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# Tree age estimates in *Fagus sylvatica* and *Quercus robur*: testing previous and improved methods

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## Abstract

The accuracy of direct (based on increment cores) and indirect (based on age-size relationships) methods of tree age estimation in *Fagus sylvatica* and *Quercus robur* was tested. This was done through increment cores and stem discs taken in an old-growth forest of Northern Spain. It was found that cross-dating was more precise than ring counting by up to 7 years per tree. Furthermore, cross-dating permitted the estimation of the age of trees with floating ring-width series, which were 7% of cored *F. sylvatica* and 40% of *Q. robur* ones. In partial cores with the arcs of the inner rings, the length of the missing radius was estimated with both a geometric method, based on the curvature of the arcs, and a new graphical method, based on the convergence of xylem rays at the pith. The graphical method was more accurate when the radial growth was eccentric, as happens in *Q. robur*, while both methods showed a similar accuracy for *F. sylvatica*, whose growth is relatively concentric. Empirical models of initial radial growth (*IRG*), built to estimate the number of missing rings, reduced the errors associated with other methods that assume constant growth rates. Age estimates obtained from the graphical method combined with the *IRG* models were within 4% of the actual age. This combination ensured age estimates with a mean accuracy of 8 years for 98% of the *F. sylvatica* trees, and 4 years for 89% of the *Q. robur*. In partial cores without the arcs of the inner rings, the length of the missing radius was estimated as the distance to the geometric centre of the tree. In that case, age estimates obtained by extrapolating the mean growth rate of the 20 innermost rings in the cores were from 10 to 20% of actual age, which coincided with results obtained in other tree species with this method. Finally, the age-diameter equations of the different cohorts produced better age estimates (from 8 to 14% of actual age) than equations of the population as a whole (from 20 to 40% of actual age). These results proved that the errors derived from doubtful assumptions, such as concentric radial growth, constant growth and recruitment rates, or the absence of anomalous rings, could be reduced by applying more realistic methods of tree age estimation.

## Introduction

Accurate age estimation is a key methodological restriction in plant population dynamics research. It is possible to determine age by using annual rings in the perennial parts of many herbaceous dicotyledonous plants, such as in the secondary root xylem (Dietz and Ullmann 1997). But in the majority of herbaceous perennials, instead of estimating age, it is necessary to classify the individuals in several "life states" with different functional and reproductive characteristics (Harper 1977). In woody species with annual growth rings, age estimates can be achieved on the basis of the exact correspondence between each ring and the calendar year in which it was formed (Stokes and Smiley 1968). Annual radial growth occurs in almost all tree species growing in temperate latitudes of both hemispheres (Fritts 1976). Furthermore, seasonal radial growth occurrence and annual ring development have been confirmed in some tropical tree species (Worbes 1999).

The removal of basal stem discs or wedges is the only sampling technique that provides a complete radial growth series of all the studied individuals (Ågren and Zackrisson 1990; Lusk and Ogden 1992; Szeicz and MacDonald 1995). But obtaining, manipulating, and surfacing stem discs is expensive and very time consuming. Disc removal is also a destructive technique, therefore it is impossible in many cases such as for protected tree species, in parks and natural reserves, or in long-term research plots used for repeated diachronic censuses. The more rapid, economic, and respectful-to-the-environment sampling technique is the extraction of increment cores.

Tree age estimation based on increment cores presents three major limitations which make it difficult to obtain the true age of an individual (Norton et al. 1987; Duncan 1989; Norton and Ogden 1990; Veblen 1992): (1) in some radial growth series it is possible to discover anomalous rings (double or absent) which cannot be identified from a single core, (2) in a partial core, which does not include the pith, there is an unknown number of missed rings, and (3) in increment cores taken above the level at which the tree was germinated, there is a loss of rings due to sampling height. In this paper issues relating to the first and second of these restrictions are studied. In relation to the third restriction, several methods of correction for sampling height have been described and tested by (Wong and Lertzman 2001).

When tree age estimation is achieved by ring counts, the probable occurrence of anomalies in radial growth can distort the final estimate. Locally missing rings and false rings can be distinguished in stem discs by their discontinuity (Johnson and Fryer 1989; Lusk and Ogden 1992). But on a single increment core these are not identifiable. The errors in age estimates due to growth anomalies can be minimized by taking the cores along the longest bole radius (Duncan 1989), or by perpendicular extraction of more than one core per tree (Mikan et al. 1994). However, with the standard cross-dating techniques (Stokes and Smiley 1968; Holmes 1983) the false or missing rings can be identified to give a correct estimation of the total number of rings on the cores (Frelich and Graumlich 1994; Szeicz and MacDonald 1995; Kelly and Larson 1997).

The most frequent causes of missing piths are the incorrect alignment of the borer, a too short length of borer relative to bole radius, and rottenness of the tree centre. The inaccuracy related to the uncertain position of the chronological centre can be reduced by applying geometric or graphical methods to estimate its position (Duncan 1989; Baker 1992; Villalba and Veblen 1997), or by assuming that the pith coincides with the geometric centre of tree bole (Norton et al. 1987). In partial cores, in addition to the distance to the pith it is also necessary to estimate the number of rings in the missing core segment. To estimate the number of missing rings several methods have been applied: age-diameter regression curves (Lorimer 1980), cumulative curves of radial growth (Villalba and Veblen 1997), and the extrapolation of the mean growth rate from either the central rings of neighboring trees (Nakashizuka and Numata 1982) or the innermost rings in the core (Norton et al. 1987; Duncan 1989; Frelich and Graumlich 1994).

When a tree cannot be cored, or the obtained cores are unusable, then age estimates must be achieved through indirect methods, such as the regression of age upon stem diameter. The age-diameter relationship should be obtained from a large sample of trees, with the complete range of size classes being uniformly represented (Veblen 1992). However, in a given forest stand individuals with quite different growth rates often coexist (Stewart 1986), so that a great variation in the age of trees belonging to the same size class is usual (Norton and Ogden 1990; Lusk and Smith 1998). Also, all the age estimates, as well as diameter measurements, are subject to error. Thus, each point in the age-diameter scatter diagrams is surrounded by an area of uncertainty which prevents the calculation of faithful predictive models of age from diameter (Ogden 1985).

The purpose of this study is to understand the errors associated with different methods of tree age estimation which can be applied in *Fagus sylvatica* and *Quercus robur*. Different methods usually adopted in the bibliography, as well as other original procedures that are proposed in this work for the first time, were evaluated on stem discs of known age. The anomalous rings included in the samples were identified by both visual and quantitative cross-dating against a master chronology. Problems relating to the estimation of the length of missing radius and the number of missing rings in partial cores were studied. To estimate the position of the chronological centre, a graphical method based on ray's convergence at the pith was developed. From a sample of cores that included the pith, a model of initial radial growth for each studied tree species was built to estimate the number of missed rings. Indirect methods of age estimation from diameter were also tested. From the results obtained, the quicker, more objective, and more accurate methods to estimate age in natural populations of *F. sylvatica* and *Q. robur*, are emphasized.

## Materials and methods

### *Study area*

The materials employed in this work were taken in the Caviedes forest, an old-growth 110 ha forest located in the coastal lowlands of west Cantabria, Northern Spain (43°20′ N, 04°18′ W). It belongs to the Oyambre Natural Park, and is to be found 6 km south of the coast, and 8 km north of the Escudo de Cabuérniga Range. The soils are deep sandy brown earths, with parent material of sandstone and clay formed in the lower Cretacean. The Caviedes forest is located on a north-east oriented slope inclined 25° at maximum. The elevation of the site ranges from 40 to 240 m above sea level. The dominant species are *Fagus sylvatica* and *Quercus robur*, both reaching a maximum estimated age of over 300 years and up to 30 m in height. The undergrowth is mainly composed of *Ilex aquifolium*. Other relevant woody species are *Salix atrocinerea*, *Pyrus cordata*, *Frangula alnus*, *Corylus avellana*, *Alnus glutinosa*, *Crataegus monogyna* and *Malus sylvestris*. Botanical nomenclature follows Tutin et al. (1964-68).

### *Sampling, tree-ring measurement and cross-dating*

Increment cores were taken from all the live *F. sylvatica* and *Q. robur* trees with a stem diameter at breast height (dbh) greater than 5 cm, that were included in a 1.35 ha forest stand. The number of *F. sylvatica* and *Q. robur* individuals cored was 469 and 121, respectively. Cores were taken with increment borers at 20 cm above ground in the trees with dbh < 30 cm, and 100 cm above ground when dbh ⩾ 30 cm. Since the forest stand is relatively level (measured slopes ranged from 3.6 to 20.7°), the direction of the maximum slope was not considered in deciding in which direction the trees should be cored. Where possible, trees were cored along the longest radius to minimize errors due to missing rings (Duncan 1989). Repetitive coring was carried out to facilitate the interception of the pith, and to avoid faults or rottenness. Usually one core per tree was taken, but up to four cores were taken in a few trees to obtain at least one appropriate core for age estimation. When more than one core was extracted from a tree, the successive cores were taken parallel and closer to the pith than the earliest, in the direction suggested by ray angles.

Cores were air dried, mounted and sanded following standard procedures (Stokes and Smiley 1968). Ring-width series from all cores were measured to the nearest 0.01 mm under a stereomicroscope with a Velmex incremental measuring device linked to a computer. To get the same number of rings which would have been obtained with ordinary ring counting on the samples, neither wood coloration nor previous cross-dating were carried out. The program COFECHA (Holmes 1983) was utilized to identify missing, partial or false rings. COFECHA accomplishes the cross-dating by calculating the better correlation coefficients for different lags between distinct segments of each individual ring-width series and a dating master series. The dating master series was calculated from those ring-width series that showed neither missing rings nor abrupt changes in growth patterns, unequivocally correctly synchronized, and highly inter-correlated. To identify each anomalous ring, the computationally generated datings were checked by visual comparisons of each radial growth series against the master dating chronology.

In the Caviedes forest 14 stem discs of *F. sylvatica* were also taken, whose diameters ranged between 24 and 60 cm, and 18 discs of *Q. robur* with diameters between 23 and 77 cm. The discs were cut with a chain-saw between 20 and 100 cm above ground level from stumps and wind-thrown trees. The trees from which discs were taken showed similar characteristics (crown-shape, trunk aspect, vigor, disease or injury signals and growth patterns) than the previously cored trees. Thus, these discs were considered a random sample illustrative of radial growth of both tree species in this locality. Discs were smoothed with a power plane and then sanded until the growth rings were clearly visible. One or two radial lines per disc were drawn from the pith to the disc boundary until 20 lines for each tree species were achieved. If two lines were drawn on a disc, these were distant enough to form an angle ⩾120°. Ring-width series along the radial lines were measured to the nearest 0.01 mm and cross-dating against the master chronologies was accomplished with both the program COFECHA and visual checking.

## *Methods for estimating pith location*

If a partial core passed close to the pith, so that the arcs of the inner rings are visible, it is possible to estimate the position of the chronological centre of the tree (Norton et al. 1987; Duncan 1989). The geometric method developed by Duncan (1989) has been used to locate the pith from the curvature of the innermost rings in different studies of tree population dynamics (Duncan 1993; Kelly and Larson 1997; Lusk and Smith 1998; Donnegan and Rebertus 1999). This method assumes concentric growth, so that the ring boundaries can be considered arcs of circumferences centered in the pith. Therefore, a valid estimation of the length of missing radius is (modified from Duncan (1989)):

$$d = \frac{L^2 + 4h^2}{8h} \qquad (1)$$

where $d$ is the estimated distance from the largest entirely visible arc in the core to the pith, and $h$ and $L$ are respectively the height and the length of these arc (Figure 1a).

Recently a new graphical method has been developed to estimate the position of the chronological centre of trees (Villalba and Veblen 1997). In this method the limits of the inner rings of different cores taken from the same tree are identified and connected with curved lines. The length of missing radius is then estimated as the radius of the innermost circle, or as one half of the average of the shortest and longest diameters of the innermost ellipse. However, this method is very time consuming (at least the innermost 30 tree-ring boundaries per sample should be carefully sketched), and it displays important sources of bias (the cores must be arranged exactly in the same relative position as in the tree, and tracing the curvature of rings may vary from one person to another). For these reasons, this graphical method has been discarded for estimating the length of the missing radius in *F. sylvatica* and *Q. robur*.

In this paper a new graphical method based on the anatomical evidence of the convergence of xylem rays at the pith is proposed. This method is especially adequate for *Quercus* spp. and *Fagus* spp., as their wood presents wide clearly-visible rays. In this method, the largest arc entirely visible on a core, and two sufficiently distant rays are sketched under magnification on a transparent tape placed onto the core (Figure 1b). The tape is then removed from the sample and fixed onto a sheet of paper and the ray sketches are extended in a straight line. The distance from the pith to the arc is then estimated as the distance between the point at which the ray extensions converge and the arc itself ($d$ in Figure 1b).

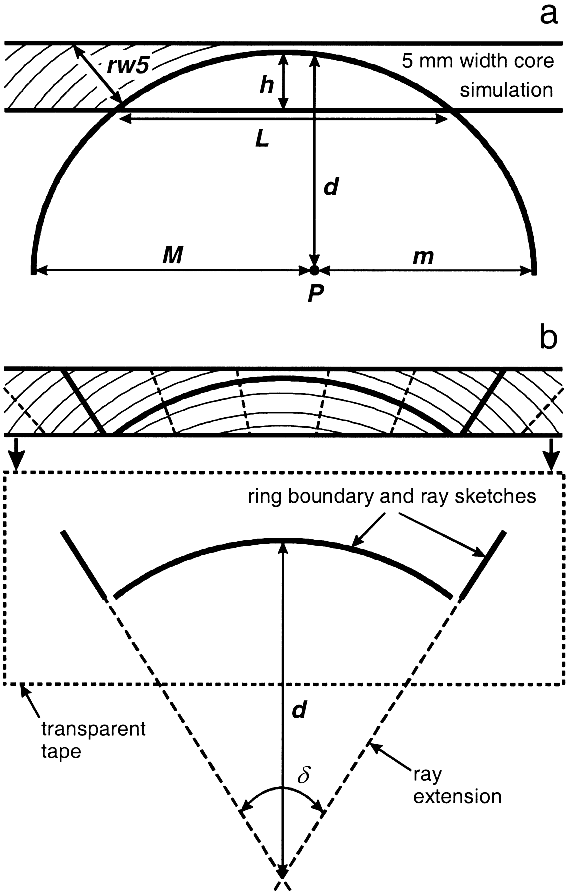

*Figure 1.* (a) Core simulation on a stem disc showing the pith ($P$), and the largest visible arc in the core (modified from Duncan (1989)). Arc height ($h$) and length ($L$), their true distance from the pith ($d$), their longest ($M$) and shortest ($m$) distances to the pith, and the width of the 5 adjacent rings to arc ($rw5$), are also showed. (b) Transverse section of a core showing the rays and ring arcs. A transparent tape is also given with the sketches of two rays and the largest visible arc, showing the ray extensions, the angle formed by them ($\delta$), and the estimated length of missing radius ($d$) according to the graphical method.

The errors associated with both the geometric and graphical methods were obtained by core simulation on the disc surface. From each radial line previously drawn on the discs, five new parallel lines were drawn at 10, 20, 30, 40 and 50 mm from the pith. A second line parallel to the first was drawn at a further 5 mm from the pith, resembling the surface of partial cores showing the arcs of the inner rings. Therefore, for each tree species a total of 100 core simulations was accomplished (20 radial lines, 5 core simulations per line). The largest visible arc was identified on each core simulation, and its length (*L*), height (*h*) and true distance from the pith (*d*) were measured with a digital caliper to the nearest 0.1 mm (Figure 1a). The length of missing radius was estimated with both the geometric method from *L* and *h*, and the graphical method from the rays and arc sketches.

The non-concentric growth close to the pith has been proposed as a main source of error in the estimation of the length of missing radii (Duncan 1989). To verify this hypothesis, an index of growth eccentricity (*E*) was defined as:

$$E = \left(1 - \frac{m}{M}\right) \cdot 100 \qquad (2)$$

where $m$ and $M$ are respectively the shortest and longest distances between the arc and the pith along the disc circumference (Figure 1a). The index $E$ ranges between 0 if the growth is ideally concentric ($m = M$), and 100 if the growth is quite eccentric ($m = 0$). To study the local geometry of radial growth in both tree species, a curvature index ($C$) was defined as:

$$C = \frac{2h}{L} \cdot 100 \qquad (3)$$

where $h$ and $L$ are as in the equation 1. This index reaches the value 0 for a straight line ($h = 0$), and 100 for a semi-circumference ($2h = L$). The eccentricity is a measure of radial growth geometry along the whole tree perimeter, while ring curvature is a local measure of growth geometry in the portion of the perimeter from which the core was taken. In addition the angle formed by the two rays, used to estimate the length of the missing radius, was measured ($\delta$ in Figure 1b).

The cores that show neither the pith nor the arcs of the inner rings, but include a sufficient percentage of the bole geometric radius, can be used to estimate tree age. This type of partial core was encountered due to decay of bole centre, or because of using too short a borer in comparison with the radius of the trunk. The procedure used to estimate the position of the pith in this case is based on the assumption that radial growth is concentric, i.e. that the tree's chronological centre coincide with its geometric centre (Norton et al. 1987). Therefore, the length of the missing radius was estimated as the difference between the geometric radius and the total core length. The length of radial lines drawn on the discs corresponds to the chronological radius. Thus, the deviations resulting from assuming concentric growth were calculated as the differences between the chronological radius minus the geometric radius of the disc (half of its diameter, excluding the bark).

### *Methods for estimating the number of rings missing from the pith*

Three methods were tested to estimate the number of missing rings on partial cores with the arcs of the inner rings. The first method assumes that radial growth rate is constant through time for a given tree, and it has been widely used for age estimation in many tree species (Norton et al. 1987; Duncan 1989; Stephenson and Demetry 1995). In this method (*RGR5*) the number of missing rings was estimated by dividing the length of the missing radius by the mean growth rate of the 5 rings adjacent to the largest visible arc on the core (calculated from *rw5* in Figure 1a).

The second method (*BAI5*) assumes a constant basal area increment through time within a tree (Stephenson and Demetry 1995). The number of absent rings was then estimated by dividing the basal area corresponding to the length of missing radius by the mean basal area increment, calculated from the 5 rings adjacent to the largest visible arc on the core (*rw5* in Figure 1a).

A third new method is proposed in this paper. It does not assume constant growth rates within a tree, but is based on the principle that the rates of initial radial growth should exhibit a common pattern of variation within a tree population. In this method an empirical model of initial radial growth (*IRG*) was applied, from which the number of missing rings was estimated as a function of both the distance from the pith, and the mean radial growth rate of the 5 rings adjacent to the largest arc visible on the core. To obtain the *IRG* equations, 55 and 40 ring-width series of *F. sylvatica* and *Q. robur*, respectively, were used. The ring widths were measured on samples showing the pith, which were taken from trees less than 90 years old.

It was assumed that these ring-width series exemplified the growth patterns of both tree species under the complete range of environmental conditions in the forest. For each measured ring the number of rings to the pith, the distance from the pith, and the mean growth rate of the 5 outer adjacent rings were calculated. 1000 rings per species, located at up to 80 mm from the pith, were randomly selected. From those rings the corresponding *IRG* models were calibrated by least-squares multiple regression. The number of rings to the pith was considered as the dependent variable, while the distance from the pith and the mean growth rate were the independent variables.

For each core simulation on the discs the number of missing rings was estimated with the three above described methods (*RGR5*, *BAI5*, and *IRG* model). The true distance from the pith, as well as estimates of the length of the missing radius obtained with the geometric and graphical methods, were used. Therefore, for each core simulation, estimates of the number of missing rings were obtained with all the possible combinations of methods appropriate for partial cores that show the arcs of the inner rings.

To estimate the number of missing rings on partial cores that did not show the arcs of the inner rings, methods based on the extrapolation of mean radial growth rates (*RGR*) and mean basal area increments (*BAI*) were tested. Taking the 20 and 50 innermost rings in a core to calculate the mean growth rate to be extrapolated, is the most frequent criterion (Norton et al. 1987; Duncan 1989; Lusk and Smith 1998). However, the mean growth rate has also been calculated from the 5 or even 3 innermost rings (Frelich and Graumlich 1994; Donnegan and Rebertus 1999). In this work the 5, 20 and 50 innermost rings visible on the cores were used to calculate the mean radial growth rate (*RGR5*, *RGR20* and *RGR50*) and the mean basal area increment (*BAI5*, *BAI20* and *BAI50*) to be extrapolated.

Among the ring width series measured along the radial lines drawn on the discs, 1000 rings located up to 200 mm from the pith were selected at random for each tree species. Each selected ring was considered as the innermost ring of a partial core simulation. For each core simulation the true number of missing rings was calculated, and the length of missing radius was estimated as the difference between the geometric radius and the length of the core simulation. The number of missing rings was estimated with the methods *RGR5*, *RGR20*, *RGR50*, *BAI5*, *BAI20* and *BAI50*, by using the length of missing radius previously estimated. If the estimated length was a negative number, then the considered number of missing rings was equal to 0 (i.e., the total number of rings on the core was the only possible estimation of tree age, because the length of the core was greater than the geometric radius due to eccentric growth).

### *Indirect methods for estimating tree age*

In the present work, indirect methods of tree age estimation based on least-squares regressions of age on bole diameter were tested. To calculate the age-diameter equations for both tree species, only complete cores were selected, i.e. those which indicated the true age of the tree at sampling height. An insufficient number of cores showing the pith was obtained for *Q. robur*. However the discs of this species were also used, as well as partial cores which showed the arcs of the inner rings, whose age was estimated by combining the graphical method and the *IRG* model.

Sampled trees of both species could be grouped in two cohorts according to their age (cohort 1: 25–86 years for *F. sylvatica*, 20–62 years for *Q. robur*; cohort 2: 175–266 years for *F. sylvatica*, 125–236 years for *Q. robur*). Thus, in addition to the age-diameter regression for the population as a whole, the regression equations for each cohort were also separately calculated. The age-diameter regression models, for populations considered as a whole, were taken as lines that passed through the origin, because when a tree is 0 years old their diameter must be 0 cm (Stephenson and Demetry 1995). By contrast, linear regression models that included a constant were applied for the separate cohorts, as it is usual (Lorimer 1980; Stewart and Rose 1990; Brodie et al. 1995; Taylor et al. 1996; Lusk and Smith 1998).

Errors in tree age estimation were calculated for each regression model by taking out trees at random with replacement, from the available samples. Five trees were randomly selected from each cohort, and the age-diameter regressions were calculated from the remaining trees. Regression equations were obtained for the overall populations as well as for each cohort separately. The ages of the 10 trees selected were estimated from their diameter with the regression equations, and the deviation of each estimate from their true age was calculated. This procedure was repeated 20 times, so that for each tree species deviations of 100 estimates were obtained considering the populations as a whole, and 100 by taking each cohort separately.

*Table 1.* Pearson's correlation coefficients between different variables measured on *F. sylvatica* and *Q. robur* stem discs, and the absolute errors in estimating the length of missing radius with the geometric (*AE-Geom*) and graphical (*AE-Graph*) methods. $n = 100$ in all tests.

| Species | Variable | *E* | *C* | δ | *AE-Geom* | *AE-Graph* |
|---|---|---|---|---|---|---|
| *F. sylvatica* | *d* | 0.14 | $-0.81^{***}$ | $-0.72^{***}$ | $0.45^{***}$ | $0.62^{***}$ |
| | *E* | | –0.07 | 0.05 | 0.18 | $0.25^{*}$ |
| | *C* | | | $0.80^{***}$ | $-0.35^{***}$ | $-0.47^{***}$ |
| | δ | | | | $-0.37^{***}$ | $-0.31^{***}$ |
| *Q. robur* | *d* | 0.02 | $-0.51^{***}$ | $-0.67^{***}$ | $0.58^{***}$ | $0.65^{***}$ |
| | *E* | | $0.35^{***}$ | $0.27^{**}$ | $0.33^{***}$ | $0.30^{**}$ |
| | *C* | | | $0.64^{***}$ | –0.02 | –0.04 |
| | δ | | | | $-0.26^{**}$ | $-0.21^{*}$ |

Variables: distance from the pith (*d*), eccentricity index (*E*), curvature index (*C*), and the angle formed by two rays (δ).
$^{*}$ $p < 0.05$;
$^{**}$ $p < 0.01$;
$^{***}$ $p < 0.001$.

## Results

### *Computation of total number of rings in the cores*

On the cores taken from the trees older than 150 years, 17110 growth rings of *F. sylvatica* were dated, among which 15 were missing rings and 195 micro-rings. Of the 6396 dated rings of *Q. robur*, only 1 missing ring and 12 micro-rings were identified. In contrast to the missing rings, the micro-rings showed some positive anatomical evidence when the cores were newly examined after quantitative cross-dating. But like the missing rings, micro-rings were not identifiable at a glance, but only by cross-dating. Thus, both missing rings and micro-rings were considered absent rings unidentifiable by means of ring counting alone. Furthermore, in outer segments of several cores, tree-ring boundaries could not be identified due to faults and periods of severe growth suppression. This occurred in 6 cores among 88 of *F. sylvatica*, and in 16 among 39 of *Q. robur*, from which floating ring-width series were obtained.

The ring-width series measured on cores taken from trees younger than 90 years, were also cross-dated quantitatively as well as visually. Cross-dating was accomplished for 381 young *F. sylvatica* trees and 82 *Q. robur*. Because of a too short ring-width series and/or deficient correspondence with the master chronology, 25% of the *F. sylvatica* series and 13% of *Q. robur* showed poor cross-dating. For these samples, ring counting was the only feasible approach in estimating the number of rings on the cores. By contrast, in the remaining radial growth series it was possible to verify if the true age of the cores was correctly determined by ring counting. The amount of young trees that showed proper dating of their ring-width series (i.e., those in which ring counts provided the true number of rings contained in the sample) was similar in both tree species: 19% for *F. sylvatica* and 22% for *Q. robur*. In 35% of the cores of *F. sylvatica* ring counting underestimated the true age while in 21% overestimated it. However, underestimates were obtained in 63% of the cores of *Q. robur*, and only in 2% of these the number of rings was overestimated.

### *Radial growth geometry*

To ascertain feasible differences in the radial growth geometry of *F. sylvatica* and *Q. robur*, correlations between the different variables measured on the central portion of the discs were computed. In both tree species, growth eccentricity (*E*) did not revealed a significant correlation with the distance from the pith (*d*) (Table 1). This result indicated that during the initial period of life, the eccentricity of radial growth was independent of the distance from the pith. However, both the curvature of the ring boundaries (*C*) and the angle of rays (δ), showed a highly significant negative correlation with *d*. Furthermore, *C* and δ were highly significantly correlated in a direct way (Table 1). These are logical consequences of radial growth progression in successively superimposed rings, and of the approximately radial arrangement of rays.

In *F. sylvatica* discs, *C* and δ were independent of *E*, while in *Q. robur* both *C* and δ showed a significant direct relationship with *E* (Table 1). Multiple regression analyses were accomplished taking *d* and *E*

*Table 2.* Absolute and percentage errors in estimating the length of missing radius. Mean errors (SE) are given for the geometric and graphical methods, and by considering the chronological center of the tree as the bole geometric center.

| Species and method | *n* | Absolute error (mm) | Percentage error (%) | U | O | $\chi^2$ s.l. |
|---|---|---|---|---|---|---|
| *Fagus sylvatica* | | | | | | |
| Geometric method | 100 | 8.8 (0.9) | 24.7 (1.9) | 80 | 20 | *** |
| Graphical method | 100 | 6.7 (0.6) | 18.1 (1.3) | 72 | 27 | *** |
| Geometric center | 20 | 20.3 (4.5) | 8.9 (1.7) | 14 | 6 | ns |
| *Quercus robur* | | | | | | |
| Geometric method | 100 | 12.1 (1.1) | 33.8 (2.5) | 77 | 23 | *** |
| Graphical method | 100 | 8.3 (0.8) | 21.7 (1.6) | 65 | 34 | ** |
| Geometric center | 20 | 66.9 (13.3) | 21.3 (3.5) | 14 | 6 | ns |

*n*: number of simulations.
U and O: number of under- and overestimates, respectively.
$\chi^2$ s.l.: significance level for the hypothesis of a similar number of under- and overestimates, according to a Chi-square test.
ns: non significant,
$^{*}$ $p < 0.05$,
$^{**}$ $p < 0.01$,
$^{***}$ $p < 0.001$.

as independent variables, and either $C$ or $\delta$ as dependent variables. In *F. sylvatica*, $C$ was only related to $d$ ($r^2 = 0.658$, $p < 0.001$), while $\delta$ was significantly related to both $d$ and $E$ ($r^2 = 0.542$, $p < 0.001$). But while $d$ explained 51.9% of angle variation, $E$ explained only 2.3% of that variation. In *Q. robur*, $C$ as well as $\delta$ were significantly related to both $d$ and $E$ ($r^2 = 0.394$ for $C$, $r^2 = 0.533$ for $\delta$, $p < 0.001$ in both tests). $d$ explained the greater proportion of the variation of dependent variables in *Q. robur* (26.6% of $C$, 44.9% of $\delta$), and $E$ explained an appreciable proportion of that variation (12.8% of $C$, 8.4% of $\delta$).

These results indicated differences in radial growth eccentricity between both species. The eccentricity measured on *F. sylvatica* discs varied between 4.6 and 54.5, while for *Q. robur* this index reached values from 15.2 to 88.1. Mean radial growth eccentricity in *Q. robur* discs was significantly greater than in *F. sylvatica* (25.9 ± 14.2 for *F. sylvatica*, 46.8 ± 18.2 for *Q. robur*, $U_{14,18} = 45.0$, $p = 0.002$, Mann-Whitney test). Thus, ring curvature and the angle of xylem rays in *F. sylvatica* were mainly related to the distance from the pith because growth eccentricity is comparatively not very important in this species. However, ring curvature and the angle of rays in *Q. robur* discs were a consequence of both the distance from the pith and the pronounced eccentricity in radial growth.

### *Estimating the length of missing radius*

In partial core simulations showing the arcs of the inner rings, the mean errors obtained with the geometric method were greater than with the graphical method for both tree species (Table 2). The mean errors obtained in the geometric and graphical methods did not differed significantly for *F. sylvatica* (paired $t = 1.55$, df = 98, $p = 0.125$, for both absolute and percentage errors). However, estimates of the length of missing radius in *Q. robur* obtained through the graphical method provided a significantly smaller error than those based on the geometric method (paired $t = 3.55$, df = 98, $p < 0.001$, for both absolute and percentage errors). With both methods and for both tree species, the true length of missing radius was significantly underestimated (Table 2).

The absolute errors obtained in estimating the length of missing radius in *F. sylvatica* were significantly and positively correlated with $d$, and independent from (or weakly correlated to) $E$, while showing a highly significant negative relationship with both $C$ and $\delta$ (Table 1). Multiple regression analyses performed taking $d$ and $E$ as independent variables, showed that absolute error obtained with the geometric method in *F. sylvatica* was only related to $d$ ($r^2 = 0.199$, $p < 0.001$). For estimates achieved with the graphical method, the absolute error was significantly related to both $d$ and $E$ ($r^2 = 0.414$, $p < 0.001$). However, this error was mainly due to the distance to the pith (38.6%), while growth eccentricity explained a minor percentage of error (2.8%).

The absolute errors obtained in estimating the length of missing radius in *Q. robur* showed a significantly positive correlation with both *d* and *E*, and a negative one with δ, while being independent of *C* (Table 1). According to multiple regression analyses, both *d* and *E* explained an appreciable proportion of the error in estimating missing core length in *Q. robur* ($r^2$ = 0.439 for geometric method, $r^2$ = 0.509 for graphical method, $p < 0.001$ in both tests). 34% of the absolute error obtained in the geometric method was related to *d*, and 9.9% to *E*. Using the graphical method, 42.6% of the absolute error was related to *d*, and 8.3% was due to *E*.

In partial cores without the arcs of inner rings, mean errors obtained when the length of missing radius was estimated in *F. sylvatica*, were considerably smaller than for *Q. robur* (Table 2). Since the radial growth of *Q. robur* in the Caviedes forest is more eccentric than that of *F. sylvatica*, it should be expected that errors in the estimation of missing radial length, under the assumption of concentric growth, will be greater for *Q. robur*. Under- or overestimates occurred when the radius in the region of bole perimeter in which the core was simulated, was smaller or greater, respectively, than the geometric radius. The peripheral points from which the cores were simulated were chosen at random. Thus, a non significantly different number of under- or overestimates was obtained (Table 2).

### *The initial radial growth models*

The best least-squares equations obtained to estimate the number of missing rings (*NMR*) were a linear function of the mean growth rate of 5 rings (*MGR5*), and a cubic polynomial function of the length of missing radius (*d*) ($NMR = 3.41 - 3.15\ MGR5 + 2.07\ d - 0.037\ d^2 + 0.0002\ d^3$, $r^2 = 0.883$ for *F. sylvatica*; $NMR = 3.37 - 2.26\ MGR5 + 1.22\ d - 0.022\ d^2 + 0.0001\ d^3$, $r^2 = 0.830$ for *Q. robur*; $n = 1000$ and $p < 0.001$ for both species; all terms significant at 0.001 level).

When the polynomial degree for *d* was enhanced, or when another model was considered for the relationship with *MGR5* (power, exponential or quadratic), the proportion of explained age increased less than 0.5%. Also, *d* explained the largest proportion of *NMR* variation (85% for *F. sylvatica* and 77% for *Q. robur*), while *MGR5* explained the poor amount of their variation (3% and 6% for *F. sylvatica* and *Q. robur*, respectively). However, this model provided more accurate estimates of *NMR* than if only *d* was used. This was particularly true for the shortest and longest distances to the pith, where the respective trend to over- and underestimate the number of missing rings was considerably corrected. Hence, this was considered the more appropriate model.

The equations were calibrated from growth rate values that ranged from 0.17 to 7.12 mm/ring for *F. sylvatica*, and from 0.25 to 7.97 mm/ring for *Q. robur*. The distances to the pith from which the equations were derived ranged from 0.38 to 79.83 mm for *F. sylvatica*, and from 0.55 to 79.58 mm for *Q. robur*. Both independent variables were more or less uniformly distributed throughout their range of variation, and they were not highly correlated ($r^2$ = 0.282 for *F. sylvatica*, $r^2$ = 0.049 for *Q. robur*).

The Figure 2 represents the initial radial growth (*IRG*) models to estimate the number of missing rings from both radial growth rate and the length of missing radius. The principal difference between both empirical equations is that, for the same growth rates and distances to the pith, the estimated number of missing rings is greater for *F. sylvatica* than for *Q. robur*. This is because the mean width of innermost *F. sylvatica* rings is significantly smaller than that of *Q. robur* (1.75 ± 1.15 mm for *Q. robur*, and 1.32 ± 1.02 mm for *F. sylvatica*, unpaired $t = 8.94$, df = 1998, $p < 0.001$).

### *Age estimates based on cores with the arcs of inner rings*

Mean errors obtained when the number of missing rings was estimated with the *IRG* models, were clearly less than those using the methods *RGR5* and *BAI5* (Table 3). This happened for both species of trees, as well as through using the true distance from the pith and the estimates of the length of missing radius obtained with both the geometric and graphical methods. Mean absolute and percentage errors obtained in *F. sylvatica* with the *IRG* model did not significantly differed when the true distance from the pith, or the length of missing radius estimated with the geometric or graphical methods, were used (paired *t* ranged from 0.73 to 1.83, *p* ranged from 0.070 to 0.466, with df = 99 in all tests).

If the number of missing rings in *Q. robur* was estimated with the *IRG* model, mean errors obtained did not significantly differed when the true distance from

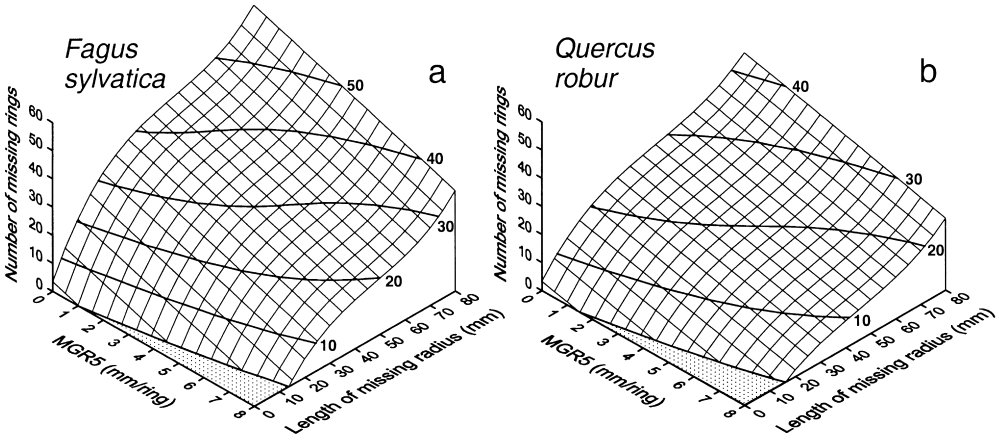

*Figure 2.* Initial radial growth models for estimating the number of missing rings in *F. sylvatica* (a) and *Q. robur* (b), as a linear function of the mean growth rate of 5 rings (MGR5), and a polynomial function of the length of missing radius. Grid divisions are at 0.5 mm/ring intervals for the growth rate, and 5 mm for the length of missing radius. The contour lines represent constant values of the number of missing rings.

*Table 3.* Absolute and percentage errors in tree ages estimated from partial cores with the arcs of the inner rings. Mean errors (SE) are given for three different methods of age estimation (*RGR5*, *BAI5*, and *IRG* model), using three different lengths of missing radius (true and estimated with the geometric and graphical methods). $n$ = 100 in all cases. Abbreviations as in Table 2.

| | | *Fagus sylvatica* | | | | | *Quercus robur* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Length of missing radius | Age estimation method | Absolute error (years) | Percentage error (%) | U | O | $\chi^2$ s.l. | Absolute error (years) | Percentage error (%) | U | O | $\chi^2$ s.l. |
| True | *RGR5* | 11.7 (1.0) | 40.9 (3.2) | 78 | 22 | *** | 5.7 (0.4) | 33.6 (1.9) | 86 | 14 | *** |
| | *BAI5* | 18.8 (1.1) | 65.9 (1.8) | 96 | 4 | *** | 11.9 (0.5) | 69.2 (1.5) | 100 | 0 | *** |
| | *IRG* | 8.8 (0.6) | 39.7 (3.3) | 33 | 67 | *** | 3.8 (0.3) | 22.5 (1.5) | 43 | 57 | ns |
| Geometric | *RGR5* | 13.3 (1.1) | 45.3 (2.4) | 84 | 16 | *** | 8.9 (0.6) | 50.0 (2.0) | 95 | 5 | *** |
| | *BAI5* | 20.3 (1.2) | 71.0 (1.8) | 98 | 2 | *** | 14.1 (0.7) | 79.6 (1.3) | 100 | 0 | *** |
| | *IRG* | 8.8 (1.1) | 33.4 (2.9) | 35 | 65 | ** | 5.2 (0.5) | 25.8 (1.8) | 72 | 28 | *** |
| Graphical | *RGR5* | 12.7 (1.1) | 43.1 (2.5) | 80 | 20 | *** | 7.5 (0.6) | 42.0 (1.9) | 90 | 10 | *** |
| | *BAI5* | 19.8 (1.2) | 68.7 (1.9) | 98 | 2 | *** | 13.2 (0.6) | 74.4 (1.4) | 100 | 0 | *** |
| | *IRG* | 8.2 (0.7) | 35.4 (3.0) | 37 | 63 | ** | 4.3 (0.5) | 21.9 (1.6) | 44 | 56 | ns |

the pith, or the length of missing radius obtained with the graphical method, were used (paired $t$ = 1.64, $p$ = 0.104 for absolute error; paired $t$ = 0.31, $p$ = 0.755 for percentage error; df = 99 in both tests). However, mean errors obtained with the *IRG* model in this species were significantly greater when the length of missing radius was estimated with the geometric method than with the graphical method (paired $t$ = 3.23, $p$ = 0.002 for absolute error; paired $t$ = 2.19, $p$ = 0.031 for percentage error; df = 99 in both tests). Therefore, the graphical method of extension of the rays combined with the *IRG* model provided the most efficient estimates of the number of missing rings on partial cores of *Q. robur*.

To underestimate the radial growth rate or basal area increment always implied an overestimation of the number of missing rings, and vice versa. Both radial growth rate and basal area increments in the missing core segment were overestimated from the core simulations. Therefore, the *RGR5* and *BAI5* methods significantly underestimated the true number of missing rings in both species (Table 3). The bias toward underestimating the number of missing rings was greater in *Q. robur*, because this species showed more cases in which the growth rate of missing segments was overestimated, and also in 100% of the cases the mean basal area increment was overestimated.

*Table 4.* Absolute and percentage errors in tree ages estimated from partial cores without the arcs of the inner rings. Mean errors (SE) are given for six different methods of age estimation, by considering the chronological center of the tree as the bole geometric center. $n$ = 1000 in all cases. Abbreviations as in Table 2, except for PU and PO: percentage of under- and overestimates, respectively.

| | *Fagus sylvatica* | | | | | *Quercus robur* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Age estimation method | Absolute error (years) | Percentage error (%) | PU | PO | $\chi^2$ s.l. | Absolute error (years) | Percentage error (%) | PU | PO | $\chi^2$ s.l. |
| *RGR5* | 39.2 (1.1) | 48.2 (1.1) | 58 | 42 | ns | 29.2 (0.7) | 58.8 (2.2) | 61 | 39 | * |
| *RGR20* | 38.0 (1.1) | 45.4 (0.9) | 55 | 45 | ns | 27.0 (0.6) | 54.4 (1.7) | 57 | 43 | ns |
| *RGR50* | 43.6 (1.2) | 50.8 (1.1) | 57 | 43 | ns | 28.1 (0.7) | 56.1 (1.5) | 54 | 46 | ns |
| *BAI5* | 42.3 (0.9) | 53.7 (0.8) | 92 | 8 | *** | 36.2 (0.7) | 61.6 (1.0) | 91 | 9 | *** |
| *BAI20* | 45.1 (1.0) | 57.9 (0.8) | 96 | 4 | *** | 38.3 (0.7) | 64.7 (0.8) | 95 | 5 | *** |
| *BAI50* | 49.1 (1.1) | 62.5 (0.9) | 96 | 4 | *** | 39.9 (0.7) | 67.1 (0.8) | 97 | 3 | *** |

However, the *IRG* model significantly overestimated the number of missing rings on partial core simulations of *F. sylvatica* (Table 3). The *IRG* model significantly underestimated the number of missing rings on partial cores of *Q. robur* only when the length of missing radius was estimated with the geometric method. When the true distance from the pith, or the estimates obtained with the graphical method, were used, the *IRG* model yielded estimates centered around the true number of missing rings (Table 3).

### *Age estimates based on cores without the arcs of inner rings*

The *RGR20* method provided superior estimates of the number of missing rings in both tree species (Table 4). Mean absolute error of age estimates obtained with the *RGR20* method in *F. sylvatica* was significantly lower than with *RGR50* (paired $t$ = 6.10, df = 999, $p$ < 0.001), but it did not differ from the error obtained with *RGR5* (paired $t$ = 1.21, df = 999, $p$ = 0.225). But mean percentage error of *F. sylvatica* age estimates, achieved with *RGR20*, was significantly lower than with both the remaining methods of radial growth rate extrapolation (paired $t$ = 2.71, $p$ = 0.007 with *RGR5*; paired $t$ = 5.97, $p$ < 0.001 with *RGR50*; df = 999 in both tests). On the other hand, mean absolute and percentage errors in *Q. robur* age estimates, obtained with the *RGR20* method, were significantly lower than with the remaining *RGR* methods (paired $t$ ranged from 2.18 to 4.70, $p$ ranged from 0.029 to be <0.001; df = 999 in all tests). The errors obtained with the *RGR20* method were also significantly lower ($p$ < 0.001 in all cases) than the ones obtained with *BAI* methods, according to paired $t$ tests achieved on 1000 partial core simulations.

Representative tree-ring series of *Q. robur* were examined to illustrate the variation of errors in age estimates obtained with *RGR* and *BAI* methods, according to radial growth patterns. When the growth rate of a tree showed a rising trend, then both *RGR* and *BAI* methods underestimated the number of missing rings (Figures 3a and 3b). If the growth rate was almost constant, the *RGR* methods provided estimates near the true number of missing rings, but *BAI* methods consistently underestimated them (Figures 3c and 3d). When radial growth rate was falling, then the *RGR* methods tended to overestimate the number of missing rings, while age underestimates were obtained with the *BAI* methods (Figures 3e and 3f). In the latter case, the magnitude of underestimates became reduced for increasingly larger distances to the pith (Figure 3f).

The ring-width series used to check these methods showed abundant transitional forms among these three types. For these reason the *RGR* methods provided a very similar (usually non significantly different) number of over- and underestimates (Table 4). Because of a more or less prolonged period of suppressed growth during the initial period in the life of many trees, to underestimate age with *RGR* methods was more frequent in close proximity to the pith, i.e. for cores with a short length of missing radius. But the rate of basal area increment in the missing core segment was generally overestimated, independent of the radial growth pattern and for any distance to the pith. Therefore, *BAI* methods mainly provided underestimates of the true number of missing rings (Table 4).

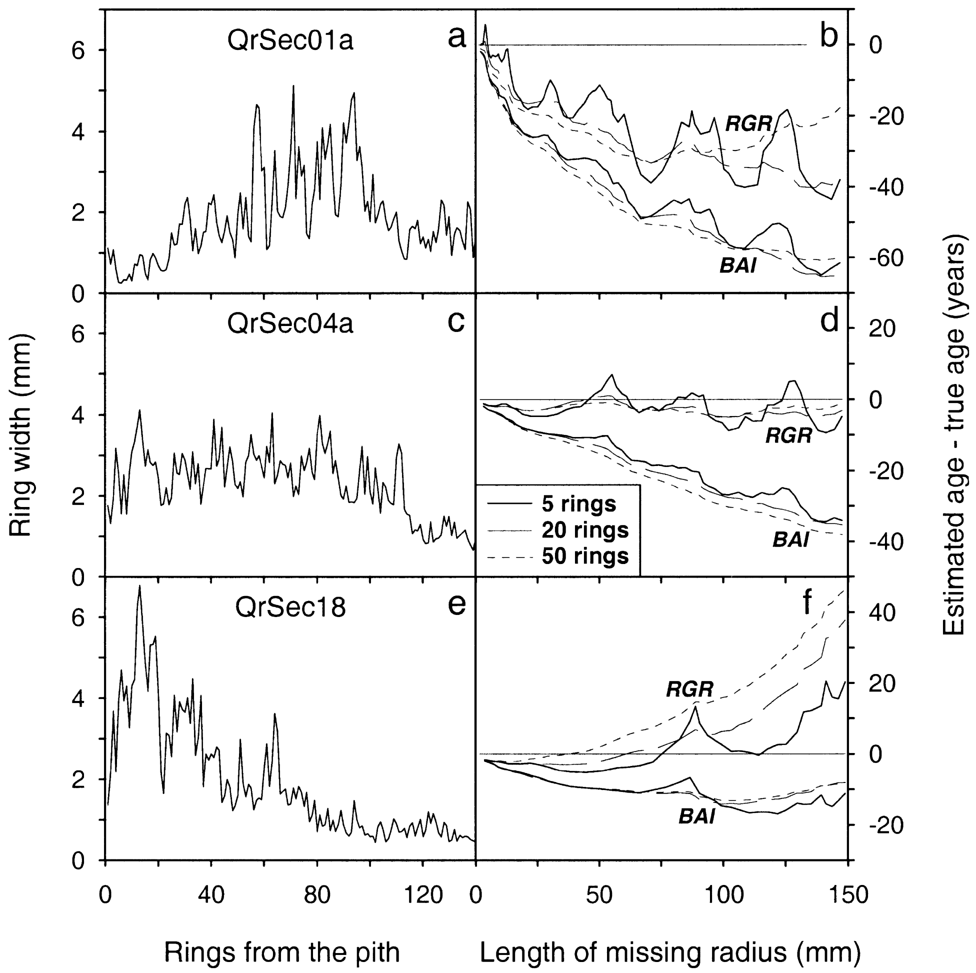

*Figure 3.* Representative ring-width series measured on *Q. robur* discs (a, c, e), with their respective deviations of age estimates for distances up to 150 mm from the pith (b, d, f). Tree age estimates were obtained by extrapolating the mean growth rate (*RGR*) and basal area increment (*BAI*) from the 5, 20 and 50 innermost rings.

### *Age estimates from bole diameter*

The regression equations obtained for age-diameter relationships in *F. sylvatica* and *Q. robur*, are shown in the Figure 4. The equations obtained for the populations considered as a whole were highly significant, with $r^2$ values greater than 0.87. The equations for the different cohorts were also significant, but $r^2$ values were considerably smaller (Table 5). The proportion of age-variance related to diameter was very similar for both cohorts of *F. sylvatica* (26–27%). By contrast, 58% of age variance was related to bole diameter in the cohort 1 of *Q. robur*, while in the cohort 2 age and diameter shared over 19% of variance (Table 5).

Age estimates obtained with cohort models were considerably more accurate and less biased than estimates obtained with the overall models (Table 6). According to the mean absolute errors obtained and the age ranges of the different cohorts, the percentage errors for *F. sylvatica* were from 6.9 to 24% of actual age (13.4% in average) in young trees, and from 6 to 9.1% (7.7% in average) in mature ones. Accordingly, percentage errors in *Q. robur* were from 8 to 25% of actual age (14.2% in average) in young trees, and from 11.4 to 21.6% of actual age (14% in average) in mature individuals.

This implied a reduction in the absolute error that ranged between 10 and 28 years, and between 6 and 26% in the percentage error, when the cohort models were used instead of the overall model. Furthermore,

*Table 5.* Regression equations for estimating tree age (*y*, years) from stem diameter (*x*, cm) for the populations considered as a whole (overall), and for each cohort separately. *n*: number of trees in each equation.

| Species | Group | *n* | Equation | $r^2$ | *p* |
|---|---|---|---|---|---|
| *Fagus sylvatica* | Overall | 209 | $y = 4.143\ x$ | 0.876 | <0.001 |
| | Cohort 1 | 179 | $y = 45.578 + 0.720\ x$ | 0.273 | <0.001 |
| | Cohort 2 | 30 | $y = 185.069 + 0.835\ x$ | 0.257 | 0.004 |
| *Quercus robur* | Overall | 116 | $y = 3.135\ x$ | 0.923 | <0.001 |
| | Cohort 1 | 87 | $y = 27.973 + 0.834\ x$ | 0.582 | <0.001 |
| | Cohort 2 | 29 | $y = 148.908 + 0.934\ x$ | 0.186 | 0.019 |

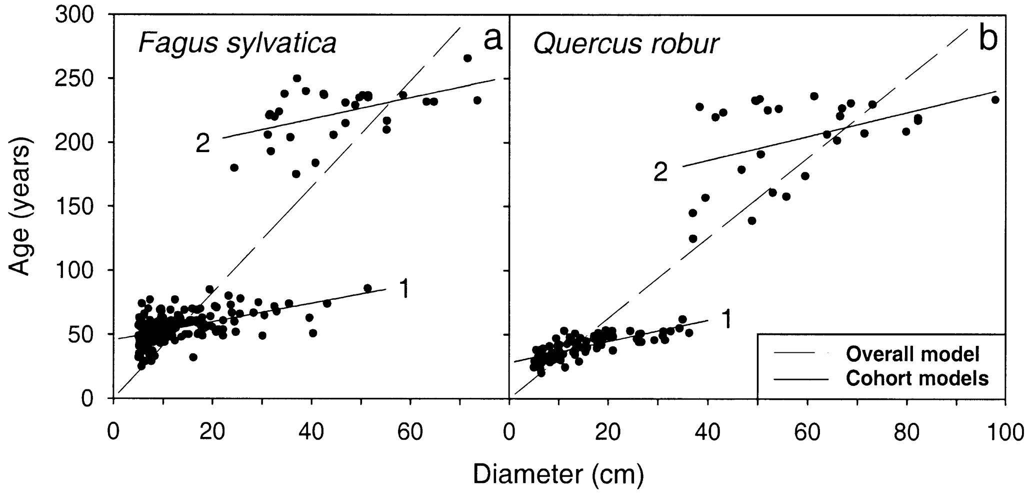

*Figure 4.* Age-diameter scatter diagrams of (a) *F. sylvatica* and (b) *Q. robur*, showing the least-squares lines obtained for the populations considered as a whole (overall model), and taking each cohort separately (cohort models). The equations that correspond to these lines are given in Table 5.

*Table 6.* Absolute and percentage errors in tree ages estimated by age-diameter equations. Mean errors (SE) are given for overall vs. cohort models based on random selection of trees. Percentage error is refereed in this case to the total age. *n* = 100 in all cases. Abbreviations as in Table 2.

| | Overall model | | | | | Cohort models | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species and cohort | Absolute error (years) | Percentage error (%) | U | O | $\chi^2$ s.l. | Absolute error (years) | Percentage error (%) | U | O | $\chi^2$ s.l. |
| *Fagus sylvatica* | | | | | | | | | | |
| Cohort 1 | 22.5 (2.2) | 39.7 (3.2) | 73 | 27 | *** | 6.5 (0.6) | 13.4 (1.6) | 46 | 54 | ns |
| Cohort 2 | 44.2 (2.9) | 19.9 (1.3) | 77 | 23 | *** | 16.3 (1.2) | 7.7 (0.6) | 58 | 42 | ns |
| *Quercus robur* | | | | | | | | | | |
| Cohort 1 | 15.2 (1.5) | 36.1 (3.0) | 48 | 52 | ns | 5.2 (0.4) | 14.2 (1.3) | 40 | 60 | ns |
| Cohort 2 | 43.1 (3.3) | 19.9 (1.4) | 57 | 43 | ns | 26.9 (1.6) | 14.0 (1.1) | 47 | 53 | ns |

when the populations of *F. sylvatica* were considered as a whole the ages were significantly underestimated (Table 6). However, if each cohort of this species was separately considered, a non significantly different number of under- and overestimates was obtained. In the case of *Q. robur*, both overall and cohort models gave age estimates almost evenly distributed around the true ages (Table 6).

## Discussion

### *Cross-dating vs. ring counting*

In mature trees, errors associated with ring counting were reduced only slightly by cross-dating, which permitted the identification of 1.2% of *F. sylvatica* rings, and 0.2% of the rings of *Q. robur*. But the principal benefit of cross-dating is that it made possible to date correctly all the floating growth series, i.e. to estimate the age of the mature trees whose cores showed anomalies in outer segments. This happened in 6.8% of *F. sylvatica* trees, in which the 6 to 117 outermost rings were unidentifiable, and in 41% of all the mature *Q. robur*, with 7 to 151 undefined final rings. These trees would otherwise have been discarded for age estimation based on increment cores.

The results obtained when cross-dating techniques were applied to cores taken from young trees can be explained by considering the porosity pattern in the wood of both species. The wood of *Q. robur* is ring-porous (Schweingruber 1990) so that ring limits are clearly distinguishable, even in the colorless sapwood of the young trees, because of the alignment of large vessels in the earlywood. Therefore it is extremely rare in this species to overestimate the number of rings by ring counting: only in 2% of the cores a single ring more than the true number was recorded.

By contrast, between 1 and 5 extra rings per core were obtained by ring counts in 21% of the samples of *F. sylvatica*. This is a diffuse-porous to semi-ring-porous tree (Schweingruber 1990), and in young trees of this species the wood is very pale and it does not show contrasting coloration between early- and latewood. Thus, variations in the density, diameter and distribution of vessels can bring about the consideration of a single ring as two. The tendency of ring counting to exaggerate age in young *F. sylvatica* trees can be reduced with a quite fine polish and by using a colorant such as phloroglucinol, in order to more easily identify adjacent rings.

In young trees of both species the occurrence of absent rings is frequent. Absent rings were more frequent in any given *F. sylvatica* tree (from 1 to 7 rings per sample) than in a *Q. robur* (1 or 2 rings per sample only). But the proportion of trees with absent rings was greater in *Q. robur* than in *F. sylvatica* (63% against 35%). Many of the absent rings identified in young *F. sylvatica* were consecutive, belonging to three periods of growth suppression: 1928–1933, 1937–1943, and 1983–1997. In the Caviedes forest, closed-canopy phases have been identified around the years 1929 and 1938, and an increase in canopy density, due to overstory accession of new young trees, has been also recognized in 1978–1996 (Rozas 2001).

Radial growth of both tree species showed a positive response to precipitation in July (Rozas 2001). The years with deficient July rain in the study area were 1928, 1935, 1943, 1968–1969, 1975 and 1986. Among these the 1928, 1943 and 1986 years coincided with absent rings in young *F. sylvatica* trees. So, absent rings in this species probably derived from an intense overshadow in closed-canopy periods and, to a lesser extent, from summer drought occurrence. But the identified absent rings in young *Q. robur* trees were not comparatively more abundant in any one year or period. Thus, underestimating the true number of *Q. robur* rings seems to be a consequence of ring wedging alone, which might be related to the pronounced pith eccentricity.

### *Improvements and applicability of graphical method*

In both tree species, and using both the geometric and graphical methods, the accuracy in estimating the length of missing radius became smaller as the distance from the pith increased. It has been previously stated that the majority of error in the estimation of the length of missing radius is due to non-concentric growth close to the pith (Duncan 1989). But this is not an appropriate conclusion of this work, because most error (20–43%) was related to the distance from the pith, while growth eccentricity explained only a minor fraction of error (0–10%). Thus, the taking of cores passing as close as possible to the pith is clearly advisable to minimize errors in estimating pith position.

Differences in accuracy between the geometric and graphical methods were evidenced by the contrasting radial growth geometry of both tree species. The radial growth of *F. sylvatica* is moderately eccentric, therefore the appearance of growth rings and rays roughly represents circumferences centered on the pith with their corresponding radii. By contrast, radial growth of *Q. robur* is not quite concentric, which violates the requisites of geometric method. Since ring boundaries of *Q. robur* cannot be considered as arcs of circumferences centered in the pith, the errors obtained from ring arcs are significantly greater than the errors obtained from rays. Thus, the graphical method is more reliable than the geometric, providing better estimates of the length of missing radius when the eccentricity in radial growth is pronounced.

Radial growth eccentricity is frequently a consequence of tree tilting, which may be due to strong winds, debris flow, snow avalanches, or soil creep in slopes (Kaennel and Schweingruber 1995). In the Caviedes forest, growth eccentricity cannot be attributed to these reasons. The sampled trees were not subjected to flood disturbances, and were not located on pronounced mountain slopes, susceptible to avalanches or mass movements of the soil. Although some stems showed a gentle angle, this was a consequence of lateral expansion of the tree to avoid the crowns of large, dominant neighbors. Thus, the more convincing explanation for the pronounced eccentricity in *Q. robur* discs is that it is characteristic of this species, and happens even if environmental conditions are not favorable for eccentric growth occurrence.

The new proposed graphical method for pith location can be widely applied in many tree species, using an adequate magnification to better identify and sketch xylem rays. European woody species may be classified into four categories on the basis of ray-widths (Wheeler et al. 1989; Schweingruber 1990). Rays exclusively uniseriate occur in gymnosperms, as well as in *Alnus* spp., *Corylus* spp., *Castanea sativa*, *Aesculus hippocastanum*, and Salicaceae. Rays 1- to 3-seriate are evident in some *Acer* species (e.g. *A. campestre*, *A. opalus*, *A. tataricum*), *Betula* spp., *Carpinus* spp., Caprifoliaceae, *Arbutus* spp., *Juglans regia*, Lauraceae, *Myrica faya*, Oleaceae, Rhamnaceae, Rosaceae Maloideae, and *Tilia* spp. Rays 4- to 10-seriate happen in *Acer platanoides*, *A. pseudoplatanus*, *Ilex* spp., *Ostrya carpinifolia*, *Erica arborea*, Leguminosae, *Platanus* spp., *Prunus* spp., and Ulmaceae. Finally, *Fagus* spp., *Quercus* spp., and *Tamarix* spp. show rays >10-seriate.

In the first and second ray-width categories, moderate magnifications (up to 40×) are required to confidently sketch rays with the help of a stereomicroscope. In many species of the third category and in all species of the fourth category, rays can be macroscopically observed on increment cores, but a low magnification (up to 20×) is necessary to confidently draw rays and ring-arcs. When cores are examined under moderate magnifications, instead of tracing the complete rays, it is advisable to put a mark on the transparent tape at two separated points on each ray. This procedure avoids probable inaccuracies due to difficulties in handling a pen magnified more than 20 times its actual size.

Other anatomical features that occur in a few taxonomic groups can facilitate the application of the graphical method. In many conifers such as *Cedrus* spp, *Larix decidua*, *Picea* spp. and *Pinus* spp., broad rays with radial resin canals are frequent, so that these can be readily observed under low magnification and used for pith location. Moreover, aggregate rays occur in many species of Betulaceae (*Alnus* spp. except *A. viridis*, *Betula humilis*) and Corylaceae (*Carpinus* spp., *Corylus* spp.). Aggregate rays are composed of a number of individual rays separated by axial elements, but so closely associated with one another that they appear macroscopically as a single large ray (Wheeler et al. 1989). However, aggregate rays may be relatively infrequent, so they could be easily overlooked or absent in the innermost segment of a core. Therefore, aggregate rays should be used only in those samples showing them in an adequate position to estimate pith location.

### *Improvements of IRG models for age estimation*

The smallest mean absolute error in estimating the number of missing rings for both tree species was obtained by combining the graphical method with the *IRG* model. The average of these errors was 8 years for *F. sylvatica* and 4 years for *Q. robur*, which corresponded to the respective deviations of ±35% and ±22% from the true number of missing rings. The sampled discs of *F. sylvatica* ranged from 184 to 250 years in age, hence this combination of methods displayed mean deviations between ±3.3% and ±4.4% of total age for mature trees of this species. The discs of *Q. robur* were from 125 to 239 years old, thus errors in total age estimation varied from ±1.8% to ±3.4%. These ranges of error are smaller than mean errors previously assessed for different methods and tree species, which are ±10% (Norton et al. 1987) and ±5% (Duncan 1989) of actual age.

The calculated errors were valid for most of the cored trees in the Caviedes forest. In *F. sylvatica*, 43.6% of cores showed the pith and 55% showed the arcs of the inner rings. In *Q. robur*, 26.4% of cores included the pith and 62.8% showed the arcs of the inner rings. The remaining individuals provided partial cores without inner ring arcs, or cores unusable for age estimation. The calculated errors are valid for partial cores with lengths of missing radii up to 55 mm, and only one *F. sylvatica* and two *Q. robur* cores were outside this distance. Thus, the tests achieved accounted for error in age estimates in 54.8% of *F. sylvatica* trees and in 61.3% of *Q. robur* ones.

The largest mean error for *F. sylvatica* might be due to the different initial growth rates of the samples used for model calibration and the ones used for its validation (1.85 ± 1.09 mm for calibration, 1.21 (±0.90 mm for validation, unpaired $t = 17.02$, df = 3050, $p < 0.001$). The errors obtained for *F. sylvatica* would be valid only for estimates achieved on cores taken from trees more than 180 years old. Probably the ages estimated in individuals with a similar age to trees used for model calibration (i.e. <90 years old), would be more accurate than for mature trees. By contrast, initial radial growth rates of *Q. robur* cores used for calibration and validation of the *IRG* model, did not differed significantly (2.05 ± 1.28 mm for calibration, 2.08 ± 1.11 mm for validation, unpaired $t = 0.56$, df = 1584, $p = 0.574$). Thus, the errors obtained for *Q. robur* would be valid for trees belonging to any age class.

These results corroborate that tree age estimation is more accurate for shade-intolerant species, which predictably grow rapidly in their youth, than for tolerant species, which can grow either rapidly or slowly in their youth (Stephenson and Demetry 1995). In light-demanding species as *Q. robur*, young trees require a high intensity of sun light for growth and survival, so their initial growth rates vary only a little in time and space. However, shade-tolerant species as *F. sylvatica*, can establish and grow under a wide range of light conditions, so that their initial growth rates will depend on the local composition and density of forest at a given time. Thus, the application of this method to shade-toleran trees involves errors due to the spatial and temporal variation of site conditions.

### *Errors from cores lacking the arcs of inner rings*

The differences between the three tested *RGR* methods were small, as has been previously stated in other tree species (Norton et al. 1987). In both species, mean ring width calculated over the innermost 20 rings gave the best results among all tested methods. The mean absolute error accounted for with the *RGR20* method was 38 years in *F. sylvatica* and 27 years in *Q. robur* (45% and 54% of the number of missing rings, respectively). Thus, for partial cores distant up to 200 mm from the pith, age estimates were from 15.2 to 20.6% of actual age in *F. sylvatica*, and from 11.3 to 21.6% of actual age in *Q. robur*. These ranges of error were similar to the errors previously noted from other species of trees with the same methods, which ranged from 10 to 20% of actual ages (Norton et al. 1987).

In general, the magnitude of errors in age estimation from growth rate extrapolation is unpredictable, and is largely dependent on radial growth pattern, the distance of the core to the pith, and the portion of the core used to growth rate extrapolation (Duncan 1989). The methods used to estimate the number of missing rings by extrapolating radial growth rates (*RGR*) or basal area increments (*BAI*), provided inferior estimates when applied to *F. sylvatica* than to *Q. robur*. This is a consequence of the relationship between the accuracy of these methods and changes in form and trend of the radial growth curves (Norton et al. 1987; Stephenson and Demetry 1995).

*F. sylvatica* growing in dense forests shows frequent growth suppressions and releases during the initial period of life. These changes in radial growth patterns produced conspicuous deviations of the mean growth rates of missing radius in comparison with mean growth rates of the inner rings in a partial core. However, percentage errors were smaller in *F. sylvatica*, because the initial mean growth rate of this species is lower than that of *Q. robur*. For the same distances to the pith, *Q. robur* showed fewer missing rings than *F. sylvatica*, giving higher values of percentage errors whereas the absolute errors were smaller.

In this work alternative methods for age estimation, based on partial cores without the arcs of the inner rings, were not considered. Thus, the doubts associated with the presumptions of concentric growth and constant growth rates were not completely avoided. Combining information from two increment cores taken at 90° or 180° from the tree, could be useful to assess pith eccentricity, and to obtain a more appropriate estimation of initial growth rates. The use of two partial cores instead of one only, has given the best age estimates and considerably reduced the tendency to underestimate age in giant conifers (Stephenson and Demetry 1995). The magnitude of errors in the *RGR* methods could be advantageously reduced by using two cores per tree instead of one only.

### *Cohort vs. overall age-diameter equations*

Trees of similar age within each cohort identified in the Caviedes forest showed a diversification in size, greater for trees established earlier, smaller for later established ones. As has been previously stated, widely different cohorts in a population of trees, each with their own age-diameter relationships, can artificially inflate the global correlation between age and diameter (Stewart 1986). Thus, the most statistically significant equation is not necessarily the most accurate predictive model with which to estimate tree age from diameter. According to the results obtained, errors in estimating age from diameter in *F. sylvatica* and *Q. robur* were notably inferior when cohort equations were used, even if equations of the complete population showed the highest and more significant $r^2$ values.

A common practice in forest dynamics research is to age a sub-sample of trees, to calculate their age-diameter relationship, and to estimate the age of the remaining trees from their diameters with the calculated equation (Veblen 1992). But doubts about the precision of age estimates, based of the age-diameter equations, have been reasonably stated (Harper 1977; Norton and Ogden 1990). According to the results obtained in this work, the ages of a stratified sub-sample of trees can be confidently estimated from cores showing the pith, and showing the arcs of the inner rings. Then, the different cohorts may be identified, so that cohort equations can be derived and used to estimate age.

The equations corresponding to cohort 1 provided age estimates with a similar accuracy to those obtained by using *IRG* models (5–6 years vs. 4–8 years in absolute errors, respectively), and clearly improved the estimates obtained with *RGR* and *BAI* methods. Moreover, the range of percentage error obtained with the equation of cohort 2 is equal to the obtained with the *RGR20* method in *Q. robur* (11–22% of actual age), and smaller than that obtained in *F. sylvatica* with the same method (6–9% vs. 15–21% of actual age). As a consequence, cohort equations based on a stratified sub-sample of trees, may be confidently used for age estimation in young trees, and may be also used in mature trees instead of *RGR* methods.

A limitation of the method is that it can be fairly applied only to trees with stem diameters similar to the ones used to calibrate the age-diameter equations. Thus, indirect methods could be applied in this forest to *F. sylvatica* trees with maximum a diameter of 80 cm, and to *Q. robur* trees with diameters up to 100 cm. But hollow *F. sylvatica* trees of more than 100 cm in diameter, and *Q. robur* trees with diameters over 150 cm are frequent in some forests at Northern Spain. Accurate age estimation in these large trees is, at the moment, clearly tentative and unrealistic.

### *Limitations of tree age estimates*

A first limitation regarding any method of total tree age estimation is that the time between germination and until the tree reached coring height is likely to be unknown (Veblen 1992). In gymnosperms and dicotyledonous plants, the germination point is located at the root collar, which constitutes the boundary between the root without pith and the stem with pith (Telewski 1993). To age sprouts it is not advisable to correct for coring height because of vigorous initial height growth (Brodie et al. 1995; Tardif and Bergeron 1999). But in trees of sexual origin, a correction factor should be applied to supply the loss of growth rings.

The correction factor can be calculated from a sub-sample of seedlings or trees, as the mean difference between the number of rings at ground level and at coring height (Henry and Swan 1974; Veblen 1989). Other alternative method can be the usage of age-height regression equations calibrated from saplings or trees sectioned at regular height intervals (Lusk and Ogden 1992; Szeicz and MacDonald 1995). To test the accuracy of these methods, many saplings and adult trees must be destructively harvested so as to identify and date the exact germination level in each one. Obviously, this is an important limitation for testing methods of total tree age estimation (see Wong and Lertzman (2001) for a new approach to assess the uncertainty around dates of tree establishment based on Monte Carlo simulations).

It must be taken into account that all the methods described and checked in this work allow an estimation of the age of a given stem, which may or may not coincide with age of the tree since germination. This is because vegetative reproduction by root suckers, root-collar sprouts, or layering is common in many species of trees (Koop 1987; Ohkubo 1992; Fernández-Palacios and Arévalo 1998). Thus, if the vegetative origin from an older individual can be discarded for a tree, then its age since germination can be estimated. However, in many studies on tree regeneration and forest dynamics, the dating of both tree germination and sprouting is equally useful (Brodie et al. 1995; Tardif and Bergeron 1999).

Tree germination dating should take into account that errors in the different methods may be additive (Duncan 1989; Villalba and Veblen 1997). The overall error could include the error of ring counting, plus the error in estimating the number of missing rings to the pith, plus the error in estimating the number of missing rings to the root-shoot boundary. These errors can be contradictory, canceling each other out. But if all the estimates are biased to either over- or underestimating the number of rings, then the errors will be cumulative. Thus, the final magnitude and sign of error cannot be predicted, even if the mean error and the bias of each method used are known (Norton and Ogden 1990). A careful sampling and analysis of these samples, and the utilization of more accurate methods, are the only guarantees of arriving at reasonable tree age estimates.

## Conclusions

Accuracy in estimating tree age is due to the conjunction of several factors, such as wood anatomical features (ring boundary distinctness, porosity pattern, ray width), growth geometry, live history traits (sexual or vegetative origin, growth patterns, shade tolerance), environmental variability (climatic fluctuations, competition intensity, disturbances), and specific faults in the samples (hidden scars, knots, local wood decay, rotten piths). Sampling procedures and methods of age estimation should consider all these factors as potential sources of error which can be minimized. As a general rule, the closer to the pith a core is taken, the more accurate is age estimation based on the core. But while bisecting the pith, or at least passing close to it, is clearly advantageous to improve tree age estimation, this alone does not definitely guarantee unbiased estimates.

The errors obtained when ring counting only is used are small and acceptable. However, a capital achievement of cross-dating is its ability to synchronize the floating ring width series, which can be relatively abundant within a set of cores. The graphical method for pith location (based on rays converging on the pith) is more accurate than the geometric (based on ring curvature) for any degree of radial growth eccentricity. The graphical method is quite simple and rapid. It can produce several hundred estimates in a day, and it is not influenced by subjective aspects that could bias the results.

The bias of age estimates in shade-tolerant species is greater. This is due to large variations in their radial growth rate in comparison to the intolerant species, which grow in a more predictable way. The initial radial growth model, as applied in this study, do not require constant growth rate over the central segment of the cores, and provide unbiased age estimates. The combination of the graphical method and the initial radial growth model is more accurate than any other combination of methods tested.

Methods of extrapolation of mean basal area increments can be used with confidence only in trees with a declining radial growth series, such as in xeric woodlands or for open-grown trees, which usually show a negative exponential growth pattern (Fritts 1976). Age-diameter models for the different cohorts provide better age estimates than if overall population models are used. An unavoidable requirement to apply age-diameter models based on cohorts, is the use of an extensive number of precise age estimates from increment cores, that clearly identify the different cohorts. If the age structure is discontinuous, with few well-differentiated cohorts, then the cohort models can be confidently used.

Numerous procedures for tree age estimation have been used in the literature, but only a few of these have been reasonably tested. Objectivity used to be the unique requirement to validate procedures for estimating tree ages. But accuracy and reproducibility are essential properties of any method used in scientific research. Thus, in order to effectively improve tree age estimates, it is essential to ignore questionable assumptions, to avoid subjective procedures, and to inquire about more accurate techniques.

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