizes of these species changed?

MATERIAL AND METHODS

Study area The nature reserve research site (Síkfõkút Project) was established in 1972 by Jakucs (1985) and is located in the Bükk Mountains (47°552 N, 20°462 E) in the north-eastern part of Hungary at an altitude of 320-340 m a.s.l. (Figure 1A). Mean annual temperature is 9.9 °C and mean annual precipitation typically about 500-600 mm. Descriptions of the geographic, climatic, soil conditions and vegetation of the forest were described in detail by Jakucs (1985, 1988,). The common forest association in this region is *Quercetum petraeae-cerridis* (Soó, 1963) (sessile oak-Turkey oak) with a dominant canopy of *Q. petraea* and *Q. cerris*. Both oak species are important native deciduous tree species of the Hungarian natural woodlands. Long-term dynamics of shrub community are described among others in works of Misik *et al*. (2013, 2014, 2017, 2020). The plots under study were made up of evenly aged temperate, mixed species deciduous forest that was at least 110 years old and had not been harvested for more than 55 years.

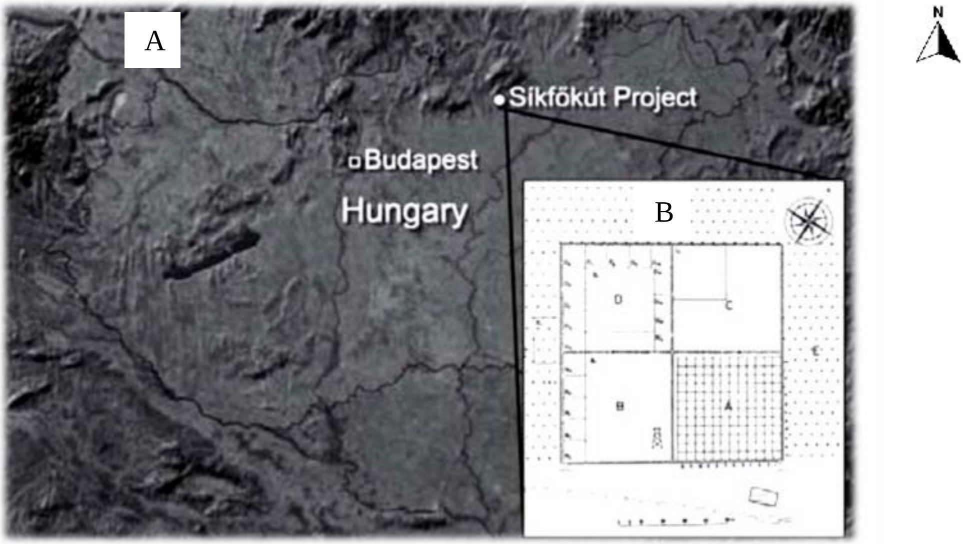

Figure 1.A. Location of the study area in Hungary. B. Study site location with plots.

Sampling and data analysis The condition of the subcanopy layer was monitored on an "A" monitoring plot at the research site, 48 m × 48 m in size; the plot was subdivided into 144 4 m × 4 m permanent subplots (Figure 1B). The "A" plot with many subplots can be found at the bottom right of the Figure 1B. The plot was established in 1972; the new layer inventories took place in 1982, 1988, 1993, 1997, 2002, 2007, 2012 and 2017, during the growing seasons.

In the new foliage layer were classified as subcanopy individuals when between 8.0–13.0 m in height. In monitoring plot the following measurements were carried out: species composition, species density; height, diameter and cover of each subcanopy species. The species' density was also determined in plot and the data was extrapolated for one hectare. Plant height was measured with a scaled pole with an accuracy of 5.0 cm and shoot diameter at 5.0 cm above the soil surface with a digital caliper and the measurement results were averaged. The foliage map was developed in a GIS environment. Based on the digitized map we estimated the foliage area of subcanopy trees with the Spatial Analysis Tools - Calculate Area function of the GIS.

The experimental data were analysed by correlation analysis to investigate the possible effects by the density, height, diameter and cover of subcanopy species on oak tree density (SPSS Statistics 19, Tulsa, USA). We used only the measured oak canopy density to the statistical analysis, because canopy cover has only been measured twice since 1972. On the other hand, oak trees have got typically monolayer foliage and they cannot significantly increase their foliage size in the gaps. In other words, the decreasing oak trees density is strong related to the oak canopy cover Statistical analysis was performed using the PAST statistical software and significant differences for all statistical tests were evaluated at the level of $^{*}P < 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$. There was no significant correlation found between the test variables at $^{n.s.}P \geq 0.05$.

RESULTS AND DISCUSSION

From the starting of oak decline, 3 native woody species were identified across the entire study area in the new subcanopy layer; *Acer campestre* L. (field maple), *Cornus mas* L. (European cornel) and *Acer tataricum* L. (Tatar maple) were present continuously as subcanopy woody species in the forest stand. *A. tataricu*m and *C. mas* individuals were not detected between the subcanopy and oak canopy layer in the last 35 years. The total density of woody species in these foliage layers increased remarkably, from 79 to 299 individuals in 3 decades. Woody species with the highest mean density in the new foliage layer was *A. campestre* with 141 shoots per hectare; followed those *C. mas* and *A. tataricum* with 17 and 11 ind. ha^{-1} (Table 1). Despite the decreasing oak density new and/or invasive species could not establish themselves in the forest community, because some native species of the understory would respond positively to change of light, thermal and moisture condition.

Table 1. Species composition and density (ind. ha^{-1}) in the subcanopy layer and under the oak canopy on the monitoring plot between 1982 and 2017.

species	**subcanopy layer (8.0-13.0 m)**							
	1982	**1988**	**1993**	**1997**	**2002**	**2007**	**2012**	**2017**
A. campestre	61	84	113	187	204	139	204	139
A. tataricum	9	4	0	13	13	17	17	13
C. mas	9	4	4	26	13	22	17	44
species	**between subcanopy and canopy layer (> 13.0 m)**							
	1982	**1988**	**1993**	**1997**	**2002**	**2007**	**2012**	**2017**
A. campestre	0	4	13	9	13	104	61	91
sum	79	96	131	235	243	282	299	287

Mean height values of subcanopy woody species changed between 8.03 and 11.40 m in the monitoring plot. The lowest and highest parameters both were recorded by A. tataricum on the basis of a few individuals. Mean height of A. campestre - as the most common species in the subcanopy – shows continuous increasing; there are two exceptions: year of 1997 and 2012. It was observed similar decreasing in height and diameter sizes of all woody species in the subcanopy layer in 2012. The size values of A. campestre increased considerably, but mean height and diameter of A. tataricum and C. mas decreased with minor stops in the last decades, especially in the last 10 years (Table 2). Acer species and C. mas responded positively to the serious oak decline. In the study site, oak decline resulted decreasing canopy cover size and led to the notable height growth of the three woody species from the shrub layer; this phenomenon is called the "Oskar"-strategy (Silvertown, 1982). Acer species typically is a genus that displays this characteristic in such circumstances.

Table 2. Long-term tendency of species' sizes (mean ± S.D.) in the subcanopy layer on the monitoring plot between 1982 and 2017.

species	**mean height in the subcanopy layer (m ± S.D)**							
	1982	**1988**	**1993**	**1997**	**2002**	**2007**	**2012**	**2017**
A. campestre	8.97±0.7	9.46±0.9	9.79±1.8	9.63±1.4	9.92±1.5	10.32±1.6	9.59±1.2	10.45±1.6
A. tataricum	8.23±0.3	8.18±0.0	-	8.73±1.2	8.03±0.0*	11.4±0.0*	8.49±0.4	8.48±0.4
C. mas	9.25±0.4	9.34±0.0	9.00±0.0	8.29±0.6	8.40±0.5	8.22±2.1	8.05±0.0	8.39±0.4
species	**mean diameter in the subcanopy layer (cm±S.D)**							
	1982	**1988**	**1993**	**1997**	**2002**	**2007**	**2012**	**2017**
A. campestre	9.37±1.9	10.11±1.3	10.43±2.0	12.64±2.8	14.48±6.0	14.44±4.9	14.37±5.4	12.19±3.3
A. tataricum	6.82±0.8	7.45±0.0	-	8.53±0.6	10.03±3.2	10.75±0.0	9.50±3.0	6.55±0.3
C. mas	6.74±1.3	7.86±0.0	8.90±0.0*	9.03±2.5	9.69±2.0	13.07±4.9	9.64±1.4	8.54±0.9

*On the basis of a single individual.

Mean cover of *A. campestre*, *C. mas* and *A. tataricum* woody species increased rapidly after the beginning of oak decline. Subcanopy foliage cover is most often dominated by *C. mas*, especially from 2002. Cover values increased continually with *C. mas* individuals, but the mean cover of maples fluctuated (lonely *A. tataricum* individuals were not considered) between 11.20 and 18.30 m^2 between 1993 and 2007. Mean cover of *C. mas* displayed high variation over the last one decade. In 2012 extraordinarily large decreasing of mean foliage cover of species was measured in the new layer (Table 3). The most important reason of this foliage loss was the extreme weather condition, because the summer was very hot and extreme dry in 2012 (Sippel and Otto, 2014).

Table 3. Long-term tendency of species' cover (mean±S.D.) in the subcanopy layer and under the oak canopy on the monitoring plot between 1982 and 2017.

species		**mean cover in the subcanopy layer (m^2 ± S.D)**			
		1982	**1988**	**1993**	**1997**
A. campestre	8.0-13.0 m	4.83±2.11	7.75±8.75	11.67±3.43	18.27±6.11
	> 13.0 m	-	-	25.43±5.76	-
A. tataricum		3.43±1.46	4.50±4.00	-	11.23±1.60
C. mas		3.64±1.13	8.50±7.00	10.38±0.00*	18.99±2.23
year		**2002**	**2007**	**2012**	**2017**
A. campestre	8.0-13.0 m	12.00±2.90	14.56±2.81	8.26±6.22	18.10±11.50
	> 13.0 m	30.24±5.32	28.14±6.93		23.33±15.19
A. tataricum		18.19±0.00*	31.74±0.00*	3.47±2.21	9.58±6.37
C. mas		27.03±1.90	34.76±5.99	11.61±5.59	19.52±5.65

*On the basis of a single individual.

We found a non-significant correlation between oak tree density and density condition of the *A. tataricum* and *C. mas* subcanopy species ($P > 0.05$). Low and negative significant relationship was between oak density and field maple and total subcanopy density ($P \leq 0.05$). Mean height and shoot diameter increment of *A. campestre* and mean height of *C. mas* correlated to oak tree density ($P \leq 0.05$). Mean sizes of *A. tataricum* and mean diameter of *C. mas* specimens increased, but non-significantly after tree decline ($P > 0.05$). The regression analysis did show a low significant association between oak canopy density and mean cover of *A. campestre* ($P \leq 0.05$). The statistical analysis recorded that after large-scale oak decline, the mean cover of *A. tataricum* and *C. mas* woody species had increased remarkably but not significantly ($P > 0.05$) (Table 4).

Observations from mature *Quercus*-dominated forests suggest throughout the eastern United States that an important part of these forests are undergoing significant compositional transformation. *Quercus* spp. are being replaced in the understory by species such as *Acer rubrum* L. (red maple) and *Acer saccharum* Marshall (sugar maple); these mesophytic, relatively shade-tolerant species are likely to become canopy dominants if current trends continue in the future (Shotola *et al*., 1992; Galbraith and Martin, 2005; Nowacki and Abrams, 2008). Röhrig and Ulrich (1991) paper described that *A. campestre* is a relatively drought tolerant species. Moreover, according to Banks *et al*. (2019) *A. campestre* shows significant seasonal drought tolerance variation. Oak species cannot successfully compete with these species (McDonald *et al*., 2002; Zaczek *et al*., 2002). At the study site, oak decline remarkably decreased canopy cover and led to the notable height growth of three species - especially *A. campestre* individuals - from the shrub layer; this phenomenon is called the "Oskar"-strategy (Silvertown, 1982). Our results support these statements, because in our study site maples showed a considerably increase in size and cover, and a low regeneration potential of canopy oak species due to detected abiotic and biotic shading effects (Jakucs, 1988; Misik *et al*., 2017).

Table 4. Statistical relationship between the structural condition of the subcanopy and the oak canopy density on the monitoring plot over the period of 1982-2017.

woody species	***r***	***P***	R^2
		density	
A. campestre	-0.77	0.02*	0.60
A. tataricum	-0.37	$0.36^{n.s.}$	0.14
C. mas	-0.46	$0.24^{n.s.}$	0.22
subcanopy	-0.79	0.02*	0.62
		height	
A. campestre	-0.75	0.03*	0.56
A. tataricum	-0.08	$0.86^{n.s.}$	0.59^{-2}
C. mas	0.74	0.03*	0.55
		diameter	
A. campestre	-0.73	0.04*	0.53
A. tataricum	-0.22	$0.60^{n.s.}$	0.05
C. mas	-0.60	$0.11^{n.s.}$	0.36
		cover	
A. campestre	-0.71	0.47^{-1}*	0.51
A. tataricum	-0.36	$0.38^{n.s.}$	0.13
C. mas	-0.62	$0.99^{-1n.s.}$	0.39

CONCLUSIONS

Our results confirm that the decreasing oak trees density led to the size and foliage cover condition changes in the shrub community in the last decades. The response of the shade and relatively drought tolerant woody species, as maples and European cornel in Síkfőkút is strong and rapid once to the oak decline; this phenomenon is so-called "Oskar"-strategy. The conclusions to be derived from the studied site are as follows: (1) the new foliage layer, the subcanopy layer was developed and improved from 1982. It was continually increasing the total density of subcanopy from 1982. (2) Three native woody species, two maples and *C. mas* composed this layer. *A. campestre* was the most common species in this foliage layer. (3) A non-significant association was obtained by the size condition of subcanopy species after the oak decline. Only mean size values of *A. campestre* and C. mas' height increased significantly over the period of 1982-2017. Better understanding understory development and possible interaction between the subcanopy layer and the oak canopy layer 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.

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