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Development of tree hollows in pedunculate oak (*Quercus robur*)

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Development of tree hollows in pedunculate oak (*Quercus robur*)

Abstract

Many invertebrates, birds and mammals are dependent on hollow trees. For landscape planning that aims at persistence of species inhabiting hollow trees it is crucial to understand the development of such trees. In this study we constructed an individual-based simulation model to predict diameter distribution and formation of hollows in oak tree populations. Based on tree-ring data from individual trees, we estimated the ages when hollow formation commences for pedunculate oak (*Quercus robur*) in southeast Sweden. At ages of about 200–300 years, 50 % of the trees had hollows. Among trees < 100 years old, less than 1 % had hollows, while all > 400-year-old trees had hollows. Hollows formed at earlier ages in fast-growing trees than in slow-growing trees, which may be because hollows are formed when big branches shed, and branches are thicker on fast-growing trees in comparison to slow-growing trees of the same age. The simulation model was evaluated by predicting the frequency of presence of hollows in relation to tree size in seven oak stands in the study area. The evaluation suggested that future studies should focus on tree mortality at different conditions. Tree ring methods on individual trees are useful in studies on development of hollow trees as they allow analysis of the variability in time for hollow formation among trees.

Key words: dendrochronology, modelling, tree cavity, tree growth, tree mortality

Introduction

Tree hollows provide important habitats for a wide range of invertebrates, birds and mammals (Gibbons and Lindenmayer, 2002; Kosinski, 2006; Ranius et al., 2005). Species dependent on tree hollows are facing decreasing habitat availability because ancient trees have declined both in forests and agricultural landscapes (Kirby and Watkins, 1998; Nilsson, 1997). For this reason, an urgent task for conservationists is to ensure that sufficient numbers of hollow trees are maintained continuously in the future. Because hollow trees do not persist for ever, it is essential to ensure that new hollow trees are generated if a given number of hollow trees is to be maintained. Furthermore, many sites have so few hollow trees that there are considerable risks of the extinction of threatened species (Ranius et al., 2005). At such sites the number of hollow trees should not only be maintained, but increased as quickly as possible. Thus, for long-term conservation planning, knowledge about the rates of formation and deterioration of hollow trees is required. Simulation models have been used to predict long-term changes in the abundance of hollow trees in forests (Ball et al., 1999; Fan et al., 2004); Fan et al. (2004) parameterised such a model based on simple statistical relationships derived from stand level data from a forest landscape in the USA, while Ball et al. (1999) focused on one eucalypt species in Australia. The latter model was parameterised inter alia from changes in trees observed through repeated measurements (Lindenmayer et al., 1997). This approach should yield reliable data. However, because the dynamics of tree hollows are slow, there may be long delays before meaningful results based on direct observations of formation and deterioration of hollow trees can be obtained. An alternative is to parameterise a model of hollow dynamics by interpreting patterns observed in snapshot studies of trees, using tree ring-based assessments of their ages.

In this study, we constructed and parameterised a dynamic model that predicted size distribution and formation of hollows in trees. In contrast to attempts to model hollow tree dynamics in Northern America and Australia, we used an individual-based model, taking into account the variability in growth rate and hollow formation among trees. This was possible because we used tree rings of individual trees to estimate the ages of trees when hollow formation commences. Our study was conducted on pedunculate oaks *Quercus robur* L. in southeast Sweden at sites largely consisting of pasture land. In Europe, pedunculate oak is the most important tree species for invertebrates associated with tree hollows (e.g. Palm, 1959; Ranius et al., 2005). Our main objective was to estimate at which age hollows are formed in trees with different growth rate. The simulation model required growth rate data, so we analysed variations in growth rate among trees and during the ageing of individual trees. By comparing model predictions with field data on tree size distribution and incidence of tree hollows at seven sites, we evaluated the model and identified gaps in our knowledge that should be filled in by future field studies.

Methods

Study sites and study trees

We conducted this study in an area south from Linköping, southeast Sweden, with one of the highest concentrations of old oaks in Northern Europe (around 58º15'N, 15º45'E; Antonsson and Wadstein, 1991). This was because samples from a large number of hollow trees are required, and for some of the analyses it was required that the trees have been growing under similar conditions, while for others a variability in e.g. growth rate was desirable. We mainly focused on seven sites with a high density of hollow oaks, situated 0.5 – 25 km from each other. The variability among these sites is representative for oak localities with high conservation value in Sweden. Five of these sites (Brokind, Kalvhagen, Orräng, Storängen, and Sundsbro) are currently grazed by cattle and situated on fertile soils dominated by deep clay soils (Johansson and Gorbatschev, 1973). At the two other sites, Långvassudde and Sturefors, there is no grazing and shallow soils are dominating. Levels of sun-exposure differ both among and within sites, but due to grazing or to the shallowness of the soils only a few trees are found in very dense situations (Fig. 1). Previously, the land was used for hay-making, which also inhibited the development of dense vegetation.

In surveys of all sites, for all trees with dbh > 10 cm we recorded circumference, whether the tree was alive or dead, and whether or not the tree had a hollow. Hollows were defined as cavities in which the inner space was wider than the entrance, and the diameter of the entrance was > 3 cm. To obtain data on the age and growth rates, sets of ten oaks per site were selected for ring sampling. The oaks were selected to match the mean diameter and proportion of hollow trees in the entire oak population at the respective sites (Table 1 and 2).

We also needed a data set from trees that have grown under similar conditions. Therefore we selected sites with similar tree growth rates (Sundsbro, Brokind, Storängen, and Kalvhagen; Table 2) and extended the tree ring sample to 53–57 trees per site (three sites: Brokind, Sundsbro, and Bjärka Säby; Bjärka Säby consists of three subsites: Storängen, Kalvhagen and Bjärka äng) for a more detailed analysis of the among-tree-variability in age at which hollow development commences (Table 3). Thus, in total we had tree ring samples from 195 trees (53 + 55 + 57 +10 + 10 + 10; two of the seven study sites were included in the Bjärka Säby site). All trees were alive except two, which had died recently. We attempted to select approximately equal numbers of trees from each of the following categories: (*i*) young trees without hollows, (*ii*) older trees without hollows, and hollow trees with (*iii*) small entrances, (*iv*) intermediately-sized entrances and (*v*) large entrances.

Model outline and tree mortality

The destiny of each tree was determined by stochastic equations that predicted tree growth, formation of hollows and tree mortality. For each simulated year, we summed the number of trees present categorised according to different tree characteristics. As we assumed the recruitment and mortality of trees and formation of hollows to occur with the same probability every year, our simulated stand of trees reached a steady state. The diameter distribution of the trees and proportion of hollow trees at the steady state was the outcome from the model.

The recruitment of young trees was assumed to be 20 trees per year, which was large enough to get a stable outcome over simulation runs. The trees were growing with different rates according to field data; growth rates were modelled for each tree by drawing numbers randomly from a normal distribution based on means and *S.D.* of growth rates for each simulated stand. The growth rate was assumed to decrease with tree age according to a function obtained from tree ring data (see *Results*). Furthermore, for each tree, the age at which hollows are most likely to form was calculated using a function based on the treespecific growth rate (see *Results*). The age at which hollows formed in individual trees was determined by drawing numbers randomly from a normal distribution, the deterministically predicted age being the mean and the estimated variability being the *C.V.*

The tree mortality of hollow oaks was estimated from observation of about 470 tree-years (number of trees multiplied by the years of study) between 1995 and 2007, during the course of investigations on the beetle *Osmoderma eremita* (e.g. Ranius and Hedin, 2001). During that time six trees died, suggesting a mortality rate for hollow oaks of about 1.3 % per year. Two of these trees fell down, while the other four trees remained standing; no tree died because the trunk was broken. For oaks in forests in Austria and Lithuania, an annual mortality rate of about 0.3 % has been reported, excluding trees affected by self-thinning (Monserud and Sterba, 1999; Ozolincius et al., 2005). Therefore, in our simulations an annual mortality rate of 0.3 % was assumed for oaks without hollows, and 1.3 % for oaks with hollows. Thus, we assume that the difference in tree mortality between these studies reflects that the stability is considerably lower in hollow trunks, at least in those with wide cavities in relation with the tree diameter. Our assumption is in line with the increased mortality generally observed among the oldest trees (Monserud & Sterba 1999), however, we assume that young trees are growing under such conditions that self thinning does not enhance mortality among them. At a tree age of 500 years, the mortality rate was assumed to be 100 %, because we never observed trees older than that (maximum estimated age: 478 years).

Estimating tree age and relating age with incidence of hollows

We estimated the age that the trees had in 2005, using the same method as Ranius et al. (2008). From each tree, two to four increment cores were taken at a height of 0.5 – 1.3 m. The cores were cross-dated using the classical memory dating method based on conspicuous pointer years (e.g. Stokes and Smiley, 1968). When the pith was reached by any of the increment cores, the age was estimated by counting the annual rings. When the pith was missed, but the best increment core reached a point less than 25 mm from the pith we estimated the distance to pith by fitting a transparent plastic with imprinted concentric circles on the sample. The number of rings missed was estimated by assuming the growth rate being equal with the three innermost rings of the core. For the remaining trees, age, *a*, was estimated using the following equation:

$$a = c + r / (k \times g) \qquad \text{eqn (1)}$$

where *c* is the number of annual rings in the longest increment core, *r* is the length of missing radius (*i.e.* distance from the innermost tree ring present to the geometric midpoint), *g* is the annual average growth rate of the innermost ten years of the increment core, and *k* is a parameter that depends on how quickly the annual growth rate decreases with tree age. We assumed that the value of *k* may vary between trees with different characteristics due to different growth patterns.

A function that predicts *k* has been obtained by using tree ring data from 95 trees with intact trunks (Ranius et al., 2008), which all were included also in the present study. From these trees, hollow trees were simulated by assuming the inner part of the trunk to be absent. The absent inner parts corresponded to multiples of ten annual rings. We weighted the data set of simulated trees to obtain the same distribution of trunk diameters and core lengths as among the trees we wanted to age. For each simulated tree, we calculated the true value of *k* from the intact annual rings. The value of *k* (or the logarithm of *k*) was used as dependent variable in a multiple linear regression model. As independent variables we used characteristics that were available for all trees and might be correlated with the growth rate pattern (trunk diameter, length of missing radius, growth rate of the inner ten years, and bark crevice depth). By including both the independent variables and their logarithms, and successively removing non-significant ($p < 0.05$) variables, we obtained the following function:

$$k = 1.66 - 0.90 \ln(g) \qquad \text{eqn. (2)}$$

where g is the growth rate (in mm yr^{-1}) of the inner ten rings of the increment core. For the simulated hollow trees, there was a strong correlation between the real age and the age estimated by the function ($R^2 = 0.839$). When eqn. (1) and (2) were used to estimate tree age in the present study, the piths were assumed to be at the geometric centres of the trunks.

Relationships between tree age and occurrence of hollows

We estimated the age at which hollow development commences using data from all seven study sites. Among the 70 oaks selected for tree-ring sampling (see *Study sites and study trees*), we analysed the relationships between the presence/absence of hollows and trunk diameter and estimated tree age by univariate logistic regression. We also constructed a multiple logistic regression model with diameter, growth rate (total radius / total age) and openness as independent variables. Diameter was replaced by growth rate, because growth rates could be directly used in the simulation model, and openness might be relevant because it may affect the wind exposure and growth of branches. In all of the multiple logistic regressions in this study, the statistical significance of the examined relationships was evaluated by calculating log likelihood ratios.

We used increment cores from 165 oaks in three relatively similar sites (see *Study sites and study trees*), to obtain a measure of the variability in tree age at which hollow formation commenced. To obtain a data set representative for the entire oak populations at these sites, we categorised the sampled trees in terms of diameter (categories: 10–40, 40–60, 60–80, 80–100, and >100 cm) and presence/absence of hollows, and weighted the categories to match the distributions of sampled trees with the entire oak population. The variability in tree age at which hollow formation commenced was estimated assuming that the difference in proportions of hollow trees between a younger age class and an older age class reflects the probability of hollow formation at a tree age among these classes. For instance, if 4 % of the trees that are 100-200 years had hollows, and 57 % of the trees that are 200-300 years had hollows, we estimated that for 53 % of the total number of trees, hollow formation commences at an age of about 200 years. From these percentages, we estimated the variability (*C.V.*) in tree ages at which hollow formation commenced.

Growth rate

We analysed growth rate data from the 165 cored oaks in Sundsbro, Brokind, and Bjärka-Säby. We analysed changes in annual ring width in relation to the ageing of trees, using all trees that were both old (> 100 years) and large (diameter > 50 cm), and in which it was possible to obtain a core to the pith (n = 77). For each of these trees, we set the mean ring width during the earliest 50 years to 1, and for every 10-year period (including the first 50 years) a relative value of growth rate was calculated. We then derived functions between tree age and relative growth rate by linear regression. We used both the variables and the logarithms of the variables (*i.e.* four different combinations are possible), to find the function with the strongest correlation (highest R^2 value).

Model evaluation

The model was used to predict the diameter distribution of the trees and incidence of hollow trees at equilibrium at the seven study sites. This was compared with field data obtained for all 1948 oaks (with a diameter > 10 cm) at the sites. Large differences between the model outcome and the field data may indicate that the model should be improved, but it may also be a consequence of variation in recruitment and mortality of trees over time, which may imply that the study stands are not in the steady state that is assumed in the simulations.

Results

Presence of hollows in age-estimated trees

Across the seven study sites, where there were wide variations in growth rates, the presence of hollows was positively related to both tree age and diameter ($p < 0.001$ for both; univariate logistic regression, $n = 70$). According to the multiple logistic regression analysis, also the age and growth rates of the trees were positively correlated with the presence/absence of hollows (p (Age) < 0.001, p (Growth rate) = 0.012, $n = 70$, model: $P / (1 - P) = \exp(-9.72 + 0.028 \text{ Age} + 1.39 \text{ Growth rate (in mm yr}^{-1}))$, where P is the probability of presence). Openness was excluded from the model, because its effect was not statistically significant ($p = 0.724$). The obtained logistic regression model was used to predict the age at which the probability that hollows would be present exceeded 50 %. At growth rates of 0.65, 1.8 and 3.4 mm yr^{-1} (the 2.5th percentile, mean and 97.5th percentile, respectively), this occurred when the oaks were 315, 258 and 178 years old, and their diameters (with bark) were 45, 101 and 132 cm, respectively.

We estimated the coefficient of variation (*C.V.*) of the age at which formation of hollows commences to be 35 %, which was used as a parameter in the model. This estimate was based on data from trees examined at the Sundsbro, Bjärka-Säby and Brokind sites, because the growth rates were similar at these three sites. Among these trees, the presence/absence of hollows was significantly related to age, but not to growth rate (p (Age) < 0.001, p (Growth rate) = 0.620, multiple logistic regression, $n = 165$, weighted samples). The *C.V.* estimate was derived from observed frequencies of hollows in each of the age classes (Fig. 2) and the fact that the youngest hollow tree found was 90 years old. We estimated that the first hollow is formed in <1, 4, 53, 15 and 29 % of trees when they are 90, 100, 200, 300 and 400 years old, respectively, which is corresponding to a C.V. of 35 %.

Growth rate and model predictions

Growth rate slightly declined as tree age increased (Fig. 3), but tree age only explained a minor part of the variability in growth rate over time ($p < 0.001$, $R^2 = 0.050$, $n = 1455$). At the study sites, there were no clear trends in the mean annual growth rate over time (Fig. 4).

For six study sites out of seven, the simulation model predicted that trees in the smallest size class would be the most frequent (Fig. 5). However, according to the field data this was only true for two sites – Storängen and Sturefors. At most of the sites, there were greater frequencies of trees of intermediate size (40 – 100 cm) than the model predicted.

As expected, the frequency of hollows increased with tree size according to both the field data and model predictions. Furthermore, at sites with relatively low growth rates (Långvassudde and Sturefors) the frequency of hollows was higher in given size classes than at sites with higher growth rates both according to field data and model predictions (Fig. 6).

Discussion

Presence of hollows in age-estimated trees

Our study is probably the first in which ring analyses of individual trees have been used to estimate the probability of hollow formation as a function of tree age. Such estimates are essential for placing the occurrence of tree hollows in a temporal perspective. We have shown that for pedunculate oak hollow formation begins rather late; in an oak with an average growth rate, the probability for the presence of a hollow reached 50 % when the tree was 258 years and in only 4 % a hollow is present at an age of 100–200 years. Because managed oak stands are subject to final felling at ages of 120–150 years (Almgren et al., 1984), this largely explains why hollows are so rare in managed oak forests. For European tree species, previous estimates of the age at which hollow formation commences have not been based on any systematically collected data. According to Speight (1989) "accumulation of tree humus can have started in rot holes" at the age of 150 years, and at ages exceeding 250-300 years, the presence of habitats for saproxylics can be "obvious". Studies of tree hollow formation have been more common in Australia than in the Northern hemisphere (Gibbons and Lindenmayer, 2002). These studies have mainly been based on general relationships between diameter and age, rather than age estimates of individual trees (e.g. Wormington et al., 2003; but see Whitford (2002) who considered the age of individual trees and the number of hollows, although not presence/absence of hollows).

We found that in fast-growing trees, hollows are generated at an earlier age than in slow-growing trees. However, when hollow formation commences, fast-growing trees have still usually reached a larger girth than slow-growing trees. Thus, the probability of presence of hollows increases with both the age and the growth rate of the trees independently. Probably most of the hollows in our study area have been formed by shedding of branches. Only if the branches are big enough, a hollow will develop in the scar. This is supported by the fact that the highest frequency of hollows was at a height of 2 – 5 m, which is the height of the largest branches (pers. obs.). Rotten centres were common in trunks of hollow trees, but very rare in trees without hollows, which indicates that the decay usually starts from a scar and goes inwards, rather than in the opposite direction. Trees that grow faster get big branches earlier, which gives an explanation to the earlier formation of hollows in fast-growing trees.

In this study we found a difference in hollow formation between fast-growing and slow-growing trees. If compararisons were made between areas with different tree species and different current and historical management regimes, the variability in the dynamics of hollow development would most likely be wider. In other regions, forest fire (Inions et al., 1989) have been found to be important for hollow development, but our study trees have not been affected by that. Pollarding may have a big influence on hollow development (Ranius et al. 2005). In Sweden, pollarding of oaks have been forbidden, but in the 18^{th} century oaks were damaged in several ways that may speed up hollow formation (Eliasson and Nilsson, 2002).

Growth rate

Growth rate, measured as the annual ring width, decreased with tree age (Fig. 3). This type of growth trend has been frequently observed in openly-grown competition-free trees (Cook, 1990). The decreasing growth rate is partly due to the geometric relationship between increments in volume and the circumference of the stem; if a given volume of wood is added to a thin stem, the diameter will grow more than if added to a larger stem (cf. Cook, 1990; White, 1998). In the trees we examined, the decline in growth rate with age was fairly small; at ages of 200–300 years, the growth rate was still > 70 % of the growth rate during the first 50 years of the trees' lifetimes (Fig. 3). In addition to low mortality rates (Ozolincius et al., 2005), the sustained growth rate of oak trees at high ages accounts for much of their ability to attain huge sizes. Consequently, oak is one of the largest tree species in Northern Europe (Nilsson, 1997).

Model predictions

Given that the establishment of oaks may vary widely over space and time due to management history (Rozas 2004), it was not surprising that there were deviations between field data and predictions of the proportions of trees in different size classes. At all study sites, we found lower proportions of small trees (diameter < 40 cm) than predicted by the model, in which constant mortality and regeneration rates were assumed (Fig. 5). The low density of small trees may be due to unsuccessful regeneration (e.g. due to grazing) or cutting of young trees. These findings imply that the density of hollow oaks will probably decrease in 100–200 years, but the length of the period in which hollow tree density is lower than it is now will depend on whether actions to promote regeneration are taken. Consequently, planning over at least two centuries is required to ensure that sufficient numbers of hollow trees are maintained at such sites.

As predicted by the model, and observed in many previous studies (e.g. Wormington et al., 2003; Harper et al., 2005), there was a strong positive relationship between the frequency of presence of hollows and tree size (Fig. 6). However, for several size classes at individual sites the model predictions fitted poorly with the field data. The most distinct deviation between the predictions and the field data was that at Långvassudde, and to lesser extents Sturefors and Kalvhagen, the model overestimated the proportions of hollow trees in the category with the biggest trees. Sturefors and Långvassudde had the lowest average growth rates, and at Kalvhagen too there were trees with low growth rates, because the growth rate varied widely among trees at this site. The reason for the deviation might be that we assumed the mortality of trees to be equal for all hollow trees, but falling rates may be higher among small hollow trees than among larger ones (Lindenmayer et al., 1997), even though there are no data supporting this hypothesis for oak. The mortality rates of the relatively small hollow trees at Långvassudde, Sturefors and Kalvhagen may be higher than predicted by our model, which may explain why hollow trees were underrepresented in the large diameter class at these sites according to our field data. Thus, better data on tree mortality rates at different circumstances would be desirable. Other deviations between predictions and field data may be due to variations in land use history (with respect, for instance, to tree regeneration, cuttings and canopy closeness; cf. Rozas, 2004) that are unknown and thus were not taken into account in the model parameterisation. Regardless of the model used, unexpected events affecting the recruitment and mortality may sometimes cause wide deviations between real and predicted outcomes.

Conclusion

Hollow oaks occur in forests as well as in more open habitats, such as oak pastures. Today, those ancient oaks that still exist in forests in Europe are often slowly growing trees in steep or rocky terrain (e.g. Ek et al., 1995), as more productive forest land is usually managed. On the contrary, oak pastures often occur on relatively fertile soils. In forests, hollow oaks can at least theoretically occur in higher densities than in pastures, but competition and often also low productivity makes the annual tree growth lower and thus, the maximum tree girth smaller. Our study points out two reasons why oaks in pastures are generally more valuable for hollow-dwelling fauna than oaks in forests. Firstly, higher growth rate implies that hollows are formed at an earlier tree age. Secondly, probably larger girth implies a lower tree mortality, and thus a longer average life-time in more open situations. Therefore, it is important that ancient trees are maintained at productive land, and not only retained at land of low economic value.

The time between the regeneration of trees and the formation of tree hollows is long (in the case of oak more than 200 years). Hence, long-term planning is necessary to ensure the persistence of fauna associated with tree hollows in many different tree species and in different forest types. The planning is facilitated by simulation models, which could be used to compare future management scenarios in terms of hollow tree dynamics. Such models become more realistic if based on tree ring methods applied on individual trees, as there may be a wide variability in growth rate and formation of hollows among trees also within sites.

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Fig. 1. Oaks (*Quercus robur*) at one of the study sites – Storängen – which is grazed by cattle.

Fig. 2. Proportions of oaks (*Quercus robur*) with hollows in different age classes. The data set was weighted, to obtain the same distribution in size categories and regarding presence/absence of hollows as seven sites with oaks in southeast Sweden. n-values in the unweighted data set: < 100 yrs, 32; 100-200 yrs, 37; 200-300 yrs, 45; 300-400 yrs, 35; > 400 yrs, 15.

Fig. 3. Relative growth rates (according to the field data and the function derived from linear regression, dotted line) in relation to tree age. Means from ln transformed values. Function: ln (Relative Growth Rate) = 0.371 – 0.127 ln (Tree Age). For each tree, the mean annual ring width at the age of 0 to 50 years was set to 1 and relative growth rates were calculated for each decade. Data from oaks (*Quercus robur*) in southeast Sweden in which the increment core was intact to the pith. The *n*-value decreases with increasing age from 77 (Age = 10) to 8 (Age = 300).

Fig. 4. Mean annual growth rate per decade in sampled oaks (*Quercus robur*) from three study sites in southeast Sweden. Only for categories including at least five trees, mean values are shown. Total number of sampled oaks: Sundsbro, 57; Bjärka-Säby, 53; Brokind, 55.

Fig. 5. Size distributions of oaks at the seven study sites in southeast Sweden. Black bars: predicted from the model, assuming constant recruitment and mortality over time. White bars: field observations.

Fig. 6. Frequency of oaks (*Quercus robur*) with hollows in different trunk diameter classes at the seven study sites in southeast Sweden. Black bars: predicted from the model, assuming constant recruitment and mortality over time. White bars: field observations.

Table 1. Frequencies of trees and characteristics of pedunculate oaks (*Quercus robur*) at the seven study sites in southeast Sweden.

	Area (ha)	Trees /ha [a]	Percentage oaks	Percentage of oaks which had hollows	Percentage of oaks which were dead	Closeness (mean) [b]	Mean diameter of hollow oaks (cm) [a]	Mean diameter of oaks with no hollows (cm) [a]
Brokind	15.5	18	52 %	17 %	1 %	0.89	101	59
Kalvhagen	9.5	60	46 %	22 %	2 %	1.00	99	74
Långvassudde	2.9	226	47 %	27 %	12 %	1.88	56	52
Orräng	4.8	78	66 %	24 %	2 %	0.85	88	74
Storängen	5.2	84	70 %	17 %	3 %	1.08	96	50
Sturefors	2.6	173	48 %	21 %	0 %	1.36	51	40
Sundsbro	7.1	69	63 %	19 %	2 %	0.80	104	62

[a] Including all trees with a diameter at breast height > 10 cm.
[b] Closeness of the surrounding canopy was estimated for each tree as free-standing (= 0), half-open (= 1) or closed (= 2).

Table 2. Characteristics of the sets of ten oaks (*Quercus robur*) from which increment cores were taken at each site, selected to match the mean diameter and proportion of hollow trees in the entire oak population at the respective sites (see Table 1).

Site	Mean growth rate [a]	C.V. growth rate [a]	Tree age, Mean (Min - Max)	Percentage hollow trees	Mean diameter of hollow trees (cm)	Mean diameter of trees with no hollows (cm)
Brokind	2.2	25%	163 (94 - 298)	20%	113	72
Kalvhagen	1.6	63%	168 (17 - 276)	30%	107	63
Långvassudde	0.7	32%	263 (177 - 305)	30%	62	46
Orräng	2.0	52%	246 (124 - 368)	20%	92	74
Storängen	1.3	38%	198 (87 - 391)	40%	107	50
Sturefors	0.8	35%	199 (105 - 299)	20%	54	36
Sundsbro	1.5	36%	181 (94 - 320)	20%	103	66

[a] Growth rates were measured for each tree as the mean width of the annual rings over the last 40 years.

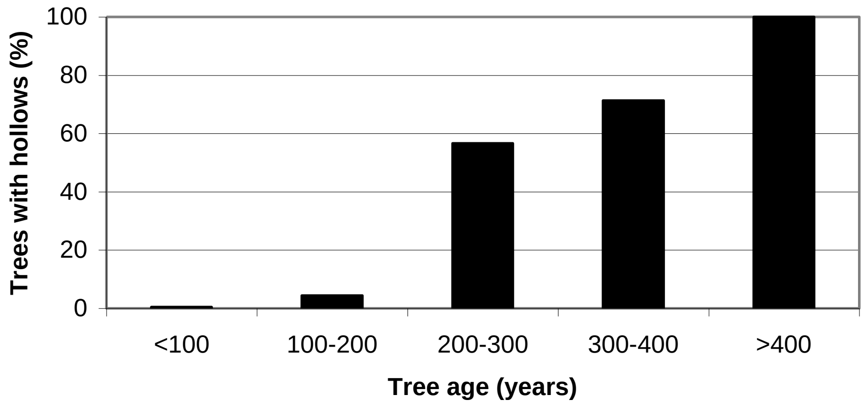
Table 3. Characteristics of oaks (*Quercus robur*) examined at the three study sites in southeast Sweden selected for a more detailed analysis of the tree growth and the variability in age at which hollow development commences among trees. Mean values (minimum and maximum values in parentheses).

Site	n	Diameter	Closeness [a]	Tree age [b]
Brokind	55	99 (10-199)	0.64 (0-2)	243 (25-478)
Bjärka-Säby	53	80 (12-166)	1.00 (0-2)	225 (17-457)
Sundsbro	57	82 (12-202)	0.72 (0-2)	211 (26-455)

[a] Closeness was estimated for each tree as free-standing (= 0), half-open (= 1) or shaded (= 2).

[b] Age estimated as described in the *Methods* section.

Fig. 1.



100
80
60
40
20
0
Trees with hollows (%)
<100
100-200
200-300
300-400
>400
Tree age (years)

Fig. 2.

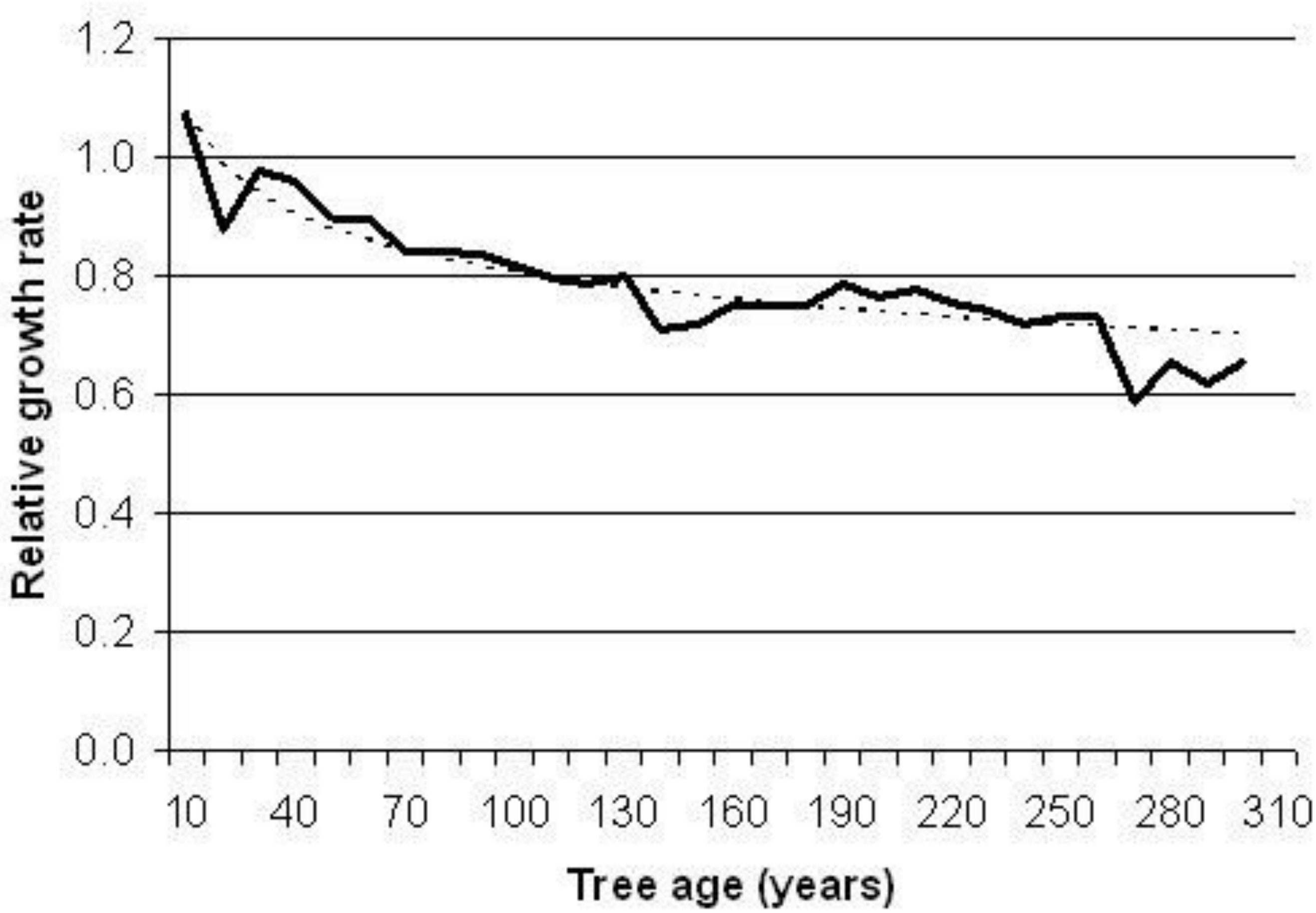

1.2
1.0
0.8
0.6
0.4
0.2
0.0
Relative growth rate
10
40
70
100
130
160
190
220
250
280
310
Tree age (years)

Fig. 3.

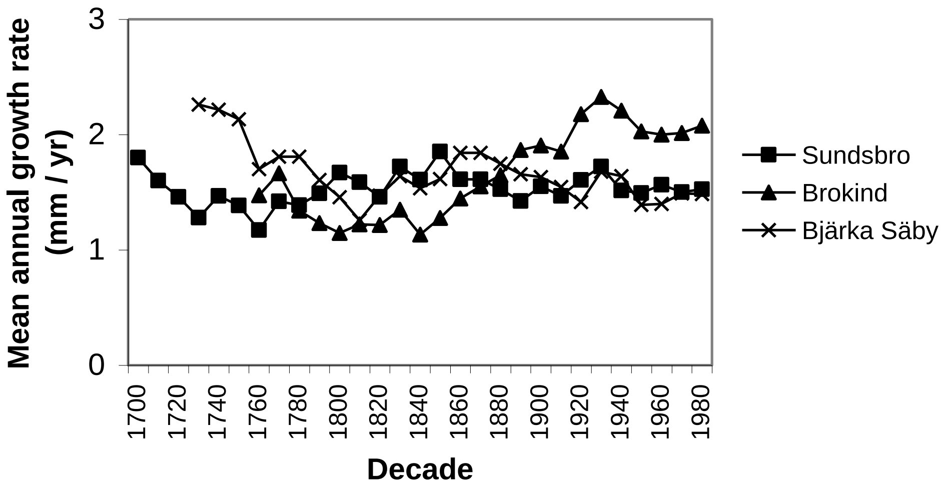
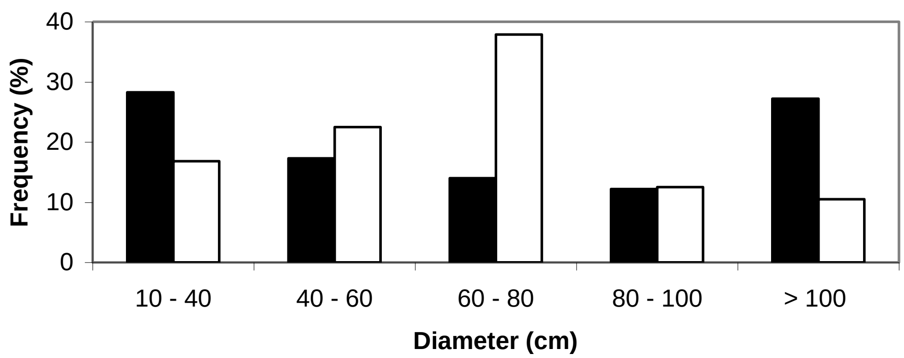
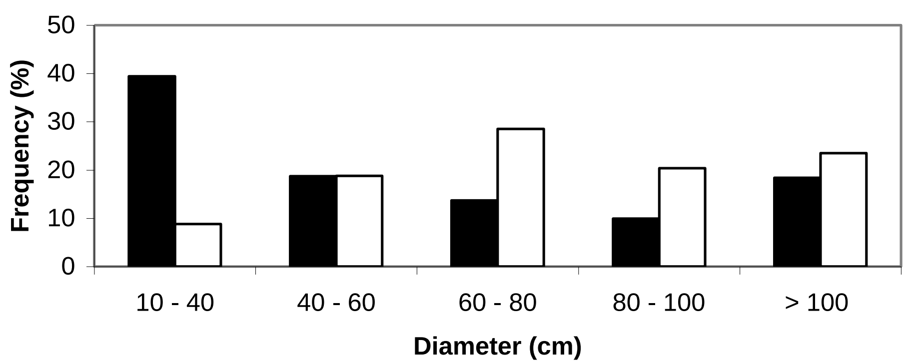

Mean annual growth rate (mm / yr)
3
2
1
0
1700
1720
1740
1760
1780
1800
1820
1840
1860
1880
1900
1920
1940
1960
1980
Decade
Sundsbro
Brokind
Bjärka Säby

Fig. 4.

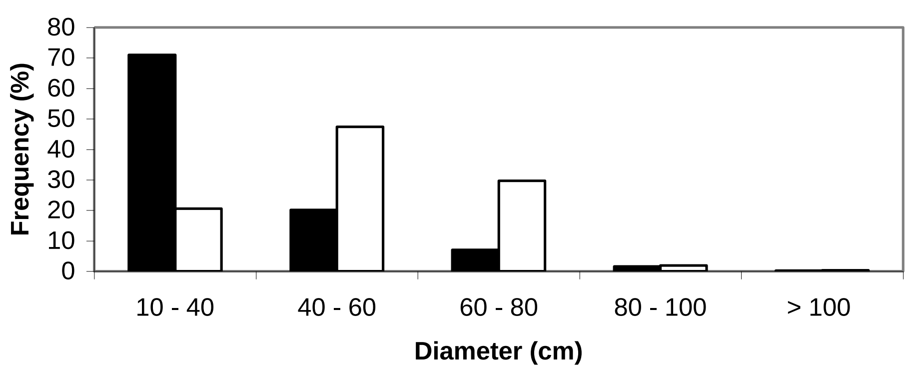
Brokind



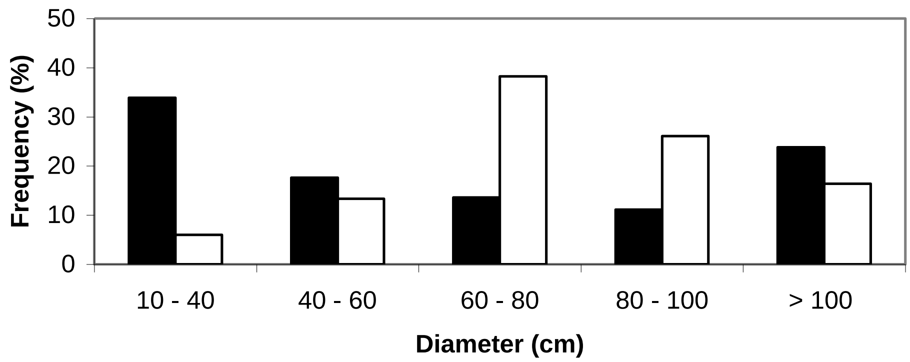
Kalvhagen



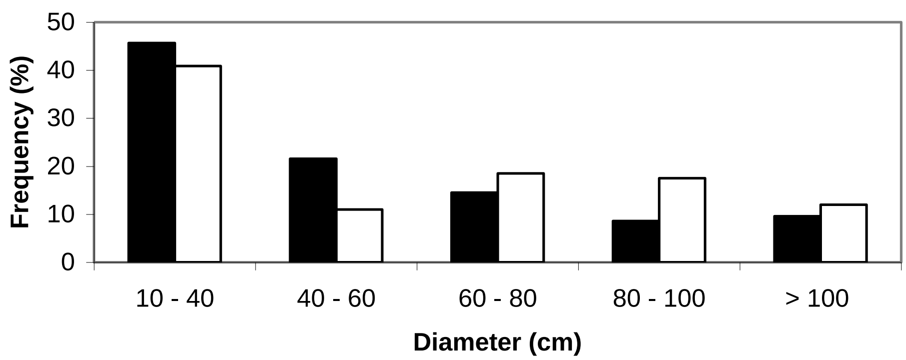
Långsvassudde



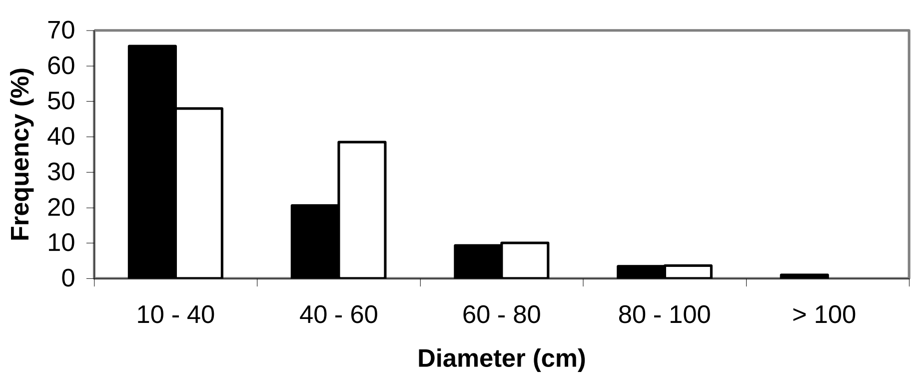
Orräng



Storängen



Sturefors



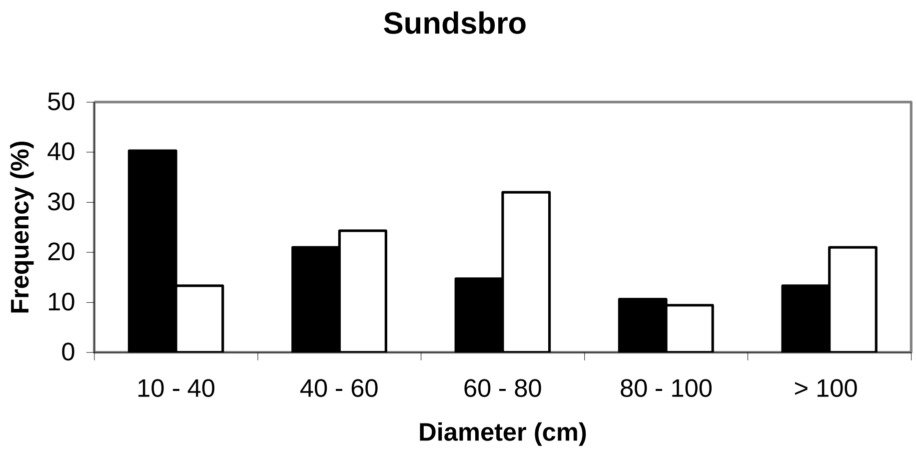
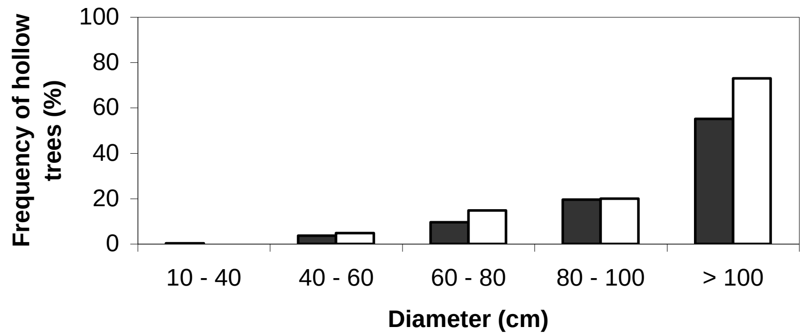
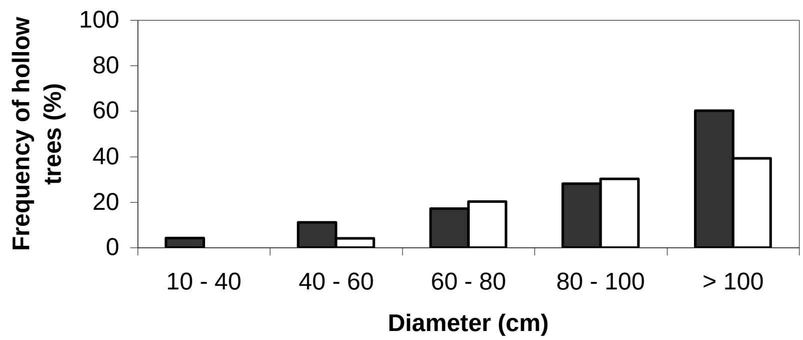

Sundsbro
Frequency (%)
50
40
30
20
10
0
10 - 40
40 - 60
60 - 80
80 - 100
> 100
Diameter (cm)

Fig. 5.

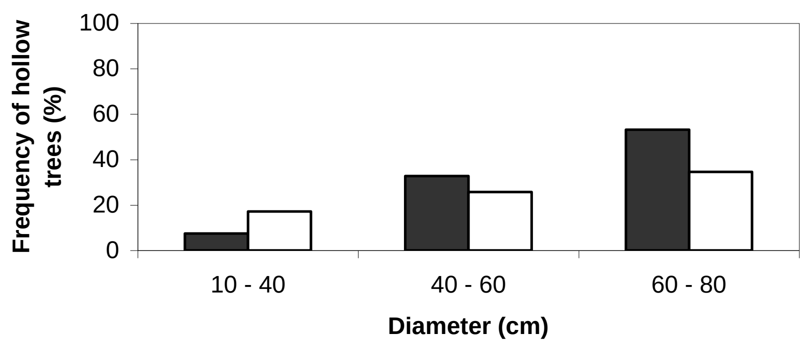
Brokind



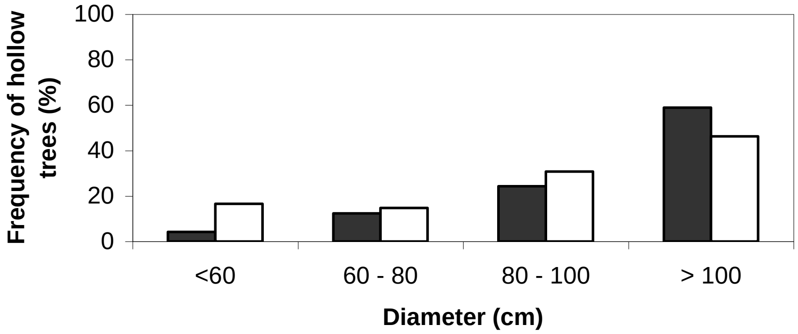
Kalvhagen



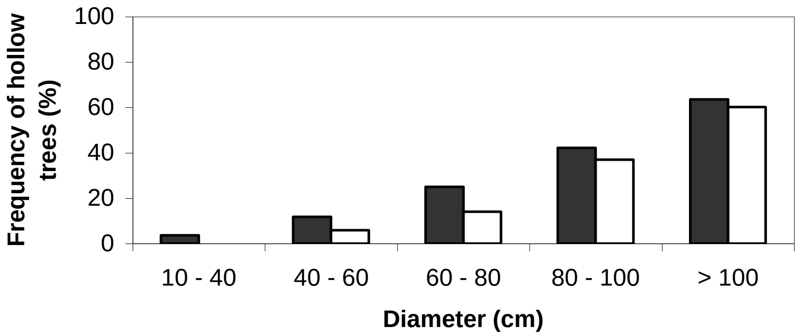
Långvassudde



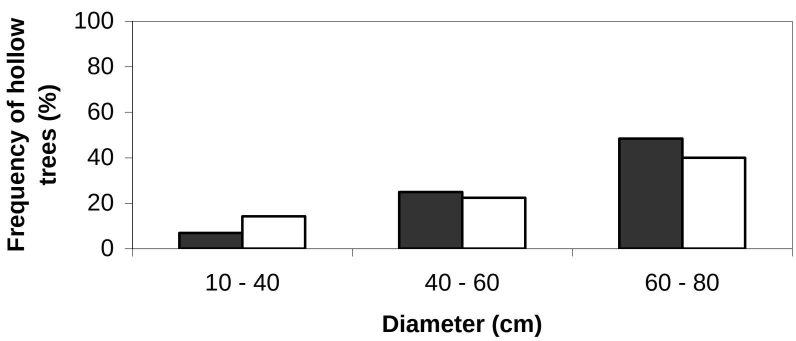
Orräng



Storängen



Sturefors



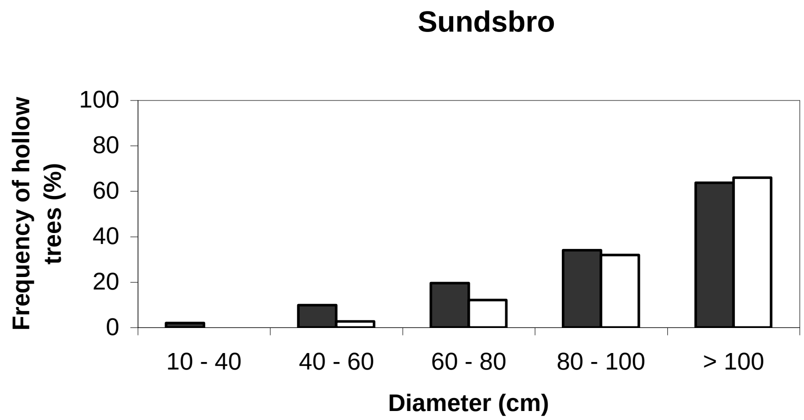

Sundsbro
Frequency of hollow trees (%)
100
80
60
40
20
0
10 - 40
40 - 60
60 - 80
80 - 100
> 100
Diameter (cm)

Fig. 6.