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Crowns of “forgotten” standards in hardwood floodplain forests

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Abstract

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Floodplain forests have traditionally been managed using the coppice-with-standards silvicultural system for centuries. After abandoning this silvicultural system approximately in the 1950s the crown of standards (mature-aged trees) developed gradually under the growing influence of their tree competitors. This study examines the crowns of remnant oak and ash standards in a hardwood floodplain forest along the Morava River in the Czech Republic. 100 oak (*Quercus robur* Linnaeus) standards and 100 ash (*Fraxinus excelsior* Linnaeus) standards were randomly selected and the basic mensuration data as well as some ecological data, such as number of large dead branches, cavities, and height of the lowest large dead and green branches, were measured. The four nearest neighbour competitors were identified for each standard, and their height, distance and azimuth were measured. The DBH of the analysed oak standards ranged between 71 and 148 cm, and the projected oak crown area ranged between 125 and 533 m^2. The ash DBH ranged between 71 and 127 cm, and projected ash crowns between 194 and 620 m^2. To assess competitive pressure, we calculated an index as a ratio of the tangents of angles of regular and compressed crowns. Distance of competing trees was more important than their height in the ash data set, but not in the oak data set.

Keywords: ash; oak; reserved trees; biodiversity; crown competition; crown projection

Modern intensive forestry often brings not only desirable outcomes such as enhancement of yield, better proportion of industrial assortments and higher labour productivity but also certain negative impacts, namely loss of biodiversity and forest stability (Winter, Möller 2008; Miller et al. 2009). Certain old-fashioned management systems, such as coppice forests or coppice-with-standards are being rediscovered and reconsidered (Kadavý et al. 2011). Examination of the forestry literature pertaining to

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coppice-with-standards and forest pastures from the 19th century reveals an unexpected degree of diversity in these two historic forms of land use (Groß, Konold 2009). However, in areas or countries where the coppice-with-standards system has been abandoned many years ago, there is now a lack of knowledge and studies assessing the development of trees in this abandoned management system, and their relationship with biodiversity.

In the Czech Republic, the management of coppices and coppice-with-standards was abruptly abandoned in the year 1950 despite the long tradition of this management in the area (Forest Management Institute 1999). However, the majority of the stands were not directly converted to high forest but were allowed to develop during the rotation cycle usually for high forests, varying from 80 to 140 years, according to site and stand type. This indirect conversion meant that the lower coppice storey from vegetative regeneration grew into the crown level of the standards that mostly regenerated generatively (Lassauce et al. 2012; Simon et al. 2014). The standards in these stands were not harvested, remained in the canopy and their crowns were gradually influenced by their competitors, recruited from the former lower storey.

The biodiversity in forests is significantly influenced by the existence of big veteran trees with dead branches, cavities and large crowns (Ranius et al. 2009; Bouget et al. 2014). These veteran trees in floodplain forests are considered as keystone species for biodiversity conservation (Machar 2012). The development and number of cavities are influenced by the existence of big dead branches, which extend to the core of a stem and enable penetration of fungal pathogens to the stem (Carey 1983; Oliver, Larson 1996). Also the wider the tree diameter, the higher the probability of cavities in stems (Holloway et al. 2007). Most of the cavities are formed by shedding of branches, but only if the branches are large enough (Ranius et al. 2009). Many standards in the former coppice-with-standards developed into such big veteran trees.

The presence of big trees supports biodiversity of saproxylic beetles (Bouget et al. 2014; Vandekerkhove et al. 2016) as well as cavity-nesting birds (Vaillancourt et al. 2008). The presence of dead wood in crowns is also important, although to a lesser extent, for biodiversity of oak-feeding xylophagous beetles (Vodka et al. 2009). At the same time, some studies stress that open forests, open landscape and semi-open woodland pastures enhance the biodiversity of organisms dependent on dead wood (Franc, Götmark 2008; Horak et al. 2014). Due to the importance of oak for biodiversity, the other tree species forming standards have been neglected. In the study area, two tree species form the standards, oak (*Quercus robur* Linnaeus) and ash (*Fraxinus excelsior* Linnaeus). While crowns of oak standards were investigated in a few studies, ash standards have stayed out of scientific interest until now.

Crown parameters, relationships between crowns and other mensurational data (Hasenauer 1997; Rouvinen, Kuuluvainen 1997; Nilsson et al. 2002; Webster, Lorimer 2003; Longuetaud et al. 2008) as well as the influence of competitors on crown irregularity have been investigated in many studies, but mainly in high forests (Osada et al. 2004; Getzin, Wiegand 2007; Getzin et al. 2008; Seidel et al. 2011). It was also noted that tree and crown competition indices are different for modelling competition between individual trees, and for the competition pressure of the entire stand (Fabrika, Pretzsch 2013). Crown changes in response to competitive pressure by its neighbour trees were analysed in conifers (Spathelf 2003). There are, however, very few studies focused on the crowns of deciduous standards dispersed in stands, and they mostly concentrate on beech (*Fagus sylvatica* Linnaeus) (Vanck, Spiecker 2004; Dobrovolný, Tesař 2010).

Attempts to reinstate management that supports the retention of standards within previously abandoned stands of coppice-with-standards require a guideline on how many standards should be retained per hectare. Foresters need to know the extent of forest land taken by the remnant standards, which would be virtually excluded from further production. This area corresponds to the total crown projection of standards. Crown projections of standards were calculated only in a few studies (Cotta 1865; Vanck, Spiecker 2004; Dobrovolný, Tesař 2010), and the proposed number of standards in coppice-with-standards varies widely from several individuals to hundreds of trees (Hochbichler 1993; Konvička et al. 2004; Coppini, Hermanin 2007; Kadavý et al. 2011) without any spatially specific studies.

The purpose of our study is to describe the crowns of oak and ash standards, and to answer the following questions:

(*i*) How large is the area covered by one standard and how many standards fill the capacity of 1 ha?

(*ii*) How is the crown structure and asymmetry affected by local competitors?

(*iii*) Does the ash also increase the capacity of hardwood floodplain forests to support biodiversity?

MATERIAL AND METHODS

Study area. We selected the area with standards according to historical studies which form part of the Regional Plans for Forest Development (Forest Management Institute 1999). The area is located in the eastern part of the Czech Republic, near the town of Kroměříž (49°18'N and 17°24'E). The climate is mild, between oceanic and continental climatic influences. The average annual temperature is 8.6°C and the annual precipitation is 599 mm (Forest Management Institute 1999). The study area of about 1,500 ha is covered by hardwood floodplain forests along the Morava River, at an altitude of 200 m a.s.l. These forests grow on alluvial soils developed from riparian sediments. The soil type is Fluvisol according to the World Reference Base for Soil Resources (FAO 1998) and the forest site type is elm floodplain (Viewegh et al. 2003).

We chose stands from 86 to 140 years old, where the standards occur. This age is the age of the former lower storey. The age was determined by the forest management plans valid for the given areas. The standards are dispersed in the stands and they do not form any clusters. Their age was estimated from the age of the former upper storey in previous coppice-with-standards and varied from 130 to 300 years. The field data were collected in 2014 and 2016.

Tree mensuration. We established two sets of standards. Each set included 100 trees. The first set included oak (*Q. robur*) standards and the second set consisted of ash (*F. excelsior*) standards. Trees of both sets were located in these hardwood floodplain forests. For each standard, a big veteran tree, randomly selected in each stand, we measured diameter at breast height using a girth tape, tree height, height of the lowest green branch which forms the crown (no epicormic branches), and height of the lowest large dead branch. Furthermore, we recorded the number of large dead branches and the number of two types of cavities – small and large cavities. Criteria for large dead branches were the minimum diameter of 10 cm at the branch attachment and minimum length of 1 m. We used the calliper with laser pointers for measuring the limit criteria for large dead branches. The criteria for small cavities were simple, no more than 10 cm in any dimension. We also used the calliper with laser pointers to measure dimensions of the cavities.

We measured the radius of the crowns from the stem in eight directions, starting from the north. The next direction was northeast, then east etc., so the angle between each direction was 45°. Eight directions were chosen based on other studies measuring the crown dimensions (Webster, Lorimer 2003; Harper 2008). We used the Vertex Laser electronic hypsometer (Haglöf Sweden AB, Sweden), which uses ultrasound to measure distances of the most distant twig from the stem in any given direction. The right angle between the horizontal plane and vertical plane, which is touched by the tip of the most distant twig, was located using a prism.

We also measured the four nearest neighbour trees, whose heights were taller than the half of the standard height. In every competitor we identified the tree species, measured its height, and distance and azimuth from the standard. In very scarce cases (three cases in the oak set and three cases in the ash set) there were less than four competitors, because the standard was located in a more open part of the stand.

Data evaluation. The total crown distance from the stem axis is the sum of two distances: measured distance between the most distant twig projections in the given direction and the diameter of the stem at breast height. To calculate the surface of the crown projection, we used formulas for triangle calculations. In each octant we had two sides of the triangle (a, b) and the angle of 45° between these sides (γ). The area of the triangle was calculated according to Eq. 1:

$$P = 0.5 \times a \times b \times \cos \gamma \tag{1}$$

where:
P – the area of the triangle.

The total crown projection is the sum of the eight triangles (eight octants).

The crown volume (V) was calculated using Eq. 2 (Assmann 1961):

$$V = 0.4 \times \frac{\pi}{4} \times \mathrm{CW}^2 \times l \tag{2}$$

where:
CW – crown width (average of measured radii),
l – crown length.

The tree volume of standards was determined according to volume tables developed for oak and ash in the Czech Republic (ÚLT 1951). To evaluate the influence of competitors on the crown irregularity (asymmetry) of standards we used a tangent of the angle between height and width of the crown (Fig. 1).

The width is the average of the eight measured radii which form the ideal regular crown. The com-

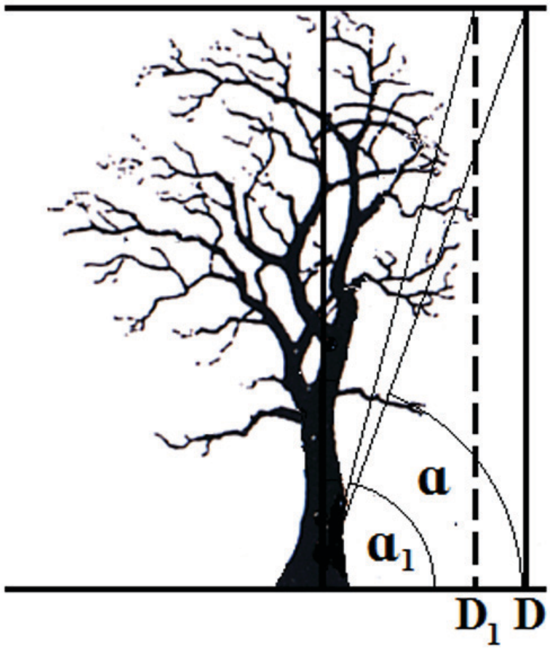

Fig. 1. Angles of average regular crown and compressed crown

D – distance for regular crown, D_1 – distance for compressed crown, α – angle for regular crown, $α_1$ – angle for compressed crown

pressed part of the crown influenced by a competitor has the lower width than the average, so the angle between its height and width is larger. The distance of the compressed crowns in direction to a certain competitor was calculated as the average of distances in the octant where the competitor was located.

The index of tangents (the tangent of regular crown divided by the tangent of compressed or extended crown) varies around the value 1. The index smaller than 1 identifies a compressed crown, and the index larger than 1 an extended crown. A relationship between this crown index of the standard and the distance and height of the competitor can be statistically evaluated, and we can assess whether distance or height of the competitor have a stronger influence on the crown of the standard. We used Microsoft Excel (Version 16.0, 2016), STATISTICA (Version 12, 2012) and R software (Version 2.15, 2013) for all analyses.

RESULTS

Each set of standards included 100 trees. DBH and height of standards were different between the oak and ash set; the oaks were wider, and the ashes were taller. The DBH of average oak was 101.1 ± 15.5 cm and height 35.1 ± 3.2 m, and the respective values of average ash were DBH 94.3 ± 11.9 cm and height 38.8 ± 3 m. The number of large dead branches was higher in oak standards but the number of cavities was higher in ash standards (Table 1).

Every crown of standards included at least one dead branch, their average number in the oak set was 8.3 and in the ash set only 2.91. The estimate of forest land occupied by standards is equal to their crown projection. Thus there can be only 29 (28.7) individuals per hectare in the oak set and 30 (29.9) individuals per hectare in the ash set at maximum.

Crowns of standards did not show any differences regarding the distance of crowns in cardinal directions, and thus the average crown of both species was symmetric. The average distance in the oak set was 10.95 ± 2.52 and 10.24 ± 2.55 m in the ash set.

The correlation matrix in Table 2 indicates the allometric relationships between dimensions and ecological data. While mensurational dimensions are highly correlated, correlations between ecological data (number of big dead branches, small and large cavities) and mensurational data were not always significant. In the oak set the highest correlation coefficient (CC) was between crown dimensions (crown volume with crown projection = 0.83; crown volume with crown length = 0.76). The diameter at breast height was positively correlated with all variables except height and crown length (crown projection = 0.53, crown volume = 0.43, dead branches = 0.32, small cavities = 0.27 and large cavities = 0.23). The number of large dead branches was positively correlated with all mensurational dimensions.

Ash standards also showed positive correlations between all mensurational dimensions but CC between these dimensions and ecological data were weaker (Table 2). In contrast to the oak standards, large dead branches were positively correlated only with DBH (CC = 0.20) and with crown dimensions (crown projection = 0.26, crown volume = 0.21). Small cavities as well as large cavities had no relationships with any variables but DBH.

Positions of large green and dead branches were also different between oaks and ashes. The number of oak standards in which the height of the lowest large dead branch was smaller or equal to the height of the lowest green branch was 78 and in the ash set only 38. The number of dead branches was correlated with the height of competitors in oak standards (CC = 0.21, $P < 0.05$).

In the oak set, we measured variables of 396 competitors, all deciduous trees comprising 13 tree

Table 1. Basic variables of oak and ash standards

	No.	Min	Max	Average	SD	CV
Oak						
DBH (cm)	100	71	148	101.1	15.58	15.41
h (m)	100	25.8	42.2	35.07	3.26	9.3
l (m)	100	13.3	33.2	23.06	4.41	19.12
CP (m^2)	100	124.92	532.89	348.09	80.41	23.1
CrV (m^3)	100	785	7,738	3,574	1,219	34.12
TV (m^3)	100	5.96	32.95	15.99	5.4	33.82
Trees with dead branches	100					
No. of dead branches		1	17	8.3	3.49	42
Trees with SC	50					
Trees with BC	18					
SC		1	4	1.4	0.67	47.86
BC		1	4	1.4	0.76	54.55
Ash						
DBH (cm)	100	71	127	94.3	11.85	12.57
h (m)	100	28.4	47.2	38.8	3.29	8.4
l (m)	100	14.4	36.8	25.39	4.38	17
CP (m^2)	100	193.65	619.56	333.65	81.76	24.5
CrV (m^3)	100	1,570	8,889	3,737	1,263	33.68
TV (m^3)	100	7.48	27.2	13.52	4.03	29.8
Trees with dead branches	100					
No. of dead branches		1	7	2.91	1.54	52.81
Trees with SC	77					
Trees with BC	18					
SC		1	6	2.07	1.22	59.1
BC		1	4	1.5	0.83	55.6

h – height, *l* – crown length, CP – crown projection, CrV – crown volume, TV – tree volume, SC – small cavities, BC – big cavities, SD – standard deviation, CV – coefficient of variation

species, and in the ash set variables of 397 competitors comprising 10 tree species. The most abundant competitors for oak standards were *F. excelsior* (58.8%), *Q. robur* (14.4%) and *Tilia cordata* Miller (8.1%), and for ash standards *F. excelsior* (53.9%), *Q. robur* (28.2%), *Alnus glutinosa* (Linnaeus) Gaertner (9.3%) and *Populus alba* Linnaeus (4.8%) (Table 3).

The angle of the regular crown shows small variability, in the oak set it was 72.60 ± 2.03° (CV = 2.78), in the ash set it was 74.51 ± 1.99° (CV = 2.88). We correlated the index with the distance and height of the competitors and we calculated the partial correlation for different tree species (only when the number of competitors within one tree species was sufficient). A significant relationship between the index and competitor heights and distances exists in the oak set only for *F. excelsior* (height and distance), *A. glutinosa* (height and distance) and *Populus* sp. (height and distance); in the ash set only for *F. excelsior* (height and distance) and *Q. robur* (distance) (Table 4).

Table 2. Correlation matrix for DBH, height (*h*), crown projection (CP), crown volume (CrV), crown length (*l*), number of dead branches (db), small cavities (SC) and big cavities (BC)

	DBH	*h*	CP	CrV	*l*	db	SC
Oak							
h	0.19						
CP	0.53*	0.26*					
CrV	0.43*	0.54*	0.83*				
l	0.15	0.65*	0.32*	0.76*			
db	0.32*	0.32*	0.21*	0.28*	0.23*		
SC	0.27*	0.04	0	0	0.03	0.15	
BC	0.23*	0.18	0.06	0.09	0.07	0.08	0.28*
Ash							
h	0.32*						
CP	0.49*	0.19					
CrV	0.45*	0.65*	0.86*				
L	0.10	0.44*	0.19	0.65*			
db	0.20*	0.06	0.26*	0.21*	–0.01		
SC	0.20*	0.07	0.14	0.06	–0.18	0	
BC	0.42*	0.09	0.15	0.12	–0.03	0.12	0.02

* relationship on the significance level of 0.05

Table 3. Variables of competitors

	No. of trees	Composition (%)	Height			Distance		
			average	SD	CV	average	SD	CV
Oak								
Robinia pseudoacacia Linnaeus	1	0.3	32.1	0	0	13.91	0	0
Acer campestre Linnaeus	2	0.5	18.6	0.15	0.81	7.15	0.56	7.83
Quercus robur Linnaeus	57	14.4	32.7	3.47	10.64	9.51	3.32	34.95
Quercus rubra Linnaeus	16	4	28.1	4.02	14.3	9.84	3.57	36.3
Carpinus betulus Linnaeus	2	0.5	20.6	0	0	9.53	0.69	7.24
Ulmus laevis Pallas	2	0.5	24.7	1.3	5.26	11.33	0.03	0.26
Fraxinus excelsior Linnaeus	233	58.8	33.0	4.81	14.57	9.18	2.90	31.56
Acer pseudoplatanus Linnaeus	6	1.5	26.6	2.51	9.45	8.66	2.76	31.83
Aesculus hippocastanum Linnaeus	6	1.5	26.5	3.66	13.86	8.31	3.26	39.29
Tilia cordata Miller	32	8.1	24.1	3.18	13.21	6.68	2.00	29.98
Alnus glutinosa (Linnaeus) Gaertner	15	3.8	25.1	3.09	12.26	9.01	2.38	26.51
Populus tremula Linnaeus	5	1.3	29.4	2.47	8.41	11.23	1.61	14.38
Populus sp.	19	4.8	38.0	3.44	9.08	10.91	3.24	29.7
Ash								
Q. robur	112	28.2	33.4	4.42	13.25	10.58	3.63	34.25
Q. rubra	1	0.3	37.2	0	0	9.75	0	0
U. laevis	1	0.3	28	0	0	5.02	0	0
F. excelsior	214	53.9	35.4	4.56	12.92	10.11	3.58	35.37
A. pseudoplatanus	1	0.3	30.8	0	0	4.16	0	0
A. hippocastanum	1	0.3	25.9	0	0	10.67	0	0
T. cordata	4	1	28.6	3.17	11.09	10.84	1.29	11.7
A. glutinosa	37	9.3	29	3.66	12.63	8.68	2.53	29.16
Populus alba Linnaeus	19	4.8	40.2	4.08	10.14	10.67	3.31	31.02
Populus sp.	7	1.8	40.3	3.31	8.21	11.28	1.83	16.2

SD – standard deviation, CV – coefficient of variation

DISCUSSION

Crowns of big veteran standards take up a relatively large area of forest land. In this hardwood floodplain forest an average oak standard occupied 348 m^2, which is more than the crown projection of 203 m^2 of the largest standard in a German hardwood forest (Cotta 1865). Ash crowns were of similar size, with an average crown projection of 333 m^2. The standards of both species in this forest had a larger crown area even than oaks growing in the open landscape. The largest oak measured in the open landscape in Austria with the diameter 100 cm had the crown width of 19 m corresponding to the crown projection of 283 m^2 (Hasenauer 1997).

The crown areas of beech reserve trees have been found to vary from 51 to 216 m^2 (DBH: 43–93 cm) (Dobrovolný, Tesař 2010), and from 202 to 356 m^2 (DBH: 84–95 cm) (Vanck, Spiecker 2004). Thus the veteran standards in a hardwood floodplain forest form some of the biggest crowns, and are then likely to play a crucial role in forming a spatial structure in these forests.

In alignment with other studies (Vanck, Spiecker 2004; Hemery et al. 2005), we found crown projection and crown volume to be related to DBH. The crowns of both species were also regular in all cardinal directions. This contrasts with the crowns of Scots pine where the frequency distribution of the directions was not random and the crowns were found to be asymmetric and enlarged toward southern, south-western and westerns directions (Rouvinen, Kuuluvainen 1997).

We calculated a maximum number of hypothetical standards per hectare based on the measured crown projections. There could be only 29 oak and 30 ash trees per hectare with the average crown size of these sites. This is a similar density to 30 living large trees (DBH > 70 cm) and 10–17 trees with DBH > 80 cm in beech-dominated forests (Nilsson et al. 2002). Cotta (1865) suggested 18 standards with the crown projection of 203 m^2 as an appropriate number but he also mentioned that in coppice-with-standards there were four storeys of standards. In addition, maximum standard volume of 200 m^3 has been proposed as a threshold above which they may have negative effects on the

Table 4. Relationship between the average tangent ratio in the crown of standards (coefficient of variation) and the competitor distance and height expressed by coefficient of correlation

	Average tangent ratio	Coefficient of variation	Coefficient of correlation	
			height	distance
Oak				
Quercus robur Linnaeus	0.970	15.192	–0.006	0.216
Quercus rubra Linnaeus	1.093	13.646	0.168	0.368
Fraxinus excelsior Linnaeus	0.958	16.401	–0.299***	0.323***
Acer pseudoplatanus Linnaeus	0.964	18.390	–0.606	0.722
Tilia cordata Miller	1.009	14.912	–0.157	0.186
Alnus glutinosa (Linnaeus) Gaertner	1.007	15.175	–0.626*	0.583*
Populus tremula Linnaeus	0.991	7.492	–0.627	0.236
Populus sp.	0.925	13.142	–0.511*	0.494*
Ash				
Q. robur	0.979	18.286	–0.148	0.255**
F. excelsior	0.951	17.271	–0.162*	0.385***
A. glutinosa	1.002	17.149	–0.134	0.170
Populus alba Linnaeus	0.967	11.779	0.211	0.262
Populus sp.	0.943	29.050	0.046	0.004

*significance level of correlation $P < 0.05$, **significance level of correlation $P < 0.01$, ***significance level of correlation $P < 0.001$

lower storey (Kadavý et al. 2011). If we adhere to the 200 m^3 threshold, there should be only 12 oak standards or 15 ash standards.

The coppice-with-standards system was abandoned in 1950 in the Czech Republic. During the development in the last 65 years the standard crowns were affected by their neighbours (broadleaved species) recruited from the former lower level originated from resprouts. The crown development seems to depend more on the competitors than on common mensurational variables such as DBH and height (Sullivan et al. 2006; Troxel et al. 2013), whereas the overall crown architecture is better explained by the actual tree height (Osada et al. 2004).

To assess the role of competitors, we used an index of the ratio between the tangent of the angle α of the regular standard crown and the tangent of the angle α_1 of the compressed crown in the direction of the competitor (Fig. 1). This method is similar to the light cone method (Biging, Dobbertin 1992). That method, however, cannot determine whether distance or height of a competitor is more important for crown irregularity, because it does not incorporate a distance between the trees (it is already addressed by the light competition cone).

A regular crown is a crown with the approximately equal crown radius in eight directions. The index calculated from tangents is the same as an index calculated only from distances (regular crown/compressed crown) because the height of the standard remains the same. It is therefore simpler to calculate an index based solely on the distance ratio, in order to measure competitor's influence. Nevertheless, we used the index of tangents, as it provides additional information, specifically a relationship between tree height and crown radius (distance of regular crown), which varies under different stocking densities. The intensity of the competition pressure is determined by the height and distance of the competing tree from the standard, canopy height and crown distance (Seidel et al. 2011). We identified the strongest competitor in both sets by correlating the distance and height of different tree species with the index of crown compression (ratio of tangents), and evaluated whether height or distance of the competitor were more important. While the main competitors of oak standards were light-demanding tree species such as ash, poplar and alder and there was no difference between the influence of competitor's height and distance, for ash standards only two species were statistically significant as competitors – ash and oak. In the ash set the distance of the competitor influenced the crown shape of the standards more than the height of competitors. Poplars, as the most light-demanding species, influenced the crowns of both standards. Their index of crown compression was the highest but the influence of their distance and height was only significant for oak standards. In both sets, ash (*F. excelsior*) is the main competitor. Ash has more rapid height growth than its neighbours (Seidel et al. 2011) and often occupies the upper storey or overstorey (Getzin et al. 2008). The overstorey trees experience very low competition in the canopy but they act as competitors to their neighbours. Competitive success of ash from the former understorey can be explained by the ability of young ash trees to penetrate to the main storey despite their lower height than the height of ash standards.

The crowns of all veteran oak standards contain large dead branches. A difference became however evident in the positions of the dead branches. While 78 oak standards had at least one dead branch either below the base of the crown or in the same position, the number of ash standards with the same type of crowns was significantly lower, only 38.

Despite the previous description of mutual shading of the branches of open-grown ash causing the primary branches at the base of the crown to die off (Hein, Spiecker 2008), only four out of 42 ash standards had one or more large dead branches below the base of the crown.

This difference in the branch mortality within the crown could be explained by lower light transmittance of oak, compared to pioneer tree species (Perot et al. 2017), related to its higher photosynthetic capacity, compared to other broadleaved species (Le Goff et al. 2004). The ash crowns are less dense, allowing light to penetrate to the crown base, with less intense self-shading and mortality of the lower branches. This has been confirmed by a comparison of the vertical distribution of foliage among *Q. robur*, *F. excelsior*, *Fraxinus angustifolia* Vahl and *T. cordata* in floodplain forests in southern Moravia, where the leaf area index (LAI) of oak was significantly higher than LAI of ash (Čermák 1998). Moreover, importance of self-shading in oak is supported by the significant effect of both competitors' distance and height. The crown shapes of the standards depend on their competitors, and their development and shape can be influenced by management targeting the competing tree species. Such management decisions affecting crown development may have implications for stand biodiversity, as certain groups of organisms associated with the presence of big veteran trees prefer different strata of the crowns (Horak et al. 2014).

Although the number of large dead branches was higher by oak standards (8.3) than by ash standards (2.9), there was no standard without a large dead branch. The large dead branches are important in supporting invertebrate biodiversity, because they provide deadwood microhabitats for saproxylic organisms, especially in the case of oak standards (Bouget et al. 2011). The positive effect that big oak trees have on biodiversity has previously been described on many sites (Ranius et al. 2009; Lassauce et al. 2012; Bouget et al. 2014). Some studies consider sun-exposed dead branches more important for biodiversity of saproxylic beetles than the remaining dead branches (Vodka et al. 2009; Horak et al. 2014). However, all types of dead branches are more important for this group of organisms than live branches. In both sets the number of large dead branches was positively correlated with DBH, which shows importance of retaining enough trees in the stand to older age to achieve the large DBH (Larrieu et al. 2017). The large dead branches are also important for forming the tree cavities, because after shedding of big branches the hollow will often develop in the scar (Carey 1983; Ranius et al. 2009). The hollows are important not only for invertebrates but also are a crucial habitat requirement for cavity-nesting birds (Carlson et al. 1998), many other vertebrates (Naďo, Kaňuch 2015) as well as lichens (Fritz, Heilmann-Clausen 2010). Our study corroborates the positive relationship of cavities to tree dimensions (Hemery et al. 2005). Although there were no differences between the two sets of standards in the number of large cavities, there were noticeable differences in the occurrence of small cavities. There was a smaller number of oak standards that had some small cavities compared to ash standards, and also their number per tree was lower in oak. The lower number of small cavities in oak could potentially be related to its wood hardness and increased difficulty in excavating these cavities (Schepps et al. 1999; Lorenz et al. 2015), although the wood hardness was usually found to play a significant role only within the same tree species (Remm, Lõhmus 2011). The difference between the oak and ash standards highlights the importance of maintaining veteran trees of multiple species in hardwood floodplain forests, as they vary in their ability to provide different aspects of wildlife microhabitat.

To answer our three questions, we conclude that:

(*i*) Both species of big veteran standards (oak and ash) had larger crowns than any other temperate floodplain tree species recorded up to now. Their number per ha is limited, because three standards take up one tenth of a hectare;

(*ii*) The most important competitor for both standards in a hardwood floodplain forest is ash growing from the former understorey. There is no difference between competitors' distance and height, except one case when the distance of oak competitor to ash standard is more important than its height. The index of crown compression of standards is the highest for poplar competitors;

(*iii*) Although ash is less important for saproxylic beetles, it forms more small cavities and is of high importance for cavity-dependent animals.

The “forgotten” standards show that even in a commercial forest, a certain number of trees should be left to develop to their physical age, as they support higher levels of biodiversity than younger trees. On the other hand, even in the areas where conservation is the primary objective, prior coppice-with-standards should be actively managed, in order to maintain the higher levels of biodiversity, previously associated with these stands (Müllerová et al. 2015). The management would vary according to the purpose of the stands and groups of organisms we want to support. Although the development of suitable crowns requires a long time, choice of the tree species of standards and their potential competitors can influence not only the shape of the crowns of standards, but also their ecological values, such as number of large dead branches, their position in crowns and number of cavities.

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