This manuscript is contextually identical with the following published paper: Bölöni, J., Ódor, P., Ádám, R., Keeton, W.S., Aszalós, R. 2017. Quantity and dynamics of dead wood in managed and unmanaged dry-mesic oak forests in the Hungarian Carpathian. Forest Ecology and Management 399: 120-131. The original article is published at https://doi.org/10.1016/j.foreco.2017.05.029.

Quantity and dynamics of dead wood in managed and unmanaged dry-mesic oak forests in the Hungarian Carpathians

Bölöni, J. [ab,*], Ódor, P. [ab], Ádám, R. [ac], Keeton, W.S. [d], Aszalós, R. [ab]

[a] MTA Centre for Ecological Research, Institute of Ecology and Botany, H-2163 Vácrátót, Alkotmány u. 2-4., Hungary.

[b] MTA Centre for Ecological Research, GINOP Sustainable Ecosystem Research Group, H-8237 Tihany, Klebelsberg u. 3., Hungary.

[c] Department of Plant Systematics, Ecology and Theoretical Botany, Eötvös Loránd University, H-1117 Budapest, Pázmány Péter sétány 1/A, Hungary.

[d] Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, USA.

E-mail addresses: boloni.janos@okologia.mta.hu (J. Bölöni), odor.peter@okologia.mta.hu (P. Ódor), helleborus42@gmail.com (R. Ádám), William.Keeton@uvm.edu (W.S. Keeton), aszalos.reka@okologia.mta.hu (R. Aszalós)

*Corresponding author, Fax: +36 28 360110, email address: boloni.janos@okologia.mta.hu, MTA Centre for Ecological Research, Institute of Ecology and Botany, H-2163 Vácrátót, Alkotmány u. 2-4., Hungary.

keywords: *Quercus*, standing dead tree, downed tree, forest management, abandoned forests, old-growth forests

Abstract

Dead wood (DW) has great importance for many wildlife species and ecological processes. The volume of DW is considered a useful indicator of the sustainability and maintenance of biodiversity in forests. Though dry-mesic oak forests cover large areas in Hungary, little is known about DW quantities or dynamics in these forests. We investigated DW conditions in five age classes of dry-mesic *Quercus petraea* and *Q. cerris* dominated forests in the Hungarian Carpathians. Stands of the first four age classes (age class 1: 40-59, age class 2: 60-79, age class 3: 80-99, age class 4: 100-119 years old) were managed and stands at least 120 years old were unmanaged at least for 30 years (age class 5). We measured the volume, density, dominance and size distribution of standing DW and volume of downed DW. We also evaluated the decay stages of DW on an ordinal scale (I-V, intact to well-decayed). The effect of age class on the derived variables such as density, dominance, volume or proportion of DW was analysed with general linear mixed models using age class as a fixed and region as a random effect. Mean total DW volume did not reach 15 m^3/ha in age class 1, 2 and 3. A much larger volume of DW was found in age class 4 and 5, where the mean total volume of DW was 36.9 and 45.1 m^3/ha, respectively. Volume and proportion of total DW over 30 cm in diameter were markedly lower in age classes 1, 2 and 3 than in age classes 4 and 5, moreover standing and downed DW over 30 cm in diameter were totally absent in stands under 100 years old. The proportion of well-decomposed (decay stage IV and V) DW was much lower (3-18% of the volume) in all five age classes than in old-growth stands of dry-mesic oak forests. After three decades of non-intervention (age class 5), the volume of DW can approach that of old-growth forests. The 40-99-year old stands contained a similarly low percentage of DW as other managed dry-mesic oak forests in Europe. Based on the results, it is likely that stands greater than 100 years old will support much higher biodiversity of saproxylic organisms compared to younger stands.

1. Introduction

Standing and downed dead wood (DW) is an important component of forest ecosystems (Franklin et al., 1987), performing an array of functions that have been well explored by research over at least three decades (Paletto et al., 2012). DW directly or indirectly provides important habitat for a great variety of forest organisms such as invertebrates, fungi, bryophytes, lichens, birds and mammals (Harmon et al., 1986; Stokland et al., 2012). Fallen DW can provide nurse logs for some types of tree regeneration (Hofgaard, 2000; Takahashi et al., 2000), while decaying DW influences microclimate heterogeneity on the forest floor and can help retain moisture during dry periods (Harmon et al., 1986; Maser and Trappe, 1984). DW also plays an important role in nutrient and carbon storage (Edmonds, 1987; Harmon et al., 1986; Janisch and Harmon, 2002; Keenan et al., 1993) and soil development (Hyvönen and Ågren, 2001; Schaetzl et al., 1989). DW often comprises 10% or more of the aboveground carbon stored in older or primary temperate forests (Keeton et al. 2011).

The density and volume of DW is considered a useful structural indicator of the sustainability and maintenance of biodiversity in forests (Corona et al., 2003; Marchetti, 2004; Paletto et al., 2012), forest naturalness (Bartha et al., 2006; Grabherr et al., 1998) and degree of old-growthness, a term implying that structure can be highly variable in late-successional forests (Bauhus et al. 2009; Lombardi et al., 2010). In Europe, the volume of DW per hectare has become one of nine pan-European indicators for sustainable forest management (criterion 4: maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems) (MCPFE, 2002).

The dynamics of DW accumulation depend on recruitment rates from tree mortality and output rates as controlled by decomposition (Siitonen, 2001). The DW input is mostly influenced by site quality, competition and self-thinning (density dependent mortality) and natural disturbances (density independent mortality; Brassard and Chen, 2008; Castagneri et al., 2010; Lombardi et al., 2008). Decay rates are influenced by species-specific wood properties, size of downed dead trees, and microclimate, particularly forest floor temperature and moisture. These factors influence the activity of decomposing organisms, mainly fungi in terrestrial ecosystems (Hytteborn and Packham, 1987, Kutszegi et al., 2015).

In managed forests, the quantity of DW, particularly in its most important forms for biodiversity (i.e. well decayed, larger sized downed dead trees) are strongly reduced by forest management (Green and Peterken, 1997; Lombardi et al., 2008; Paletto et al., 2014). In many managed European forests, most of the merchantable timber is ultimately harvested, thereby reducing the potential for DW recruitment as compared to unmanaged forests (Gibb et al., 2005; Marage and Lemperiere, 2005; Vandekerkhove et al., 2009). Forest management also influences the size distribution of DW: in managed forests, DW is predominantly composed of fine woody debris (thinner than 10 cm diameter; Kruys et al., 1999; Siitonen et al., 2000).

Though oak forests dominate large areas in Central and Southern Europe, little is known about their DW accumulation or dynamics in these systems. Research has only recently begun to explore DW dynamics in European oak systems (Bobiec, 2002; Petritan et al., 2012; Sweeney et al., 2010) and this topic is poorly investigated in dry-mesic oak forests in particular (Lombardi et al., 2008; Rahman et al. 2008). Under-attention to the topic of DW in unmanaged and old-growth oak forests reflects the general rarity of these systems in Europe, making it difficult to find relatively untouched mixed dry-mesic sessile oak (*Quercus petraea*) dominated forests (Korpel, 1995; Rahman et al., 2008; Saniga et al., 2014). This contrasts with beech and montane beech-fir zones, for which near-natural reference sites are far more abundant in Europe and for which DW inventory data are more widely available (Christensen et al., 2005).

To address this knowledge gap, this study investigates DW in managed and unmanaged dry-mesic sessile oak and Turkey oak (*Q. cerris*) dominated forests affected by human activity of various intensity in North Hungary (i.e. the Hungarian Carpathians). We assessed the quantity and quality – distribution according to DW types (downed versus standing), size categories and decay stages – of DW in five stand age classes. Our results were compared with DW data reported by previous research from old-growth dry-mesic oak forests. The overall goals of this study are:

(1) to investigate how DW quantity and quality change with the age of dry-mesic oak forests stands in Hungary,

(2) to investigate whether and under what circumstances managed stands can sometimes develop DW characteristics similar to old-growth forests,

(3) to formulate recommendations for sustainable forest management and biodiversity conservation approaches, including DW retention practices.

In this study, significantly larger quantity of DW is hypothesized to accumulate in older as compared to younger oak-dominated stands, primarily due to decreasing impact of management activity. Silvicultural management also affects the quality of DW, hence the density of larger diameter and well-decayed DW are expected to be higher in the older age classes. We also hypothesised that in managed stands older than 120 years the volume of DW will reach the level of old-growth stands, but the proportion of well-decomposed, large sized downed dead trees will be lower due to removal of recruitment sources (i.e. harvested large standing trees).

2. Methods

2.1 Study sites

Typical habitat types in the hilly regions of the Carpathian Basin are dry-mesic oak forests dominated by *Quercus petraea*, *Q. pubescens*, *Q. robur* and *Q. cerris*, forming two characteristic Natura 2000 habitat types; 91H0 Pannonian woods with *Quercus pubescens* and 91M0 Pannonian-Balkanic turkey oak-sessile oak forests (European Commission DG Environment, 2013). They cover about 180 000 hectares in Hungary (Bölöni et al., 2008, 2011). Dry-mesic oak forests occupy a forest zone between 200 and 700 m a.s.l. in the Hungarian Carpathians (Fig. 1). The climate of the Hungarian Carpathians is temperate with an average annual precipitation of 600-700 mm and a mean annual temperature of 8.0-9.5 ˚C (Dövényi, 2010; Halász, 2006). The depth of the soil organic layer varies widely within this zone depending on topography. The main soil types are leptosols and cambisols (Krasilnikov et al., 2009), their physical and chemical conditions strongly specific to the bedrock because vulcanic, limestone, sandstone and loess also occur.

The upper tree layer of investigated forests is dominated by *Q. petraea* and *Q. cerris*. The second canopy layer is usually removed or formed by a small number of *Acer campestre, Sorbus torminalis, Fraxinus ornus, F. excelsior*. The shrub layer is naturally dense and consists predominantly of *Crataegus monogyna, Ligustrum vulgare, Cornus mas, Rosa canina* and saplings of associated tree species, or is often artificially removed. The herb layer is typically composed of grasses (e.g. *Poa nemoralis, Dactylis polygama, Melica uniflora*), and a mixture of light-demanding and drought-tolerant forest herbs (e.g. *Campanula persicifolia, Galium schultesii, Tanacetum corymbosum, Vincetoxicum hirundinaria*), forest generalists (e.g. *Veronica chamaedrys, Viola odorata, Fragaria vesca*), and potentially of a few species of the mesic forests (e.g. *Stellaria holostea, Viola rechenbachiana*).

In these dry-mesic oak forests the main silvicultural system historically was coppicing with intensive masting, grazing and firewood collection (Járási, 1997; Johann et al., 2011; Magyar, 1993; Szabó, 2005). Since the 19th century this has been replaced by a uniform shelterwood silvicultural system, converting these forest stands to high forests with a rotation period of 80-100 years (Danszky, 1972; Savill, 2004). The structure of these forests has been relatively uniform: in mature stands, the upper layer is dominated by oaks of circa 20 m in height and 30 cm in diameter at breast height (DBH). These relatively low productivity forests possess 300-350 m^3/ha volume of living wood in their mature state (80-100 years old).

2.2 Data collection

Managed (age class 1 to 4) and unmanaged (age class 5) dry-mesic oak forest stands were selected for the recent study. We selected the unmanaged stands based on the following criteria; (1) dry-mesic *Quercus petraea-Q. cerris* dominated site, (2) older than 120 years old, (3) has highly protected conservation status or form core area of forest reserve and (4) has not been managed for at least 30 years. In the studied regions we found 19 forest subcompartments in 7 forests stands that have met the criteria, and assigned 160 sample plots, 1-35 in each forest subcompartment (Table 1, age class 5). The management unit of forestry in Hungary is subcompartment, which covers an approximately 3-6 ha area with relatively homogenous site conditions. The number of the assigned sample plots depended on the size of the forest subcompartment and on the number of neighbouring stands with similar age and condition. These sampling plots displayed an aggregated pattern, hence there are just a few stands older than 120 years, which were unmanaged at least in the last three decades (Fig. 1).

The investigated managed stands were selected by a stratified random sampling from the Hungarian Forest Stand Database, which contains basic stand compositional, structural and management information for the Hungarian forest stands (ÁESZ, 2008). Only forest subcompartments representing the dry-mesic sessile and Turkey oak forest zone were included for the stratified random sampling using the following inclusion criteria: (1) minimum proportion of sessile and Turkey oak of 95%; (2) maximum proportion of shade tolerant tree species of mesic forests (e.g. *Carpinus betulus, Fagus sylvatica, Tilia spp*.) of 5%; (3) stand age 40-119 years, (4) elevation between 250 and 700 m a.s.l., (5) southern exposure or ridge top. Eighty subcompartments were selected by this process for the study. As a secondary stratification, the subcompartments were classified according to the age of the dominant trees, differentiating the following age classes: age class 1 – 40-59 years old, age class 2 – 60-79 years old, age class 3 – 80-99 years old, age class 4 – 100-119 years old (Table 1). We assigned 1-6 sampling plots in each forest subcompartments depending on the size of the given subcompartment, thereby we selected 178 managed sampling plots altogether. The minimum distance between the centre of sampling plots and minimum distance from roads to avoid edge effect was 50 m.

These forest stands were subjected to forest management with different intensity. The rotation period is generally between 80 and 100 years in these forest stands, some management practice is implemented in every 10 years in average, first tending and improvement cuttings, then cleaning cuttings and thinnings at the end. Living trees are extracted during these processes, but DW is generally also removed. There were significant forest management within 10 years in most of them, while in some forest stands the management was less intensive, even 20 years elapse time between the treatments. Field sampling was carried out from 2009 to 2014. The sampling plots were geographically separated in three regions, but all categories were represented in each region (Fig. 1). The greater number of sampling plots of stands over 120 years old was considered necessary due to the greater heterogeneity of these stands. Altogether we assigned 338 sampling plots in 99 managed and unmanaged forest subcompartments.

The sampling plots of this study were represented by spatial points, and all derived variables were related to these points, because different variables were measured by different methods in the field, including line, relascope and circular plot based methods. All measurements were centred on the same point. In each sampling plot an 8.92 m radius circular plot (250 m^2) was defined for the measurement of living trees and standing entire and broken dead trees between 5 and 25 cm DBH. In the case of larger trees a point relascope method with a factor 2 prism relascope was used to identify trees added to the sample. DW and living trees were measured separately in each sampling plot. For each individual living and dead trees, the species, the DBH and the crown position (dominant, codominant, intermediate, supressed) of all trees were recorded. The height of 1-3 dominant tree individual(s) and height of 1-3 supressed tree(s) were measured by Haglöf Vertex III height and distance meter in each sampling plot. For other individuals it was estimated based on the measurements and crown position.

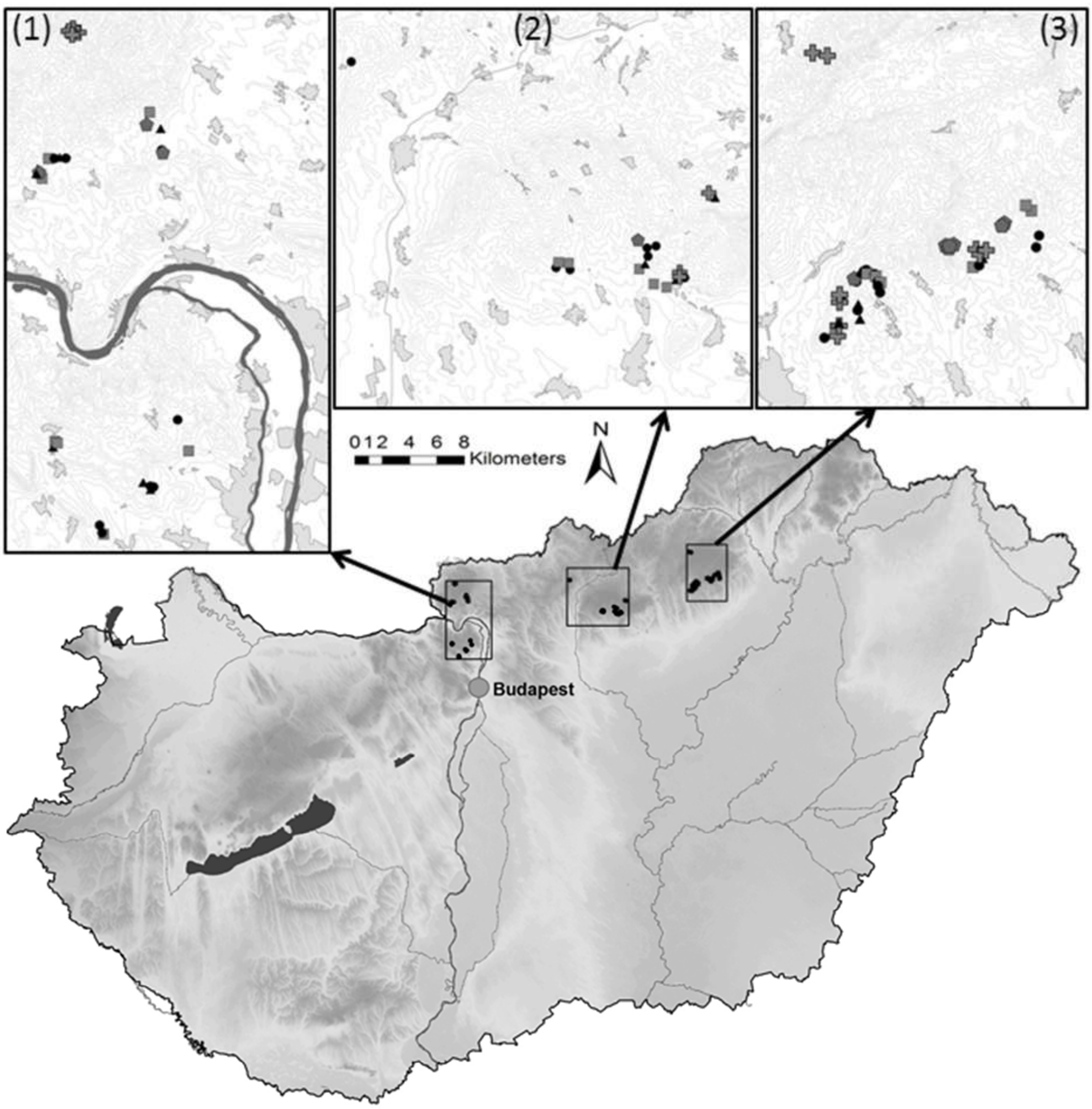
Table 1

Stand characteristics and living wood by age classes. Values are means ± standard deviations.

Age class	1	2	3	4	5
Age in 2010 (year)	40-59	60-79	80-99	100-119	120-165
Number of sampling plots	37	62	52	27	160
Density (stems/ha)	1443 ± 571	725 ± 296	511 ± 273	472 ± 218	515 ± 279
Basal area (m^2/ha)	27.52 ± 3.72	27.46 ± 5.14	27.62 ± 6.28	32.49 ± 6.74	27.85 ± 6.26
Volume (m^3/ha)	246 ± 38	291 ± 65	303 ± 99	400 ± 102	312 ± 85
Stand height (m)	15.6 ± 1.9	18 ± 2.6	18.3 ± 3.3	20.9 ± 3.1	18.8 ± 3.3
DBH (cm)	16.0 ± 3.3	22.7 ± 4.8	26.9 ± 6.1	31.2 ± 6.0	29.7 ± 10.2

Fig. 1

Study sites in three regions of the northern Hungarian Carpathian Mountains (1 – Visegrádi-hegység – Börzsöny; 2 – Mátra; 3 – Bükk). Legend: Black triangle = age class 1, black dots = age class 2, grey squares = age class 3, grey pentagons = age class 4, grey crosses = age class 5.



DW was divided into groups of standing dead wood (SDW), downed dead wood (DDW), stumps and DW on living trees. In this study we concentrated on SDW and DDW, their sum is referred as total dead wood (TDW). SDW had two forms, entire standing dead trees and broken standing dead trees with an absence of crown with a DBH >5 cm. Broken standing dead trees with height of 0.5-2.0 m were also measured, in these cases mid-diameter was recorded instead of DBH. DDW contained downed dead trees or pieces of stem or branches that have fallen with a mid-diameter >5 cm and length >0.5 m. The separation of DDW from SDW was at a 45° angle.

The volume of DDW was estimated by line-intercept sampling method using three transect lines of 16 m in length from the centre of the sampling plot at 0, 120 and 240 degrees (Ståhl et al., 2001; Van Wagner, 1968; Warren and Olsen, 1964). The measurements consisted of the diameter (to the nearest cm) at each intersection point. The data of the three lines per unit were merged. The decay stages of DW were evaluated on an ordinal scale (I-V, Spetich et al., 1999), numbers I-V indicate codes used for decomposition classes where class I is the least decomposed and class V is the most decomposed.

2.3 Data analysis

Inputs for the data analysis consisted of DBH and the height values of each tree. The volume of each living and standing entire dead individual tree (containing majority of branches) was calculated using tree volume functions (Sopp and Kolozs, 2000). Broken standing dead trees were considered as cylinder and volume was approximated using the formula $V=H*D^2*\pi/4$, where V is the volume, H the height of the dead tree and D the mid-diameter of the trunk. Volume per hectare values were calculated based on the total volume of individual trees. The size of sampling plots was 250 m^2 (8.92 m radius) for trees DBH 5-25 cm and according to critical distance of point relascope method for larger trees (DBH >25 cm). For DDW volume estimation Van Wagner's (1968) formula was used: $V=\pi^2*\sum d^2/8L$, where V is the volume per unit area, d the diameter at intersection and L is the length of sample line (in our case L was 48 m).

For the purpose of the analyses, well-decayed DW was a classification assigned to decay classes IV and V. A large tree was defined as a tree with a DBH larger than 30 cm (for downed dead trees intersection diameter was used instead of DBH).

The analysed derived variables and their units are listed in Table 2. The effect of age class on the derived variables was analysed by general linear mixed models (Faraway, 2006) using age class as a fixed and region as a random effect. The dependent variables were "ln" transformed, the normality of the residuals and their variance homogeneity was checked. The significance of the fixed factor was tested by maximum likelihood method, and the random factor by restricted likelihood method using chi-square tests (Faraway, 2006; Zuur et al., 2009). In case of significant fixed (age class) effects the differences between the age classes were analysed by Tukey HSD multiple comparisons (Zar, 1999). The analyses were carried out in R 3.0.2 statistical environment (R Development Core Team, 2013) using the "lattice" (Sarkar, 2008), "multcomp" (Hothorn et al., 2008), and "nlme" (Pinheiro et al., 2015) packages. Nomenclature follows Tutin et al. (1964-1993).

3. Results

The mean total DW (TDW) volume of five age classes forms two significantly separated groups. Stands in age classes 1, 2 and 3 contained mean TDW volume under 15 m^3/ha (Fig 2, Table 2). A much higher volume of DW was found in age class 4 and 5, where the mean total volume of DW reached 36.9 and 45.1 m^3/ha, respectively. The difference between 36.9 and 45.1 m^3/ha appeared rather important, but not significant. DW proportion related to total above ground biomass (living trees volume + DW volume) in age class 1-3 was smaller than 5.5%, stands at least 100 years old had more than 8% (Table 2).

Density of SDW varied between 28 to 39 stem/ha in all age classes with the exception of age class 1, which had a density of 114 stem/ha. Mean basal area of SDW in stands 40-99 years old (age classes 1 to 3) was under 1 m^2/ha and mean volume under 8 m^3/ha. Sampling plots in stands older than 100 years had SDW with a basal area of more than 1.6 m^2/ha and a mean volume of 14-17 m^3/ha (Table 2). The mean diameter of SDW was significantly higher in three age classes over 80 years old (age classes 3 to 5) than in the younger age classes. Based on the mean volume of DDW age classes were divided into two significant groups. The average volume of DDW was less than 9 m^3/ha in age classes 1, 2 and 3, while it was more than 20 m^3/ha in the older stands. The SDW ratio was 37-39%, except in age class 3, where it reached 56%.

The density of SDW over 30 cm in diameter (large dead trees) was significantly higher (12 stem/ha) in age class 5 than in other age classes. The number of standing large dead trees in age classes 1-4 varied between 0 stem/ha in age class 1 and 4 stem/ha in age class 4, but these differences were not significant. Unmanaged stands (age class 5) had significantly higher volume and proportion of large DW than other stands (Table 2).

The diameter distribution of SDW was nearly even in age class 3 and 4, while stands in age class 1 and 2 more than 95% of SDW units were under 20 cm in DBH (Fig. 3a). In age class 5 SDW under 10 cm and above 30 cm in diameter were most frequent.

Table 2

Dead wood characteristics of the age classes and the statistics (Chi^2 and p values) of the general linear mixed models. Values are means ± standard deviations. Different letters indicate significant differences based on multiple comparisons between age classes. TAV=total above ground volume.

Stand type	1	2	3	4	5	Chi^2	p-value
Standing DW density, stem/ha	114^{a} ± 100	35^{b} ± 61	28^{b} ± 56b	39^{b} ± 43	36^{b} ± 40	93.24	<0.0001
Standing DW basal area, m^2/ha	0.85^{ab} ± 0.70	0.61^{a} ± 1.09	0.97^{ab} ± 1.89	1.68^{bc} ± 1.77	2.06^{c} ± 2.30	47.24	0.0001
Standing DW volume, m^3/ha	5.0^{ab} ± 4.5	4.4^{a} ± 8.5	8.0^{ab} ± 16.1	14.3^{bc} ± 18.5	17.3^{c} ± 24.0	39.29	0.0006
Standing DW DBH, cm	10.4^{a} ± 3.5	14.4^{a} ± 5.6	22.2^{ab} ± 9.2	24.0^{b} ± 6.5	30.9^{b} ± 18.5	130.15	<0.0001
Downed DW volume, m^3/ha	8.6^{ab} ± 5.4	7.1^{a} ± 7.6	6.2^{a} ± 8.5	22.5^{b} ± 21.9	27.8^{b} ± 45.1	69.62	<0.0001
Downed DW diameter, cm	7.4^{a} ± 1.2	7.9^{a} ± 2.7	9.3^{a} ± 3.6	13.8^{b} ± 6.5	13.4^{b} ± 5.6	169.76	<0.0001
Total DW volume, m^3/ha	13.6^{a} ± 6.4	11.5^{a} ± 10.1	14.2^{a} ± 19.9	36.9^{b} ± 31.1	45.1^{b} ± 53.1	84.32	<0.0001
Standing DW in total DW volume, %	36.8	38.3	56.3	38.8	38.4		
Total DW in TAV, %	5.3^{ab} ± 2.2	3.9^{a} ± 3.6	4.7^{a} ± 5.7	8.3^{b} ± 6.5	11.8^{b} ± 11.2	40.28	<0.0001
Standing DW over 30 cm in diameter density, stem/ha	0.0^{a} ± 0.0	0.4^{a} ± 2.8	2.0^{a} ± 6.3	4.1^{a} ± 8.8	12.0^{b} ± 16.1	154.50	<.0001
DW volume over 30 cm in diameter	0.0^{a} ± 0.0	0.4^{a} ± 2.8	2.2^{ab} ± 7.6	10.5^{bc} ± 20.2	25.3^{c} ± 43.9	202.22	<0.0001

Fig. 2

Boxplots of the total dead wood volume (m^3/ha) in age classes. Letters indicate significant differences based on multiple comparisons (p<0.05).

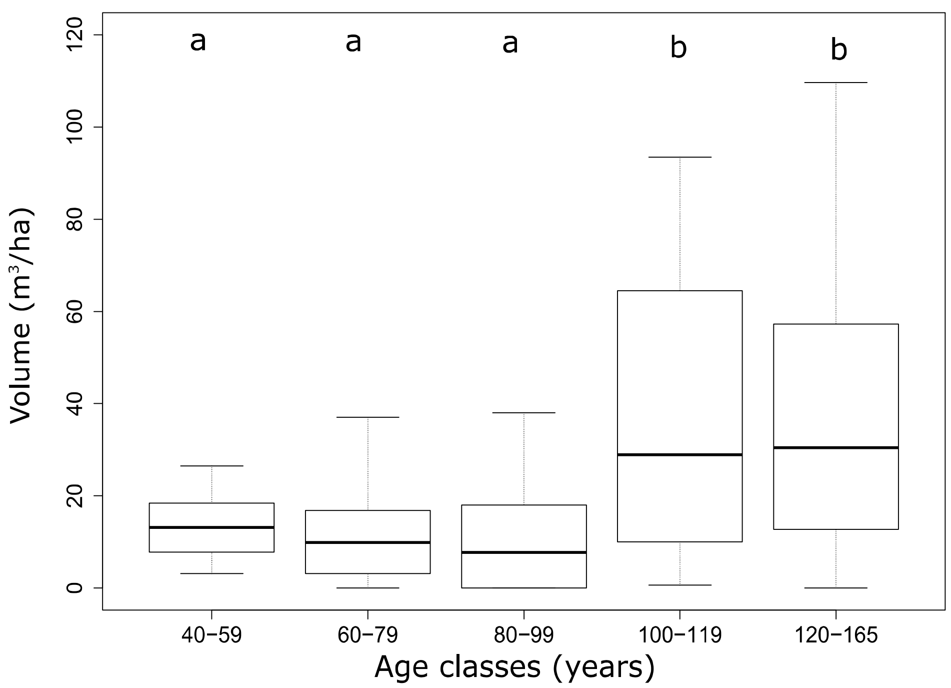
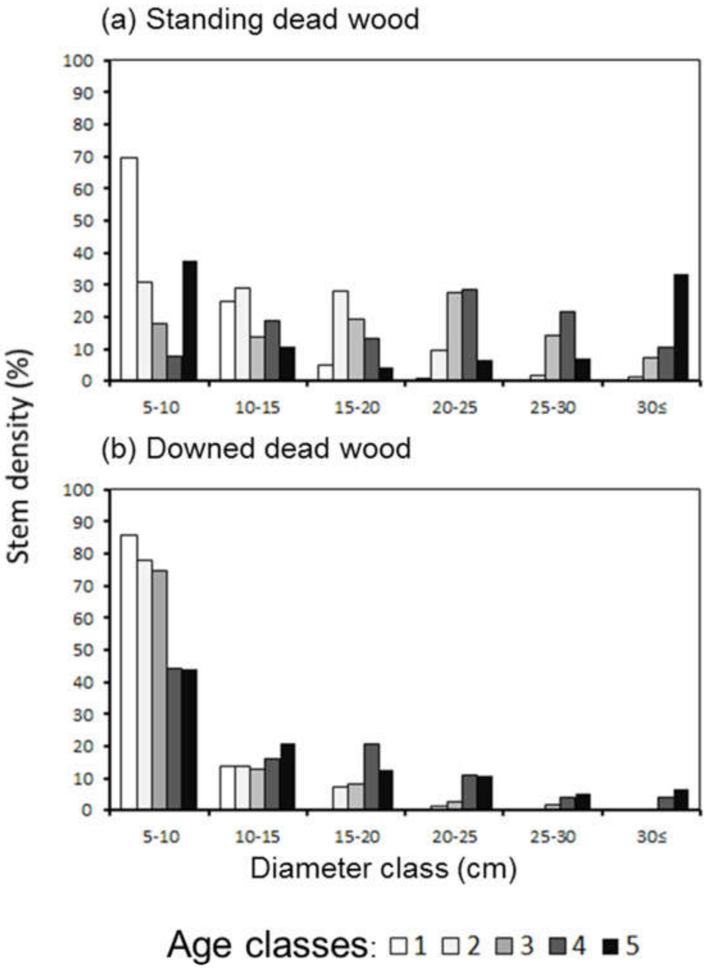


Fig. 3

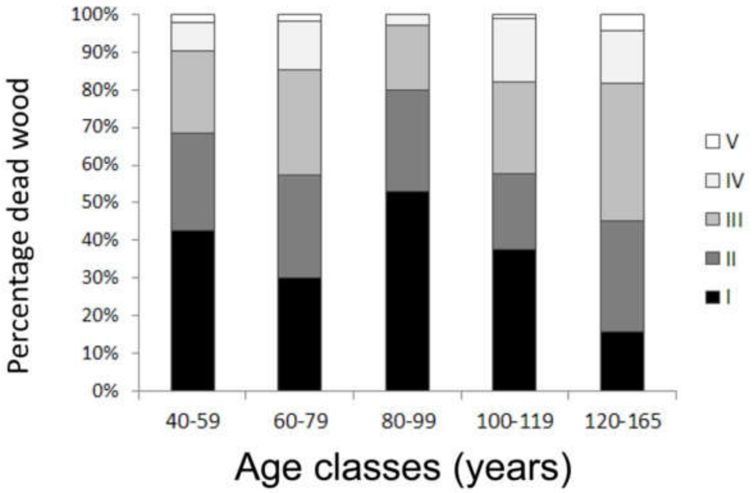
Diameter distribution of standing (a) and downed (b) dead wood density (%) in different age classes.



The diameter distribution of DDW followed a reverse-J shape for all age classes (Fig. 3b). In all five age classes, the majority of downed dead trees were under 20 cm in diameter. In age class 1, the predominance (86 %) of downed dead trees was smaller than 10 cm, while only 44 % was in this size range in age class 4. Stands of age classes 1-3 did not contain downed dead trees over 30 cm in diameter at all, moreover downed dead trees thicker than 25 cm were found only in stands older than 80 years (Fig. 3b). Although small in absolute number, large-diameter standing and downed dead trees had comparatively large volumes per piece and account for the significant difference in observed volume of DW between age classes 4-5 and 1-3. The volume and percentage of more decomposed DW (decay stages IV-V) was very low in all stands (Fig. 4). In age class 4-5 the proportion was higher (more than 18%) than in age classes 1-3 (under 15%).

Fig. 4

Percentage of dead wood in age classes 1-5 in each decay stage (I-V).



4. Discussion

4.1 Volume of total dead wood

The average volume of TDW in 40-99 years old stands (age class 1 to 3) is similar to values reported previously for managed mesic and dry-mesic oak forests in Europe (Table 3), although there is slightly higher volumes of TDW in mesic stands. However, data from dry-mesic oak forests in Italy (Barreca et al., 2008; Lombardi et al., 2008; Paletto et al., 2014) indicate lower volumes (5-9 m^3/ha) than observed in this study. A common characteristic of the managed stands we studied is that the TDW volume comprising less than 5% of the total aboveground living and DW volume. According to these results, and compared to other regularly managed forests, the 11-14 m^3/ha average of the studied dry-mesic managed forests can be considered relatively high. Relative scarcity of downed and standing dead trees is reported in other studies as well (Colak et al., 2009; Kirby et al., 1998), particularly for the larger size classes of standing and fallen dead trees (Sweeney et al., 2010). DW was generally removed from the majority of European forest via intensive forest management activity, sometimes resulting in a complete purge of all coarse downed material (Debeljak, 2006).

On the basis of TDW volume, stand age of 100 years seems to be a threshold: under this age it is below 15 m^3/ha in all age classes, it is relatively high (45m^3/ha) in unmanaged stands older than 120 years, while stands between 100 and 120 years (age class 4) represent a transition, but they are rather similar to unmanaged ones (36 m^3/ha).

Table 3

Volume of dead wood (standing and downed, without stumps) in managed forests. TAV=total above ground volume.

Country	DT	Standing DW, m^3/ha	Downed DW, m^3/ha	Total DW, m^3/ha	Total DW in TAV, %	age, years	Source
Dry-mesic oak forests							
Italy	1a			4.5	1.7		Lombardi et al., 2008
Italy	1b			2.4	1.4		Lombardi et al., 2008
Italy	1b	3.6	5.3	8.9		51-280	Barreca et al., 2008
Italy	1c	2.7	3.4	6.1		30-45 / 100	Paletto et al., 2014
Hungary	1d	5.8	7.2	12.9	4.6	40-99	this study
Mesic mixed oak forests							
Hungary	2a	12.2	10.1	22.3		70-100	Márialigeti et al., 2016
England	2b		11.9-23.1				Kirby et al., 1991
Poland	2b		2.0-9.5			50-70	Kirby et al., 1991
Poland	2b	0-5	0-1	1-6	1.4		Bobiec, 2002
France	2b	10.3	1.6	11.9		20-25	Lassauce et al., 2012
Ireland	2c		20.7-27.1				Sweeney et al., 2010

DT=Dominant tree species:

1a – *Quercus cerris*; 1b – *Q. frainetto*; 1c – *Q. cerris*, *Q. pubescens*, *Q. ilex*; 1d – *Q. petraea, Q. cerris*

2a – *Q. petraea, Q. robur, Fagus sylvatica, Pinus sylvestris*, 2b – *Q. robur, Carpinus betulus, Tilia cordata*; 2c – *Quercus spp., Fraxinus excelsior*.

Differences in the volume of DW in stands under and over 100 years can be explained by the distinct forest management regime of the two groups. The majority (71%) of the 40-99-year-old stands are intensively managed according to forest management plans following rotation forestry systems. The rotation period of *Q. petraea* and *Q. cerris* dominated forests is 80-100 years in Hungarian forestry practice, thus the number of extant 100-119 year old managed stands are relatively low. Less intensive forest management is more typical in these older stands; about 67% of them have some form of less intensive management. Extended entry cycles for selection harvests (e.g. 20 years) and less intensive thinning operations lead to greater accumulations of DW across all size classes.

Studied stands older than 120 years (age class 5) are left unmanaged for at least 30 years, thus it was expected to contain significant volume of TDW. DW accumulation in the studied unmanaged stands approximates, but does not reach the DW volume of old-growth dry-mesic oak forests. The volume of TDW found in age class 5 (45 m^3/ha) is in the lower half of the range of similar old-growth or abandoned dry-mesic oak forests, which are dominated by canopy trees over 110-150 years, and some cases exceeded 200-300 years (Carvalho, 2011; Goebel and Hix, 1996; Hale et al., 1999; Hart et al., 2012; Shifley et al., 1997) (Table 4). Among the old-growth dry-mesic oak forests the

Boky Forest Reserve in Slovakia has the most similar tree species composition and site characteristics to the studied forests of the Hungarian Carpathians. In Boky since the 1970s, a monitoring program has measured the quantity of DW. Reported total volume of DW for the Boky Reserve is 43 m^3/ha on average, having continuously increased over the monitoring timeframe from 17 m^3/ha initially and reaching 65 m^3/ha in the 2000s (Saniga and Schütz, 2002; Saniga et al., 2014). In Italy 32 m^3/ha TDW volume was reported from Turkey oak dominated stands after 50 years of non-intervention (Lombardi et al., 2008), and 83 m^3/ha in sessile oak-Turkey oak dominated Austrian stands abandoned 80 years ago (Rahman et al., 2008). In Portugal, various mesic and dry-mesic mixed oak stands have 6.9 m^3/ha (early stage) and 65.4 m^3/ha (late stage) TDW on average (Carvalho, 2011). Similar values (34-79 m^3/ha) were measured in North-American old-growth dry-mesic oak forests (Goebel and Hix, 1996; Muller and Liu, 1991; Shifley et al., 1997). Abandoned and old-growth mesic oak forest stands have 2-5 times more DW – usually exceeding 100 m^3/ha – than dry-mesic oak forests with a similar history and structure (Table 4; Bobiec, 2002; Meyer et al., 2006; Petritan et al., 2012; Rahman et al., 2008), as the volume of DW increases in direct proportion to site productivity (Harmon et al., 1986; Nilsson et al., 2002; Spetich et al., 1999).

The ratio of TDW compared to total aboveground biomass varies between 3.9 and 5.3% in the younger age classes (1, 2, 3) investigated in our study, which is quite low compared to unmanaged stands. In European unmanaged dry-mesic oak forests, the ratio of TDW compared to total aboveground biomass varies between 7 and 19% (Lombardi et al., 2008; Saniga and Schütz, 2002; Saniga et al., 2014), but exceptionally can exceed these ratios (25%, Rahman et al. 2008). The average ratio of TDW compared to total aboveground biomass is 11.8% in age class 5, similar DW ratio was found in previously managed European mesic oak forests abandoned at least 30 years ago (6-30%, average 13%; Vandekerkhove et al, 2009). Nevertheless, the ratio of TDW compared to total aboveground biomass is typically higher than 20% in the majority of the observed mesic old-growth oak forests in Europe (Bobiec, 2002; Meyer et al., 2006; Petritan et al., 2012; Rahman et al., 2008). It seems that mesic oak forests have not only higher productivity, but also contain higher volume and proportion of DW than dry-mesic oak forests (Burrascano et al., 2013).

Table 4

Dead wood in old-growth (OG) and abandoned (AB) dry-mesic and mesic oak forests. TAV=total above ground volume. Old-growth and abandoned stands are dominated by trees at least 110-150 years old.

Country	DT	Min. DBH/ D	Standing DW basal area, m^2/ha	Standing DW volume, m^3/ha	Downed DW volume, m^3/ha	Total DW volume, m^3/ha	Standing dead wood in total DW volume, %	Total DW in TAV, %	age, years	Source
Dry-mesic oak forests										
Slovakia, EU, OG	1a					17-65		6-19		a
Austria, EU, AB	1a	5		31.6	51.5	83.1	38	25		b
Italy, EU, AB	1b	5				32		7		c
Portugal, EU, OG	1c	5				6.9-65.4				d
Hungary, EU, AB	1a	5	2.06	17.3	27.8	45.1	38	12	120-165	this study
Ohio, USA, OG	1d	10	2	19	30	48	38			e
Missouri, USA, OG	1e	10	1.5-2.4	8-14	24-49	34-58	15-29			f
Tenessee, USA, OG	1f	5	2.44							g
Maryland, USA, OG	1g	7.5			54					h
Kentucky, USA, OG	1h	20				79				i
Mesic oak forests										
Romania, EU, OG	2a	5		38	97	134	28	19		j
Poland, EU, OG	2b	4		13	119	132	9	23		k
Poland, EU, OG	2b	10	3.7	16						l
Poland, EU, OG	2b	10	4.2	27						l
Germany, EU, AB	2c			46	163	209	32	30		m
Austria, EU, AB	2d			22.8	95.4	118.2	19	29		b
Minnesota, USA, OG	2e	10		27	48	75	36			n
Georgia, USA, OG	2f	20			66					o
Ohio, USA, OG	2g				131					p
Ohio, USA, OG	2g				204					p
Indiana, USA, OG	2h	5	3.03		49					q
Illinois, USA, OG	2i	10	2.4		81					r
Missouri, USA, OG	2j	2	2.15		39					s
Illinois, USA, OG	2k	6.6	4.2							t

DT=Dominant tree species:

1a – *Quercus petraea, Q. cerris*; 1b – *Q. cerris*; 1c – *Q. robur, Q. pyrenaica*, *Q. suber, Fraxinus angustifolia*; 1d – *Q. alba, Q. prinus, Q. velutina, Acer rubrum*; 1e – *Q. alba, Q. velutina, Q. rubra, Carya* spp.; 1f – *Q. alba, Q. coccinea, Q. velutina, A. rubrum, Pinus echinata*; 1g – *Q. prinus, Q. rubra, Betula lenta, A. rubrum*; 1h – *Q. prinus, Q. velutina, A. saccharum.*

2a – *Q. petraea, Fagus sylvatica*; 2b – *Q. robur, Carpinus betulus, Tilia cordata*; 2c – *Q. robur, Q. pertaea, C. betulus*; 2d – *Q. petraea, C. betulus*; 2e – *Q. rubra*; 2f – *Q. alba, P. strobus*; 2g – *Q. alba, Q. rubra, F. grandifolia*; 2h – *Q. alba, Q. velutina, Q. rubra, F. grandifolia, A. saccharum*; 2i – *Q. alba, A. saccharum, T. Americana*; 2j – *A. saccharum, Q. rubra, Q. muehlenbergii*; 2k – *A. saccharum, Q. velutina, Q. rubra, Q. alba*;

Source:

a – Saniga et al., 2014; b – Rahman et al., 2008; c – Lombardi et al., 2008; d – Carvalho, 2011; e – Goebel and Hix, 1996; f – Shifley et al., 1997; g – Hart et al., 2012; h – Dodds and Smallidge, 1999; i – Muller and Liu, 1991; j – Petritan et al., 2012; k – Bobiec, 2002; l – Nilsson et al., 2002; m – Meyer et al., 2006; n – Hale et al., 1999; o – Hardt and Swank, 1997; p – McCarthy et al., 2001; q - Schmelz et al., 1974; MacMillan, 1981; r - Roovers and Shifley, 1997; s - Richards et al., 1995; t - Shotola et al., 1992.

Bormann and Likens (1994) suggested that DW volume decreases after the cessation of forest management, but returns to pre-logging levels after about 50 years. According to other estimates, this process may take 60 to 100 years (Peterken, 1996; Vandekerkhove et al., 2009). Beside many factors, the age of the dominant trees is one of the most determining variables in TDW recruitment dynamics. The volume of TDW in mature stands, where the age of the dominant trees can reach their natural lifetime is comparable to that of virgin forests (Vandekerkhove et al., 2005; von Oheimb et al., 2005, 2007). This statement is in line with the observations made in the present unmanaged stands studied, where the canopy layer is dominated by older individuals, the spontaneous decay of trees is typical, active forest management has been discontinued several decades (30-40 years) ago, and TDW volume approaches the expected levels of the old-growth stands of this forest type. Slow decomposition rate of *Quercus* species (Kahl et al., 2017; Schowalter et al., 1998) can also contribute to relatively high volume of DW in unmanaged dry-mesic oak forests of Central Europe.

4.2 Standing dead wood

Unfortunately, the number of standing dead trees given in stem/ha is often not comparable between studies due to the dissimilar threshold of minimum diameter and different diameter distributions. In old-growth dry-mesic oak forests in the USA, the density of SDW ranges between 30 and 130 stem/ha (Dodds and Smallidge, 1999; Hart et al., 2012; Goebel and Hix, 1996; McComb and Muller, 1983; Shifley et al., 1997; Spetich et al., 1999), although values above 100 stems/ha are rare. The number of standing DW surpasses 100 stem/ha only in the stands younger than 60 years, however, in these stands the number of living stems is also much higher than in the other age classes (Table 1). Proportion of standing DW compared to the living trees is between 5-8% in all age classes including the stands older than 120 years. This ratio ranges between 9 and 12% in the dry-mesic old-growth oak forests of the USA (Hart et al., 2012; Goebel and Hix, 1996; McComb and Muller, 1983; Shifley et al., 1997; Spetich et al., 1999), rarely reaching even 25% (Dodds and Smallidge, 1999). As an evident result of previous management activities, the ratio of standing DW does not reach the values typical in the old-growth forests nor in managed, neither in the unmanaged stands of the recent study.

In dry-mesic old-growth forests, the average basal area of SDW is around 2 m^2/ha in stands (1.50-2.44 m^2/ha; Goebel and Hix, 1996; Hart et al., 2012; Shifley et al., 1997). The latter was found in cases of unmanaged stands (2.06 m^2/ha) in this study. A DW volume of 17.3 m^3/ha was found in the studied dry-mesic unmanaged stands. The only available data for SDW originated from a European dry-mesic oak stand, abandoned long time ago, is higher than our value (32 m^3/ha, Rahman et al. 2008), but similar (19 m^3/ha, Goebel and Hix, 1996), and a bit lower values (10 m^3/ha, Shifley et al., 1997) are reported from two North-American forest sites.

4.3 Downed dead wood

The only relevant European data from dry-mesic abandoned oak forests is from the Lange-Leitn Natural Forest Reserve, Austria, with a DDW volume of 52 m^3/ha (Rahman et al., 2008), which is much higher than the average values measured in this study (27.8 m^3/ha for class 5). Old-growth dry-mesic oak forests in the USA produce usually more than 24 m^3/ha logs (24-54 m^3/ha, Dodds and Smallidge, 1999; Goebel and Hix, 1996; Shifley et al., 1997). Mesic oak old-growth forests contain evidently higher volume of both standing and downed DW, e.g. the volume of DDW generally approaches (Petritan et al., 2012; Rahman et al., 2008) or even exceeds 100 m^3/ha (Bobiec, 2002; Meyer et al., 2006) in the old-growth mesic oak dominated forests of Europe (Table 4).

DDW typically has a higher volume than SDW in temperate deciduous forests (e.g. Bobiec, 2002; Christensen et al. 2005; Hale et al., 1999; Korpel, 1995, 1997; Meyer et al., 2003; Nilsson et al., 2002). The ratio of SDW and TDW volumes is between 9-38% both in dry-mesic and mesic old-growth oak forests in Europe and North America (Bobiec, 2002; Goebel and Hix, 1996; Hale et al., 1999; Meyer et al., 2006; Rahman et al., 2008; Petritan et al., 2012; Shifley et al., 1997). We found 38% of DDW in studied unmanaged oak forests as a result of higher proportion of SDW volume, which can be attributed to former forest management activity. The perished tree individuals are relatively fresh, many of them still standing, gradually adding to the volume and ratio of downed trees when they fall.

The dynamics of the managed stands are evidently determined by forest management activities until their age of 100 years. The natural DW dynamics is more pronounced in the stands older than 100 years, as a result of the less intensive management activity. The elapsed time since the last forest intervention (10-40 years) is generally not enough for the accumulation of DW in similar volume than in the old-growth forests, and proportion of DDW is generally lower. These results are in line with the findings of investigations from Central- and Western-Europe, where data were purchased form previously managed mesic oak forests, and the time of non-intervention was at least 30 years. The average ratio of standing DW was still higher than 40% (44%, 10-70%, Vandekerkhove et al., 2009).

4.4 The density of large dead wood

Density of standing dead trees with a DBH >30 cm varies between 0 and 4 stems/ha in age classes 1 to 4, which is evidently a very low value. The time from forest recruitment until the cutting age (80-100 years) is not enough to the tree individuals to grow larger trunks in these low productivity sites. The retention of veteran trees were not typical during earlier cuttings either, however these trees could form the present source of large standing or downed DW. The proportion of large DW in total DW volume is very low in managed dry-mesic oak forests in the Hungarian Carpathians, due to the general forest management regime, like in other managed oak forests in Europe (e.g. Kirby et al., 1991; Paletto et al., 2014; Sweeney et al., 2010).

On the other hand, 12 stems/ha standing dead trees with DBH larger than 30 cm on average were found in the unmanaged stands (age class 5) of the study. This value approaches or even reaches the number of large DW of old-growth forests. The density of standing dead tree individuals with a DBH >30 cm usually ranges between 11 and 24 stems/ha, and for trees with a DBH >50 cm around 8 stems/ha in old-growth temperate mesic deciduous and mixed coniferous stands in Europe and in the USA (Hura and Crow, 2004; Nilsson et al., 2002; von Oheimb et al., 2007). Fewer large standing dead trees (<10 stems/ha) were found in the investigated dry-mesic oak forests in the size category of DBH >30 cm then in the dry-mesic oak forests of the USA (Dodds and Smallidge, 1999; Hart et al., 2012). The difference between our dry-mesic oak dominated sites and the North American ones can be explained by the fact that Hungarian sites have been managed since the medieval ages, reaching 90-100 years of age with relatively high density and homogeneous size distribution. DW comes from the relatively numerous and thick living tree individuals during the period that has elapsed since abandonment, thus many of them have DBH >30 cm. On the other hand, the density of standing DW with DBH >50 cm is lower in our study than in dry-mesic old-growth oak forests, which indicates shortage of mature and really large tree individuals.

4.5 Decay stages

According to the data from dry-mesic old-growth oak forests, downed dead trees are predominantly in decayed phases (decay stages IV and V). Their ratio is typically higher than 50% (66%, Dodds and Smallidge, 1999; 57%, Hart et al., 2012), sometimes 35% (Shifley et al., 1997). Mesic stands are characterised by similar values (63%, MacMillan, 1981; 73%, McCarthy et al., 2001; 26%, Richards et al., 1995). These values range between 3 and 18% in our study, indicating a much lower volume of downed DW with advanced decay stages. Decay stage is usually estimated in DW studies, although different classifications are used. Furthermore, since the speed of decay depends on several background factors, the comparison of data is not straightforward.

This phenomenon can be explained by two obvious facts. The first one is that the stands had been managed in the past, resulting in an absence of old and consequently intensely decayed DDW. These forests have been unmanaged for the past 40 years, but signs of past removal of DW were still evident, which explain the low proportion of advanced decay classes in DW. The second reason is the slow decomposition of *Q. petraea* (in line with other oak species) under dry site conditions (Schowalter et al., 1998). Accordingly, the decay of sessile oak is markedly slow in these relatively dry and cool sites, even those sessile oak individuals are only in decay stage III, which have been laying on the forest floor for a several decades.

4.6 The limitations of this study

The comparison of the DW in forest stands published in different papers is not straightforward as forest stand surveys use different minimal DBHs (or diameter for DDW),which is in most cases ranging from 5 to 10 cm (Hardt and Swank, 1997; Muller and Liu, 1991; Richards et al., 1995). In our study DW between 5-10 cm accounts for 5-6% (2.3 m^3/ha) of DW volume in age class 4 and 5. In many cases, TDW volume is not even published, as only standing or only DDW is measured. Furthermore, in many cases the units of measurement used are also different (e.g. m^2/ha for SDW and m^3/ha for DDW). The lack of standard measurement necessitates a cross-checking of the amount of SDW and DDW separately, beside the comparison of the total volume. Furthermore, in the case of SDW, a comparison of density, basal area and volume data is also required. The lack of data also makes it necessary to compare the results not only with dry-mesic oak stands but also with higher productivity oak dominated stands on mesic sites, and, eventually, with other deciduous forests.

4.7 Management recommendations

The industrial, timber-oriented silvicultural systems of the last centuries have resulted in very low density and volume of DW in dry-mesic oak forests in Central Europe based on our results. Therefore, we recommend that management for biodiversity should maintain higher density and volume of DW in these forests. This, recommendation applies generally at the European scale (Sweeney et al., 2010; Vandekerkhove et al. 2009), but particularly in Hungary where the low level of DW in managed forests is outstanding (Bölöni, 2015; Márialigeti et al., 2016). In dry-mesic oak forests the maintenance of higher levels of DW is an essential conservation target. As old-growth dry mesic forests contain approximately 50 m^3 DW per hectare on average, we recommend to leave at least the half of that, 25-30 m^3/ha, in case of these habitat types for the benefit of biodiversity. This recommendation is consistent with previous studies (Bauhus et al., 2009; Bütler and Schlaepfer, 2004; Hodge and Peterken, 1998), including those finding a strong correlation between intermediate levels of DW and positive biodiversity responses (see, for example, Dove and Keeton, 2015; McKenny et al., 2006). This volume could be achieved by leaving DW after thinning and harvesting in the forest, by active felling (leaving downed dead trees) and girdling (to create SDW) of selected trees in protected areas. Managers could also leave naturally generated DW, for example where disturbances such as low to moderate severity wind throw are recruiting downed wood (Sweeney et al., 2010, Burrascano et al., 2013).

Size of standing and downed dead trees are considerably low not only in the actively managed stands, but also in the older stands, except the unmanaged sites (age class 5), which possess similar density of large DW as old-growth forests. Several specific saproxylic organisms depend on the large dead units. The very low frequency of large standing and downed dead trees could be enhanced by active conservation management by the felling and girdling of large-diameter trees, or in case of absence of large trees, by importing large downed dead trees (Sweeney et al., 2010, Burrascano et al., 2013). Retention of approximately 10-15 m^3/ha DW over 30 cm in diameter is recommended in protected dry-mesic oak forest sites, with 5-10 stem/ha standing dead tree density as a minimum target, to achieve biodiversity conservation targets, as suggested also in previous studies (Bauhus et al., 2009; Bütler and Schlaepfer, 2004; Hodge and Peterken, 1998). Although the volume of DW can reach the value typical in old-growth forests within a few decades, decomposition needs more time. Beside large DW, the well-decomposed fine woody debris are also needed for biodiversity conservation.

5. Conclusions

In managed stands 40-99 years old, we found very low quantities of DDW (under 15 m^3/ha) regardless of stand age, a finding similar to that reported for managed dry-mesic oak forests elsewhere in Europe (Barreca et al., 2008; Lombardi et al., 2008; Paletto et al., 2014). One hundred years of stand development can be considered a threshold for large wood recruitment in these systems. Above this age both less intensively managed and the unmanaged stands are capable of recruiting relatively high volume of DW (36.9 and 45.1 m^3/ha respectively), in some cases approaching the volume found in old-growth dry-mesic oak forests. From this point of view forest stands above 100 years show old-growth features in case of dry-mesic oak habitat type. Our results support a conclusion that after cessation of management, a relatively short period – approximately 20-30 years – is enough to produce DW volumes and biomass similar to old-growth forests, provided that the stand was at least 80 year-old at the time of the abandonment. DW appears to be is one of the first structural features to regenerate after cessation of intensive forest management based on our results and previous research (Carvalho, 2011; Lombardi et al., 2008; Rahman et al., 2008; Saniga et al., 2014).

Size of standing and downed dead trees are considerably low in the actively managed stands, large-diameter downed dead trees (DBH>30cm) are totally absent from the stands younger than 100 years. Large-diameter standing and downed dead trees only in the unmanaged sites (age class 5) possess similar density and volume of large DW as old-growth forests. Furthermore, the low rate of decayed DW indicates the influence of former intensive forest management. The volume of well-decayed DW is considerably low even in the stands abandoned at least 30 years ago. Three decades of non-intervention were not enough time interval for the development of high volume of well-decayed DW.

Acknowledgement

Our research is supported by the Hungarian Research Fund (OTKA K 105896) and the National Research, Development and Innovation Office (GINOP-2.3.2-15-2016-00019) project. The authors thank the long-term support of the Hungarian Forest Reserve Programme (Ministry of Agriculture). Many thanks to Borbála Balázs, Ferenc Horváth, Péter Jeszenszky, Katalin Mázsa, Tamás Pásti, Tamás Sigmond for their great assistance in the fieldwork. We are grateful for the two anonymous reviewers for their helpful comments and suggestions that substantially improved the manuscript.

References

ÁESZ, 2008. Magyarország erdőállományai, 2006. (Forest stands of Hungary, 2006). Hungarian Forest Service, Budapest., http://www.nebih.gov.hu/erdeszet_cd/index.htm

Barreca, L., Cutini, A., Mercurio, R., 2008. Caratterizzazione della necromassa in boschi di farnetto (*Quercus frainetto* Ten.) della Calabria. Forest@ 5, 187–194.

Bartha, D., Ódor, P., Horváth, T., Tímár, G., Kenderes, K., Standovár, T., Bölöni, J., Szmorad, F., Bodonczi, L., Aszalós, R., 2006: Relationship of tree stand heterogeneity and forest naturalness. Acta Silvatica et Lignaria Hungarica 2, 7–22.

Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. Forest Ecol. Manage. 258, 525–537.

Bobiec, A., 2002. Living stands and dead wood in the Bialowieza Forest: suggestions for restoration management. Forest. Ecol. Manage. 165, 121–136.

Bölöni, J., (Ed.), 2015. Tanulmányok a félszáraz tölgyesek ökológiai viszonyairól [Studies on ecology of dry-mesic oak forests]. MTA Ökológiai Kutatóközpont Tanulmányai 1, MTA Ökológiai Kutatóközpont, Tihany.

Bölöni, J., Molnár, Zs., Biró, M., Horváth, F., 2008. Distribution of the (semi-)natural habitats in Hungary II. Woodlands and shrublands. Acta Bot. Hung. 50 (suppl.), 107–148.

Bölöni, J., Molnár, Zs., Kun, A. (Eds.), 2011. Magyarország élőhelyei. (Habitat types of Hungary). MTA ÖBKI, Vácrátót.

Bormann, F.H., Likens, G.E., 1994. Pattern and process in a forested ecosystems. New York, Springer-Verlag.

Brassard, B.W., Chen, H.Y.H., 2008. Effects of forest type and disturbance on diversity of coarse woody debris in boreal forest. Ecosystems 11, 1078–1090.

Burrascano, S., Keeton, W.S., Sabatini, F.M., Blasi, C., 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: a global review. Forest Ecology and Management, 291, 458-479.

Bütler, R., Schlaepfer, R., 2004. Wie viel Totholz braucht der Wald? Schweiz. Z. Forstwes. 155, 31–37.

Carvalho, J.P.F., 2011. Composition and structure of natural mixed-oak stands in northern and central Portugal. For. Ecol. Manage. 262, 1928–1937.

Castagneri, D., Garbarino, M., Berretti, R., Motta, R., 2010. Site and stand effects on coarse woody debris in montane mixed forests of Eastern Italian Alps. For. Ecol. Manage. 260, 1592–1598.

Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., Vrska, T., 2005. Dead wood in European beech (Fagus sylvatica) forest reserves. For. Ecol. Manage. 210, 267–282.

Colak, A.H., Tokcan, M., Rotherham, I.D., Atici, E., 2009. The amount of coarse dead wood and associated decayrates in forest reserves and managed forests, northwest Turkey. Investigación Agraria: Sistmas y Recursos Forestales 18, 350–359.

Corona, P., Köhl, M., Marchetti, M., 2003. Advances in forest inventory for sustain-able forest management and biodiversity monitoring. Forestry Sciences series 76. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Danszky, I., 1972. Erdőművelés. Irányelvek, eljárások, technológiák I. Erdőfelújítás, erdőtelepítés, fásítás. (Forest cultivation. Guidelines, methods, techniques I. Forest regeneration, artificial planting, reforestation.), first ed. Mezőgazdasági Könyvkiadó Vállalat, Budapest.

Debeljak, M., 2006. Coarse woody debris in virgin and managed forest. Ecol. Ind. 6, 733–742.

Dodds, K.J., Smallidge, P.J., 1999. Composition, vegetation, and structural characteristics of a presettlement forest in Western Maryland. Castanea 64, 337–345.

Dove, N.C, Keeton, W.S., 2015. Structural complexity enhancement increases fungal species richness in northern hardwood forests. Fungal Ecol. 13, 181–192.

Dövényi, Z. (Ed.), 2010. Magyarország kistájainak katasztere. (Inventory of Microregions in Hungary). MTA Földrajztudományi Kutatóintézet, Budapest.

Edmonds, R.L., 1987. Decomposition rates and nutrient dynamics in small-diameter woody litter in four forest ecosystems in Washington, U.S.A. Can. J. For. Res. 17, 499–509.

European Commission DG Environment, 2013. Interpretation Manual of European Union Habitats - EUR28.

Faraway, J.J., 2006. Extending the linear model with R. Chapman and Hall, London.

Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. BioScience 37, 550–556.

Gibb, H., Ball, J.P., Johansson, T., Atlegrim, O., Hjalten, J., Danell, K., 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. Scand. J. For. Res. 20, 213–222.

Goebel, P.C., Hix, D.M., 1996. Development of mixed-oak forests in southeastern Ohio: a comparison of second-growth and old-growth forests. For. Ecol. Manage. 84, 1–21.

Grabherr, G., Koch, G., Kirchmeir, H., Reiter, K., 1998. Hemerobie österreichischer Waldökosysteme. Veröffentlichungen des Österreichischen MaB-Programmes, Band 17, Universitätsverlag Wagner, Innsbruck.

Green, P., Peterken, G.F., 1997. Variation in the amount of dead wood in woodlands of the Lower Wye Valley, UK, in relation to the intensity of management. For. Ecol. Manage. 98, 229–238.

Halász, G. (Ed.), 2006. Magyarország erdészeti tájai. (Forest regions of Hungary). Állami Erdészeti Szolgálat, Budapest.

Hale, C.M., Pastor, J., Rusterholz, K.A., 1999. Comparison of structural and compsitional characteristics in old-growth and mature, managed forests of Minnesota. Can. J. For. Res. 29, 1479–1489.

Hardt, R.A., Swank, W.T., 1997. A comparison of structural and compositional characteristics of Southern Appalachian young second-growth, maturing second-growth, and old-growth stands. Nat. Areas J. 17, 42–52.

Harmon M.E., Franklin J.F., Swanson F.J., Sollins P., Gregory S.V., Lattin J.D., Anderson N.H., Cline S.P., Aumen N.G., Sedell J.R., Lienkaemper G.W., Cromack Jr. K. and Cummins K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302.

Hart, J.L., Clark, S.L., Torreano, S.J., Buchanan, M.L., 2012. Composition, structure, and dendroecology of an old-growth Quercus forest on the tablelands of the Cumberland Plateau, USA. For. Ecol. Manage. 266, 11–24.

Hodge, S.J., Peterken, G.F., 1998. Deadwood in British forests: priorities and a strategy. Forestry 71, 99–112.

Hofgaard, A., 2000. Structure and regeneration pattern in a virgin Picea abies forest in northern Sweden. J. Veg. Sci. 4, 601–608.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous Inference in General Parametric Models. Biometrical J. 50, 346–363.

Hura, C.E., Crow, T.R., 2004. Woody debris as a component of ecological diversity in thinned and unthinned northern hardwood forests. Nat. Areas J. 24, 57–64.

Hytteborn, H., Packham, J.R., 1987. Decay rate of Picea abies logs and the storm gap theory: a reexamination of Sernander plot III, Fiby urskog, Central Sweden. Arboric. J. 11, 299–311.

Hyvönen, R., Ågren, G.I., 2001. Decomposer invasion rate, decomposer growth rate, and substrate chemical quality: how they influence soil organic matter turnover. Can. J. For. Res. 31, 1594–1601.

Janisch, J.E., Harmon, M.E., 2002. Successional changes in live and DW carbon stores: implications for net ecosystem productivity. Tree Physiol. 22, 77–89.

Járási, L. 1997. Erdőgazdálkodás Bánkúttól Nagymilicig. (Forest management from Bánkút to Nagymilic). Észak-Magyarországi Erdőgazdasági Rt., Miskolc.

Johann, E., Agnoletti, M. Bölöni J., Erol, S. C., Holl, K., Kusmin, J., Latorre, Jesus G., Latorre, Juan G., Molnár Zs., Rochel, X., Rotherham, J. D., Saratsi, E., Smith, M., Tarang, L., van Benthem, M., van Laar, J., 2011: Chapter 6. Europe. In: Parrotta, J.A., Trosper, R.L., (Eds.), Traditional Forest-Related Knowledge: Sustaining Communities, Ecosystems and Biocultural Diversity. World Forest Series vol. 12. Springer, Dordrecht, pp. 203–249.

Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., Buscot, F., Floren, A., Heibl, C., Hessenmöller, D., Hofrichter, M., Hoppe, B., Kellner, H., Krüger, D., Linsenmair, K.E., Matzner, E., Otto, P., Purahong, W., Seilwinder, C., Schulze, E.D., Wende, B., Weisserm, W.W., Gossner, M.M., 2017. Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. For. Ecol. Manage. 391, 86–95.

Keenan, R.J., Prescott, C.E., Kimmins, J.P., 1993. Mass and nutrient content of woody debris and forestfloor in western redcedar and western hemlock forests on northern Vancouver Island. Can. J. For. Res. 23, 1052–1059.

Keeton, W.S., Whitman, A.A., McGee, G.C., Goodale, C. L., 2011. Late-successional biomass development in northern hardwood-conifer forests of the northeastern United States. Forest Science, 57, 489-505.

Kirby, K.J., Reid, C.M., Thomas, R.C., Goldsmith, K.B., 1998. Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. J. Appl. Ecol. 35, 148–155.

Kirby, L.J., Webster, S.D., Antczak, A., 1991. Effects of forest management on stand structure and the quantity of fallen dead wood: some British and Polish examples. For. Ecol. Manage. 43, 167–174.

Korpel', S., 1995. Die Urwalder der Westkarpaten. Gustav Fischer Verlag, Stuttgart-Jena-New York.

Korpel', S., 1997. Totholz in Naturwaldern und Konsequenzen fur Naturschutz und Forstwirtschaft. Forst und Holz 52, 619–624.

Krasilnikov, P., Ibanez Marti, J.-J., Arnold, R., Shoba, S. (Eds.), 2009. A Handbook of Soil Terminology, Correlation and Classification. Earthscan, London.

Kruys, N., Fries, C., Jonsson, B.G., Lamas, T., Stahl, G., 1999. Wood inhabiting cryptogams on dead Norway spruce (Picea abies) trees in managed Swedish boreal forests. Can. J. For. Res. 29, 178–186.

Kutszegi, G., Siller, I., Dima, B., Takács, K., Merényi, Zs., Varga, T., Turcsányi, G., Bidló, A., Ódor, P. 2015. Drivers of macrofungal species composition in temperate forests, West Hungary: functional groups compared. Fungal Ecology 17: 69-83.

Lassauce, A., Anselle, P., Lieutier, F., Bouget, C., 2012. Coppice-with-standards with an overmature coppice component enhance saproxylic beetle biodiversity: A case study in French deciduous forests. For. Ecol. Manage. 266, 273–285.

Lombardi, F., Chirici, G., Marchetti, M., Tognetti, R., Lasserre, B., Corona, P., Barbati, A., Ferrari, B., Di Paolo, S., Giuliarelli, D., Mason, F., Iovino, F., Nicolaci, A., Bianchi, L., Maltoni, A., Travaglini, D., 2010. DW in forest stands close to oldgrowthness under Mediterranean conditions in the Italian Peninsula. Italia Forestale e Montana 65, 481–504.

Lombardi, F., Lasserre, B., Tognetti, R., Marchetti, M., 2008. DW in relation to stand management and forest type in Central Apennines (Molise, Italy). Ecosystems 11, 882–894.

MacMillan, P.C., 1981. Log decomposition in Donaldson's Woods, Spring Mill State Park, Indiana. Am. Midl. Nat. 106, 335–344.

Magyar, E., 1993. Erdőgazdálkodás a 18. századi Magyarországon. (Forest management in Hungary in the 18th century). In: R. Várkonyi, Á., Kósa, L., Várkonyi, G. (Eds.), Európa híres kertje. (Famous garden of Europe). Orpheusz, Budapest, pp. 141–163.

Marage, D., Lemperiere, G., 2005. The management of snags: A comparison in managed and unmanaged ancient forests of the Southern French Alps. Ann. For. Sci. 62, 135–142.

Marchetti, M., 2004. Monitoring and indicators of forest biodiversity in Europe - from ideas to operationality. EFI Proceedings No. 51, Joensuu, Finland.

Márialiget, S., Tinya, F., Bidló, A., Ódor, P., 2016. Environmental drivers of the composition and diversity of the herb layer in mixed temperate forests in Hungary. Plant Ecol. 217, 549–563.

Maser, C., Trappe, J.M., 1984. The seen and unseen world of the fallen tree. Gen. Tech. Rep. PNW-164. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, U.S.

McCarthy, B.C., Small, C.J., Rubino, D.L., 2001. Composition, structure and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio. For. Ecol. Manage. 140, 193–213.

McComb, W.C., Muller, R.N., 1983. Snag densities in old-growth and second-growth Appalachian Forests. J. Wildlife Manage. 47, 376–382.

McKenny, H.C., Keeton, W.S., Donovan, T.M., 2006. Effects of structural complexity enhancement on eastern red-backed salamander (*Plethodon cinereus*) populations in northern hardwood forests. For. Ecol. Manage. 230, 186–196.

MCPFE, 2002. Improved Pan-European Indicators for Sustainable Forest Management. MCPFE Liaison Unit, Vienna, Austria, http://www.foresteurope.org/documentos/improved_indicators.pdf

Meyer, P., Tabaku, V., Lüpke, B.V., 2003. Die Struktur albanischer Rotbuchen-Urwalder-Ableitungen fur eine naturnahe Buchenwirtschaft. Forstwissenschaftliches Centralblatt 122, 47–58.

Meyer, P., von Krüger, A.W., Steffens, R., Unkrig, W., 2006. Naturwälder in Niedersachsen - Schutz und Forschung Band 1. NW-FVA, Göttingen.

Muller, R.N., Liu, Y., 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Can. J. For. Res. 21, 1567–1572.

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusiński, G., Ranius, H., 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. For. Ecol. Manage. 161, 189–204.

von Oheimb, G., Westphal, C., Härdtle, W., 2007. Diversity and spatio-temporal dynamics of dead wood in a temperate near-natural beech forest (Fagus sylvatica). Eur. J. For. Res. 126, 359–370.

von Oheimb, G., Westphal, C., Tempel, H., Härdtle, W., 2005. Structural pattern of a near-natural beech forest (Fagus sylvatica) (Serrahn, North-east Germany). For. Ecol. Manage. 212, 253–263.

Paletto, A, De Meo, I., Cantiani, P., Feretti, F., 2014. Effects of forest management on the amount of DW in Mediterranean oak ecosystems. Ann. For. Sci. 71, 791–800.

Paletto, A., Ferretti, F., De Meo, I., Cantiani, P., Focacci, M., 2012. Ecological and environmental role of DW in managed and unmanaged forests. In: Diez, J.J. (Ed.), Sustainable Forest Management - Current Research. InTech, Available from: http://www.intechopen.com/books/sustainable-forest-management-current-research/ecological-and-environmental-role-of-DW-in-managed-and-unmanaged-forests

Peterken, G.F., 1996. Natural Woodland. Ecology and Conservation in Northern Temperate Regions. Cambridge University Press, Cambridge.

Petritan, A.M., Biris, I.A., Merce, O., Turcu, D.O., Petritan, I.C., 2012. Structure and diversity of a natural temperate sessile oak (Quercus petraea L.) – european beech (Fagus sylvatica L.) forest. For. Ecol. Manage. 280, 140–149.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team (2015). _nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-120. URL: http://CRAN.R-project.org/package=nlme

R Development Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org

Rahman, M.M., Frank, G., Ruprech, H., Vacik, H., 2008. Structure of coarse woody debris in Lange-Leitn Natural Forest Reserve, Austria. J. For. Sci. 54, 161–169.

Richards, R.H., Shifley, S.R., Rebertus, A.J., Chaplin, S.J., 1995. Characteristics and dynamics of an upland Missouri old-growth forest. In: Gottschalk, K.W., Fosbroke, S.L.C. (Eds.), Proceedings of the 10th Central Hardwood Forest Conference; 1995 March 5-8; Morgantown, pp. 11–22.

Roovers, L.M., Shifley, S.R., 1997. Composition and dynamics of Spitler Woods, an old-growth remnant forest in Illinois (USA). Nat. Areas J. 17, 219–232.

Saniga, M., Balanda, M., Kucbel, S., Pittner, J., 2014. Four decades of forest succession in the oak-dominated forest reserves in Slovakia. iForest 7, 324–332.

Saniga, M., Shütz, J.P., 2002. Relation of dead wood course within the development cycle of selected virgin forests in Slovakia. J. For. Sci. 48, 513–528.

Sarkar, D., 2008. Lattice: Multivariate Data Visualization with R. Springer, New York.

Savill, P., 2004. Sylvicultural systems. In: Burley, J., Evans, J., Youngquist, J.A. (Eds.), Enciclopedia of forest sciences, Elsevier, Amsterdam, pp. 1003-1011.

Schaetzl, R.J., Burns, S.F., Johnson, D.L., All, T.W., 1989. Tree uprooting: review on impacts on forest ecology. Vegetatio 79, 165–176

Schmelz, D.V., Barton, J.B., Lindsey, A.A., 1974. Donaldson's Woods: two decades of change. Proceedings of the Indiana Academy of Science 84, 234–243.

Schowalter, T.D., Zhang, Y.L., Sabin, T.E., 1998. Decomposition and nutrient dynamics of oak (Quercus spp.) logs after five years of decomposition. Ecography 21, 3–10.

Shifley, S.R., Brookshire, B.L., Larsen, D.R., Herbeck, L.A., 1997. Snags and down wood in Missouri old-growth and mature second-growth forests. Northern J. Appl. Forestry 14, 165–172.

Shotola, S.J., Weawer, G.T., Robertson, P.A., Ashby, W.C., 1992. Sugar maple invasion of an old-growth oak-hickory forest in southwestern Illinois. Am. Midl. Nat. 127, 125–138.

Siitonen, J., Martikainen, P., Punttila, P., Rauh, J., 2000: Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. For. Ecol. Manage. 128, 211–225.

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41.

Sopp, L., Kolozs, L. (Eds.), 2000, Fatömegszámítási táblázatok [Volume tables]. Állami Erdészeti Szolgálat, Budapest.

Spetich, M.A., Shifley, S.R., Parker, G.R., 1999. Regional distribution and dynamics of coarse woody debris in midwestern old-growth forests. For. Sci. 45, 302–313.

Ståhl, G., Ringvall, A., Fridman, J., 2001. Assessment of coarse woody debris – a methodological overview. Ecol. Bull. 49, 57–70.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge.

Sweeney, O.F.McD., Martin, R.D., Irwin, S., Kelly, T.C., O'Halloran, J., Wilson, M.W., McEvoy, P.M., 2010. A lack of large-diameter logs and snags characterises dead wood patterns in Irish forests. For. Ecol. Manage. 259, 2056–2064.

Szabó, P., 2005. Woodland and forests in medieval Hungary. Archaeopress, Oxford.

Takahashi, M., Sakai, Y., Ootomo, R., Shiozaki, M., 2000. Establish-ment of tree seedlings and water-soluble nutrients in coarse woody debris in an old-growthPicea–Abiesforest in Hokkaido, northern Japan. Can. J. For. Res. 30, 1148–1155.

Tutin, T.G., Burges, N.A., Chater, A.O., Edmondson, J.R., Heywood, V.H., Moore, D.M., Valentine, D.H., Walters, S.M., Webb, D.A., 1964-1993. Flora Europaea. Vols. 1-5 and Vol.1, ed.2. Cambridge: Cambridge University Press.

Van Wagner, C.E., 1968. The line intersect method in forest fuel sampling. For. Sci. 14, 20–26.

Vandekerkhove, K., De Keersmaeker, L., Baeté, H., Walleyn, R., 2005. Spontaneous re-establishment of natural structure and related biodiversity in a previously managed beech forest in Belgium after 20 years of non intervention. For. Snow Landsc. Res. 79, 145–156.

Vandekerkhove, K., De Keersmaeker, L., Menke, N., Meyer, P., Verschelde, P., 2009. When nature takes over from man: Dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. For. Ecol. Manage. 258, 425–435.

Warren, W.G., Olsen, P.F., 1964. A line intersect technique for assessing logging waste. For. Sci. 10, 267–276.

Zar, J.H., 1999. Biostatistical analysis. Prentice Hall, New Jersey.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G., 2009. Mixed effects models and extension in ecology with R. Springer, New York.