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Age estimation of large trees: New method based on partial increment core tested on an example of veteran oaks

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ABSTRACT

Knowledge about tree age is critical to forestry, nature conservation and ecological studies. Direct age determination of large diameter trees through increment cores is complicated by various obstacles, primarily because of rot and insufficient borer length. Here, we aim to (1) test the accuracy of various methods (tree-ring width, basal area increment, age-size relationship) for tree age estimation, (2) select the most accurate approach and (3) enable age estimation of large individuals of *Quercus robur*. This was done through increment cores collected in an alluvial forest in the Czech Republic. We achieved 75 age estimates for each tree, including our novel approach, which reduces the effect of decreasing tree-ring width and increasing basal area increment during tree life. The extrapolation of mean ring width to missing radius generally overestimates the number of missing rings (by up to 27.5% of actual age) and the level of overestimation increases with decreasing partial core length, while the application of basal area increment largely underestimates the age estimation (by up to 20.5%). Thus, to eliminate the over- and underestimation caused by natural tree ring width decrease and basal area increase during the tree senescence and increasing size, we averaged the number of estimated rings by these two methods. This technique obtained the most reliable age estimates, with an error up to 3.5%. Thus it is suggested here that this technique provides a relatively accurate age estimate for trees where it is impossible to directly determine the age; at least for light-demanding species. Moreover, the proposed technique does not require complicated analysis and is not time consuming. However, future research should test the applicability of this technique for tree species with various ecological strategies, i.e. shade-tolerant species. Finally, we estimate that the age of large oaks in our study area does not exceed 400 years. Due to such fast growth, it is possible to keep the continuity of these keystone structures in a given landscape and thus preserve the associated biodiversity.

1. Introduction

Large trees are keystone structures in various types of landscape. They provide critical habitats for the maintenance of biodiversity for a wide range of organisms (Sebek et al., 2013; Edman et al., 2016) and play an important role in carbon storage and dynamics (Stephenson et al., 2014). For management, conservation and forest ecology purposes it is also crucial to have an age estimation for large trees. Age determination is fundamental to understanding forest structure and dynamics and should serve as a basis for conservation action to ensure the continuous presence of large trees in a landscape.

Several methods currently exist for tree age estimation. The age of large trees or trees which cannot be cored may be estimated indirectly, most commonly with the dependence of stem diameter on age. The advantage of such an approach is that information can be obtained for a large number of trees in a relatively short time. On the other hand, the relation between age and size can be quite poor depending on e.g. tree species and the past and present growth conditions (Altman et al., 2013b). In addition, trees with quite different growth rates often coexist locally and so trees of similar size can show great variation in their age.

Tree rings are widely used for age estimation and additional dendrochronological techniques can be applied to identify missing and/or false rings and provide accurate age estimation with annual resolution. The most common non-destructive technique for age estimation is based on increment cores. Several problems can be

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encountered when estimating the age of large trees in this way, making the whole process difficult or even impossible (Stephenson and Demetry, 1995; Rozas, 2003; Clark and Hallgren, 2004). The principal problems (and potential solutions) are:

(1) Cores do not reach the pith because of eccentric tree radial growth or just simply because of difficult alignment of the increment borer. The potential solution is additional coring as the pith position is estimated on the basis of the first core (Frelich and Reich, 1995).
(2) The impossibility of reaching the pith because of wood decay. Additional sampling at a different height and/or on the opposite side of the stem can help to reach the pith or at least get longer increment cores as the rotten part in the centre can be asymmetric. However, increased caution is necessary during the coring of rotten trees as there is a risk that the borer will become lodged (Loader and Waterhouse, 2014).
(3) The impossibility of reaching the pith because of a large tree diameter and a lack of adequate borer length. This is especially true for trees with stem diameters exceeding 2 m, as commonly-available increment borers do not exceed 1 m. Despite the fact that such instruments exist (Krottenthaler et al., 2015) they have their own disadvantages (see Stephenson and Demetry, 1995). Moreover, in our experience, increment borers longer than 40 cm are costly and, more importantly, prone to bending, especially if hardwood is sampled. Thus, shorter increment cores are usually collected.
(4) Coring is usually performed above the oldest part of tree, i.e. the tree base. Various methods for height correction exist (Wong and Lertzman, 2001; Niklasson, 2002; Altman et al., 2016). For the purpose of age determination itself, it seems that the best approach is to core trees at ground level. However, the real age can still be underestimated for samples taken here (DesRochers and Gagnon, 1997). Additionally, age determination is not always the main purpose of coring so dendrochronologists often take the samples at least 20–40 cm above the ground, most commonly at breast height (1.35 m), for several reasons: (1) a lower probability of growth anomalies, fire scars and rot (Frelich and Reich, 1995) and (2) the higher sensitivity of radial growth to climate (Kerhoulas and Kane, 2012).

The importance of these four factors in age estimation from increment cores increases with increasing tree diameter which makes the age estimation of large trees challenging when compared to smaller ones. Although several approaches for estimating the pith offsets exist (Rozas, 2003; Pirie et al., 2015), the majority of studies test various methods and determine the potential error in age estimation on trees of known age. However the next step, i.e. the application of these findings for age estimation of trees with unknown age, is rare.

The common assumption in estimating the number of missing rings on partial/off-centre increment cores is that both radial growth and basal area increments are constant through time for a given tree (Norton et al., 1987). However, trends in the growth usually reflect the stand history and differ between life-strategies (i.e. light-demands vs. shade-tolerance) of individual species. In a simplified way, the general growth trend of light-demanding species is that radial growth decreases with increasing age (and size) and basal area increases with age due to increasing diameter. On the contrary, the radial growth patterns of shade-tolerant species have more complex growth trends and reflect more environmental changes, especially disturbances (Altman et al., 2013a). The main difference between the growth trends of light-demanding and shade-tolerant species is in the juvenile phase and the length of time growing under light suppression. Such trees exhibit always much slower growth rates than canopy trees overhead (Frelich, 2002). While light-demanding species can only sustain a few years of suppression, shade-tolerant species can tolerate a longer period (up to few centuries) of extreme suppression (Frelich and Lorimer, 1991). The assumption of there being a constant growth/basal area is then always an unrealistic scenario which causes bias in age estimation, as the mean ring width/basal area of the partial core (or its part) are extrapolated for the missing radius (Norton et al., 1987; Stephenson and Demetry, 1995; Rozas, 2003). Consequently, there is a real need to reduce the errors derived from such doubtful assumptions and effectively improve tree age estimates (Rozas, 2003).

The aim of this study was to test the efficiency of various methods of age estimation and determine the age of large individuals of *Quercus robur*, a light-demanding species, for which only partial cores are available because of rot. Our aims were: (1) to test various methods for age estimation of partial increment cores and describe the attendant uncertainty, (2) to select the most applicable method for age estimation, and (3) to estimate the age of large oaks.

2. Methods

2.1. Study area

This study was performed in alluvial woodlands along the lower Morava (March) and Dyje (Thaya) rivers. This area is a biodiversity hot-spot in Central Europe (Rozkošný and Vaňhara, 1996) and is extremely rich in saproxylic organisms. This is due to the large numbers of old, open-grown trees, fragments of open woodland, the high variability in past and current woodland management and a large continuous woodland area (Miklín and Čížek, 2014). The terrain is flat and abiotic conditions were rather homogenous within the study area which makes it an ideal model for studying tree growth, as trees are minimally affected by environmental differences. Large open-grown trees are scattered across the area in various densities and their numbers are decreasing rapidly (Miklín and Čížek, 2014). Age estimation of these large oaks is therefore urgently needed as a sound basis for conservation management.

2.2. Data collection and analyses

During the summers of 2012–2015 we collected 337 core samples from pedunculate oak (*Quercus robur*) from the study area. Coring was carried out at a height of 1.3 m above ground level using a steel borer of maximum length 80 cm. All cores were dried and a thin layer of wood was sliced off from each core using a core microtome (Gartner and Nievergelt, 2010) to highlight the tree-ring boundaries. Rings were counted from pith to bark and tree-ring widths were measured to the nearest 0.01 mm using the TimeTable measuring device and PAST4 software (http://www.sciem.com). Ring-sequences were visually cross-dated using the pattern of wide and narrow rings (Yamaguchi, 1991), and verified by percentage parallel variation (Gleichläufigkeit; see Eckstein and Bauch (1969)) and the similarity of growth patterns between individual series (Baillie-Pilcher's t-value; see Baillie and Pilcher (1973)).

All cores were first placed in one of the following three categories according the distance to pith: (1) trees with pith, (2) trees with an arc of the inner rings, and (3) partial cores (which did not contain either pith or an arc). To estimate the number of missing rings to the pith, we applied a graphical method (for details see Rozas, 2003) to cores from the second category. Since the estimated number of missing rings to the pith was quite low (minimum 1, maximum 11, and mean 4.5 years), we combined trees from the first and second category (i.e. cores with pith and arc) into the common category "complete cores". However, the theoretical length of estimated missing rings, i.e. the number of rings multiplied by the average of 5 innermost rings, was added to the length of the cores with an arc (i.e. sum of all visible rings). This correction will minimize the underestimation of the length from bark to pith and make the data more accurate for further analysis. Table 1 presents information about trees and cores in the three categories.

To determine whether the radial growth of the studied trees was concentric or eccentric, geometric (including bark) and chronological radii were compared for complete cores. The geometric radius was calculated from the diameter at sampling height and it is simply the radius of the tree. The chronological radius is the length of complete increment cores. Tree growth is concentric if the geometric and chronological radii are similar and tree growth is eccentric if they differ.

2.3. Testing the accuracy of tree age estimation

Different approaches for determining the number of missing rings from partial cores were tested based on cores with a known number of rings (i.e. cores with pith or arc). Firstly, we produced five groups of partial cores by deleting 10%, 20%, 30%, 40%, and 50% of the innermost rings. For each group, the known number of rings for every core was compared with age estimations calculated by following three methods.

(1) Mean radial growth (RG) of the 5, 10, 20, and 50 innermost rings (RG5, RG10, RG20 and RG50) as well as the total mean radial growth (RGT). The number of missing rings was estimated by dividing the known missing core length by RG5, RG10, RG20, RG50 and RGT, respectively.

(2) Mean basal area increments (BAI) of the 5, 10, 20 and 50 innermost rings (BAI5, BAI10, BAI20 and BAI50) and whole partial core (BAIT), i.e. the sum of the basal area of all visible increments. The number of missing rings was estimated by dividing the known missing core basal area by BAI5, BAI10, BAI20 and BAI50 and BAIT, respectively.

(3) To balance the commonly-described growth trend of decreasing tree-ring widths and increasing basal area increments during the life tree, we averaged the number of missing rings estimated by RG and BAI, i.e. for each core, the pairs of corresponding results were averaged (RG5 with BAI5, RG10 with BAI10 and so on).

The methods described above yielded 75 (25 per method) age estimates for every tree. For each method, the estimated age was calculated as the sum of the estimated number of missing rings and the number of visible rings on the partial core. The absolute error (i.e. absolute difference between estimated age and known tree age), standard error and percentage of underestimates and overestimates were calculated for each estimation method. The Wilcoxon–Mann–Whitney test was employed to test if the age estimation of individual methods differed from the known age.

2.4. Age estimation of partial increment cores

For each tree with a partial increment core, we determined the missing radius by subtraction of the partial core length from the geometric radius. To estimate the number of rings to pith on the missing radius of partial cores, methods showing the highest similarity with original age in testing the accuracy of tree age estimation were selected. Specifically, to capture the variability of individual approaches, we selected the number of innermost rings to be averaged according to the highest similarity with the original age for all partial core lengths for both RG and BAI. The number of missing rings was estimated by dividing the missing radius and missing basal area by the mean of the "best fit" innermost rings of RG and BAI, respectively. However, missing radius now includes the bark, which causes age overestimation. The bark width was estimated from the difference between the geometric radius at coring height and the length of the complete core. The mean bark width was then subtracted from the missing radius and this value was used for missing ring estimation. However, please note that our calculation of bark width also includes growth eccentricity.

Tree age at coring height was estimated as the sum of the number of visible rings on the partial core and the estimated number of missing rings:

$$AGE = N + ((GR - PCL - MBW)/MRW_n)$$

where N is the sum of the number of visible rings on the partial core, GR = geometric radius, PCL = partial core length, MBW = mean bark width, and MRW_n = mean ring width of the last n rings (for BAI method are instead of missing radius (GR – PCL – MBW) and MRW_n used missing BA and mean BAI for the last n rings, respectively).

Moreover, linear least-squares regression was developed to determine relationship between age and diameter at coring (breast) height (DBH). To get a regression trend estimating the age for a wide range of DBH, an age-DBH equation was calculated for complete cores together with age estimation for partial cores by selected reliable method, i.e. age estimation which is not significantly different ($p > 0.05$) from real age (or which is closest to real age in the case that all age estimations significantly differ from real age).

All analyses and figures were performed in R (R Core Team, 2016) with packages "dplR" (Bunn, 2008) and "ggplot2" (Wickham, 2009).

3. Results

3.1. Radial growth symmetry

The regression analysis detected a strong, significant relationship ($R^2 = 0.8$, $p < 0.001$) between stem radius and the length of complete cores (Fig. S1). Overall, the increment core length was shorter than the stem radius (in 99%). This difference is caused by bark width (including growth eccentricity), which makes the

Table 1
Number (N) of cores (=trees) included in our analyses together with information about mean, maximum and minimum DBH and number of measured tree rings.

	N	DBH			Number of rings		
		Mean	Max	Min	Mean	Max	Min
Pith	10	34.6	49	21.3	126.1	168	73
Arc	142	35.1	69.9	7.9	109.5	188	34
Partial	185	55.8	93.6	40.3	139.4	287	74

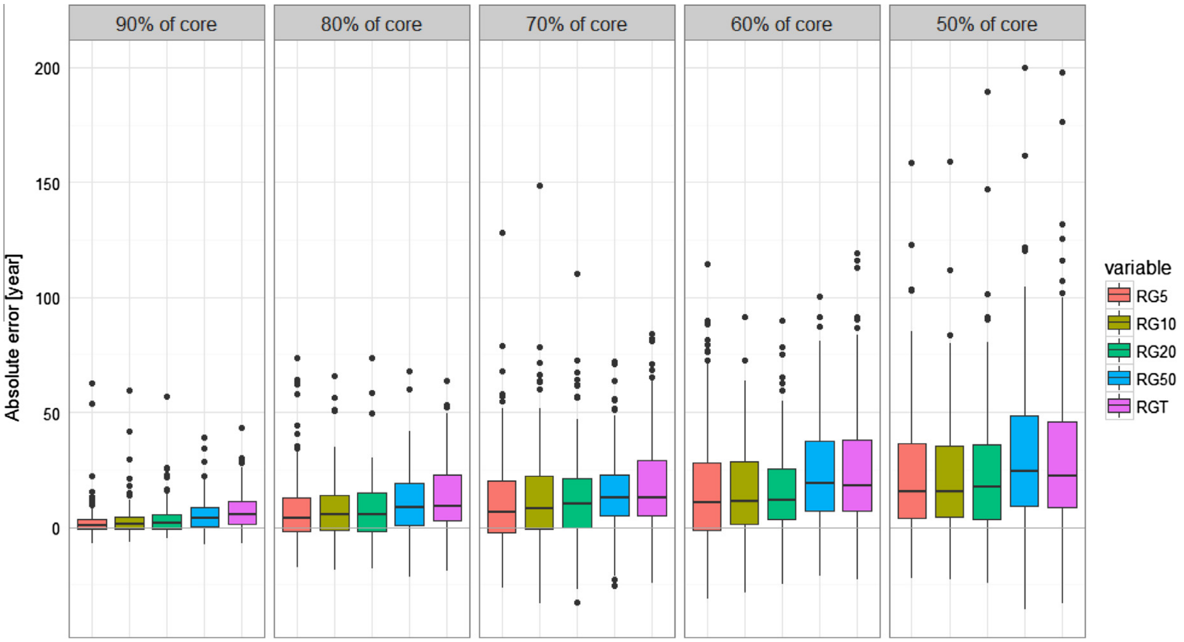

Fig. 1. Absolute deviation from true age for calculation using the mean radial growth of the innermost 5, 10, 20, 50 and all rings for each partial core length (90%, 80%, 70%, 60%, and 50% of complete core). Boxes represent 25–75% of values, black strips medians, whiskers 1.5 interquartile ranges, and open dots outliers.

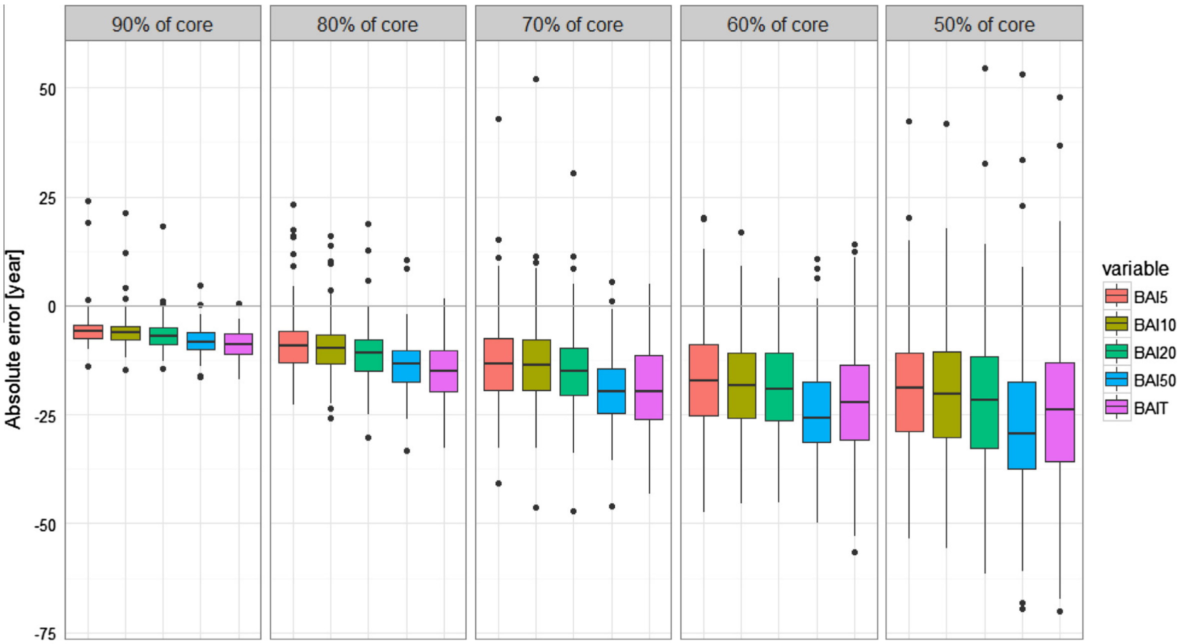

Fig. 2. Absolute deviation from true age for calculation using the mean basal area increment of the innermost 5, 10, 20, 50 and all rings for each partial core length (90%, 80%, 70%, 60%, and 50% of complete core). Boxes represent 25–75% of values, black strips medians, whiskers 1.5 interquartile ranges, and dots outliers.

stem radius longer. The length of the increment core was longer than the stem radius for only two trees (i.e. growth was eccentric and the core was collected on the side with the shorter chronological radius). In both cases, differences were up to 0.7 cm, pith was absent (in both cases two rings were missing to pith) and trees were quite small (radius = 8.6 and 8 cm) with very thin bark. Generally, our results indicated that concentric growth prevailed in our study site, as we did not identify large negative differences between the stem radius and the core length and positive differences are caused by a reasonable bark width (Fig. S2).

We detected a strong, well-fitting significant relationship ($R^2 = 0.42$, $p < 0.001$) between stem radius and estimated bark width (Fig. S2A). Thus, we suggest that the influence of growth eccentricity is negligible and the difference between the geometric radius and the length of the complete core predominantly indicates bark width. The estimated mean bark width is 6.7 cm (Fig. S2B) and this value was further used as the bark width for age estimation of trees with partial cores.

3.2. Testing the accuracy of tree age estimation

The error in age estimation increases as partial core length decreases for both the RG and BAI methods (Figs. 1 and 2). Generally, age estimation by RG methods is overestimated, while BAI

Table 2

Accuracy of age estimation of various methods based on radial growth (RG), basal area increment (BAI) and average between RG and BAI (*m* RG BAI) for individual partial core lengths (50–90%). Mean absolute (A.E.) and percentage (P.E.) errors together with standard error (S.E.) as well as percentage of underestimates (P.U.) and overestimates (P.O.) are shown. Significance (*p*) between real and estimated age is shown: n.s.- non significant, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

Age estimation method	Partial core length																								
	90%					80%					70%					60%					50%				
	A.E. (SE)	P.E. (SE)	P.U.	P.O.	*p*	A.E. (SE)	P.E. (SE)	P.U.	P.O.	*p*	A.E. (SE)	P.E. (SE)	P.U.	P.O.	*p*	A.E. (SE)	P.E. (SE)	P.U.	P.O.	*p*	A.E. (SE)	P.E. (SE)	P.U.	P.O.	*p*
RG5	2.6 (0.6)	1.8 (0.5)	40	59	n.s.	7.9 (1.2)	6 (1)	36	64	n.s.	11.8 (1.7)	9.2 (1.4)	33	67	*	16.5 (2.1)	13.7 (1.7)	29	71	**	22.4 (2.4)	19.3 (1.9)	20	80	***
RG10	3.1 (0.6)	2.1 (0.5)	34	66	n.s.	7.6 (1.1)	5.8 (0.9)	35	65	*	12.8 (1.8)	10.1 (1.4)	29	71	*	15.6 (1.7)	13.5 (1.5)	22	78	**	21.9 (2.2)	19.3 (1.8)	18	82	***
RG20	3.6 (0.6)	2.6 (0.5)	31	69	n.s.	7.5 (1)	6 (0.8)	32	68	*	12.8 (1.6)	10.6 (1.3)	26	74	**	16.8 (1.6)	14.7 (1.3)	19	81	***	24.2 (2.5)	21.3 (2)	22	78	***
RG50	5.1 (0.6)	4 (0.5)	24	76	*	10.4 (1.1)	8.3 (0.9)	22	78	***	15.6 (1.6)	12.2 (1.2)	16	85	***	23.4 (2.3)	17.7 (1.7)	16	84	***	33.4 (3.7)	25 (2.7)	14	86	***
RGT	7.1 (0.7)	5.5 (0.5)	16	84	*	13 (1.2)	10.7 (0.9)	16	84	**	18.5 (1.7)	15.6 (1.3)	13	87	***	24.6 (2.1)	21.2 (1.7)	14	86	***	31.6 (2.9)	27.5 (2.3)	15	85	***
BAI5	−5.5 (0.3)	−5.1 (0.3)	98	2	n.s.	−8.7 (0.6)	−8.1 (0.5)	91	9	**	−12.5 (0.8)	−11.5 (0.7)	91	9	***	−15.9 (1)	−14.3 (0.8)	88	13	***	−18.7 (1.2)	−16.5 (1)	91	9	***
BAI10	−5.9 (0.3)	−5.6 (0.2)	97	3	n.s.	−9.8 (0.5)	−9 (0.4)	95	5	**	−13 (0.9)	−12.1 (0.7)	93	7	***	−17.4 (0.9)	−15.5 (0.7)	94	6	***	−20.1 (1.2)	−17.6 (0.9)	95	5	***
BAI20	−6.7 (0.3)	−6.2 (0.2)	97	3	*	−11.3 (0.5)	−10.4 (0.4)	97	3	***	−14.7 (0.8)	−13.5 (0.6)	93	7	***	−18.8 (0.8)	−16.7 (0.7)	97	3	***	−21.5 (1.3)	−18.4 (1)	94	6	***
BAI50	−8.1 (0.2)	−7.1 (0.2)	99	1	n.s.	−13.7 (0.5)	−11.7 (0.4)	99	1	**	−19.1 (0.7)	−15.6 (0.6)	98	2	***	−24 (1.1)	−18.2 (0.8)	96	5	**	−26.7 (1.8)	−19.9 (1.3)	93	8	**
BAIT	−8.8 (0.2)	−7.8 (0.1)	99	1	**	−14.8 (0.5)	−13 (0.3)	99	1	***	−19.1 (0.8)	−16.8 (0.5)	97	3	***	−22 (1)	−19.2 (0.8)	96	4	***	−23.5 (1.4)	−20.5 (1.1)	93	7	***
m RG BAI 5	−1.5 (0.5)	−1.7 (0.4)	82	18	n.s.	−0.4 (0.9)	−1.1 (0.7)	63	37	n.s.	−0.4 (1.2)	−1.1 (1)	63	37	n.s.	−0.3 (1.5)	−0.3 (1.3)	61	39	n.s.	1.8 (1.8)	1.4 (1.5)	56	44	n.s.
m RG BAI 10	−1.4 (0.4)	−1.7 (0.4)	80	20	n.s.	−1.1 (0.8)	−1.6 (0.6)	63	37	n.s.	−0.1 (1.3)	−1 (1.1)	60	40	n.s.	−0.9 (1.2)	−1 (1.1)	57	43	n.s.	0.9 (1.6)	0.9 (1.4)	54	46	n.s.
m RG BAI 20	−1.6 (0.4)	−1.8 (0.3)	78	22	n.s.	−1.9 (0.7)	−2.2 (0.6)	60	40	n.s.	−1 (1.1)	−1.4 (0.9)	59	41	n.s.	−1 (1.2)	−1 (1)	59	41	n.s.	1.3 (1.8)	1.5 (1.5)	51	49	n.s.
m RG BAI 50	−1.5 (0.4)	−1.5 (0.3)	73	27	n.s.	−1.7 (0.8)	−1.7 (0.6)	60	40	n.s.	−1.7 (1.1)	−1.7 (0.9)	61	40	n.s.	−0.3 (1.7)	−0.2 (1.3)	57	43	*	3.3 (2.7)	2.6 (2)	57	43	*
m RG BAI T	−0.9 (0.4)	−1.1 (0.3)	69	31	n.s.	−0.9 (0.7)	−1.2 (0.6)	63	37	n.s.	−0.3 (1.1)	−0.6 (0.9)	55	45	n.s.	1.3 (1.5)	1 (1.2)	53	47	n.s.	4 (2.1)	3.5 (1.7)	51	49	n.s.

methods strongly underestimate the tree age (Figs. 1 and 2, Table 2). The mean percentage error was at least 2.6% and −5.1% and as high as 27.5% and −20.5% for the RG and BAI methods, respectively (Table 2). Averaging fewer innermost rings resulted in smaller errors in age estimation for both the RG and BAI methods (Figs. 1 and 2, Table 2). As well the larger length of partial increment cores, the smaller variation in age estimation was recorded for both RG and BAI methods (Figs. 1 and 2, Table 2). Non-significant differences between true tree age and age estimation were recorded for 90% length of partial core by RG5, RG10, RG20, BAI5, BAI10 and BAI50 and for 80% length of partial core by RG5 only (Table 2).

Our newly-proposed technique, which averaged the results gained by the RG and BAI methods (for a given length and number of innermost rings of the partial core) provided the most reliable age estimates (Fig. 3, Table 2). The mean percentage error was at least −0.2% and as high as 3.5% (Table 2). The accuracy of age estimation with this novel approach decreased with increasing length of missing radius in similar way to the RG and BAI methods (Fig. 3, Table 2). No obvious influence of the number of tree rings used in averaging was identified, compare to RG and BAI methods (Table 2). Mostly, age estimation does not significantly differ from the true tree age, only the extrapolation of the result for the 50 innermost rings for the 50% and 60% length of partial core showed significant difference (Table 2).

3.3. *Age estimation of partial increment cores*

The age of trees with only partial cores was estimated with the most precise method for every category, i.e. RG5 and BAI5. Both methods showed similar results of age estimation (Fig. S3; Wilcoxon–Mann–Whitney test; $p = 0.25$). Age estimation was higher in 74% by RG5 and in 26% for BAI5 and was consistent between RG5 and BAI5 for a partial core length >70% of the geometric radius (excluding bark width), while for shorter cores BAI5 tends to have higher age estimations compared to RG5 (Fig. S4A). We also identified high consistency between both methods for trees with lower stem radius, however, a higher age estimation for BAI5 was recorded independently of stem radius (Fig. S4B).

We finally utilized two groups of trees to get a linear least-squares regression for indirect tree age estimation based on age and DBH: (1) trees with complete cores and (2) trees with partial cores where the age was estimated by an average between RGT and BAIT. Total RG and BAI was selected as it doesn't significantly differ from the true tree age (Table 2) and it is easy to get this value and make an age estimation, even in the field (compare this to the application of a selected number of inner rings). The proportion of age-variance related to stem radius obtained by linear regression was highly significant (Fig. 4).

4. Discussion

Currently, there is a relatively large variety of methods looking to improve tree age estimation when it is not possible to determine the tree age directly (Villalba and Veblen, 1997; Niklasson, 2002; Rozas, 2003; Pirie et al., 2015). However, these methods are always developed on the basis of virtual cores or complete cores, but rarely applied for age estimation because of (1) high uncertainty, (2) high time consumption or (3) limited application to various species.

Our results have confirmed the previously documented trend of decreasing accuracy of age estimation with increasing length of missing radius (Norton et al., 1987; Rozas, 2003), regardless of the method employed. Moreover, age estimation depends significantly on the number of tree rings used for averaging in both RG

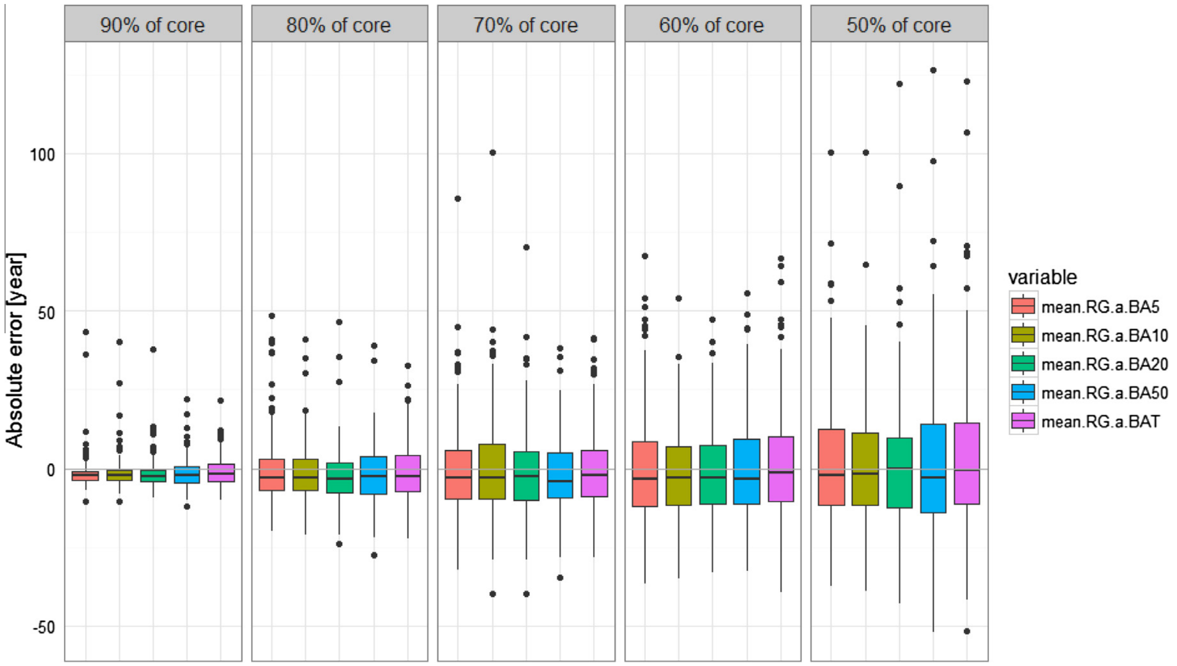

Fig. 3. Absolute deviation from true age for calculation using the average between age estimations gained by RG and BAI methods for the innermost 5, 10, 20, 50 and all rings of each partial core length (90%, 80%, 70%, 60%, and 50% of complete core). Boxes represent 25–75% of values, black strips medians, whiskers 1.5 interquartile ranges, and dots outliers.

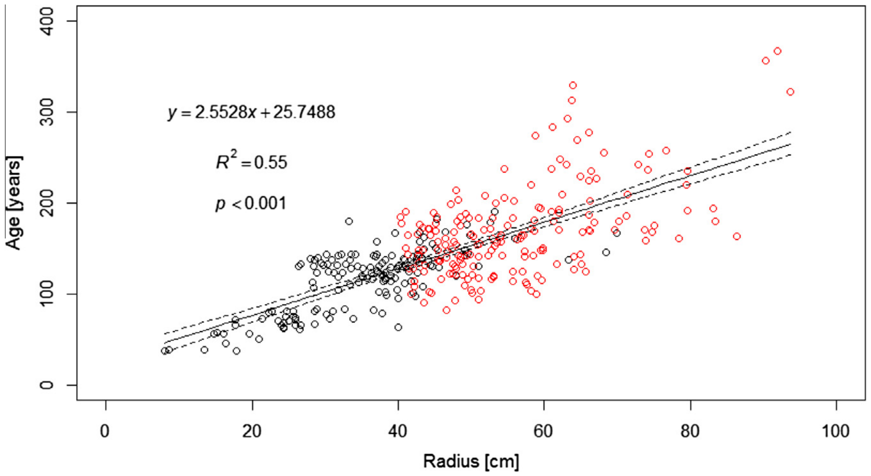

Fig. 4. Relationship of age and DBH for complete cores (black circles) and estimated age for partial cores based on the mean between RGT and BAIT (red circles). Fitted linear model with 95% confidence interval (dashed lines) is shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and BAI approaches. Generally, the lower number of inner tree rings used for averaging yields the most precise age estimation. Hence, the combination of a short length of missing radius and a lower number (5–10) of tree rings used for averaging provided the most precise age estimation. However, the utilization of a lower number of tree rings for averaging can be a potential source of error and thus does not guarantee an unbiased estimate. The mean RG or BAI calculated from a short section of tree-ring chronology can be more affected by short to middle-term growth variation caused by abrupt or suppressed growth after a disturbance event (Altman et al., 2014) or climate anomalies (Briffa et al., 1998). Consequently, the mean calculated on the basis of such an exceptional segment increases the error in the age estimation. Caution is therefore needed, especially for shade tolerant species and individuals which are more frequently affected by disturbances and other factors affecting their growth trend (Frelich, 2002).

It is shown here that the RG method overestimates the true number of missing rings and thus the age of the tree. On the contrary, the BAI method generally underestimates the age. These general trends in the errors of age estimation are caused by (1) the declining growth trend, which is common for light-demanding species (RG) and (2) the low basal area of inner rings (BAI) (Duncan, 1989). Thus, the mean RG of inner rings is always lower than wider rings in the centre of the trunk and leads to overestimation. Similarly, the large basal area of mean BAI of inner rings compared to the small basal area of rings in the centre of the trunk leads to underestimation. Although, in our case, the studied species exhibited exclusively declining (i.e. negative exponential) growth trends and thus we have a relatively homogenous direction of error in the age estimation, future research should focus on the growth trend of studied species. The level of under- and overestimation is strongly dependent on the growth trend, which can vary within species (Rozas, 2003). In principle, the RG method should give the best age estimation if the radial growth trend is flat. However, this is relatively rare, especially for large trees. In contrast, methods extrapolating BAI can be used with confidence for trees with a declining radial growth trend (Rozas, 2003).

To eliminate the contrasting errors of age estimation by RG (overestimation) and BAI (underestimation) methods, we propose a new approach which averages the age estimations gained by RG and BAI methods. The resulting age estimation was the most accurate of all applied approaches and estimated ages do not generally differ significantly for the whole dataset (with exceptions of the mean of 50 inner rings for 60% and 50% partial core lengths). The maximum error (both under- and overestimation) is in all cases lower with the application of our RG-BAI averaging approach when compared with the utilization of RG or BAI methods separately. The accuracy of age estimation with the RG-BAI averaging approach decreases with increasing length of missing radius similarly to the RG and BAI methods, but the errors (both absolute and percentage) are markedly lower in our novel approach. In addition, there is no obvious influence of the number of tree rings used in averaging when compared to RG and BAI methods. For that reason, we suggest the application of averaging between mean RG and mean BAI for the whole core. This is very easy to calculate and can be used for preliminary age estimation, even in the field, if necessary. However, as already mentioned, our dataset is specific with relatively concentric growth and a prevailingly declining growth trend. Hence, the averaging of age estimation made by RG and BAI methods should be tested in future on other species or trees with higher growth variation due to competition.

It was previously noted that trees with large diameters are not suitable for accurate age estimation (Rozas, 2003). However, this is valid mainly for age-diameter equations and we applied our new technique on partial cores from large oaks. Previous age estimations of these large oaks in the Czech Republic was about 400 up to 800 years (Vrška et al., 2006). Nevertheless, our analysis suggests that they are most probably 400 years old at most. It must be noted that we did not include the time needed from germination to reach coring height in our age estimation. However, as our study species is light-demanding, trees were mostly solitary from the beginning of their lives and soil in the area was nutrient rich. Thus we suggest that our studied trees need only a few years (up to 5) to reach the coring height and this error is negligible when compared to other uncertainties in age estimation based on partial cores. In addition, future research should determine if the application of our method is appropriate to light-demanding species "only" or if it will find application across species with various ecological strategies, i.e. shade-tolerant species. Due to fast radial growth of oaks in our study area, we suggest that it is possible to keep the continuity of large oaks as keystone structures in the given landscape and thus preserve the associated biodiversity. However, to maintain the character of this landscape it is necessary to plant solitary oaks as the present generation of large oaks is retreating rapidly. Together with the planting, it is important to open up the canopies of existing closed forests by applying management techniques such as partial cutting, selective harvesting, coppicing and wood pasturing. These would thus change the current course of habitat deterioration in a relatively simple manner (Miklín and Čížek, 2014).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.08.033.

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