

Errors in estimating tree age: implications for studies of stand dynamics

Carmen M. Wong and Ken P. Lertzman

Abstract: Errors in estimates of tree ages from increment cores can influence age-class distributions, affecting inferences about forest dynamics. We compare methods of height correction of increment cores taken above ground level by examining how resulting errors affect age-class distributions of ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco). We compared the sapling (corrections based on the average basal age of breast high saplings) and the ground methods (corrections based on the average difference in age between ground and coring height) with a regression model we developed to overcome traditional assumptions of temporal and spatial homogeneity in early growth. Where early growth differed among mature trees or between modern saplings and mature trees, the regression method estimated age better than the two other methods. All methods of height correction over- or under-estimated tree age by at least 10 years and up to 30 years, indicating that age cannot be related to independent events of periodicities less than 10–20 years, such as El Niño, without accounting for error. Monte Carlo simulations demonstrated that error from height corrections affected the shape of age-class distributions by generating spurious regeneration pulses. We suggest that the magnitude of this error should govern the width of analytical age-classes to scale interpretations within the confidence of age estimates.

Résumé : Les erreurs dans les estimés de l'âge des arbres faits à partir de carottes peuvent influencer la distribution des classes d'âge affectant ainsi les inférences sur la dynamique forestière. Nous avons comparé les méthodes qui corrigent pour la hauteur des carottes prises au-dessus du sol en examinant de quelle façon les erreurs qui en résultent affectent la distribution des classes d'âge du pin ponderosa (*Pinus ponderosa* Dougl. ex P. & C. Laws.) et du douglas bleu (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco). La méthode basée sur l'âge basal moyen des jeunes tiges dont la taille correspond à la hauteur de poitrine et la méthode basée sur la différence moyenne d'âge entre le sol et la hauteur de prélèvement des carottes ont été comparées à un modèle de régression que nous avons développé pour contourner les hypothèses traditionnelles d'homogénéité temporelle et spatiale durant la phase de croissance juvénile. Lorsque la croissance juvénile diffère parmi les arbres matures ou entre les jeunes tiges actuelles et les arbres matures, le modèle de régression estime l'âge mieux que les deux autres méthodes. Toutes les méthodes de correction pour la hauteur surestiment ou sous-estiment l'âge de l'arbre d'au moins 10 ans et jusqu'à 30 ans. Ceci montre que l'âge ne peut être relié aux événements dont la périodicité est inférieure à 10–20 ans, tel El Niño, sans tenir compte de l'erreur d'estimation. Les simulations Monte Carlo ont démontré que les erreurs de correction pour la hauteur affectent la forme de la distribution des classes d'âge en générant des pulsations artificielles de régénération. Nous suggérons que l'amplitude de cette erreur intervienne dans la détermination de la largeur des classes d'âge pour ajuster l'interprétation des résultats à l'intérieur des limites de confiance des estimés de l'âge.

[Traduit par la Rédaction]

Introduction

Estimating the dates of tree establishment is a key requirement for research in the disturbance ecology of many forests. Approximate estimates are suitable for studies not concerned with relating tree establishment with independent temporal data. However, more accurate estimates are needed for purposes such as estimating time since fire (Johnson and Gutsell 1994) and for correlating tree establishment with cli-

mate (Savage et al. 1996; Villalba and Veblen 1997) or chronologies of disturbances (e.g., Romme and Knight 1981). Forest ecologists traditionally use peaks in static age-class distributions to identify disturbance initiated cohorts or pulses of tree establishment (Johnson et al. 1994; Oliver and Larson 1996). Errors in the dates of establishment can affect the shape of these distributions (Palik and Pregitzer 1995). Few studies on forest disturbance have evaluated the sensitivity of their results to the degree of error in the estimates of establishment dates.

Error in estimates of tree establishment arises primarily from the nature of the method used to sample the age of individual trees (Norton and Ogden 1990). To estimate the establishment dates of trees nondestructively, one would ideally sample the root–shoot boundary of every tree with an increment borer. Even with destructive sampling, however, it is difficult and laborious to identify the root–shoot boundary of trees accurately (Savage et al. 1996; DesRochers and

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Gagnon 1997). Studies based on increment boring typically rely on cores taken at a predetermined height, such as breast height (1.3–1.4 m) or 20–40 cm above ground (e.g., Henry and Swan 1974; Lorimer 1980; Veblen et al. 1991). Coring at these heights is less laborious and avoids problems associated with boring at the base of trees where trees are more likely to have fire scars, rot, or flare beyond the size of the borer making complete cores impossible (Frelich and Reich 1995; Stephenson and Demetry 1995).

Boring at a specified height above ground, when used to estimate dates of establishment, encounters three possible sources of error: (i) assigning calendar dates to tree rings, particularly of species tending to have missing or false rings; (ii) estimating the number of years to the pith on cores which miss or fall short of the pith, and (iii) estimating the number of years to grow to the height at which the tree is bored (Norton and Ogden 1990). The magnitude of error for each of these sources varies from a few years to a few decades depending on patterns of tree growth and coring height (Norton and Ogden 1990; Palik and Pregitzer 1995). Various methods have been used to minimize error from the first two sources, such as visual or computer-assisted cross dating to eliminate dating errors (Yamaguchi 1991; Grissino-Mayer and Holmes 1993) and modeling the number of missing years on cores that fail to hit the pith (Norton et al. 1987; Duncan 1989; Stephenson and Demetry 1995; Villalba and Veblen 1997). Various methods are also used to height correct cores not taken at ground level, but no study has compared the adequacy of these methods. In this paper we compare various methods of height correction by assessing how resulting errors affect interpretations of forest dynamics from age-class distributions.

One of two methods is typically used for estimating a “height correction” (h_c), the number of years it takes a tree to grow to coring height. One method of height correction involves cutting saplings at the root collar and determining a height correction from either the average basal age of saplings of the coring height (“sapling method”) (e.g., Veblen et al. 1991) or less commonly from a regression between sapling height and age (e.g., Mast et al. 1998). Some studies defined general categories of growth and used the average age of fast-growing saplings for fast-growing mature trees, and the age of slow-growing saplings for slow-growing mature trees (Romme and Knight 1981). Most methods using saplings without stratifying for differences in site conditions or tree position in the canopy assume the growth conditions of current saplings are similar to those experienced by older canopy trees (Villalba and Veblen 1997). A second method is to add the average difference in age between pairs of cores taken at ground level and at coring height from mature trees to every sample (Henry and Swan 1974). We call this the “ground method.” Both the sapling and the ground methods assume that an average of several trees accurately describes the early growth of any one tree. Averages provide accurate height correction only when variability in early tree growth is low and normally distributed (Palik and Pregitzer 1995). It is likely that these two assumptions of temporal and spatial homogeneity in early growth rates are violated in many forests. Successional stage, microhabitat, genotype, topography, changing climate, and disturbance regimes can cause the

growth rates of young trees to vary over time and space. Studies that do not try to link tree age to independent data like climate or disturbances, often simply report tree age at coring height. This too, is only valid where trees have similar rates of early growth over time and space (Palik and Pregitzer 1995).

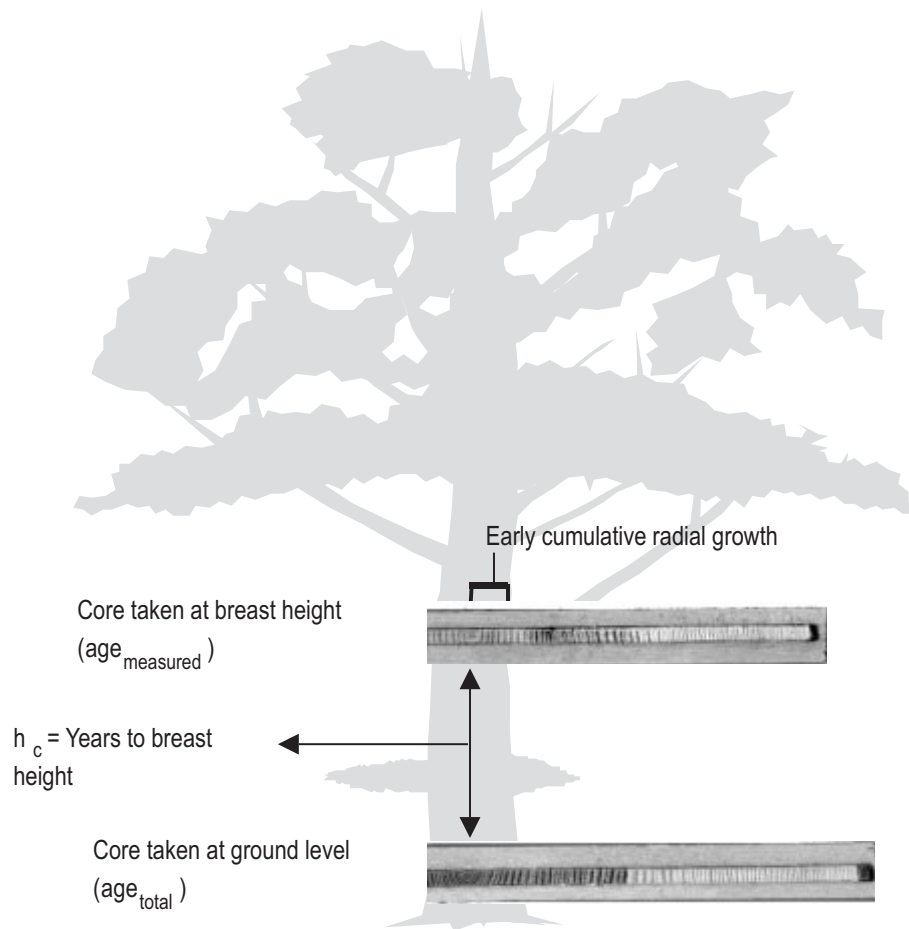
In this paper, we (i) develop a regression method for height correction that overcomes assumptions of temporal and spatial homogeneity in early growth rates, (ii) compare three methods of height correction (sapling, ground, and regression), and then (iii) illustrate how to account for error when interpreting forest dynamics from age-class distributions. We first test whether regression between early radial growth measured at breast height (1.3 m) and early height growth can estimate the number of years mature trees required to grow to breast height in a ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) – Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) forest. Height growth in young trees tends to be positively correlated with radial growth except when trees are stressed by moisture, injury, or insect attack (Kulman 1971; Oliver and Larson 1996). Other variables, such as tree height and diameter at breast height (DBH), are thought to be poorly related to tree age in multi-aged stands (Johnson et al. 1994). The sensitivity of the regression model to cores that miss the pith was also examined. We then compare the three height correction methods (sapling, ground and regression, and uncorrected data) by analyzing the influence of the resulting error on age-class distributions. In the ponderosa pine – Douglas-fir forest, the regression method should correct for coring height more accurately than the other methods, because it requires less assumptions of homogeneity in early radial growth. We illustrate how to account for uncertainty in dates of tree establishment by using Monte Carlo simulations to determine the appropriate resolution of age-classes for analysis. We also examine the hypothesis that uncertainty in height corrections is enough to cause spurious peaks in age-class distributions at some resolution and that the sensitivity of age-class distributions to error in tree ages may be more pronounced at finer resolutions, i.e., using narrower classes in age-class distributions may cause more spurious pulses of tree establishment than using wider classes.

Methods

Study site and context

We conducted this study in the lower canyon of the Nlaka'pamux Stein Valley Heritage Park in the interior of British Columbia, Canada (50°15'N, 121°40'W). Forests here are open (mean density 429 trees/ha) and transitional between the dry hot variants of the Ponderosa Pine (PPxh2) and the Interior Douglas-fir biogeoclimatic subzones (IDFxh2) of British Columbia's biogeoclimatic classification system (Lloyd et al. 1990; Meidinger and Pojar 1991; MacKinnon et al. 1992). We cored trees in seven natural stands (28 ha total) dominated by Douglas-fir (73% of trees) and ponderosa pine (23%) on flat river terraces, each bounded by the Stein River and steep slopes. This study is part of a larger study of forest disturbance in which we integrate patterns of tree establishment with data on low-severity fires to infer the relative roles of disturbances of different severity in the seven stands (Wong 1999). We cored trees at ground and breast height and used these ages to compare three methods of height correction.

Fig. 1. Components of the regression method for the height correction of increment cores. The number of years a tree requires to reach breast height (h_c) was estimated from the early cumulative radial growth measured on the core taken at breast height. We added h_c to the ages of cores taken at breast height ($\text{age}_{\text{measured}}$) to obtain ages from height corrected ring counts. These were compared with the age of cores taken at ground level ($\text{age}_{\text{total}}$).



Three methods of height corrections

Height corrections of increment cores sampled above ground level follow the general equation

$$[1] \quad \text{Age}_{\text{measured at coring height}} + h_c + e_{\text{estimate of years to pith}} + e_{\text{estimate of missing/false rings}} = \text{age}_{\text{total}}$$

Because we used cross-dated cores that intersected the pith, we did not need to estimate years to the pith or missing or false rings. For the sapling method we estimated the height correction (h_c) as the average age of current saplings at ground level. The value of h_c was estimated from 15 ponderosa pine and 15 Douglas-fir saplings close to breast height randomly selected over the study area. Saplings were 1.3 ± 0.12 m high (mean \pm SD); approximately half were growing in relatively open space and half in patches of small trees. We cut these saplings at ground level and sanded and dated basal cross sections using standard dendrochronological methods (Stokes and Smiley 1968; Yamaguchi 1991).

For the ground method and to develop a height correction regression, we calculated h_c from pairs of cores taken at ground level and at breast height from 17 ponderosa pine and 24 Douglas-fir trees (Fig. 1). We stratified our sampling of these 41 trees according to the number of trees sampled on each terrace in the larger disturbance study. For example, 40% of the trees used for the disturbance study were from one terrace, so we cored approximately 40% of the 41 trees used for the height correction on this terrace.

Sampling points were placed along a transect in each stand at regular intervals based on the number of sampling points and the size of the stand. At each sampling point, we cored and measured the total tree height and DBH of the three closest trees that met the following criteria: (i) >5 cm DBH; (ii) one of the three trees was a different species than the other two; and (iii) one was >20 cm DBH. The 41 cored trees ranged from 6 to 46 cm DBH. We took two increment cores from the same side of each tree; one at breast height (1.3 m) and one at ground level (mean height 0.19 m). To core close to the ground, we dug pits in the soil in which the handle of the increment borer could turn, used the handle of a 10-in. increment borer (1 in. = 2.54 cm) on an 18-in. borer, or instead of a handle, used a ratchet to drill in the shaft of the borer and an adjustable wrench to extract the shaft. An adapter to connect the ratchet to the borer shaft was made from two 0.375-in. drive sockets joined by a piece of 0.5-in. hex bar. We only used pairs of cores for analysis if both the ground level and breast height cores intersected pith or were within what we judged to be 1 year of the pith. Cores were mounted, sanded, and visually cross-dated using standard dendrochronological methods (Stokes and Smiley 1968; Yamaguchi 1991) and existing tree-ring width chronologies (Riccius 1998). The number of years to breast height, h_c , was calculated as the absolute difference in age between each pair of ground level and breast height cores. For the ground method, h_c for each species was simply the average of this difference (Henry and Swan 1974).

For regression method, we used measurements of early radial growth, height, and DBH of the 41 trees described above to develop regressions. We measured the widths of the first 15 rings on the cores taken at breast height using a sliding-stage micrometer. We examined the strength of least squares linear, log-linear, and various nonlinear regression models (negative exponential, power, and quadratic) regressions between years to breast height and the following variables: (i) cumulative radial growth in the first 5, 10, or 15 years on cores sampled at breast height; (ii) total tree height; and (iii) DBH. We selected the final model based on the distribution of the residuals, the magnitude of the mean square error (MSE) and the coefficient of variation (Ratkowsky 1990).

Sensitivity of height correction regression to missing pith

Since it is common for increment cores to miss the pith of a tree, we examined the sensitivity of our model to errors arising from this. When the pith is missed, information about the earliest years of a tree is not known. We evaluated how well later periods of radial growth estimate early height growth to assess the adequacy of cores that deviated from the pith by up to 15 years. To do this, we substituted the variable of cumulative radial growth in the first 5 years at breast height with later periods of 5-year growth, e.g., growth from year 5 to year 10 and from year 10 to year 15. We calculated the error of each estimate of years to breast height, h_c , as the absolute difference between observed and estimated values. We tested for differences in the distributions of error from using each of these periods of growth in the regression with a Kolmogorov–Smirnov two-sample test (K–S test). We are unaware of an existing correction for the K–S statistic for multiple comparisons.

Comparing methods of height corrections

To evaluate which method of height correction produced the best estimates, we compared the distributions of residual error from each method (sapling, ground, regression) and reporting age at coring height (uncorrected ages). Error of these estimates was calculated as the absolute difference between observed (age at ground level) and height-corrected ages. Height corrections, h_c , generated by each method were added to the age determined from each of the 41 cores taken at breast height. We tested for significant differences between the distributions of error from each of the four methods using the K–S test. We also compared interpretations of age-class distributions resulting from the various methods of height correction.

Implications of uncertainty in establishment dates

We analyzed the influence of error in estimates of tree age on the apparent number and position of pulses of tree establishment in histograms. We first used the regression between radial growth in the first 5 years and years to breast height to estimate establishment dates of the 466 Douglas-fir cored at breast height in the larger disturbance study (Wong 1999). These corrected dates constituted the estimated distribution of establishment dates. We compared this estimated distribution with a simulated distribution representing the possible proportion of trees in each date class if the height corrections were wrong. The simulated distribution was created using Monte Carlo methods to simulate possible age distributions that included error from the regression method. To do this, we defined the probability of a certain magnitude of error as its frequency of occurrence when height correcting the present study's 24 trees. For each of the 466 trees, we randomly selected an error from this probability distribution, added this error to the estimated establishment date, and placed the tree into an appropriate date class. We did this 1000 times for each tree and summarized the results of the 1000 age distributions in one simulated distribution

where the proportion in each date class was an average of the 1000 scenarios.

To examine the hypothesis that the sensitivity of age-class distributions to error is dependent on the resolution of analysis, we compared the estimated and simulated distributions at two resolutions. We used date classes of coarse (20 years wide) and fine (5 years) resolution. At each resolution we (i) tested for significant differences in the shape of the estimated and simulated distributions (K–S test), (ii) correlated the estimated and simulated proportions in each date class (Pearson coefficient), and (iii) compared the apparent number and position of pulses of tree establishment. For the latter, we identified pulses as bell-shaped peaks (Oliver and Larson 1996) where the number of trees was at least 50% greater than the preceding date class for coarse resolution or the preceding four date classes for fine resolution (Wells et al. 1998).

Results

Sapling and ground methods

Modern saplings took approximately twice as long to grow to breast height as did the currently mature trees when they were saplings. On average, modern ponderosa pine saplings of breast height were 35 ± 10 years old (median 30) and modern Douglas-fir saplings were 37 ± 11 years old (median 39). Based on the ground method, mature ponderosa pine, on average, required 16 ± 12 years (median 12) and mature Douglas-fir required 20 ± 10 years (median 20; Fig. 2) to reach breast height when they were young.

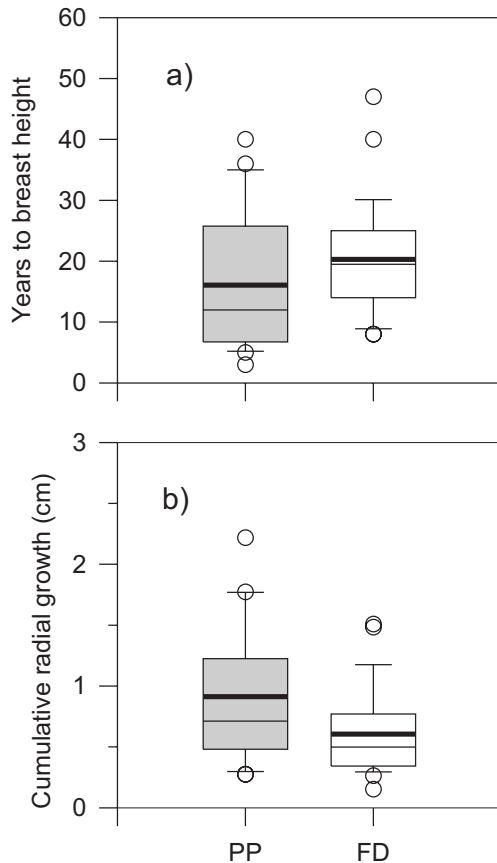
Regression method

The variable that best estimated the height correction of increment cores taken at breast height was cumulative radial growth in the first 5 years. The relationship between years to breast height (y) and cumulative radial growth during the first 5 years on the breast height core (x) was best described by a power function ($y = ax^{-b}$, where a controls the slope and b influences the shape of the curve). Other models using cumulative radial growth in the first 10 or 15 years exhibited heteroscedastic residuals. Compared with the power function, other regression functions between radial growth and years to breast height had lower MSEs, coefficients of variation, and poorer distributions of residuals. The power model explained most of the variance in years to breast height for ponderosa pine ($R^2 = 0.70$) but only about one-third of the variance in that for Douglas-fir ($R^2 = 0.31$; Fig. 3). Weak linear relationships existed between years to breast height and total tree height or DBH (height: all R^2 values < 0.29 , $p > 0.026$; DBH: all R^2 values < 0.156 , $p > 0.112$).

Sensitivity of regression to missing pith

The distributions of error from the regression between years to breast height and cumulative radial growth during the first 5 years on the breast height core were centered around zero for both ponderosa pine and Douglas-fir (mean error 0.09 years; Fig. 4). For Douglas-fir, using radial growth measured progressively farther from the pith did not significantly change the distribution of error around height corrections (Fig. 4; K–S test: all p values > 0.675). For ponderosa pine, the further radial growth was measured from the pith, the more our model tended to overestimate height corrections and, thus, total tree ages, but it did not significantly

Fig. 2. Summary of the parameters used to estimate the number of years to coring height: (a) difference in years between ground level and breast height cores; (b) cumulative radial growth in the first 5 years at breast height. Thick lines in the boxes are the mean, and thin lines are the median; shaded and open boxes are for ponderosa pine (PP) ($n = 17$) and Douglas-fir (FD) ($n = 24$), respectively. Open circles are values outside the 10th and 90th percentiles.

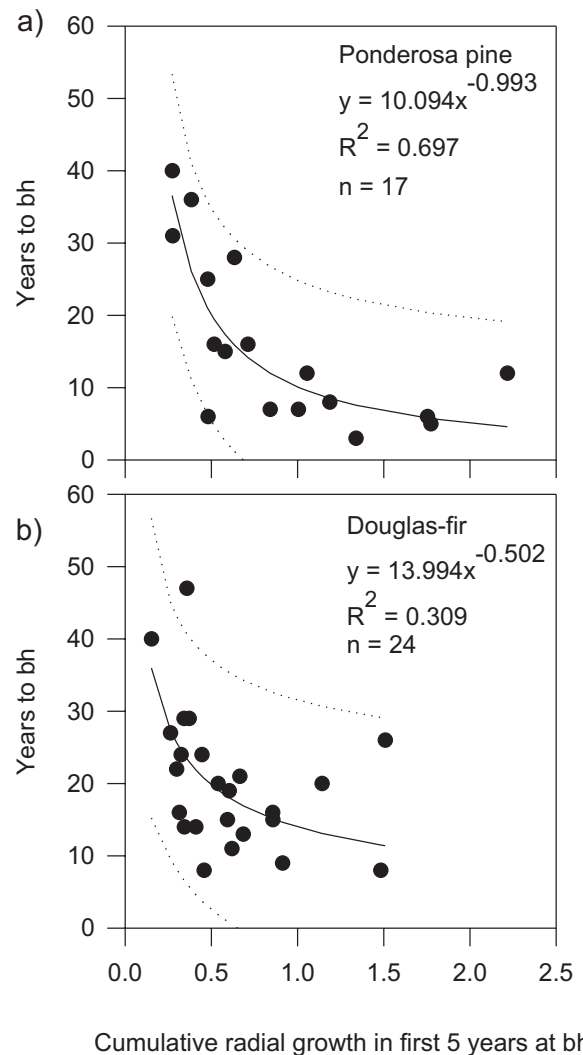


change the distribution of error (Fig. 4; K-S test: all p values > 0.312).

Methods of height corrections differed

The four methods of height correction differed in their accuracy of estimates of years to breast height (Fig. 5). Age at breast height underestimated total tree age by up to 50 years (mean error 16 years for pine and 20 years for Douglas-fir), while the average age of saplings of breast height overestimated total age by up to 50 years (mean error 19 years for pine and 16 years for Douglas-fir). In contrast, using the ground or regression method resulted in distributions of error in estimates that were centered close to zero (mean error 0.05 and 0.09 year for pine and 0.29 and 0.09 year for Douglas-fir). The distributions of error from the ground and regression methods differed significantly from reporting the age at coring height and the sapling methods (K-S test: all p values < 0.001) but did not differ from each other (K-S test: p values > 0.240). However, for ponderosa pine, the range of possible error (-13 to 24 years) from the ground method was greater than from the regression method (-15 to 12 years).

Fig. 3. Nonlinear regression between years to breast height and cumulative radial growth (cm) in the first 5 years at breast height (bh). Broken lines are 95% confidence intervals around estimated values.

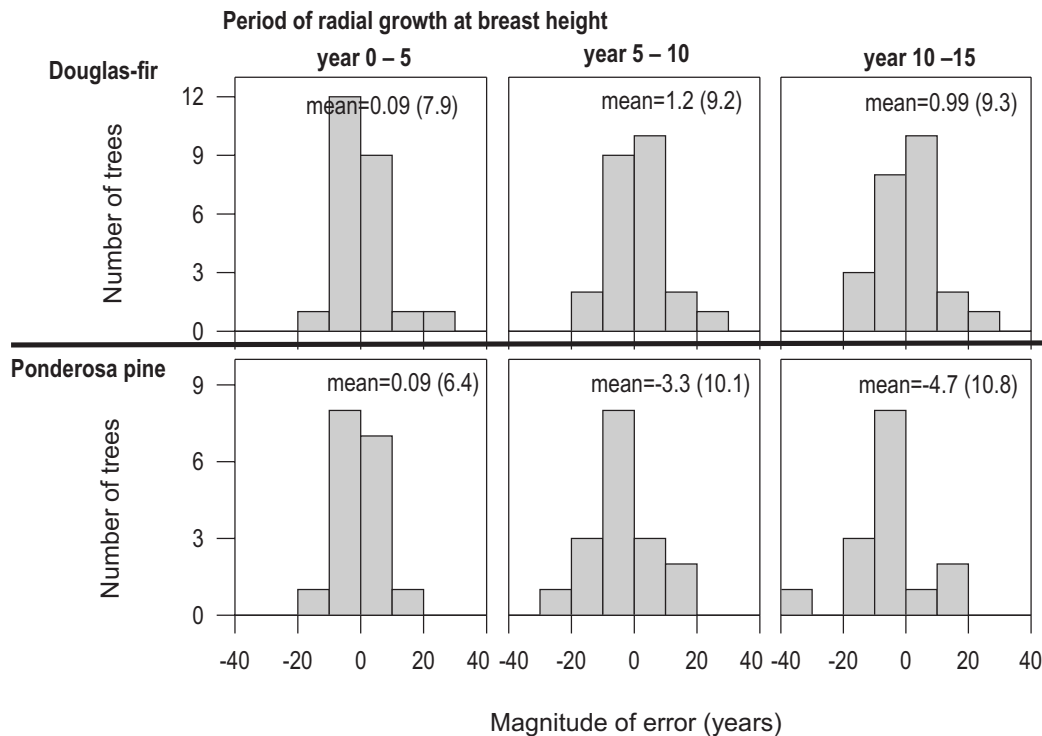


For Douglas-fir, ranges of possible error from these two methods were essentially the same (-12 to 26 years).

Error affected distributions of tree establishment

Error in establishment dates can significantly change the shape of age-class distributions if the resolution of analysis is too fine. This is illustrated when estimated age distributions determined from height-corrected ring counts differ from simulated distributions that summarized possible scenarios if these height corrections were wrong (Fig. 6). When class widths of 20 years were used (coarse resolution), estimated and simulated distributions of dates of establishment were not significantly different in location, dispersion, and skewness (K-S test: $p = 0.89$; Fig. 6a). However, these two distributions significantly differed when classes were 5 years wide (fine resolution) (K-S test: $p = 0.031$; Fig. 6c). The trade-off between error and resolution of data analysis is further emphasized in Figs. 6b and 6d. When histograms of fine resolution were used, there was greater deviation from a per-

Fig. 4. Comparing the distribution of error in estimates of years to breast height from our regression method when cores with pith were used versus cores 10 or 15 years off pith at breast height. Values in parentheses are SDs.



fect correlation between the estimated and simulated proportion of trees in each age-class, i.e., increased scatter around the 1:1 relationship; Pearson coefficients: coarse (0.995), fine (0.954) (Figs. 6b and 6d).

Error in establishment dates and resolution of analysis affected the number and position of regeneration pulses that we were able to identify. When analyzing the coarse resolution histograms, estimated and simulated distributions displayed the same number and position of regeneration pulses. Using the criterion of proportions of trees 50% greater than the preceding date class, one pulse, establishing around 1855, was identified for both estimated and simulated distributions. Under fine-resolution analysis, more pulses were identified in the estimated distribution than the simulated simulation: three pulses were identified in the estimated distribution originating in 1940, 1855, and 1795, while only one pulse in 1850 was identified in the simulated distribution.

Discussion

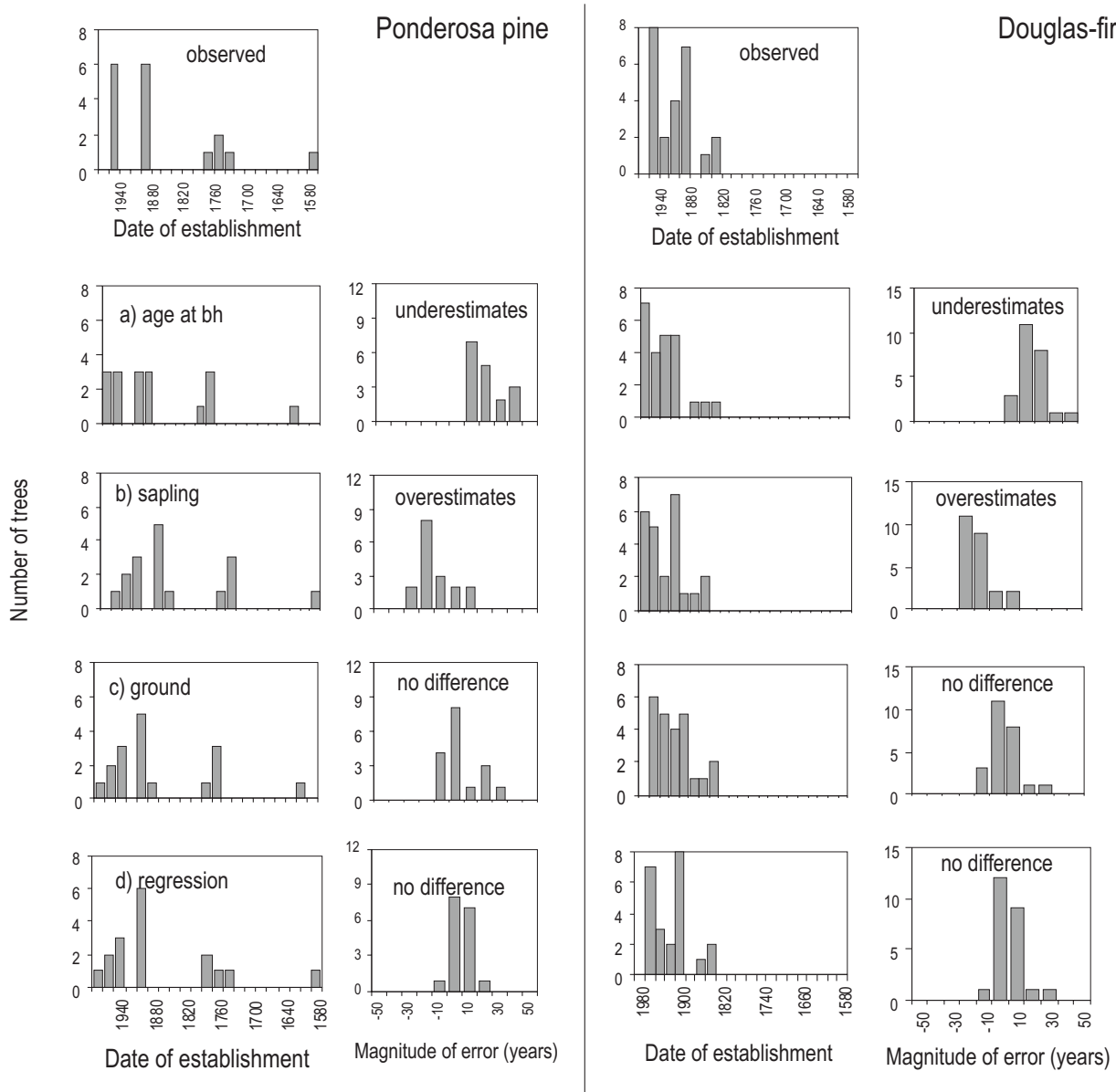
Each method has an appropriate context

Why did the regression method estimate height corrections better than the sapling method? The sapling method assumes temporal and spatial homogeneity in the growth rates of young trees. If modern saplings are growing under conditions similar to the older overstory, then the average basal age of saplings at the coring height should provide accurate height corrections. In our study area, modern saplings appeared suppressed relative to growth rates exhibited by older trees. These older trees likely established under different competitive regimes from modern saplings, because frequent low-severity fires, thought to historically maintain open for-

ests, have now been mostly excluded from the study area since 1936 (Riccius 1998). The sapling method, therefore, tended to overestimate total tree age relative to the regression model (Fig. 5). Some of this overestimation may be caused by being unable to sample true age at ground level; for the regression method we sampled age on average at 20 cm above the ground, and root collars may be below ground level. In boreal forests, root collars of spruce are likely to be below ground because of adventitious root formation (DesRochers and Gagnon 1997). However, in our study area these factors are unlikely to have caused the degree of overestimation observed from the sapling method because (i) even at the slowest rate of height growth, it took up to only 6 years to grow 20 cm in height (based on the observation that it took current Douglas-fir saplings 37 years to grow to breast height (1.3 m)) and (ii) the soil and organic layers are too rocky and shallow to permit much organic buildup around the root collar.

Why did the regression method estimate height corrections better than the ground method for ponderosa pine but not for Douglas-fir? There are two possible answers. Ponderosa pine may meet the assumptions of the regression method better than Douglas-fir. The regression method assumes early radial growth is a good estimator of early height growth and that the cores taken at breast height record perfect information about the early growth of that tree. For most shade-intolerant species like ponderosa pine these are not unreasonable assumptions, because these species are not likely to be suppressed in the understory as saplings. Douglas-fir, however, is shade tolerant in these dry ecosystems and can remain suppressed in the understory. Periods of short suppression during the first few years of a tree's life may not have been

Fig. 5. Estimates of dates of tree establishment (left columns) and error of these estimates (right columns) from observed dates (labeled observed) for uncorrected data and three different methods used to estimate the number of years ponderosa pine and Douglas-fir require to grow to breast height (bh). Methods are (a) reporting age at breast height; (b) sapling; (c) ground; and (d) regression. Error is expressed as observed – estimated values, and we indicate whether the method underestimates or overestimates observed dates of establishment.

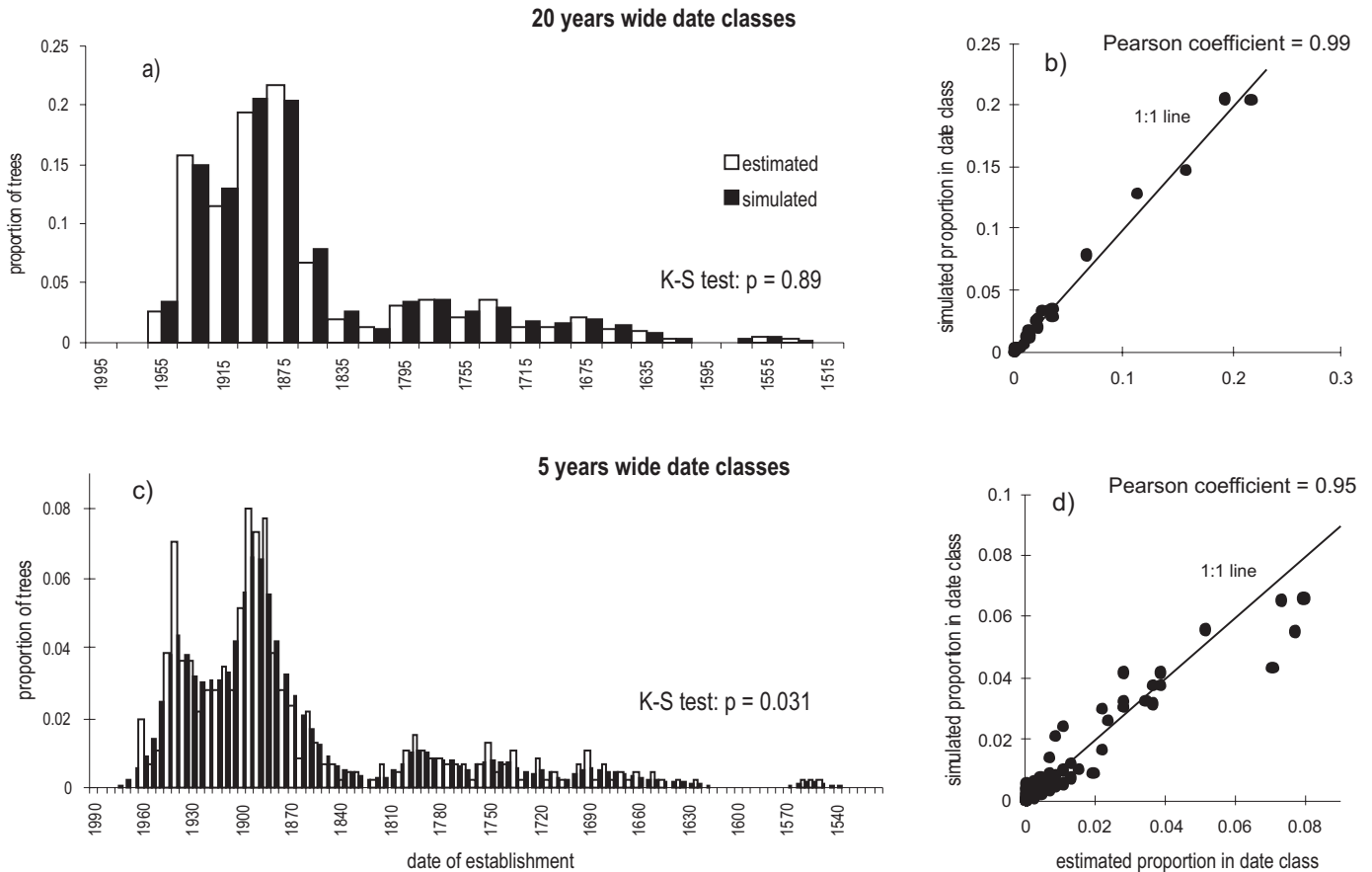


recorded on some cores taken at breast height, i.e., early growth may not be temporally homogeneous within a tree. Thus, radial growth on the innermost segment of the core taken at breast height of such trees will overestimate the actual rate of early radial growth. This underestimates the number of years to coring height and may partly explain the relatively poorer fit of the power function to the Douglas-fir data (Fig. 3). In other forests where competition, climatic stress, herbivory, insect defoliation, or injury can reduce the growth of seedlings for a few years (Kulman 1971; Carlson and Schmidt 1989; Clinton et al. 1997), this may be a larger source of error and limit the applicability of the regression method. Because the regression method assumes temporal

homogeneity in radial growth between coring height and ground level within a tree, the regression method predicted ponderosa pine better than Douglas-fir (Fig. 5). This suggests that the regression method estimates shade-intolerant species better than shade-tolerant ones.

Douglas-fir may also meet the assumptions of the ground method better than ponderosa pine. On our site, there was little variability in the early height and radial growth of Douglas-fir relative to ponderosa pine (Fig. 2). Because the ground method assumes there is little spatial variability among trees during early growth, the ground method predicted Douglas-fir better than ponderosa pine. Since the range of error in height corrections resulting from the ground and re-

Fig. 6. Comparing distributions of estimated and simulated dates of establishment of Douglas-fir using class widths of 20 years (a) and 5 years (c). Open bars are estimated proportions of trees from height corrected ring counts. Solid bars are what the proportions might actually be if height corrections were wrong (calculated by adding expected error to height corrected ring counts with Monte Carlo simulations). Assessing the strength of the correlation between estimated and simulated proportions in matching date classes for class widths of 20 years (b) and 5 years (d). Class width of 20 years better represented the potential influence of error from height corrections.



gression methods was similar (Fig. 5), it would have been more efficient to use the ground method instead of the regression method to height correct Douglas-fir cores.

Each of the three methods of height correction considered here requires certain assumptions about the growth of young trees and, thus, will estimate better in certain circumstances than others. The sapling method works when the growth rate of trees is the same over time and space. This is not true in many forests, particularly in ponderosa pine – Douglas-fir forests where stands have become denser because of climate, fire suppression, and grazing (Fulé et al. 1997). The ground method works where the growth of young trees is similar over space. This also is not true in many forests. For example, *Austrocedrus chilensis* (D. Don) seedlings in northern Patagonia varied in height growth with microsite and the proximity of large trees (Villalba and Veblen 1997). If no evidence exists to indicate that the radial and height growth of young trees has been temporally and spatially homogeneous, then the regression method provides a unique height correction for each mature tree and, thus, overcomes these assumptions. The regression method is appropriate for forests where (i) boring close to the ground is difficult or impossible, (ii) modern saplings are absent, (iii) modern saplings do not represent historical saplings, or (iv) early growth was highly

variable between mature trees. If we had enough samples, developing a regression for each stand or stratifying according to site conditions may have increased the accuracy of height correction. The regression method does not work as well when radial growth varies greatly between ground level and coring height within a tree. An alternative is to avoid height corrections by taking all increment cores as close to the ground as possible and accepting the associated error. The magnitude of error, however, may be enough to influence interpretations of age-class distributions or preclude relating dates of tree establishment to independent data (Fig. 5).

Error in height corrections limits inferences that can be made from age-class distributions. All methods of height correction, even with the regression method, which involves the fewest assumptions, over- or under-estimated height corrections by at least 10 years and up to 30 years (Fig. 5). This level of error does not permit relating tree establishment to independent events, such as El Niño events, of periodicities less than 10 years. Even if age structure is not related to independent events, error can affect conclusions about stand dynamics. For example, the ground and regression methods of height correction indicated that, for ponderosa pine, there has been a gradual pulse of establishment beginning in 1940,

whereas the actual ages indicate one very narrow window of establishment in 1961–1980 (Fig. 5). Additional sources of error, such as estimating the number of years to the pith on cores that miss the pith, can increase this level of error and may in some forests, particularly with large trees like giant sequoias (*Sequoiadendron giganteum* (Lindley) Buchholz), be larger than the error involved in height corrections (Stephenson and Demetry 1995).

It is important to assess uncertainty

Since only bole excavations followed by fine sectioning of cross sections of the stem can date the actual germination year of trees, some degree of error in tree ages should be expected when using increment cores. How can one deal with error in dates of tree establishment to make appropriately scaled inferences about forest dynamics? We advocate using Monte Carlo simulations to formally assess the uncertainty around dates of tree establishment estimated from height correcting or extrapolating to the pith. The magnitude of error expected from height corrections should govern the width of date- or age-classes to scale interpretation of histograms within the confidence in the estimates of dates or ages. Since the majority (88%) of errors for Douglas-fir estimates in this study were between –10 to 10 years from actual ages, we were confined to the coarse resolution of 20-year widths for histogram analysis. We verified that 20 years was an appropriate scale of analysis for the expected amount of error, because the estimated age distribution (determined from height corrected ring counts) did not differ from the simulated distribution (determined from simulating possible scenarios if height corrections were wrong; Fig. 6). If we had analyzed histograms using date classes 5 years wide, the indicated three regeneration pulses could have been misinterpreted as a forest structured by multiple, moderate-severity disturbances. In contrast, the histogram with date classes 20 years wide indicated that the forest was more likely structured by one moderate-severity disturbance that did not kill all the old trees and was followed by a long 60-year period of regeneration. These two interpretations of the data have different implications for disturbance frequency and severity, and therefore, it is critical to analyze the influence of error on conclusions derived from static age distributions. The degree to which error modifies age-class distributions depends on the magnitude of the error in conjunction with the resolution of the age-classes. If the distribution of error from height corrections or extrapolating to the pith is unknown, then hypothetical distributions can be used in simulations to examine how sensitive the shapes of age-class distributions are to error.

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References

- Carlson, C.E., and Schmidt, W.C. 1989. Influence of overstory removal and western spruce budworm defoliation on growth of advance conifer regeneration in Montana. USDA For. Serv. Res. Pap. INT-409.
- Clinton, B.D., Elliott, K.J., and Swank, W.T. 1997. Response of planted eastern white pine (*Pinus strobus* L.) to mechanical release, competition, and drought in the southern Appalachians. *South. J. Appl. For.* **21**: 19–23.
- DesRochers, A., and Gagnon, R. 1997. Is ring count at ground level a good estimation of black spruce age? *Can. J. For. Res.* **27**: 1263–1267.
- Duncan, R.P. 1989. An evaluation of errors in tree age estimates based on increment cores of Kahikatea (*Dacrycarpus dacrydioides*). *N.Z. Nat. Sci.* **16**: 31–37.
- Freligh, L.E., and Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecol. Monogr.* **65**: 325–346.
- Fulé, P.Z., Covington, W.W., and Moore, M.M. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecol. Appl.* **7**: 895–908.
- Grissino-Mayer, H.D., and Holmes, R.L. 1993. International tree-ring data bank program library. Laboratory of Tree Ring Research, University of Arizona, Tucson.
- Henry, J.D., and Swan, J.M.A. 1974. Reconstructing forest history from live and dead plant material—an approach to the study of forest succession in southwest New Hampshire. *Ecology*, **55**: 772–783.
- Johnson, E.A., and Gutsell, S.L. 1994. Fire frequency models, methods and interpretations. *Adv. Ecol. Res.* **25**. pp. 239–285.
- Johnson, E.A., Miyanishi, K., and Kleb, H. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta* – *Picea engelmannii* forest. *J. Ecol.* **82**: 923–931.
- Kulman, H.M. 1971. Effects of insect defoliation on growth and mortality of trees. *Annu. Rev. Entomol.* **16**: 289–324.
- Lloyd, D.L., Angove, K., Hope, G., and Thompson, C. 1990. A guide to site identification and interpretation for the Kamloops Forest Region, Parts 1 and 2. Research Branch, B.C. Ministry of Forests, Victoria.
- Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology*, **61**: 1169–1184.
- MacKinnon, A., Meidinger, D., and Klinka, K. 1992. Use of the biogeoclimatic ecosystem classification system in British Columbia. *For. Chron.* **68**: 100–120.
- Mast, J.N., Veblen, T.T., and Linhart, Y.B. 1998. Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone. *J. Biogeogr.* **25**: 743–755.
- Meidinger, D.V., and Pojar, J. 1991. Ecosystems of British Columbia. B.C. Ministry of Forests, Research Branch, Victoria. Spec. Rep. Ser. 6.
- Norton, D.A., and Ogden, J. 1990. Problems with the use of tree rings in the study of forest population dynamics. *In* *Methods of dendrochronology: applications in the environmental sciences.* Edited by E.R. Cook and L.A. Kairiukstis. Kluwer Academic Publishers, Norwell, Mass. pp. 284–288.

- 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.
- Oliver, C.D., and Larson, B.C. 1996. *Forest stand dynamics*. 2nd ed. John Wiley & Sons, Inc., New York.
- Palik, B.J., and Pregitzer, K.S. 1995. Variability in early height growth rate of forest trees: implications for retrospective studies of stand dynamics. *Can. J. For. Res.* **25**: 767–776.
- Ratkowsky, D.A. 1990. *Handbook of nonlinear regression models*. Marcel Dekker, Inc., New York.
- Riccus, E. 1998. Scale issues in the fire history of a fine grained landscape. Master's thesis, Simon Fraser University, Burnaby, B.C.
- Romme, W.H., and Knight, D.H. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology*, **62**: 319–326.
- Savage, M., Brown, P.M., and Feddema, J. 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. *Ecoscience*, **3**: 310–318.
- Stephenson, N.L., and Demetry, A. 1995. Estimating ages of giant sequoias. *Can. J. For. Res.* **25**: 223–233.
- Stokes, M.A., and Smiley, T.L. 1968. *An introduction to tree ring dating*. University of Chicago Press, Chicago, Ill.
- Veblen, T.T., Hadley, K.S., Reid, M.S., and Rebertus, A.J. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology*, **72**: 213–231.
- Villalba, R., and Veblen, T.T. 1997. Improving estimates of total tree ages based on increment core samples. *Ecoscience*, **4**: 534–542.
- Wells, A., Stewart, G.H., and Duncan, R.P. 1998. Evidence of widespread, synchronous, disturbance-initiated forest establishment in Westland, New Zealand. *J. R. Soc. N.Z.* **28**: 333–345.
- Wong, C.M. 1999. Memories of natural disturbances in ponderosa pine – Douglas-fir age structure, southwestern British Columbia. Master's thesis, Simon Fraser University, Burnaby, B.C.
- Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* **21**: 414–416.