## NOTE / NOTE

# A new, proportional method for reconstructing historical tree diameters 

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#### Abstract

Accurate methods of reconstructing historical tree diameters from increment cores are important because diameter is used in allometric equations to predict stand characteristics and to study stand dynamics. The conventional reconstruction method assumes that the pith is in the centre of the stem. This is often incorrect, as evidenced by a pith increment index quantifying the deviation between the geometric radius of the stem and the chronological radius of a core. I propose a new method which assumes that growth is proportional around the stem and, unlike the conventional method, cannot yield negative historical diameters. These methods were evaluated by calculating the deviations between reconstructed diameters and historical diameter measurements from 164 ponderosa pine (Pinus ponderosa Dougl. ex P. \& C. Laws.) trees from permanent plots in Arizona and New Mexico. Deviations varied with pith increment index for the conventional method but not for the proportional method, and varied with tree age for both methods at one site. These methods could be used in tandem, with the proportional method applied where the increment from outer ring to pith is measured and the conventional method applied where this increment cannot be measured.

Résumé : Il est important que les méthodes utilisées pour reconstituer le diamètre passé des arbres à partir de carottes soient précises parce que le diamètre est utilisé dans des équations allométriques pour prédire les caractéristiques des peuplements et étudier leur dynamique. La méthode de reconstitution conventionnelle assume que la moelle est dans le centre de la tige. Cela est souvent erroné comme le montre un indice d'accroissement de la moelle qui quantifie l'écart entre le rayon géométrique de la tige et le rayon chronologique d'une carotte. L'auteur propose une nouvelle méthode qui assume que la croissance est proportionnelle autour de la tige et qui, contrairement à la méthode conventionnelle, ne peut produire de diamètres passés négatifs. Ces méthodes ont été évaluées en calculant l'écart entre les diamètres reconstitués et les diamètres mesurés dans le passé sur 164 tiges de pin ponderosa (Pinus ponderosa Dougl. ex P. \& C. Laws.) dans des places échantillons permanentes en Arizona et au Nouveau-Mexique. Les écarts variaient en fonction de l'indice d'accroissement de la moelle pour la méthode conventionnelle mais pas pour la méthode proportionnelle et ils variaient avec l'âge des arbres pour les deux méthodes dans une station. Ces méthodes pourraient être utilisées en tandem en appliquant la méthode proportionnelle lorsque l'accroissement est mesuré du dernier cerne annuel jusqu'à la moelle et la méthode conventionnelle lorsque cet accroissement ne peut être mesuré.


[Traduit par la Rédaction]

## Introduction

Tree diameter is used in allometric equations to estimate many variables, including tree biomass (Gholz et al. 1979; Omdal et al. 2001), understory production (e.g., BojorquezTapia et al. 1990), and forest carbon stocks and fluxes (Jenkins et al. 2003). Studies of stand structural dynamics (Foster et al. 1996) also often require the reconstruction of historical tree diameters. Accurate diameter reconstructions are therefore important for understanding and modeling forest dynamics and for making management decisions.

[^0]A stem cross section provides the complete radial growth series of a tree but can only be obtained by killing it, which is unacceptable in most situations (Rozas 2003). In addition, results from studies of cross sections may not be applicable in the field, as they require information about stem geometry that cannot be obtained without sectioning the tree (e.g., Biging and Wensel 1988). Increment cores provide a nondestructive and operationally feasible method of obtaining growth data. Multiple cores per tree can increase the accuracy of diameter growth estimates (Matérn 1961; Iles 1974), but also greatly increase the processing time, effort, and core storage space required. I sought a method of reconstructing historical diameters that could be applied to a single increment core per tree, regardless of where around the stem it was obtained.

Much attention has been devoted to methods for correctly identifying tree age (Duncan 1989; Villalba and Veblen 1997; Wong and Lertzman 2001; Rozas 2003; Clark and Hallgren 2004; Gutsell and Johnson 2004) but less attention has been

Fig. 1. Idealized stem cross sections illustrating the reconstruction of historical diameter using the conventional method $\left(\mathrm{DBH}_{\mathrm{HC}}\right)$ and proportional method $\left(\mathrm{DBH}_{\mathrm{HP}}\right)$. Reconstructions are based on the current inside-bark diameter (outer circle; 40 cm in these examples) and a single increment core (thick vertical line). Increments are measured on the core from the outer ring to the historical date of interest $\left(I_{\mathrm{H}}\right.$; required for both methods) and from the outer ring to the pith (chronological radius; $I_{\mathrm{P}}$; required for the proportional method). The historical diameter (inner circle) is 10 cm in these examples but in practice is unknown. The pith increment index (PII) is a measure of the difference between the chronological radius of the core and the geometric radius of the stem, and $G$ is the proportion of radial growth that occurred before the historical date of interest. If the pith and geometric centre of the stem are equal (A), both methods correctly reconstruct the historical diameter. If the pith is off-centre ( $B$ and $C$ ), the broken lines indicate where the chronological and geometric radii are equal. The proportional method correctly reconstructs the historical diameter regardless of where the core is taken, while the conventional method can underestimate it (B) or overestimate it (C).

given to methods for quantifying radial growth increment (e.g., Biging and Wensel 1988) or reconstructing historical tree diameter (Dolph 1981). In this paper I describe a new method for reconstructing historical diameters and compare it with the conventional method by calculating the deviations between diameters reconstructed by each method and historical diameter measurements of trees on permanent plots.

## Description of reconstruction methods

## Stem geometry

The pith, or chronological centre of a stem (sensu Norton et al. 1987), often does not correspond to the geometric centre (Williamson 1975; Biging and Wensel 1988; Singleton et al. 2003). Analysis of the deviation between these two points requires a stem cross section (e.g., Singleton et al. 2003). However, an increment core can be used to describe the difference between the chronological and geometric radii using a pith increment index (PII):

$$
\begin{equation*}
\mathrm{PII}=\frac{2 I_{\mathrm{P}}-\mathrm{DIAM}_{\mathrm{IB}}}{\mathrm{DIAM}_{\mathrm{IB}}} \times 100 \tag{1}
\end{equation*}
$$

where $I_{\mathrm{P}}$ is the radial increment from outer ring to pith (chronological radius) on an increment core, and DIAM $\mathrm{IB}_{\mathrm{IB}}$ is the inside-bark diameter at coring height (twice the geometric radius). PII is positive when the chronological radius is greater than the geometric radius, zero when the chronological radius is equal to the geometric radius, and negative when the chronological radius is less than the geometric radius. If the pith is off-centre, the chronological radius varies
around the stem, and PII therefore varies among cores taken at different locations around the stem.

## The conventional and proportional methods

Conventional diameter reconstructions involve measuring the radial increment between the outer ring and the historical date of interest $\left(I_{\mathrm{H}}\right)$ and subtracting twice this measurement from the inside-bark diameter (e.g., Fulé et al. 1997). This method assumes that the chronological and geometric centres are equal and that radial growth has been symmetric. When PII is positive, it can yield negative reconstructed diameters.

The proportional diameter-reconstruction method involves multiplying the current diameter by the proportion of radial growth that occurred before the historical date of interest $(G) . G$ is calculated as
[2] $\quad G=\frac{I_{\mathrm{P}}-I_{\mathrm{H}}}{I_{\mathrm{P}}}$
This method assumes that growth has been proportional around the stem, which is not always so (Norton et al. 1987), but is a less restrictive assumption than those of the conventional method. In particular, no assumption is made about the location of the pith relative to the geometric centre of the stem. Also, reconstructed diameters are always positive, since $G \geq 0$.

An example (Fig. 1) illustrates these methods. An increment core that intersects the pith of a tree with a current inside-bark diameter of 40 cm is used to reconstruct the tree's historical diameter ( 10 cm ; in practice this is unknown) at the date of interest. The stem is assumed to be circular and growth to have been proportional around the stem.

Table 1. Summary statistics for trees from plots on the Coconino and Cibola National Forests (COC and CIB, respectively) used to reconstruct outside-bark diameter at breast height $\left(\mathrm{DBH}_{\mathrm{OB}}\right)$ in 1914-1915 from $\mathrm{DBH}_{\mathrm{OB}}$ measurements and increment cores obtained in 1997-2001.

|  | COC ( $n=102$ ) |  | CIB ( $n=62$ ) |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Mean $\pm$ SD | Range | Mean $\pm$ SD | Range |
| $\mathrm{DBH}_{\text {OB }}$ in 1997-2001 (cm) | $52.5 \pm 10.2$ | 36.1-86.6 | 38.8 $\pm 9.4$ | 14.7-64.5 |
| $\mathrm{DBH}_{\text {OB }}$ in 1914-1915 (cm) | $28.5 \pm 12.8$ | 10.2-63.5 | $24.6 \pm 7.3$ | 9.9-45.5 |
| Stump height centre date | $1844 \pm 49$ | 1702-1905 | $1824 \pm 44$ | 1606-1896 |
| Rings-to-pith ${ }^{\text {a }}$ | $6 \pm 4$ | 0-20 | $5 \pm 4$ | 0-17 |
| Pith increment index (\%) | $-5.2 \pm 9.8$ | -28.0 to 25.3 | $-9.5 \pm 13.4$ | -40.0 to 30.5 |
| Percentage of radial growth before 1914-1915 (G) | $51 \pm 17$ | 21-82 | $57 \pm 11$ | 31-88 |

${ }^{a}$ Estimated number of rings between the inner ring of the core and the pith.

If the chronological and geometric centres are identical, growth was radially symmetric and both methods yield the correct reconstructed diameter (Fig. 1a). Similarly, both methods yield the correct reconstructed diameter if the pith is off-centre but the core is taken where the chronological and geometric radii are equal (broken lines in Figs. $1 b$ and $1 c$ ). The points where these radii are equal cannot be identified in the field, however, so it is unlikely that cores will be taken at these points. For cores taken elsewhere around the stem, the proportional method yields the correct reconstructed diameter, since $G$ is unaffected by PII (Figs. $1 b$ and $1 c$ ). In contrast, diameters reconstructed by the conventional method vary with core location, as illustrated by the extremes presented here. The conventional method underestimates the historical diameter if PII is positive (Fig. 1b) and overestimates it if PII is negative (Fig. 1c).

## Case studies

## Data collection

The conventional and proportional reconstruction methods were tested on 102 trees from a permanent plot in Arizona and validated on 62 trees from permanent plots in New Mexico. These plots were established in the early 1900s as part of a long-term study of growth and yield in ponderosa pine (Pinus ponderosa Dougl. ex P. \& C. Laws.) (Pearson 1923). The Arizona plot (COC S1A; hereinafter COC) is in the Fort Valley Experimental Forest, Coconino National Forest, 10 km northwest of Flagstaff. The New Mexico plots (CIB S1A and CIB S2A; hereinafter jointly referred to as CIB) are in the Cibola National Forest, 30 km south of Magdalena. Historical data are stored in the Fort Valley Archives, US Forest Service Rocky Mountain Research Station, Flagstaff, Arizona.

Contemporary measurements were gathered as part of a larger project (Moore et al. 2004). For this study I used data from all live ponderosa pine trees that $(i)$ had been tagged and measured in 1914 or 1915 (COC and CIB, respectively), and (ii) had cores on which $I_{\mathrm{P}}$ could be measured (i.e., no broken cores or heart rot). Sampled trees were $\geq 100$ years old and spanned a $70-\mathrm{cm}$ range of diameter at breast height (DBH; 137 cm ) (Table 1). Small trees were not included because historical measurements were restricted to trees $\geq 9.14 \mathrm{~cm}$ DBH.

Cores were extracted at stump height $(40 \mathrm{~cm})$ because the larger project required a more accurate assessment of tree
age than was possible with cores taken at breast height. Cores were mounted, sanded, and cross-dated using standard dendrochronological techniques (Stokes and Smiley 1968). For cores that missed the pith, the pith location and number of rings between the inner ring of the core and the pith (hereinafter rings-to-pith) were estimated with a pith locator (Applequist 1958). Use of a pith locator is rapid and efficient but assumes that radial growth has been symmetric and constant near the centre of the tree (Rozas 2003). $I_{\mathrm{P}}$ and $I_{\mathrm{H}}$ were measured to the nearest millimetre. On cores that missed the pith, $I_{\mathrm{P}}$ was measured by positioning the pith locator on the core and measuring from the centre of the pith locator to the outer ring. PII and $G$ were calculated for each increment core (Table 1).

Outside-bark diameter at stump height $\left(\mathrm{DSH}_{\mathrm{OB}}\right)$ was measured and inside-bark diameter $\left(\mathrm{DSH}_{\mathrm{IB}}\right)$ was calculated using Myers' (1963) bark-thickness equations for old-growth ponderosa pine. $\mathrm{DSH}_{\mathrm{IB}}$ for each tree at the historical measurement date ( 1914 for COC, 1915 for CIB) was reconstructed using the conventional and proportional methods, and reconstructed diameters were then converted to $\mathrm{DBH}_{\mathrm{OB}}$ for comparison with historical diameter measurements. Conversions were made using Myers' (1963) bark-thickness equations and a DSH-DBH regression developed from other ponderosa pine trees on the Coconino and Cibola National Forests (J. Bakker, M. Moore, and A. Sánchez Meador, unpublished data):
[3] $\mathrm{DBH}_{\mathrm{OB}}=-0.5413+0.9313 \mathrm{DSH}_{\mathrm{OB}}$

$$
\left(r^{2}=0.9928, p<0.0001 ; n=3387\right)
$$

I used this regression because published equations (e.g., Hann 1976) do not use the same stump height as this study.

## Comparisons with historical diameters

Reconstructed diameters were compared with actual diameters measured in 1914-1915. The deviation $\left(D_{\mathrm{m}}\right)$ between the diameter reconstructed by each method $\left(\mathrm{DBH}_{\mathrm{Hm}}\right)$ and the historical diameter $\left(\mathrm{DBH}_{\mathrm{H}}\right)$ was calculated as
[4] $\quad D_{\mathrm{m}}=\mathrm{DBH}_{\mathrm{Hm}}-\mathrm{DBH}_{\mathrm{H}}$
where $\mathrm{m}=\mathrm{C}$ for the conventional method and $\mathrm{m}=\mathrm{P}$ for the proportional method. Since $D$ is expected to be correlated with historical diameter, I calculated the percent deviation $\left(\% D_{\mathrm{m}}\right)$ between reconstructed and historical DBH values as

Table 2. Deviations $(D)$ and percent deviations ( $\% D$ ) between historical diameters (Table 1) and reconstructed diameters using the conventional and proportional methods for trees from the Coconino and Cibola National Forests (COC and CIB, respectively).

|  | COC $(n=102)$ |  |  |  | CIB $(n=62)$ |
| :--- | :--- | :--- | :--- | :--- | :--- |
|  | Mean $\pm$ SD | Range |  | Mean $\pm$ SD | Range |
| Conventional method |  |  |  |  |  |
| $\quad D(\mathrm{~cm})$ | $0.7 \pm 4.0$ | -9.5 to 10.3 |  | $-0.7 \pm 3.4$ | -8.6 to 6.7 |
| $\% D$ | $8.3 \pm 22.5$ | -31.1 to 86.0 |  | $-1.3 \pm 16.9$ | -27.2 to 56.0 |
| Proportional method |  |  |  |  |  |
| $\quad D(\mathrm{~cm})$ | $-0.7 \pm 2.8$ | -9.1 to 4.7 |  | $-2.3 \pm 2.8$ | -10.1 to 3.8 |
| $\% D$ | $0.1 \pm 11.9$ | -27.6 to 31.5 | $-8.6 \pm 12.2$ | -40.7 to 25.2 |  |

Note: A positive or negative deviation indicates that the historical diameter was overestimated or underestimated, respectively.

$$
\begin{equation*}
\% D_{\mathrm{m}}=\frac{D_{\mathrm{m}}}{\mathrm{DBH}_{\mathrm{H}}} \times 100=\frac{\mathrm{DBH}_{\mathrm{Hm}}-\mathrm{DBH}_{\mathrm{H}}}{\mathrm{DBH}_{\mathrm{H}}} \times 100 \tag{5}
\end{equation*}
$$

Percent $D_{\mathrm{m}}$ is $>0$ when the historical diameter is overestimated and $<0$ when it is underestimated.

Wilcoxon signed ranks tests were used to determine whether mean $\% D_{\mathrm{m}}$ was significantly different from 0 at each forest. Chi-square goodness-of-fit tests determined whether the observed proportion of trees for which each method performed best (i.e., had smallest $|\% D|$ ) differed significantly from those expected by chance at each forest.

I postulated that $\% D_{\mathrm{m}}$ might be related to PII, tree age, and rings-to-pith. Since PII is a proxy for the deviation between the chronological and geometric centres of a stem, $\% D_{\mathrm{C}}$ should be related to it but $\% D_{\mathrm{P}}$ should not (Fig. 1). While correlation with historical diameter was accounted for, age-diameter relationships are weak for ponderosa pine (Pearson 1950) and $\% D_{\mathrm{m}}$ might be related to tree age (i.e., the age at stump height when historical diameters were measured). The ability to identify the location of the pith decreases as the distance between the inner ring and pith increases (Rozas 2003), so $\% D_{\mathrm{P}}$ might be related to rings-topith (since it requires the radial increment from outer ring to pith), while $\% D_{\mathrm{C}}$ shoud not.

I used model selection to quantify the importance of explanatory variables (for details, see Burnham and Anderson (2002; section 4.4) and Johnson and Omland (2004)). The three variables (PII, tree age, rings-to-pith) were combined in all seven possible combinations for each method at each forest. The model containing all variables was assessed for overall significance; if it was not significant, further testing was not warranted. If it was significant, the fit between model $i$ and the data was examined by calculating an Akaike Information Criterion $\left(\mathrm{AIC}_{\mathrm{c}}\right)$ score normalized as an Akaike weight $\left(w_{i}\right)$. The relative importance of a variable is $\Sigma w_{i}$ (maximum $=1$ ) for all models containing that variable, and the model-averaged coefficient for the variable is the sum of the products of the coefficient from model $i$ and $w_{i}$ (Burnham and Anderson 2002).

## Results

At COC, the conventional method overestimated historical diameter $\left(\mathrm{DBH}_{\mathrm{H}}\right)$ by $8.3 \%$ (Wilcoxon $T^{+}=-884.5, p=0.003$; Table 2), while the proportional method overestimated it by only $0.1 \%\left(T^{+}=198.5, p=0.510\right)$. The proportional method performed best for $64.7 \%$ of trees $\left(\chi^{2}=8.82, p=0.003\right)$.

Percent $D_{\mathrm{C}}$ was negatively related to PII (Fig. 2a) and tree age (Fig. 2b), but there was little evidence of a relation with rings-to-pith (Table 3). Percent $D_{\mathrm{P}}$ was not related to PII (Fig. 2c) or rings-to-pith, but was negatively related to tree age (Table 3, Fig. 2d).

At CIB, the conventional method underestimated $\mathrm{DBH}_{\mathrm{H}}$ by $1.3 \%\left(T^{+}=207.5, p=0.147\right.$; Table 2$)$, while the proportional method underestimated it by $8.6 \%\left(T^{+}=678.5, p<\right.$ 0.001 ). The proportional method performed best for $53.2 \%$ of trees $\left(\chi^{2}=0.26, p=0.612\right)$. Percent $D_{\mathrm{C}}$ was negatively related to PII (Fig. 2a) but was not related to tree age (Fig. 2b) or rings-to-pith (Table 3). Percent $D_{\mathrm{P}}$ was not related to any of the explanatory variables (Table 3, Figs. $2 c$ and $2 d$ ).

## Discussion

The case studies provide support for using the proportional method to estimate historical tree diameter. Diameters reconstructed via the proportional method were unrelated to PII (Table 3, Fig. 2c), while those reconstructed via the conventional method (Fig. 2a) were overestimated when PII was negative (chronological radius < geometric radius) and underestimated when PII was positive (chronological radius $>$ geometric radius).

The fact that the proportional method is not affected by core location (Fig. 1) has practical advantages during fieldwork. For example, a common practice is to measure stump height on the uphill side of the tree but to obtain increment cores from the side slope to minimize reaction wood and get the most accurate assessment of growth possible from a single core (Stokes and Smiley 1968). If cores are to be used to reconstruct historical diameters via the proportional method, they could be taken where stump height is measured, or elsewhere around the stem if necessary.

Deviations between historical and reconstructed diameters differed between forests (Table 2), indicating that variables other than core location were also important. While this difference may reflect variation in growth form between sites, it may also relate to tree age, which was an important explanatory variable at COC but not at CIB (Table 3). More young trees were sampled at COC ( 27 trees vs. 1 tree $<20$ years old at CIB), and historical diameters of young trees were more likely to be overestimated, especially via the conventional method (Fig. 2b). The reason for this overestimation is unclear, but may relate to juvenile growth rates and patterns. The proportional method reduced the range of $\% D$ values

Fig. 2. Scatterplots of percent deviation (\%D; Table 2) between historical diameters (Table 1) and reconstructed diameters using the conventional method ( A and B ) and proportional method ( C and D ) for trees from plots on the Coconino and Cibola National Forests (COC and CIB, respectively). For the conventional method, $\% D$ is negatively related to PII at both sites (A) and to tree age at COC (B). For the proportional method, $\% D$ is not related to PII at either site (C) but is negatively related to tree age at COC (D). Horizontal and vertical zero lines are shown for reference. Model-selection results are presented in Table 3.


Table 3. Results of model selection estimating the relative importance of three explanatory variables to the percent deviation (\%D) between historical diameters (Table 1) and reconstructed diameters using the conventional and proportional methods for trees from the Coconino and Cibola National Forests (COC and CIB, respectively).

|  | COC $(n=102)$ |  |  | CIB $(n=62)$ |  |
| :--- | :--- | :--- | :--- | :--- | :--- |
|  | $\sum w_{i}$ | Coefficient |  | $\sum w_{i}$ | Coefficient |
| Conventional method |  |  |  |  |  |
| $\quad$ PII | 1 | -1.34 |  | -0.66 |  |
| Tree age | 1 | -0.17 |  | 0.4059 | -0.02 |
| $\quad$ Rings-to-pith | 0.2526 | -0.02 |  | 0.2399 | -0.01 |
| Proportional method |  |  |  |  |  |
| $\quad$ PII | 0.5188 | -0.09 |  | - |  |
| $\quad$ Tree age | 0.9974 | -0.09 | - | - |  |
| Rings-to-pith | 0.2516 | 0 | - | - |  |

[^1]for these young trees much more than it affected the range of $\% D$ values for older trees (Fig. 2d).

The conventional method is most likely to yield negative diameters when reconstructing small historical diameters, but reconstruction methods could not be compared on small trees because historical diameter measurements were only made on trees with DBH $\geq 9.14 \mathrm{~cm}$. An assessment of the implications of the reconstruction method on stand characteristics would require a detailed study of all trees on a site, including these smaller trees, and would require multiple cores per tree to account for the effect of core location on diameters reconstructed using the conventional method.

Deviations between reconstructed and historical diameters were not related to rings-to-pith (Table 3), possibly because most cores missed the pith by only a few rings (Table 1). For cores that miss the pith by a large amount or lack the arcs of inner rings (Rozas 2003), the proportional method cannot be used because $I_{\mathrm{P}}$ cannot be measured accurately. Although the conventional method is affected by core location, it remains useful for these cores and for others that do not reach the pith because of heart rot, exceptionally large stem diameter, or other factors.

I suggest that these methods be used in tandem, with the proportional method applied where the increment from outer ring to pith is measurable and the conventional method ap-
plied where this increment cannot be measured. Such an approach should be less biased than using the conventional method alone, although the implications of combining the two methods in a study should be further studied.

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## References

Applequist, M.B. 1958. A simple pith locator for use with offcentre increment cores. J. For. 56: 141.
Biging, G.S., and Wensel, L.C. 1988. The effect of eccentricity on the estimation of basal area and basal area increment of coniferous trees. For. Sci. 34: 621-633.
Bojorquez-Tapia, L.A., Ffolliott, P.F., and Guertin, D.P. 1990. Herbage production - forest overstory relationships in two Arizona ponderosa pine forests. J. Range Manage. 43: 25-28.
Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
Clark, S.L., and Hallgren, S.W. 2004. Age estimation of Quercus marilandica and Quercus stellata: applications for interpreting stand dynamics. Can. J. For. Res. 34: 1353-1358.
Dolph, K.L. 1981. Estimating past diameters of mixed-conifer species in the central Sierra Nevada. U.S. For. Serv. Res. Note PSW-353.
Duncan, R.P. 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (Dacrycarpus dacrydioides). N.Z. Nat. Sci. 16: 31-37.
Foster, D.R., Orwig, D.A., and McLachlan, J.S. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. Trends Ecol. Evol. 11: 419-424.
Fulé, P.Z., Covington, W.W., and Moore, M.M. 1997. Determining reference conditions for ecosystem management in southwestern ponderosa pine forests. Ecol. Appl. 7: 895-908.
Gholz, H.G., Grier, C.C., Campbell, A.G., and Brown, A.T. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Oreg. State Univ. For. Res. Lab. Res. Pap. 41.

Gutsell, S.L., and Johnson, E.A. 2004. Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. J. Ecol. 90: 153-166.
Hann, D.W. 1976. Relationship of stump diameter to diameter at breast height for seven tree species in Arizona and New Mexico. U.S. For. Serv. Res. Note INT-212.

Iles, K. 1974. Geometrical considerations affecting the determination of basal area growth by increment boring methods. M.Sc. thesis, Oregon State University, Corvallis, Ore.
Jenkins, J.C., Chojnacky, D.C., Heath, L.S., and Birdsey, R.A. 2003. National-scale biomass estimators for United States tree species. For. Sci. 49: 12-35.
Johnson, J.B., and Omland, K.S. 2004. Model selection in ecology and evolution. Trends Ecol. Evol. 19: 101-108.
Matérn, B. 1961. On the precision of estimates of diameter growth from increment borings. In Proceedings of the 13th Congress of the International Union of Forest Research Organizations, Vienna, Austria, September 1961. Part 2(2), Sect. 25/8. IUFRO Vienna.
Moore, M.M., Huffman, D.W., Fulé, P.Z., Covington, W.W., and Crouse, J.E. 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. For. Sci. 50: 162-176.
Myers, C.A. 1963. Estimating past diameters of ponderosa pines in Arizona and New Mexico. U.S. For. Serv. Res. Note RM-7.
Norton, D.A., Palmer, J.G., and Ogden, J. 1987. Dendroecological studies in New Zealand. 1. An evaluation of tree age estimates based on increment cores. N.Z. J. Bot. 25: 373-383.
Omdal, D.W., Jacobi, W.R., and Shaw, C.G., III. 2001. Estimating large-root biomass from breast-height diameters for ponderosa pine in northern New Mexico. West. J. Appl. For. 16: 18-21.
Pearson, G.A. 1923. Natural reproduction of western yellow pine in the southwest. USDA Bull. 1105.
Pearson, G.A. 1950. Management of ponderosa pine in the southwest as developed by research and experimental practice. USDA For. Serv. Agric. Monogr. 6.
Rozas, V. 2003. Tree age estimates in Fagus sylvatica and Quercus robur: testing previous and improved methods. Plant Ecol. 167: 193-212.
Singleton, R., DeBell, D.S., Marshall, D.D., and Gartner, B.L. 2003. Eccentricity and fluting in young-growth western hemlock in Oregon. West. J. Appl. For. 18: 221-228.
Stokes, M.A., and Smiley, T.L. 1968. An introduction to tree-ring dating. University of Chicago, Chicago, Ill.
Villalba, R., and Veblen, T.T. 1997. Improving estimates of total tree ages based on increment core samples. Ecoscience, 4: 534542.

Williamson, R.L. 1975. Out-of-roundness in Douglas-fir stems. For. Sci. 21: 365-370.
Wong, C.M., and Lertzman, K.P. 2001. Errors in estimating tree age: implications for studies of stand dynamics. Can. J. For. Res. 31: 1262-1271.


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[^1]:    Note: Larger summed Akaike weights ( $\sum w_{i}$; maximum $=1$ ) indicate increased importance of a variable relative to the other variables in the model set (for details, see Burnham and Anderson (2002) and Johnson and Omland (2004)). Summed Akaike weights and coefficients were not calculated for the proportional method at CIB, as the model containing all variables was not significant ( $p=0.989$ ). The model containing all variables was significant for the proportional method at COC $(p=0.0006)$ and for the conventional method at $\operatorname{COC}(p<0.0001)$ and CIB $(p=0.0001)$.

