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How old are the largest southern Swedish oaks? A dendrochronological analysis

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In the southern Scandinavian landscape, large oaks *Quercus robur* provide habitat for a wide range of species, including a large number species on the national Red list and the EU habitat directive. Since most of these trees are hollow and have likely been growing in conditions different from the ones of an "average" oak in today's more forested landscape, direct inference of their age from diameter may be biased. To provide support for the management of these trees, we estimate their age by combining inventory data on diameter distribution of the largest oaks (n = 236) in the Swedish county of Scania and data on ring width distribution for large (>1 m in stem diameter) oaks collected in seven oak-dominated stands (both woodland-type and denser closed-canopy forests) in southern Sweden (n_{trees} = 69, n_{rings} = 12399). The mode of ring-width distribution was 1.26 mm yr^{-1}. The central 90% of ring width distribution was within 0.54 and 3.38 mm, demonstrating the high growth plasticity of the species. Both ring width distribution in large oaks, divided into 16 width classes, and cumulative 20-yr diameter increments (19 classes) were well approximated by the log-normal function. The largest oaks in Scania are unlikely to exceed 1000 yr, the most probable age estimates of the majority of the inventoried oaks were centered around 500–700 yr. The age distribution of 18 large (69.4–178 cm dbh) non-hollow oaks suggest the maximum age being around 400–600 yr. Conservation-oriented management of oak populations should address the need for preservation of such old trees.

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Oak-dominated woodland and closed-canopy forests have been an important part of the southern Swedish landscape in the past centuries (Nilsson 1992, Eliasson and Nilsson 1999, Lindbladh et al. 2003, Ranius et al. 2008). Extensive logging and conversion of woodland habitats into both agricultural fields and conifer monocultures during the last centuries are all believed to play a role in decline of the area covered by oak forests (Eliasson and Nilsson 1999, Lindbladh et al. 2003). Since large oaks commonly provide habitat to a large number of lichens, bryophytes and insect species associated with large-diameter living, or dead trees (Ranius and Jansson 2000, Manning et al. 2006, Paltto et al. 2008, Ranius et al. 2008), this development has had a negative impact on landscape biodiversity. Old oaks may also be important for local oak regeneration (Götmark 2007) and for preservation of species genetic diversity (Jensen et al. 2002).

Conservation of oak-dominated woodland requires a better knowledge on tree longevity, since such knowledge provides ground for the analysis of tree population dynamics and its modelling which can support long-term planning of conservation actions. Pedunculate oak *Quercus robur* is known to commonly achieve an age of several centuries across most of its distribution range in Europe (Prentice and Helmisaari 1991, Rushforth 1999). However, almost all large oak trees become hollow, which precludes exact estimation of tree age (Ranius et al. 2009). Partly due to this, available inventories of large oaks in Sweden do not provide information on tree ages (Blomberg 2004a, b).

Pedunculate oak is a rather shade-intolerant tree (Grime et al. 1988), which has led many to assume that for this species the size of the tree is indicative of its age. This assumption is probably valid when conditions are more or less open and given that soil conditions across sites are similar. Extending the diameter-age relationship obtained on young and mature trees (<150 yr old) towards older cohorts (>150 yr) is the simplest way to guess the age of large hollow trees (Ranius et al. 2009). However, for the very large trees the estimation of the tree's age from its diameter may be biased. The source of this bias is likely differences in growth conditions between "average" oaks and trees that have achieved a large size. In other words, using a simple regression between diameter and age would inevitably make very large trees very old, which may not necessarily be the case.

The main purpose of this study was to provide age estimates for a population of large oak trees in southern Sweden. We assembled and analysed the distribution of tree-ring increments from large oaks sampled across a range of sites in southern Sweden. This ring width distribution was contrasted against diameter distribution of the largest (>1 m in stem diameter) known oaks in the southern Swedish county of Scania (Fig. 1), available from the literature (Blomberg 2004a, b). By estimating the age of big and likely old oaks with the help of ring-width distribution recorded from such large trees, we avoid possible growth-related bias. We assess uncertainty of resulting age estimates by using independent data from precisely-dated non-hollow oaks. Finally, we compare our results with published data on oak growth rates and maximum ages.

Material and methods

Study area

The data analyzed in the paper originated in the Swedish counties of Scania, Halland, Västra Götaland, and Stockholm (Fig. 1, Table 1). The mean annual temperature in this part of southern Sweden is between 5°C and 8°C. The mean temperature in January varies between –4°C and 0°C, and between 15°C and 16°C in July. There is a large variation in precipitation between the western (up to 1200 mm yr^{-1}) and the eastern (500 mm yr^{-1}) part of the region. Western or south-western winds prevail (Raab and Vedin 1995). The growing period with mean daily temperature >5°C lasts for 180–240 d (Nilsson 1996). The soils of the study region bear a history of glacial dynamics and were formed on sandy and stony moraines (Fredén 2002). The region is situated in the nemoral and boreo-nemoral vegetation zones (Sjörs 1999). Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* are the main coniferous species. Oaks *Quercus robur* and *Q. petraea*, European beech *Fagus sylvatica*, and small-leaved species (the birches *Betula pendula* and *Betula pubescens* and aspen *Populus tremula*) represent the deciduous component in the forest cover (Nilsson 1996). Sites with sampled large oak trees (Table 1) represented two main habitat types for this species in the region – a) forested and mostly closed-canopy stands and b) open woodland stands often used for grazing (Table 1). Since the type of the oak-dominated forest might have been different in the past, this classification represented the state of the stands at the time of sampling only (Niklasson et al. 2002, Niklasson and Nilsson 2005).

Oak inventory data

Data on diameter of the largest oaks (>1 m in stem diameter) was obtained in the published database on the largest trees for the southern Swedish county of Scania (Blomberg 2004a, b; Fig. 1). In most of the cases the oaks recorded during the inventory were initially reported by laymen, who perceived them as "very large", i.e. above the commonly observed size range for this tree. Due to this nature of the data, it carried a clear sampling artefact: on part of the distribution (trees <145 cm in diameter) the number of trees recorded increased with size. In other words, the low numbers of oaks <145 cm dbh (Fig. 3) were a result of not taking into consideration large trees which did not appear "large enough" to be reported.

Acquisition of tree-ring data

To analyze the growth rates of large oaks (>1 m in diameter at breast height, dbh), tree-ring chronologies of 69 such trees were developed from seven localities in southern Sweden (Fig. 1). Most of the data originated from the oak-dominated woodland of Hallands Väderö, a nature reserve located on the island with same name outside the Swedish southwestern coast of the Kattegatt strait (Fig. 1, Table 1).

Trees were cored with an increment corer along two radii. After being dried and mounted on wooden plates, they were polished with up to 400 grit sand paper. The cores were measured using an ANIOL measuring stage controlled by the CATRAS software (Aniol 1983). Each radius was cross-dated and verified by use of signature years (Stokes and Smiley 1968) and through the application of two computer programs: CATRAS (Aniol 1983) and COFECHA. The latter program is a part of the Tree-Ring Data Bank Program Library (Grissino-Mayer et al. 1997). The two radii were averaged into single tree chronologies by simple averaging of two series. No statistical pre-treatment of chronologies was undertaken since the focus of the study was on statistical distribution of absolute ring widths, and not on the temporally-resolved growth histories. All measured tree rings (number of rings = 12 399) were used to obtain statistical properties of their ring width distribution.

Statistical analyses

The age estimation process consisted of the following steps: 1) analysis of aggregated ring-width distribution

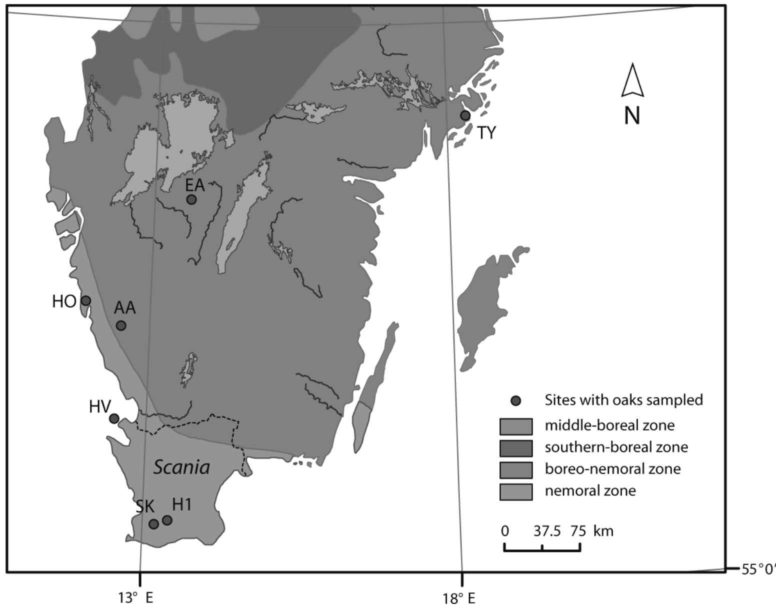

Figure 1. Location of sites with large (>1 m dbh) oaks sampled for constructing ring width distribution. Boundaries of the vegetation zones are according to the Swedish National Atlas (Nilsson 1996). Dashed line is the border of the Swedish county of Scania where the largest oak trees were inventoried by Blomberg et al. (2004a, b).

of large oaks, 2) generation of diameter distribution for 20-yr segments for each tree, 3) conversion of independently collected dbh distribution of large oaks into their age distribution by using the central 90% of the distribution for 20-yr segments, and finally 4) verification of the regression results on independently collected data on exact age of large (>1 m dbh) non-hollow oaks.

To assess the variation of ring increments over time within a single tree we calculated the distribution parameters for 20-yr consecutive ring segments in each tree. We used this procedure to lower the variation in the trees' growth data and to decrease the uncertainty range for conversion of diameter data into age estimates. This procedure was justified by our observation that tree ring pattern of naturally growing oaks is typically a mixture of periods with higher and lower increments. Oaks with consistently high or low increments over most of their lifespan are very rare. We obtained the mode, i.e. the most frequently occurring value, and the 5 and the 95% thresholds of ring width distribution for 20-yr ring segments, which were later used to convert tree diameter distribution into age distribution. Cutting-off the lower and the higher 5% of the distribution translated into 90% probability of our age estimates being within its "true" values.

Table 1. Characteristics of the sites where large oak trees were sampled. n refers to the number of large oak trees sampled in each site. Site type: F – forest, closed canopy stand; W – woodland, savanna-like typically grazed areas. Dbh and age data refer to the stand characteristics. Ring width average and mode refer to sub-population of non-hollow oaks within a site. See Fig. 5 for age/size data of non-hollow oaks for all sites combined.

Site ID	Coordinates	Site type	Canopy dominants	Dbh ± SD, cm	Age ± SD, yr	$n_{hollow}/n_{non\text{-}hollow}$	Ring width average/mode
TY	59°11´N, 18°22´E	W	Oak	80 ± 27.8	214 ± 84.4	2/4	1.38/0.88
EA	58°26´N, 13°40´E	F	Oak, beech, elm	75 ± 25.0	126 ± 14.8	1/0	–
HO	57°30´N, 11°58´E	F	Oak, maple, aspen	82 ± 40.0	174 ± 80.0	5/3	1.82/1.34
AA	57°15´N, 12°13´E	W	Oak	66 ± 29.0	142 ± 94.8	1/2	1.19/1.12
HV	56°27´N, 12°33´E	W	Oak	61 ± 20.5	181 ± 67.1	54/2	0.86/0.65
H1	55°34´N, 13°27´E	F	Oak, beech	89 ± 25.5	143 ± 46.0	3/2	1.87/1.28
SK	55°32´N, 13°14´E	F	Oak, beech, spruce, hornbeam	74 ± 37.6	134 ± 75.2	3/5	1.20/1.08

To evaluate how well the age estimates may represent the actual age of large trees, we collected a separate data set data on large oaks from the same sites with pith present (non-hollow oaks, Table 1, Appendix) and plotted actual ages together with regression lines based on mode, 5 and 95% distribution thresholds of 20-yr segments. In this sub-sample, selected oak trees had fully visible pith or pith located within a few (<3–5) rings from the oldest sampled ring.

Our approach did not carry any assumption about expected tree age nor any age trend (Appendix) in ring increments within a tree. We, however, assumed that the annual growth variation over 2002–1750, the principal period contributed to ring width distribution, was the same as during previous centuries, i.e. the period not covered by trees used to produce the ring width distribution.

Results

The modes of the ring width and 20-yr cumulative increment distributions were 1.26 and 33.05 mm, respectively. The tree-ring increment in 69 large oaks analysed showed considerable variation (Fig. 2). The lower 5% and

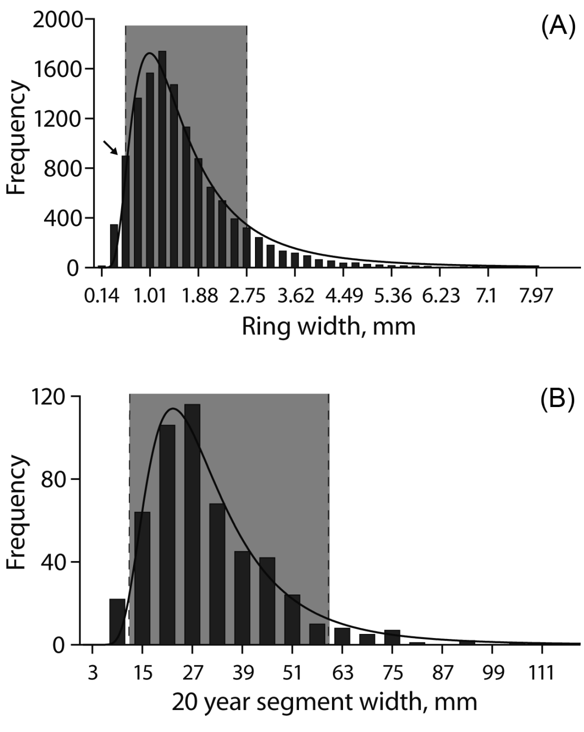

Figure 2. Distribution of ring widths in oak trees larger than 1 m in dbh (A) and distribution of 20-yr width increments obtained on the same data (B). The arrow points to the average annual increment for inventoried oaks in Scania over the period 1953–2002 (0.49 mm yr^{-1}, Blomberg et al. 2004a). The grey area indicates central 90% of the ring width distribution. Log-linear functions are fitted to the observed distributions.

the higher 95% limits of the ring width distribution were 0.54 and 3.38 mm yr^{-1}, respectively. In case of 20-yr increments, the central 90% of its distribution was within 17.07 and 58.54 mm.

The distribution of the raw ring widths was fitted to a log-exponential function (Fig. 2A):

$$Y = \exp(11.74 - 4.29/X - 4.29 \times \ln(X)),$$

where Y was the ring width class frequency (0.22 mm class width), and X was the mid-point of the width class. The amount of explained variation (R^2) and Durbin-Watson statistic were 97.7% and 1.35%, respectively. Similarly, the distribution of the 20-yr cumulative increments was fitted to

$$Y = \exp(30.26 - 138.95/X - 6.22 \times \ln(X)),$$

with R^2 = 96.4% and Durbin-Watson statistic = 2.46 (Fig. 2B) and given 6-mm wide classes.

The mode and the corresponding 5 and 95% limits of the 20-yr increment distribution were subsequently used to convert diameter data on the largest oaks in Scania (Fig. 3) into age estimates (Fig. 4).

The majority of the reported oaks (90%) were between 480 and 720 yr old (Fig. 4), as estimated by the conversion of the 20-yr increment distribution mode (33.05 mm) into age estimates. The large plasticity of growth, however, considerably extended the range of ages within 90% confidence limits from 280 to 1320 yr for all diameter classes combined.

To verify age estimates, ages of 18 big oaks with their piths present were linearly regressed against their dbh (Fig. 5):

$$Y = 1.204 \times X + 191.55,\ R^2 = 0.14.$$

The regression was not significant (p = 0.128). The resulting regression line was plotted together with three oth-

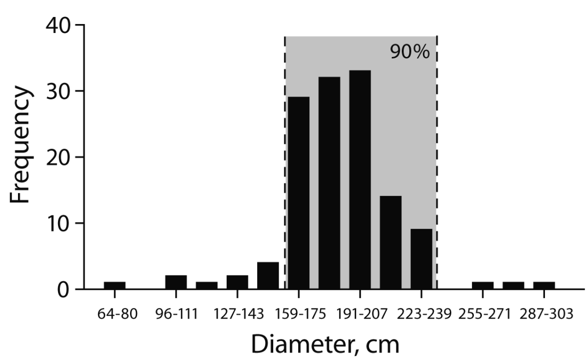

Figure 3. Diameter distribution of large oak trees in Scania as reported by Blomberg (2004a, b). The grey area refers to the 90% of the total amount of oak trees reported in the inventory.

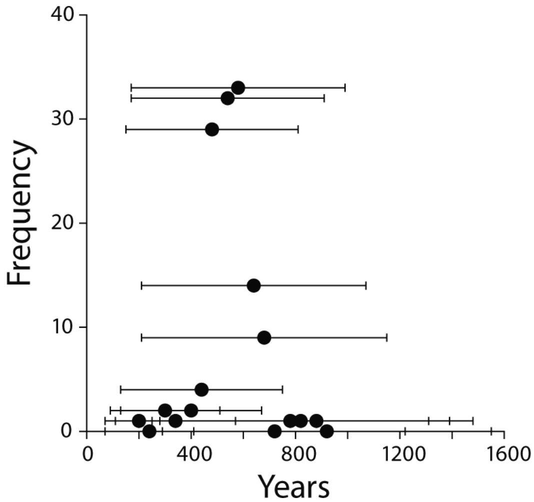

Figure 4. Reconstructed age distributions of the large oaks in Scania. Age distribution was obtained by combining data on the distribution of ring widths (Fig. 2) and diameter distribution of large oak trees (Fig. 3). Mode and central 90% distribution limits (5 and 95%) of the ring width distribution were used to convert means of 16 diameter size classes into age estimates (dots) and provide respective uncertainty estimates.

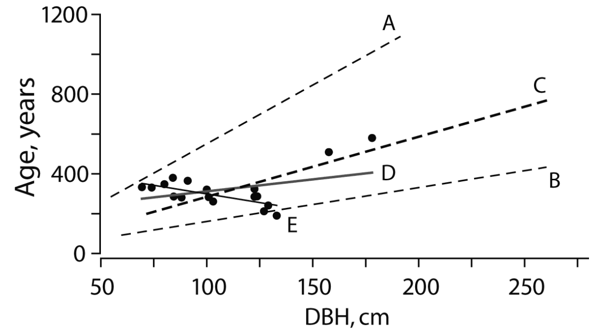

Figure 5. Validation of the age-diameter regression for large oaks in Scania. Dots refer to the 18 non-hollow oaks with precisely estimated age.The solid line (D) is a regression line based on the age-dbh relationship among these trees. Dashed lines are age-dbh regressions based on the higher 95% (A), lower 5% (B), and the mode (C) of ring width distribution in large oaks. Line E represents regression of age against the dbh with two oldest and largest trees excluded.

er regressions representing the mode, the lower 5% and the higher 95% of 20 yr increment of large oaks (dashed lines on Fig. 5). The regression equation based on the mode of the ring width distribution had the form:

$$Age = 3.01 \times dbh - 16.45.$$

By plotting all regression lines together with the exact ages of non-hollow oaks, it was possible to assess potential deviation of reconstructed ages from its "true" estimates. Although average tree dbh in the verification dataset was lower than in the inventory dataset (109.3 vs 187.7 yr), their dbh ranges did overlap (69.4–178 vs 68.5–294.8 cm) and therefore justified the comparison.

Regressions produced from tree ring data were satisfactory when verified on the independent dataset of precisely aged 18 non-hollow oaks. Only one tree (6% of the total amount of trees) fell outside the area limited by the regression lines based on 5 and 95% limits of increment distribution. This number was smaller than the theoretically expected number of trees falling outside the area limited by regression lines based on 5 and 95% distribution thresholds (lines A and B in Fig. 5), given a sample of 18 trees (18 × 0.9 = 1.6 trees). Importantly, trees with the largest diameters stayed close to the regression line, which indicated that predictions based on our linear model did not deteriorate with increase in tree diameters. In turn, the regression line obtained directly from the age–dbh relationship among these non-hollow trees did not adequately represented age-dbh relationship for the oldest trees (Fig. 5, line D). In fact, while considering all but the two oldest trees, the regression line suggested that age decreased with increasing dbh (Fig. 5, line E). In other words, in the dbh range of 100–140 cm the increase in dbh was due to increase in growth rate and not in the tree ages. The respective linear regression (Age = –1.736 dbh + 472.64) explained 43% of age variation and was significant at $p = 0.002$.

Discussion

Growth rate of large oaks

Our study showed that large variability in the oak growth rates, both at the scale of a single year and over 20-yr periods, was the main source of uncertainty in age estimation of large oaks. Although the mode of ring-width distribution was 1.26 mm yr^{-1}, 5% of the ring widths were above 3.38 mm and another 5% of the ring widths were below 0.54 mm, clearly demonstrating the high growth plasticity of this tree species. These calculations assumed absence of missing rings, i.e. rings with zero width in a particular year. Taking missing rings into account while calculating properties of oak ring width distribution would lower the mean and the mode of the ring distribution. Our own experience with cross-dating of oak samples, however, suggests that missing rings are extremely rare in southern Swedish oaks. No missing rings were observed in the dataset used in the current study and we therefore believe that ignoring missing rings in calculating ring width distribution properties in oak did not introduce sizable error in our analyses.

Ring width distribution in large oaks was well approximated by the log-normal function, indicating the presence of a well-defined distribution mode. The mode of distribution obtained in our study was intermediate compared with the range of other published rates. Average ring widths for oaks, growing across a range of site types in England, varied between 2.5 and 5 mm (White 1998), which was substantially higher than growth rates of southern Swedish oaks (1.26 mm). We attribute this difference to the fact that Swedish oaks represent the northern limit of European oak distribution range (Dahl 1998), and experience therefore generally less favorable growth conditions (lower sum of growing season temperatures and higher incidence of cold periods in the beginning of the growing season), as compared to the oaks in Britain. The difference might also arise due to the fact that our ring width distribution represented all tree life stages, whereas rates of British oaks referred to the "mature stage" in a trees' lifespan, which might precede age-related growth declines (White 1998). Moreover, systematic difference in growth rates might exist in rates calculated for very large oaks (our dataset) and oaks of average size (UK dataset). Closer to our estimate was an average diameter increment rate obtained in 250-yr old upland oak forests at the forest-steppe border in Europe – 0.85 mm yr^{-1} (Neshataev et al. 1974). Average diameter increment as derived from repeated inventories in 1953 and 2002 (Blomberg 2004a) was 0.49 mm yr^{-1} and lower than the mode of distribution in our dataset of large oaks. These figures are representing growth rates of trees in the later part of their life, often in a stage of growth decline. In line with this suggestion, this rate was in good agreement with estimates of growth rate for English oaks in the stage of age-related growth decline (<0.5 mm – White 1998). Similarly to European oaks, the average growth rate of 300-yr old white oaks *Quercus alba* in Pennsylvania was estimated to be below 0.75 mm (Abrams and Downs 1990).

In the current study we took advantage of direct measurements of ring widths in large oaks and made no assumptions about timing of different growth periods (initial fast growth and crown expansion, mature stage of growth stabilization, and period of age-related growth decline) in the trees' lifespan. For cases when coring of the trees is not possible (a "no destructive sampling" policy), White (1998) proposed an alternative approach for age estimation, based on the timing of different growth periods. Capitalizing on the large dataset of tree ring measurements, the method provides average species – and site type – specific growth rates for each of the growth periods. However, in regions where strong climatic controls over tree growth are coupled with high variation in site-level conditions, ring-width analysis apparently represents the only consistent method of age estimation in hollow trees.

Age of oaks

Age estimation based on analysis of tree-ring width distribution suggested that the largest oaks (within the dbh range between 68 and 295 cm) in Scania are unlikely to exceed 1000 yr of age. The most likely age estimates of the majority of the oaks inventoried by Blomberg (2004a, b) are to be centred around 500–700 yr. A limited dataset of non-hollow trees with known ages pointed to similar ages. Our estimates are higher than the ones in the database of maximum tree ages compiled by Brown (1996) where the maximum ages of different oak species, though showing large variation within the genius, tend not to exceed 400 yr.

A regression based on the mode of ring width distribution, identified in this study, was a better predictor of the age of the two oldest non-hollow oaks than diameter-age regression based exclusively on the dataset of non-hollow oaks (Fig. 5). This observation, together with the fact that regressions based on 5 and 95% ring width distribution limits covered >90% of the variation in the actual ages, provided support for our age reconstruction. The dataset of non-hollow oaks revealed a generally poor association between age and tree size. Disregarding the two oldest trees in the dataset would effectively eliminate the positive dbh-age relationship. As we originally suggested, the size of the trees (at least within the range of 100–140 cm dbh) was to a larger degree an indication of its growth rate and not its age (Fig. 5, line E). This suggested that site- and tree-specific growing conditions which could also vary in time are the main contributors to variability in the age-diameter relationship. To explore the possibility to incorporate site-level variables in the age estimation procedure, Ranius et al. (2009) included openness and fertility of the habitat as independent variables in the age-diameter regression equation, which improved age predictions for small and moderate diameter oaks (mostly below 60 cm dbh).

Little predictive power of the tree diameter in respect to age estimation poses a challenge during an inventory of old oak trees, since old trees may not be necessarily large. Analysis of the dataset on non-hollow oaks pointed to the absence of positive diameter-age correlation around 50–150 cm dbh (Fig. 5), which was close to a subjective threshold guiding the decision of a field observer to consider a tree as large (Fig. 3). To ensure that old but slowly growing trees are included in the future oak inventories, we advocate the use of a clearly defined lower diameter threshold for a tree to be included in the inventory. We therefore propose 70 cm dbh as such a provisional threshold. We would further advice to consider site conditions as an additional factor in choosing the trees, with more xeric conditions indicative of older ages (Ranius et al. 2009).

Management considerations

With the possible exception of the oldest specimens of yew *Taxus baccata* and juniper *Juniperus communis*, our results support the view of the oak as the longest living tree in southern Scandinavia. This result argues for development of conservation management specifically oriented towards preservation of large and old oaks across the landscape (Alexander et al. 1996, Götmark 2007, Franc and Götmark 2008). In southern Sweden, a number of localities exist where oak populations may contain a high proportion of trees approaching 300–400 yr (Nilsson et al. 1999, Lannér et al. 2004). Our study demonstrates the potential of using region-wide datasets of ring increments to provide age estimates of such trees. The presented regression equation, developed mostly with data from sites on sandy and stony moraines, provides a tool to assess the age of such trees and, therefore, improves site evaluation in the context of its biological and historical values.

A discussion on oak maximum ages is not complete without a brief review of factors responsible for mortality of old and typically large oak trees. The current mean annual mortality rate of oaks older than 200 yr in a large sample of southern Swedish oaks is 1.0% with variation among different diameter classes being 0.2 to 3.2% (Drobyshev et al. 2008). There is little empirical knowledge on dominant mortality factors for large and old oaks, and the exceptional ability of these trees to survive as broken and hollowed complicates this picture. There is general agreement that decline in physical properties of the main stem wood, making trees more susceptible to high wind speed episodes, is an important mortality factor of these trees (Niklasson and Nilsson 2005). Wood decay in old oaks is primarily related to natural scarring of the tree and changes in the wood moisture content (Boddy and Rayner 1983). However, the timing of decay development and actual tree mortality in oak show little correlation as a vast majority of old trees are hollow. We speculate that mortality of large oaks is driven by an interaction between a long-term decrease in wood physical properties of the main stem and the occurrence of more short-term "trigger" events. For example, both published studies (Führer 1999, Gaertig et al. 2002, Drobyshev et al. 2008) and our field observations suggest that an increase in stand density and alteration of soil water regime, commonly resulting from changes in land-use pattern, may be important factors behind mortality of old oak trees.

Better age estimates for old oaks, coupled with data on mortality rates for such trees, may be of value for biological monitoring purposes. Differences in the mortality rates of "equally-old" trees among stands, parts of the landscape, or large geographical areas may be indicative of the variation in growing conditions and survivorship rates among analysed populations. This knowledge should add to a better understanding of oak population dynamics under changing environmental conditions.

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Appendix

Examples of growth patterns of non-hollow oaks, illustrating large growth variability and difficulty in defining a common age trend. Data are raw ring width averaged from two radii of the same tree.