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

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27   **Abstract**

28   Dead wood (DW) has great importance for many wildlife species and ecological processes. The volume of DW is

29   considered a useful indicator of the sustainability and maintenance of biodiversity in forests. Though dry-mesic oak

30   forests cover large areas in Hungary, little is known about DW quantities or dynamics in these forests. We

31   investigated DW conditions in five age classes of dry-mesic *Quercus petraea* and *Q. cerris* dominated forests in the

32   Hungarian Carpathians. Stands of the first four age classes (age class 1: 40-59, age class 2: 60-79, age class 3: 80-

33   99, age class 4: 100-119 years old) were managed and stands at least 120 years old were unmanaged at least for 30

34   years (age class 5). We measured the volume, density, dominance and size distribution of standing DW and volume

35   of downed DW. We also evaluated the decay stages of DW on an ordinal scale (I-V, intact to well-decayed). The

36   effect of age class on the derived variables such as density, dominance, volume or proportion of DW was analysed

37   with general linear mixed models using age class as a fixed and region as a random effect. Mean total DW volume

38   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

39   the mean total volume of DW was 36.9 and 45.1 m^3/ha, respectively. Volume and proportion of total DW over 30

40   cm in diameter were markedly lower in age classes 1, 2 and 3 than in age classes 4 and 5, moreover standing and

41   downed DW over 30 cm in diameter were totally absent in stands under 100 years old. The proportion of well-

42   decomposed (decay stage IV and V) DW was much lower (3-18% of the volume) in all five age classes than in old-

43   growth stands of dry-mesic oak forests. After three decades of non-intervention (age class 5), the volume of DW

44   can approach that of old-growth forests. The 40-99-year old stands contained a similarly low percentage of DW as

45   other managed dry-mesic oak forests in Europe. Based on the results, it is likely that stands greater than 100 years

46   old will support much higher biodiversity of saproxylic organisms compared to younger stands.

47

48   **1. Introduction**

49   Standing and downed dead wood (DW) is an important component of forest ecosystems (Franklin et al., 1987),

50   performing an array of functions that have been well explored by research over at least three decades (Paletto et al.,

51   2012). DW directly or indirectly provides important habitat for a great variety of forest organisms such as

52   invertebrates, fungi, bryophytes, lichens, birds and mammals (Harmon et al., 1986; Stokland et al., 2012). Fallen

53   DW can provide nurse logs for some types of tree regeneration (Hofgaard, 2000; Takahashi et al., 2000), while

54   decaying DW influences microclimate heterogeneity on the forest floor and can help retain moisture during dry

55   periods (Harmon et al., 1986; Maser and Trappe, 1984). DW also plays an important role in nutrient and carbon

56   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).

88 To address this knowledge gap, this study investigates DW in managed and unmanaged dry-mesic sessile oak and

89 Turkey oak (*Q. cerris*) dominated forests affected by human activity of various intensity in North Hungary (i.e. the

90 Hungarian Carpathians). We assessed the quantity and quality – distribution according to DW types (downed

91 versus standing), size categories and decay stages – of DW in five stand age classes. Our results were compared

92 with DW data reported by previous research from old-growth dry-mesic oak forests. The overall goals of this study

93 are:

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

95 (2) to investigate whether and under what circumstances managed stands can sometimes develop DW

96   characteristics similar to old-growth forests,

97 (3) to formulate recommendations for sustainable forest management and biodiversity conservation approaches,

98   including DW retention practices.

99 In this study, significantly larger quantity of DW is hypothesized to accumulate in older as compared to younger

100 oak-dominated stands, primarily due to decreasing impact of management activity. Silvicultural management also

101 affects the quality of DW, hence the density of larger diameter and well-decayed DW are expected to be higher in

102 the older age classes. We also hypothesised that in managed stands older than 120 years the volume of DW will

103 reach the level of old-growth stands, but the proportion of well-decomposed, large sized downed dead trees will be

104 lower due to removal of recruitment sources (i.e. harvested large standing trees).

105

106 **2. Methods**

107 2.1 Study sites

108 Typical habitat types in the hilly regions of the Carpathian Basin are dry-mesic oak forests dominated by *Quercus*

109 *petraea*, *Q. pubescens*, *Q. robur* and *Q. cerris*, forming two characteristic Natura 2000 habitat types; 91H0

110 Pannonian woods with *Quercus pubescens* and 91M0 Pannonian-Balkanic turkey oak-sessile oak forests (European

111 Commission DG Environment, 2013). They cover about 180 000 hectares in Hungary (Bölöni et al., 2008, 2011).

112 Dry-mesic oak forests occupy a forest zone between 200 and 700 m a.s.l. in the Hungarian Carpathians (Fig. 1).

113 The climate of the Hungarian Carpathians is temperate with an average annual precipitation of 600-700 mm and a

114 mean annual temperature of 8.0-9.5 ˚C (Dövényi, 2010; Halász, 2006). The depth of the soil organic layer varies

115 widely within this zone depending on topography. The main soil types are leptosols and cambisols (Krasilnikov et

116 al., 2009), their physical and chemical conditions strongly specific to the bedrock because vulcanic, limestone,

117 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

149 proportion of sessile and Turkey oak of 95%; (2) maximum proportion of shade tolerant tree species of mesic

150 forests (e.g. *Carpinus betulus, Fagus sylvatica, Tilia spp*.) of 5%; (3) stand age 40-119 years, (4) elevation between

151 250 and 700 m a.s.l., (5) southern exposure or ridge top. Eighty subcompartments were selected by this process for

152 the study. As a secondary stratification, the subcompartments were classified according to the age of the dominant

153 trees, differentiating the following age classes: age class 1 – 40-59 years old, age class 2 – 60-79 years old, age

154 class 3 – 80-99 years old, age class 4 – 100-119 years old (Table 1). We assigned 1-6 sampling plots in each forest

155 subcompartments depending on the size of the given subcompartment, thereby we selected 178 managed sampling

156 plots altogether. The minimum distance between the centre of sampling plots and minimum distance from roads to

157 avoid edge effect was 50 m.

158 These forest stands were subjected to forest management with different intensity. The rotation period is generally

159 between 80 and 100 years in these forest stands, some management practice is implemented in every 10 years in

160 average, first tending and improvement cuttings, then cleaning cuttings and thinnings at the end. Living trees are

161 extracted during these processes, but DW is generally also removed. There were significant forest management

162 within 10 years in most of them, while in some forest stands the management was less intensive, even 20 years

163 elapse time between the treatments. Field sampling was carried out from 2009 to 2014. The sampling plots were

164 geographically separated in three regions, but all categories were represented in each region (Fig. 1). The greater

165 number of sampling plots of stands over 120 years old was considered necessary due to the greater heterogeneity of

166 these stands. Altogether we assigned 338 sampling plots in 99 managed and unmanaged forest subcompartments.

167 The sampling plots of this study were represented by spatial points, and all derived variables were related to these

168 points, because different variables were measured by different methods in the field, including line, relascope and

169 circular plot based methods. All measurements were centred on the same point. In each sampling plot an 8.92 m

170 radius circular plot (250 m^2) was defined for the measurement of living trees and standing entire and broken dead

171 trees between 5 and 25 cm DBH. In the case of larger trees a point relascope method with a factor 2 prism

172 relascope was used to identify trees added to the sample. DW and living trees were measured separately in each

173 sampling plot. For each individual living and dead trees, the species, the DBH and the crown position (dominant,

174 codominant, intermediate, supressed) of all trees were recorded. The height of 1-3 dominant tree individual(s) and

175 height of 1-3 supressed tree(s) were measured by Haglöf Vertex III height and distance meter in each sampling

176 plot. For other individuals it was estimated based on the measurements and crown position.

177

178 Table 1

179 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

180

181

182 Fig. 1

183 Study sites in three regions of the northern Hungarian Carpathian Mountains (1 – Visegrádi-hegység – Börzsöny; 2

184 – Mátra; 3 – Bükk). Legend: Black triangle = age class 1, black dots = age class 2, grey squares = age class 3, grey

185 pentagons = age class 4, grey crosses = age class 5.

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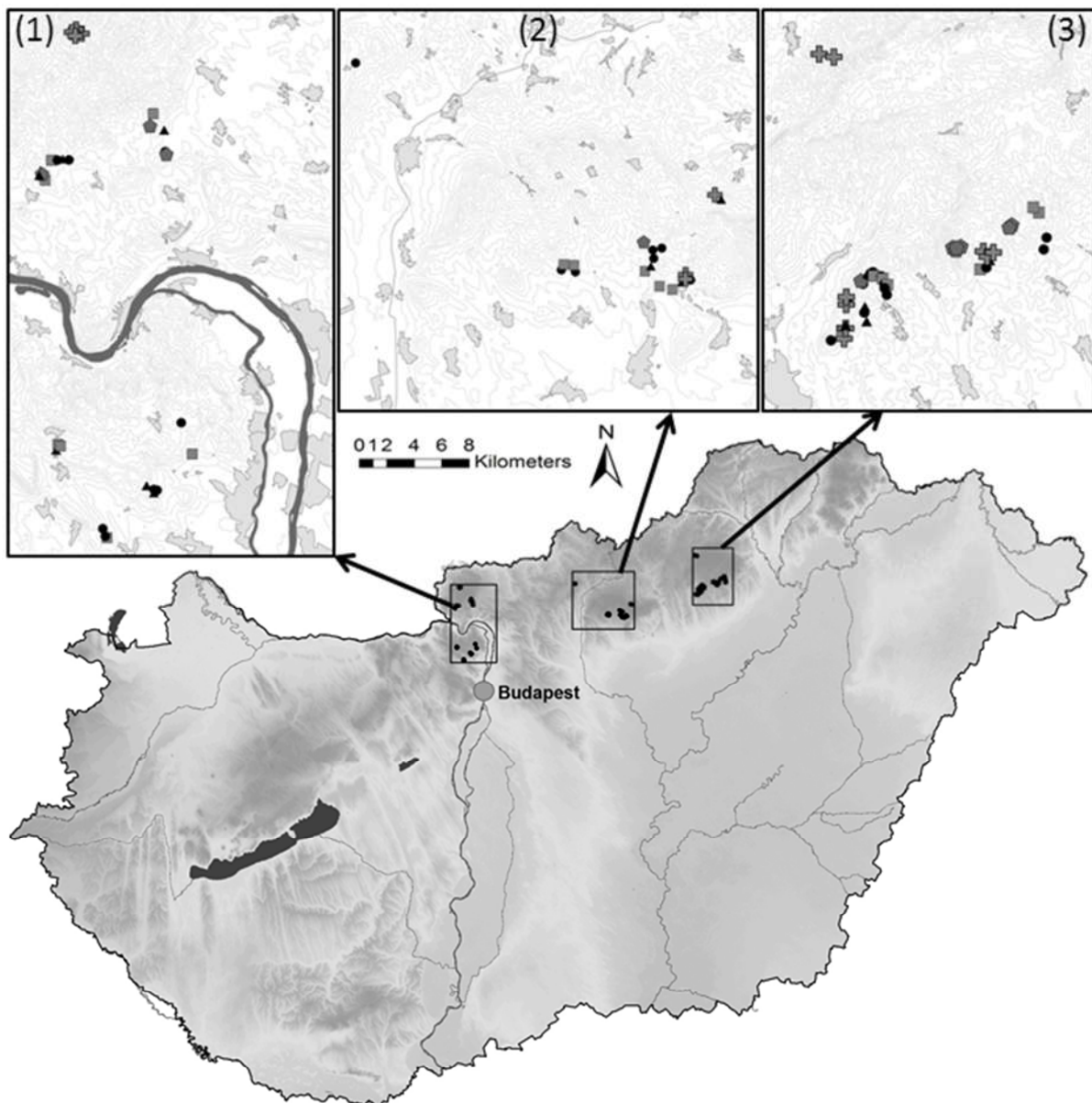
187 DW was divided into groups of standing dead wood (SDW), downed dead wood (DDW), stumps and DW on living

188 trees. In this study we concentrated on SDW and DDW, their sum is referred as total dead wood (TDW). SDW had

189 two forms, entire standing dead trees and broken standing dead trees with an absence of crown with a DBH >5 cm.

190 Broken standing dead trees with height of 0.5-2.0 m were also measured, in these cases mid-diameter was recorded

191 instead of DBH. DDW contained downed dead trees or pieces of stem or branches that have fallen with a mid-

192 diameter >5 cm and length >0.5 m. The separation of DDW from SDW was at a 45° angle.

193 The volume of DDW was estimated by line-intercept sampling method using three transect lines of 16 m in length

194 from the centre of the sampling plot at 0, 120 and 240 degrees (Ståhl et al., 2001; Van Wagner, 1968; Warren and

195 Olsen, 1964). The measurements consisted of the diameter (to the nearest cm) at each intersection point. The data

196 of the three lines per unit were merged. The decay stages of DW were evaluated on an ordinal scale (I-V, Spetich et

197 al., 1999), numbers I-V indicate codes used for decomposition classes where class I is the least decomposed and

198 class V is the most decomposed.

199

200 2.3 Data analysis

201 Inputs for the data analysis consisted of DBH and the height values of each tree. The volume of each living and

202 standing entire dead individual tree (containing majority of branches) was calculated using tree volume functions

203 (Sopp and Kolozs, 2000). Broken standing dead trees were considered as cylinder and volume was approximated

204 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

205 the trunk. Volume per hectare values were calculated based on the total volume of individual trees. The size of

206 sampling plots was 250 m^2 (8.92 m radius) for trees DBH 5-25 cm and according to critical distance of point

207 relascope method for larger trees (DBH >25 cm). For DDW volume estimation Van Wagner's (1968) formula was

208 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

209 sample line (in our case L was 48 m).

210 For the purpose of the analyses, well-decayed DW was a classification assigned to decay classes IV and V. A large

211 tree was defined as a tree with a DBH larger than 30 cm (for downed dead trees intersection diameter was used

212 instead of DBH).

213 The analysed derived variables and their units are listed in Table 2. The effect of age class on the derived variables

214 was analysed by general linear mixed models (Faraway, 2006) using age class as a fixed and region as a random

215 effect. The dependent variables were "ln" transformed, the normality of the residuals and their variance

216 homogeneity was checked. The significance of the fixed factor was tested by maximum likelihood method, and the

217 random factor by restricted likelihood method using chi-square tests (Faraway, 2006; Zuur et al., 2009). In case of

218 significant fixed (age class) effects the differences between the age classes were analysed by Tukey HSD multiple

219 comparisons (Zar, 1999). The analyses were carried out in R 3.0.2 statistical environment (R Development Core

220 Team, 2013) using the "lattice" (Sarkar, 2008), "multcomp" (Hothorn et al., 2008), and "nlme" (Pinheiro et al.,

221 2015) packages. Nomenclature follows Tutin et al. (1964-1993).

222

223 3. Results

224 The mean total DW (TDW) volume of five age classes forms two significantly separated groups. Stands in age

225 classes 1, 2 and 3 contained mean TDW volume under 15 m^3/ha (Fig 2, Table 2). A much higher volume of DW

226 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

227 difference between 36.9 and 45.1 m^3/ha appeared rather important, but not significant. DW proportion related to

228 total above ground biomass (living trees volume + DW volume) in age class 1-3 was smaller than 5.5%, stands at

229 least 100 years old had more than 8% (Table 2).

230 Density of SDW varied between 28 to 39 stem/ha in all age classes with the exception of age class 1, which had a

231 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

232 and mean volume under 8 m^3/ha. Sampling plots in stands older than 100 years had SDW with a basal area of more

233 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

234 in three age classes over 80 years old (age classes 3 to 5) than in the younger age classes. Based on the mean

235 volume of DDW age classes were divided into two significant groups. The average volume of DDW was less than

236 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%,

237 except in age class 3, where it reached 56%.

238 The density of SDW over 30 cm in diameter (large dead trees) was significantly higher (12 stem/ha) in age class 5

239 than in other age classes. The number of standing large dead trees in age classes 1-4 varied between 0 stem/ha in

240 age class 1 and 4 stem/ha in age class 4, but these differences were not significant. Unmanaged stands (age class 5)

241 had significantly higher volume and proportion of large DW than other stands (Table 2).

242 The diameter distribution of SDW was nearly even in age class 3 and 4, while stands in age class 1 and 2 more than

243 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

244 diameter were most frequent.

245

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

250

251

252 Fig. 2

253 Boxplots of the total dead wood volume (m^3/ha) in age classes. Letters indicate significant differences based on
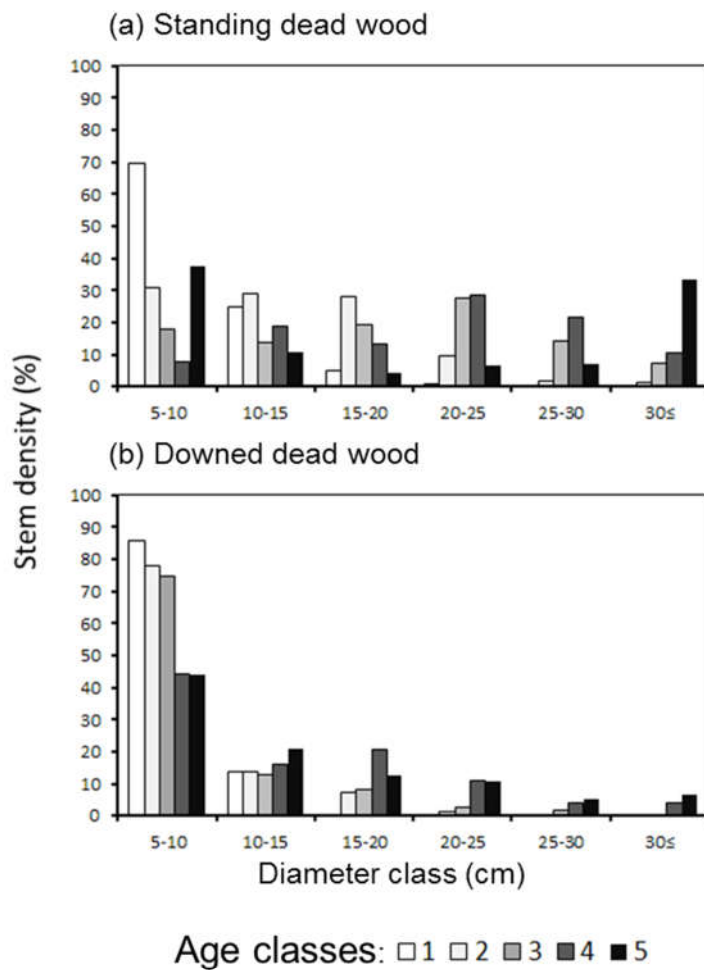
254 multiple comparisons (p<0.05).
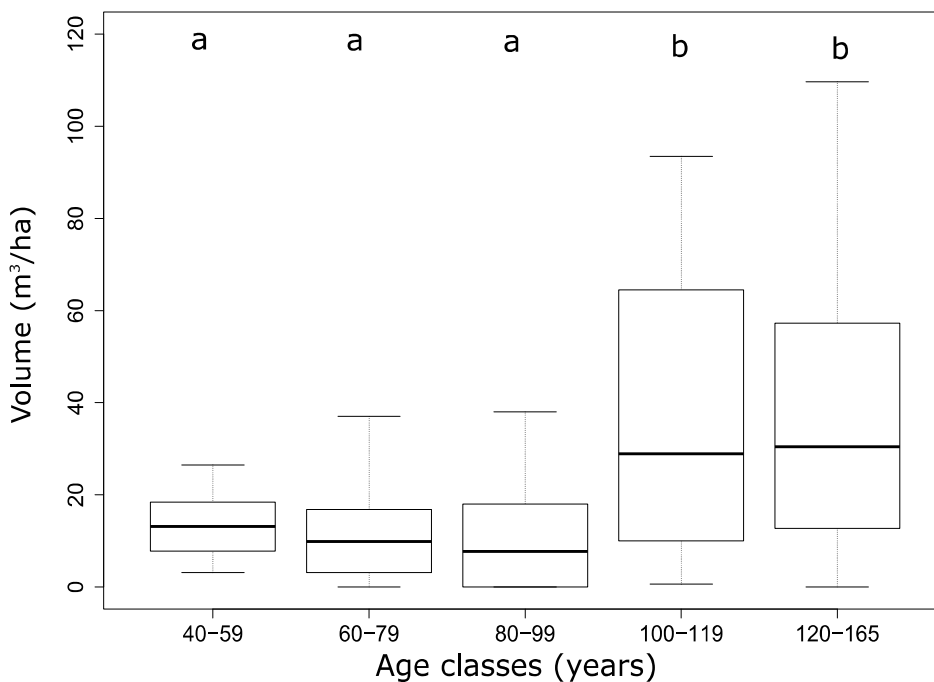
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256

257   Fig. 3

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

(a) Standing dead wood

(b) Downed dead wood

Stem density (%)

Diameter class (cm)

Age classes: □1 □2 ▨3 ■4 ■5

259

260   The diameter distribution of DDW followed a reverse-J shape for all age classes (Fig. 3b). In all five age classes,

261   the majority of downed dead trees were under 20 cm in diameter. In age class 1, the predominance (86 %) of

262   downed dead trees was smaller than 10 cm, while only 44 % was in this size range in age class 4. Stands of age

263   classes 1-3 did not contain downed dead trees over 30 cm in diameter at all, moreover downed dead trees thicker

264   than 25 cm were found only in stands older than 80 years (Fig. 3b). Although small in absolute number, large-

265   diameter standing and downed dead trees had comparatively large volumes per piece and account for the significant

266   difference in observed volume of DW between age classes 4-5 and 1-3. The volume and percentage of more

267   decomposed DW (decay stages IV-V) was very low in all stands (Fig. 4). In age class 4-5 the proportion was higher

268   (more than 18%) than in age classes 1-3 (under 15%).

269

270   Fig. 4

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

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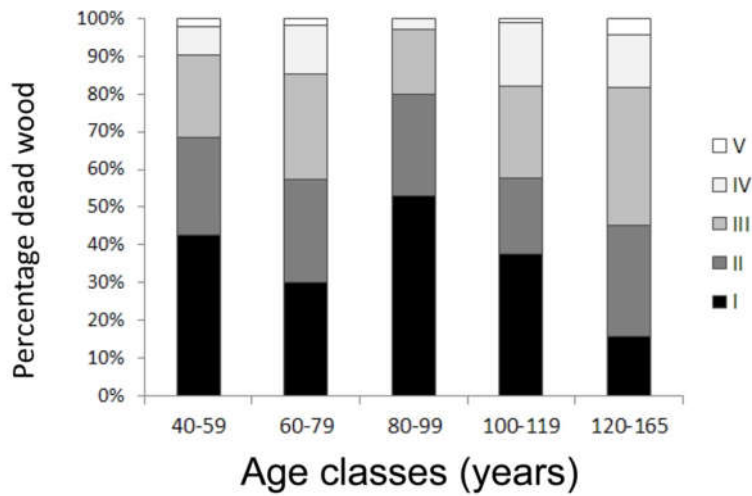
4. Discussion

275   4.1 Volume of total dead wood

276   The average volume of TDW in 40-99 years old stands (age class 1 to 3) is similar to values reported previously for

277   managed mesic and dry-mesic oak forests in Europe (Table 3), although there is slightly higher volumes of TDW in

278   mesic stands. However, data from dry-mesic oak forests in Italy (Barreca et al., 2008; Lombardi et al., 2008;

279   Paletto et al., 2014) indicate lower volumes (5-9 m^3/ha) than observed in this study. A common characteristic of the

280   managed stands we studied is that the TDW volume comprising less than 5% of the total aboveground living and

281   DW volume. According to these results, and compared to other regularly managed forests, the 11-14 m^3/ha average

282   of the studied dry-mesic managed forests can be considered relatively high. Relative scarcity of downed and

283   standing dead trees is reported in other studies as well (Colak et al., 2009; Kirby et al., 1998), particularly for the

284   larger size classes of standing and fallen dead trees (Sweeney et al., 2010). DW was generally removed from the

285   majority of European forest via intensive forest management activity, sometimes resulting in a complete purge of

286   all coarse downed material (Debeljak, 2006).

287   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

288   all age classes, it is relatively high (45m^3/ha) in unmanaged stands older than 120 years, while stands between 100

289   and 120 years (age class 4) represent a transition, but they are rather similar to unmanaged ones (36 m^3/ha).

290

291 Table 3

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

293 volume.

Country	DT	Standing DW, m³/ha	Downed DW, m³/ha	Total DW, m³/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

295 DT=Dominant tree species:

296 1a – *Quercus cerris*; 1b – *Q. frainetto*; 1c – *Q. cerris, Q. pubescens, Q. ilex*; 1d – *Q. petraea, Q. cerris*

297 2a – *Q. petraea, Q. robur, Fagus sylvatica, Pinus sylvestris*, 2b – *Q. robur, Carpinus betulus, Tilia cordata*; 2c –

298 *Quercus spp., Fraxinus excelsior*.

299

300 Differences in the volume of DW in stands under and over 100 years can be explained by the distinct forest

301 management regime of the two groups. The majority (71%) of the 40-99-year-old stands are intensively managed

302 according to forest management plans following rotation forestry systems. The rotation period of *Q. petraea* and *Q.*

303 *cerris* dominated forests is 80-100 years in Hungarian forestry practice, thus the number of extant 100-119 year old

304 managed stands are relatively low. Less intensive forest management is more typical in these older stands; about

305 67% of them have some form of less intensive management. Extended entry cycles for selection harvests (e.g. 20

306 years) and less intensive thinning operations lead to greater accumulations of DW across all size classes.

307 Studied stands older than 120 years (age class 5) are left unmanaged for at least 30 years, thus it was expected to

308 contain significant volume of TDW. DW accumulation in the studied unmanaged stands approximates, but does not

309 reach the DW volume of old-growth dry-mesic oak forests. The volume of TDW found in age class 5 (45 m³/ha) is

310 in the lower half of the range of similar old-growth or abandoned dry-mesic oak forests, which are dominated by

311 canopy trees over 110-150 years, and some cases exceeded 200-300 years (Carvalho, 2011; Goebel and Hix, 1996;

312 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, m²/ha	Standing DW volume, m³/ha	Downed DW volume, m³/ha	Total DW volume, m³/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*;

352   Source:

353   a – Saniga et al., 2014; b – Rahman et al., 2008; c – Lombardi et al., 2008; d – Carvalho, 2011; e – Goebel and Hix,

354   1996; f – Shifley et al., 1997; g – Hart et al., 2012; h – Dodds and Smallidge, 1999; i – Muller and Liu, 1991;

355   j – Petritan et al., 2012; k – Bobiec, 2002; l – Nilsson et al., 2002; m – Meyer et al., 2006; n – Hale et al., 1999; o –

356   Hardt and Swank, 1997; p – McCarthy et al., 2001; q - Schmelz et al., 1974; MacMillan, 1981; r - Roovers and

357   Shifley, 1997; s - Richards et al., 1995; t - Shotola et al., 1992.

358

359   Bormann and Likens (1994) suggested that DW volume decreases after the cessation of forest management, but

360   returns to pre-logging levels after about 50 years. According to other estimates, this process may take 60 to 100

361   years (Peterken, 1996; Vandekerkhove et al., 2009). Beside many factors, the age of the dominant trees is one of

362   the most determining variables in TDW recruitment dynamics. The volume of TDW in mature stands, where the

363   age of the dominant trees can reach their natural lifetime is comparable to that of virgin forests (Vandekerkhove et

364   al., 2005; von Oheimb et al., 2005, 2007). This statement is in line with the observations made in the present

365   unmanaged stands studied, where the canopy layer is dominated by older individuals, the spontaneous decay of

366   trees is typical, active forest management has been discontinued several decades (30-40 years) ago, and TDW

367   volume approaches the expected levels of the old-growth stands of this forest type. Slow decomposition rate of

368   *Quercus* species (Kahl et al., 2017; Schowalter et al., 1998) can also contribute to relatively high volume of DW in

369   unmanaged dry-mesic oak forests of Central Europe.

370

371   4.2 Standing dead wood

372   Unfortunately, the number of standing dead trees given in stem/ha is often not comparable between studies due to

373   the dissimilar threshold of minimum diameter and different diameter distributions. In old-growth dry-mesic oak

374   forests in the USA, the density of SDW ranges between 30 and 130 stem/ha (Dodds and Smallidge, 1999; Hart et

375   al., 2012; Goebel and Hix, 1996; McComb and Muller, 1983; Shifley et al., 1997; Spetich et al., 1999), although

376   values above 100 stems/ha are rare. The number of standing DW surpasses 100 stem/ha only in the stands younger

377   than 60 years, however, in these stands the number of living stems is also much higher than in the other age classes

378   (Table 1). Proportion of standing DW compared to the living trees is between 5-8% in all age classes including the

379   stands older than 120 years. This ratio ranges between 9 and 12% in the dry-mesic old-growth oak forests of the

380   USA (Hart et al., 2012; Goebel and Hix, 1996; McComb and Muller, 1983; Shifley et al., 1997; Spetich et al.,

381   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,

412 where data were purchased form previously managed mesic oak forests, and the time of non-intervention was at

413 least 30 years. The average ratio of standing DW was still higher than 40% (44%, 10-70%, Vandekerkhove et al.,

414 2009).

415

416 4.4 The density of large dead wood

417 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

418 evidently a very low value. The time from forest recruitment until the cutting age (80-100 years) is not enough to

419 the tree individuals to grow larger trunks in these low productivity sites. The retention of veteran trees were not

420 typical during earlier cuttings either, however these trees could form the present source of large standing or downed

421 DW. The proportion of large DW in total DW volume is very low in managed dry-mesic oak forests in the

422 Hungarian Carpathians, due to the general forest management regime, like in other managed oak forests in Europe

423 (e.g. Kirby et al., 1991; Paletto et al., 2014; Sweeney et al., 2010).

424 On the other hand, 12 stems/ha standing dead trees with DBH larger than 30 cm on average were found in the

425 unmanaged stands (age class 5) of the study. This value approaches or even reaches the number of large DW of

426 old-growth forests. The density of standing dead tree individuals with a DBH >30 cm usually ranges between 11

427 and 24 stems/ha, and for trees with a DBH >50 cm around 8 stems/ha in old-growth temperate mesic deciduous and

428 mixed coniferous stands in Europe and in the USA (Hura and Crow, 2004; Nilsson et al., 2002; von Oheimb et al.,

429 2007). Fewer large standing dead trees (<10 stems/ha) were found in the investigated dry-mesic oak forests in the

430 size category of DBH >30 cm then in the dry-mesic oak forests of the USA (Dodds and Smallidge, 1999; Hart et

431 al., 2012). The difference between our dry-mesic oak dominated sites and the North American ones can be

432 explained by the fact that Hungarian sites have been managed since the medieval ages, reaching 90-100 years of

433 age with relatively high density and homogeneous size distribution. DW comes from the relatively numerous and

434 thick living tree individuals during the period that has elapsed since abandonment, thus many of them have DBH

435 >30 cm. On the other hand, the density of standing DW with DBH >50 cm is lower in our study than in dry-mesic

436 old-growth oak forests, which indicates shortage of mature and really large tree individuals.

437

438 4.5 Decay stages

439 According to the data from dry-mesic old-growth oak forests, downed dead trees are predominantly in decayed

440 phases (decay stages IV and V). Their ratio is typically higher than 50% (66%, Dodds and Smallidge, 1999; 57%,

441 Hart et al., 2012), sometimes 35% (Shifley et al., 1997). Mesic stands are characterised by similar values (63%,

442   MacMillan, 1981; 73%, McCarthy et al., 2001; 26%, Richards et al., 1995). These values range between 3 and 18%

443   in our study, indicating a much lower volume of downed DW with advanced decay stages. Decay stage is usually

444   estimated in DW studies, although different classifications are used. Furthermore, since the speed of decay depends

445   on several background factors, the comparison of data is not straightforward.

446   This phenomenon can be explained by two obvious facts. The first one is that the stands had been managed in the

447   past, resulting in an absence of old and consequently intensely decayed DDW. These forests have been unmanaged

448   for the past 40 years, but signs of past removal of DW were still evident, which explain the low proportion of

449   advanced decay classes in DW. The second reason is the slow decomposition of *Q. petraea* (in line with other oak

450   species) under dry site conditions (Schowalter et al., 1998). Accordingly, the decay of sessile oak is markedly slow

451   in these relatively dry and cool sites, even those sessile oak individuals are only in decay stage III, which have been

452   laying on the forest floor for a several decades.

453

454   4.6 The limitations of this study

455   The comparison of the DW in forest stands published in different papers is not straightforward as forest stand

456   surveys use different minimal DBHs (or diameter for DDW),which is in most cases ranging from 5 to 10 cm (Hardt

457   and Swank, 1997; Muller and Liu, 1991; Richards et al., 1995). In our study DW between 5-10 cm accounts for 5-

458   6% (2.3 m³/ha) of DW volume in age class 4 and 5. In many cases, TDW volume is not even published, as only

459   standing or only DDW is measured. Furthermore, in many cases the units of measurement used are also different

460   (e.g. m²/ha for SDW and m³/ha for DDW). The lack of standard measurement necessitates a cross-checking of the

461   amount of SDW and DDW separately, beside the comparison of the total volume. Furthermore, in the case of

462   SDW, a comparison of density, basal area and volume data is also required. The lack of data also makes it

463   necessary to compare the results not only with dry-mesic oak stands but also with higher productivity oak

464   dominated stands on mesic sites, and, eventually, with other deciduous forests.

465

466   4.7 Management recommendations

467   The industrial, timber-oriented silvicultural systems of the last centuries have resulted in very low density and

468   volume of DW in dry-mesic oak forests in Central Europe based on our results. Therefore, we recommend that

469   management for biodiversity should maintain higher density and volume of DW in these forests. This,

470   recommendation applies generally at the European scale (Sweeney et al., 2010; Vandekerkhove et al. 2009), but

471   particularly in Hungary where the low level of DW in managed forests is outstanding (Bölöni, 2015; Márialigeti et

472   al., 2016). In dry-mesic oak forests the maintenance of higher levels of DW is an essential conservation target. As

473   old-growth dry mesic forests contain approximately 50 m^3 DW per hectare on average, we recommend to leave at

474   least the half of that, 25-30 m^3/ha, in case of these habitat types for the benefit of biodiversity. This

475   recommendation is consistent with previous studies (Bauhus et al., 2009; Bütler and Schlaepfer, 2004; Hodge and

476   Peterken, 1998), including those finding a strong correlation between intermediate levels of DW and positive

477   biodiversity responses (see, for example, Dove and Keeton, 2015; McKenny et al., 2006). This volume could be

478   achieved by leaving DW after thinning and harvesting in the forest, by active felling (leaving downed dead trees)

479   and girdling (to create SDW) of selected trees in protected areas. Managers could also leave naturally generated

480   DW, for example where disturbances such as low to moderate severity wind throw are recruiting downed wood

481   (Sweeney et al., 2010, Burrascano et al., 2013).

482   Size of standing and downed dead trees are considerably low not only in the actively managed stands, but also in

483   the older stands, except the unmanaged sites (age class 5), which possess similar density of large DW as old-growth

484   forests. Several specific saproxylic organisms depend on the large dead units. The very low frequency of large

485   standing and downed dead trees could be enhanced by active conservation management by the felling and girdling

486   of large-diameter trees, or in case of absence of large trees, by importing large downed dead trees (Sweeney et al.,

487   2010, Burrascano et al., 2013). Retention of approximately 10-15 m^3/ha DW over 30 cm in diameter is

488   recommended in protected dry-mesic oak forest sites, with 5-10 stem/ha standing dead tree density as a minimum

489   target, to achieve biodiversity conservation targets, as suggested also in previous studies (Bauhus et al., 2009;

490   Bütler and Schlaepfer, 2004; Hodge and Peterken, 1998). Although the volume of DW can reach the value typical

491   in old-growth forests within a few decades, decomposition needs more time. Beside large DW, the well-

492   decomposed fine woody debris are also needed for biodiversity conservation.

493

494   **5. Conclusions**

495   In managed stands 40-99 years old, we found very low quantities of DDW (under 15 m^3/ha) regardless of stand

496   age, a finding similar to that reported for managed dry-mesic oak forests elsewhere in Europe (Barreca et al., 2008;

497   Lombardi et al., 2008; Paletto et al., 2014). One hundred years of stand development can be considered a threshold

498   for large wood recruitment in these systems. Above this age both less intensively managed and the unmanaged

499   stands are capable of recruiting relatively high volume of DW (36.9 and 45.1 m^3/ha respectively), in some cases

500   approaching the volume found in old-growth dry-mesic oak forests. From this point of view forest stands above

501   100 years show old-growth features in case of dry-mesic oak habitat type. Our results support a conclusion that

502   after cessation of management, a relatively short period – approximately 20-30 years – is enough to produce DW

503 volumes and biomass similar to old-growth forests, provided that the stand was at least 80 year-old at the time of

504 the abandonment. DW appears to be is one of the first structural features to regenerate after cessation of intensive

505 forest management based on our results and previous research (Carvalho, 2011; Lombardi et al., 2008; Rahman et

506 al., 2008; Saniga et al., 2014).

507 Size of standing and downed dead trees are considerably low in the actively managed stands, large-diameter

508 downed dead trees (DBH>30cm) are totally absent from the stands younger than 100 years. Large-diameter

509 standing and downed dead trees only in the unmanaged sites (age class 5) possess similar density and volume of

510 large DW as old-growth forests. Furthermore, the low rate of decayed DW indicates the influence of former

511 intensive forest management. The volume of well-decayed DW is considerably low even in the stands abandoned at

512 least 30 years ago. Three decades of non-intervention were not enough time interval for the development of high

513 volume of well-decayed DW.

514

522

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