

TREE AGE ESTIMATION FOR THE TROPICS: A TEST FROM THE SOUTHERN APPALACHIANS

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Abstract. The lack of annual growth rings in the majority of tropical tree species greatly limits our understanding of the long-term dynamics of tropical forests. To address this problem, several methods have been developed to estimate the age of tropical trees from diameter growth data. These past approaches, however, suffer from two major flaws: (1) they assume a deterministic age–size relationship for a tree species, and (2) they have not been verified with independently derived age data. In this paper, I present a new approach that uses diameter growth rates, independent of tree size, that are stratified by crown class to estimate the age of individual trees. Past approaches have assumed that when present-day canopy trees were juveniles they grew at rates similar to conspecifics currently in the understory. In contrast, the crown class model assumes that present-day canopy trees have grown at rates similar to conspecifics in the same crown class, irrespective of size, throughout ontogeny.

The crown class model was compared to a periodic annual increment (PAI) model typical of past approaches in mixed oak-hardwood forest in the southern Appalachians, USA. Tree ages were obtained independently from tree cores from three stands of differing age structure. Comparisons between the two models were made for species' population age structures (independent of stands) and stand age structures (independent of species).

Age estimation errors for the crown class model were lowest for relatively shade-intolerant species such as yellow poplar (*Liriodendron tulipifera*) and chestnut oak (*Quercus prinus*), but increased with the increasing shade tolerance of the species. The PAI model followed the opposite pattern, providing the most accurate age estimates for shade-tolerant species. These results were consistent with the underlying ecological assumptions of each model.

When predicted age distributions for individual stands were compared to the true age distributions, the PAI approach had higher estimation errors than the crown class model in almost every case. In addition, the PAI model had a strong tendency to overestimate tree ages. A mixed model that used crown class age estimates for shade-intolerant species and PAI model age estimates for shade-tolerant species generated the most accurate estimates of stand age distribution. The results of this study suggest new opportunities for the study of long-term dynamics in tropical forests and underscore the importance and utility of validating models with independent data.

Key words: age estimation; Appalachian forest, southern; crown class; model testing; periodic annual increment; stand dynamics; suppression; temperate forests; tropical forests.

INTRODUCTION

One of the greatest impediments to advancing the understanding of tropical forest dynamics is the inability to accurately determine the ages of the trees in the absence of reliable annual growth rings (Ashton 1981, Bormann and Berlyn 1981). The study of forest stand dynamics in the temperate zone has progressed rapidly in recent decades as a consequence of dendroecological studies (e.g., Henry and Swan 1974, Swetnam and Lynch 1993) that use annual growth rings to infer historical patterns of change in forest stands

(Oliver and Larson 1996). Because tree species with annual rings are rare in tropical forests, few retrospective studies have been undertaken in the tropics.

Without accurate estimates for the ages of individual trees, the current understanding of temporal dynamics of tropical forests relies heavily on extrapolation of short-term growth trends. Investigations into the temporal dynamics of tropical forests have depended almost exclusively on permanent study plots; however, few permanent plots are more than 20 years old, a fraction of the lifespan of the majority of the canopy tree species in a forest. The development of methodologies to accurately estimate tree ages based on short-term growth data would provide tropical foresters and ecologists an important tool to study long-term forest stand dynamics. Because tree diameter is an easy and inexpensive measurement to obtain, and in many cases such data already exist, the focus of this study is on

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age estimation models that use diameter growth as the principal variable.

Past approaches to estimating tree age

The periodic annual increment (PAI) approach is the oldest of the age estimation models that have been applied in tropical forests. Brown and Mathews (1914) used it to estimate tree ages in Philippine dipterocarp forests nearly a century ago. It is a simple means of obtaining age estimates from size and increment data and is the conceptual basis for most subsequent age estimation procedures. The PAI method requires a sample of trees spanning the entire size range of a species. Diameter classes are defined for the entire size range. The time required to pass through a diameter class for a tree growing at the mean growth rate for that diameter class is calculated for each diameter class. Age–diameter curves are then developed by plotting the cumulative time required to pass through each diameter class (Nicholson 1965).

A practical shortcoming of the PAI approach is that, in many cases, growth data may either not be available for every size class or may be limited by small sample sizes to a few individuals whose growth may or may not be “characteristic” of the size class. To alleviate this problem, Condit et al. (1993) and Terborgh et al. (1997) proposed using regression techniques to buffer the influence of erratic fluctuations in small samples and extrapolate growth patterns across size classes without data. The regression approach develops a polynomial relationship between tree size and annual diameter increment (Condit et al. 1993). The resultant equation is integrated to produce a lifetime growth trajectory.

Terborgh et al. (1997) modified the regression approach of Condit et al. (1993) in two ways. First, they replaced the polynomial regression with loess regression, a nonparametric, locally weighted, smoothing algorithm, because it better described the complex relationships between size and growth. Second, they weighted individual tree contributions to the regression by the probability of mortality given tree size (relative to size at maturity) and growth increment. The reason for weighting growth performance is straightforward: Trees that are smaller or growing slowly have a lower probability of surviving to become canopy trees. Therefore, giving their contribution an equal weighting biases the lifetime growth trajectory and is unlikely to accurately reflect the early growth patterns of trees that currently occupy the canopy.

Another limitation of the traditional PAI approach is that it does not incorporate individual variation in growth rates. Lieberman and Lieberman (1985) developed a probabilistic approach to the PAI concept that captures individual tree variation. The Liebermans’ method simulates hundreds of growth trajectories of trees using a matrix of data consisting of $\text{dbh}(t_0)$ and growth rate $[\text{dbh}(t_1) - \text{dbh}(t_0)]$ for individual trees spanning the entire range of sizes within the population.

This is achieved in several steps (see Lieberman and Lieberman 1985 for details and several examples of simulated age–size trajectories). Data bin widths are defined to include n trees (where typically $5 < n < 100$ trees). A tree is then randomly selected from the smallest n trees. The size of the selected tree is the initial tree size for the simulated growth trajectory [i.e., $\text{dbh}(t_0)$]. The size of the selected tree at t_1 [i.e., $\text{dbh}(t_1)$] is obtained by adding the growth of the tree to $\text{dbh}(t_0)$. The closest tree in size to $\text{dbh}(t_1)$ is selected from the data matrix. This tree serves as the midpoint of a new group of n trees. The next tree is randomly selected from this group of trees. The growth of the new tree is added to $\text{dbh}(t_1)$ to obtain $\text{dbh}(t_2)$. This process is repeated until the maximum tree size is reached. Simulating many growth trajectories (e.g., 100–1000) permits statistical analyses of age–size relationships such as mean and median growth trajectories and minimum and maximum tree ages.

Limitations of past approaches

Each of these age estimation methods suffers from one of two basic flaws that limit their application. The first problem is ecological: The estimated lifetime growth trajectories imply that tree growth is deterministic (i.e., a tree of a given size must be a certain age). The second problem is methodological: The model predictions were not tested against independently derived age data to evaluate their performance (Clark 1986). In addition, the PAI approach, which is the basis of all the age estimation methods, makes implicit assumptions about stand development patterns that may not always hold (see *Methods: Model descriptions and assumptions: PAI regression method*).

The PAI approach assumes that individual tree development follows a relatively deterministic time course; that is, an individual of a given species and age must be a specific size (Lieberman and Lieberman 1985). Clearly this is not the case; tree growth is indeterminate. For a given species, size is more likely to be a function of available resources, historical growing conditions, and other factors, than of age alone (Harper 1977). Studies of stand dynamics in temperate zone forests have repeatedly demonstrated that tree size and age are poorly correlated (e.g., Oosting and Billings 1951, Oliver 1980, Veblen 1986, Cherubini et al. 1996). As Harper (1977) noted:

It is wholly unrealistic and very dangerous to assume any relationship between the size of trees and their age, other than the vague principle that the largest trees in the canopy are likely to be old. However, it cannot be argued conversely that small trees are likely to be young: they may be as old as the main occupants of the canopy. If a tree is very young it is likely to be small, but if it is small it may be any age.

While there may be a general positive correlation (occasionally supported by a statistically significant F value in a linear regression), the strength (and predictive power) of the relationship is typically poor, most of the variance being in the error term.

Brown and Matthews (1914), Condit et al. (1993), and Terborgh et al. (1997) all appreciated this problem and addressed it in a variety of ways. Brown and Matthews (1914) developed age–size curves using a fast-growing subset of trees for each species. Condit et al. (1993) developed an additional age–size relationship that was one standard deviation above the mean growth trajectory. Terborgh et al. (1997) developed a mean lifetime growth trajectory using unweighted data as well as a “best estimate lifetime growth trajectory” using a weighting variable that decreased the influence of slow-growing trees. In each case, a tree could have two possible sizes for a given age. However, there was no a priori reason to assign a particular tree to one or the other age–size trajectories.

In contrast, the Lieberman's (1985) method directly addressed the shortcomings of the deterministic approach by using a probabilistic resampling technique. In so doing, they went to the other extreme. The resampling approach produced a range of age estimates for a given diameter and provided reasonable estimates for minimum and maximum ages (Lieberman and Lieberman 1985). While the resampling approach is useful for addressing general questions of life history variation among different guilds of tree species, it offers little guidance for estimating the age of individual trees or the age structure of specific stands.

The continued use of a deterministic age estimation model may have been abetted by the lack of independently derived age data to test the models. The only attempt to validate age estimates comes from Terborgh et al. (1997). They used a successional chronosequence and point bar accretion rates along the Manu River in Peru to test the accuracy of tree age estimates. Their even-aged stands were dominated by several early successional tree species and followed relatively predictable patterns of forest development following riverbank formation (Terborgh and Petren 1991). While variation in interspecific patterns of size and growth rate certainly occurred, the estimated ages of all individuals in each site should have been approximately the same, irrespective of species. Their results supported this hypothesis, although there was considerable variation at some sites. The tree age estimates were also compared to expected site ages estimated from the point bar accretion rates. The tree age estimates were found to be within 3–20% of the site age that was predicted by the accretion rates (Terborgh et al. 1997).

An improved age estimation method must address both of the problems that have limited the application of past approaches. First, the model should offer a compromise between deterministic vs. probabilistic growth trajectories; specifically, for a tree of a given size more

than one age estimate should be obtainable, but there should not be such a wide range of age estimates that choosing a single age becomes an arbitrary process. Ideally, different age estimates for a tree of a given size should be chosen based on a readily quantifiable field measurement that can be mechanistically related to growth potential. Second, the model must be validated using independently derived age data. The validation process provides important information on the relative strengths and weaknesses of a model as well as the general applicability of a model (Jackson et al. 2000). In addition, testing model outputs against independent data can shed light on hidden assumptions that may exist in the model.

In this paper, I describe an age estimation technique that provides several possible ages for a tree of a given size and species, based on relative crown illumination (hereafter, the crown class model). The relative availability of light is a strong determinant of growth performance and survival in temperate and tropical trees (Bazzaz 1979, Bazzaz and Pickett 1980). Trees that grow under high light conditions generally have higher probabilities of survival and higher growth rates (Kobe et al. 1995, Davies 2001). The relative availability of incident light can be quickly and consistently characterized in the field by crown class (Smith 1986) or as crown illumination index (Dawkins 1958, Clark and Clark 1992) and can explain much of the variation in recent diameter growth of individual trees (Clark and Clark 1992, Moravie et al. 1999). The crown class model and its assumptions are described in detail below (see *Methods: Model descriptions and assumptions: Crown class method*).

I evaluated the predictive ability of the crown class model and the PAI regression model developed by Condit et al. (1993), which is broadly representative of PAI-based age estimation methods historically used in tropical forests in its general assumptions. However, to effectively evaluate the age estimation models requires forest stands that have long-term permanent plot data to parameterize the model and tree species that possess annual growth rings to test the model. Comparing the estimated ages of trees with their true ages permits analysis of model accuracy and bias in predicting stand age structure, as well as population age structures within stands. While many tropical forests have permanent plots and many tropical tree species have been shown to have annual growth rings, few tropical forests have both. Consequently, it is not yet possible to perform a detailed evaluation of the age estimation model in a tropical forest. Instead, I tested the models in a (relatively) species-rich temperate broad-leaved forest in the southeastern U.S. for which both permanent plot data and dendrochronological data were available. Specifically, I applied the models to three oak–hardwood stands of varying age structure from the southern Appalachians, USA, and evaluated the accuracy of their

age estimates using age data independently obtained from dendrochronological analyses of the study trees.

METHODS

Study site

The study was conducted at the Bent Creek Research and Demonstration Forest (BCEF; 35°30' N, 82°37.5' W), near Asheville, North Carolina, USA. The BCEF watershed is ~2400 ha and is dominated by forests typical of upland southern Appalachian hardwoods. Common canopy species include white oak (*Quercus alba* L.), chestnut oak (*Q. prinus* L.), and yellow poplar (*Liriodendron tulipifera* L.); red maple (*Acer rubrum* L.) and blackgum (*Nyssa sylvatica* Marsh) are common in the midstory (Braun 1950). The forests are relatively species-rich with ~25 mid-story and canopy tree species known to occur within the BCEF watershed (D. Loftis, *personal communication*). Three temporary plots were established in stands of differing age structure within the Bent Creek watershed. Two plots were located in the Hard Times Ridge (HTR) tract. Stand HTR1 was an even-aged stand that had established in the mid-1800s; stand HTR2 was a two-aged stand with one age cohort that had established in the late 1800s and a second age cohort of relict trees that had established in the early 1700s. The third plot (RP) was located in the Rice Pinnacle tract and was a multiple-cohort stand that showed four discrete periods of recruitment over the past 300 years (see *Results: Stands* for more detailed descriptions of the age structure of each stand). Plot sizes varied from 27 × 27 m (HTR1) to 45 × 45 m (RP1) in order to include a minimum number of individuals ($n = 3-5$) in each age cohort. In each of the three study plots, every tree ≥ 10 cm dbh was mapped to plot coordinates, measured for dbh and height, and scored for crown class. Diameter increment data were obtained from permanent plot installations at BCEF. The dataset included individual tree records from a network of plots measured over a 20-yr period (1975–1995), with plots remeasured every 5 yr. In each plot, tree height and dbh were measured for all individuals > 5 cm dbh. Censuses between 1975 and 1990 also included crown class.

Several different classification systems exist to describe the relative illumination of a tree's crown within the forest canopy. The traditional forestry classification recognizes four crown classes within a canopy stratum: dominant, codominant, intermediate, and suppressed (Smith 1986). However, in studies of tropical forests, this has been amended to include as many as 13 different crown classes (Dawkins 1958, Clark and Clark 1992, Moravie et al. 1999). The ability to consistently identify crown classes is critical to the application of such a qualitative scheme. Typically, as the complexity of the classification system increases, the repeatability of the measurement decreases. I chose to use the relatively simple four-class system in the present study

primarily because the permanent plot data set from BCEF used it. However, given the ease and repeatability of the classifications, and the high level of variation in diameter growth rates among co-occurring trees that the four crown classes explained, little would be gained in adopting a more complex classification scheme.

Model descriptions and assumptions

Crown class method.—The crown class method uses two variables to estimate the age of individual trees: dbh and crown class. Mean diameter growth rates for each crown class were obtained for each of the study species from the permanent plot dataset. Mean diameter increment was calculated using the 1985–1990 increment because it was the most recent census that included crown class data, and the 5-yr time interval was comparable to intercensus intervals of large-scale permanent plots in tropical forests (Condit 1995). To calculate the age of an individual tree with the crown class method, the dbh of that tree was divided by the mean diameter growth rate for trees of that crown class and species. For example, if mean diameter growth of suppressed chestnut oaks was 0.25 cm/yr, then the estimated age of a suppressed chestnut oak that was 20 cm dbh would be 80 years.

The crown class approach makes specific assumptions about how individual trees in a stand develop through time. In particular, the crown class model assumes that a tree that is currently in a given crown class has been in that crown class throughout its ontogeny. There are few published studies that examine this assumption. One long-term permanent plot study in temperate broadleaf deciduous forests in the northeastern USA has shown that most individuals remain in either the same crown class or the immediately inferior or superior crown class throughout stand development; crown class transitions of more than one class are extremely rare (Ward and Stephens 1993, 1994, 1996, 1997). In the BCEF permanent plot data, ~70% of all trees stayed in the same crown class during the 5-yr census intervals. Crown class transitions of more than one crown class occurred in $< 2\%$ of the trees. The underlying assumption of this model, then, is that the relative dominance of individuals within a stand is set during the earliest stages of stand development. Many studies of stand development patterns in temperate zone forests have documented this pattern, particularly in stands developing after catastrophic, stand-replacing disturbances, and particularly for shade-intolerant tree species (Oliver and Larson 1996:238–250). In addition, the crown class model assumes that diameter growth is constant throughout ontogeny (i.e., linear). As a result, there are two classes of trees for which we expect this model to be less appropriate: (1) trees that reach large diameters and (2) trees that are capable of enduring long periods of suppression while maintaining the ability to grow rapidly upon release.

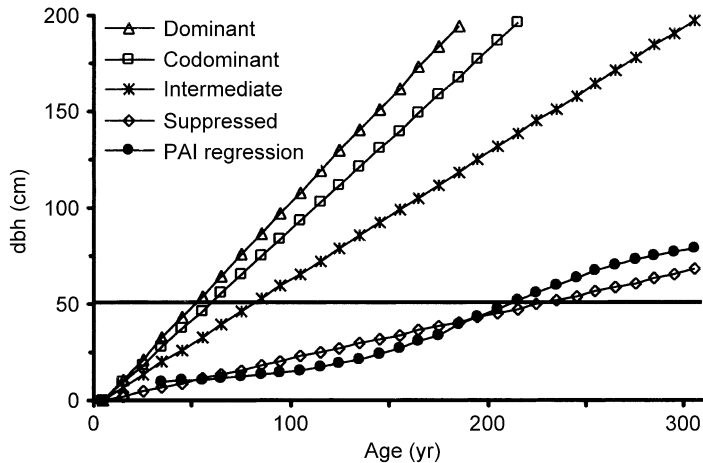


FIG. 1. Examples of growth trajectories for chestnut oak calculated by the crown class and periodic annual increment (PAI) regression age estimation models. The crown class age estimates generates four linear trajectories (one for each crown class). The PAI regression model creates a single growth trajectory. The horizontal line shows the range of potential age estimates that could be obtained for a chestnut oak of 50 cm dbh given the different models.

In trees that reach large diameters, decreasing diameter increment is a simple consequence of geometry. However, developing and parameterizing nonlinear functions to address this problem would require considerably larger datasets than were available and based on exploratory analyses provided very little improvement over the crown class model. For trees that can survive long periods of suppression, age–size relationships will be specific to individual trees, and it is unlikely that any age estimation method could provide accurate results. Based on these assumptions of the crown class model, I predicted that age estimates would be most accurate for shade-intolerant species and poorest for shade-tolerant species (i.e., the absolute differences between estimated and true ages should be positively correlated with shade tolerance).

PAI regression method.—The PAI regression method was developed by Condit et al. (1993) to assess the growth histories of native tree species in a large-scale permanent forest dynamics plot in Panama. It fitted polynomial regressions to instantaneous growth rates as a function of log-transformed dbh. Each function represented a differential equation for dbh and their solutions provided dbh trajectories as a function of tree age (Condit et al. 1993). Using instantaneous growth rates carries the basic PAI concept to the extreme by dividing a diameter distribution into an infinite number of size classes. For a detailed discussion of the methodology see Condit et al. (1993). For each species, a lifetime growth trajectory was calculated using the BCEF permanent plot dataset (1985–1990). However, the growth trajectory for individuals smaller than 10–15 cm dbh was asymptotic in most species because of the nature of the differential equations and the minimum diameter of the BCEF census data (5 cm). To account for this problem, I calculated the growth trajectory for each species from an initial diameter of 10 or 15 cm, depending on the species. The mean number of years required to reach the initial diameter was calculated directly from the tree-ring data and then added

to the PAI regression age estimates for each species at each plot. This introduces a bias when comparing the two age estimation procedures. The ages of trees that are 10–15 cm dbh will be relatively accurate for the PAI regression method because it is based on actual tree-ring data from the sample population. Extending the growth trajectory predicted by the PAI regression method to trees substantially smaller than 10–15 cm dbh would likely increase the estimated ages substantially. As such, the results of the PAI regression analyses described here should be considered best estimates for the PAI regression approach.

The underlying assumptions of the PAI regression approach differ significantly from those of the crown class approach. The PAI regression method assumes that a tree that is currently in the canopy formerly grew in the same manner as an “average” individual that is currently in the understory. This assumption is based on the traditional concept of forest succession in which understory trees eventually grow into the canopy (Johnson et al. 1994). As Terborgh et al. (1997) discuss, the assumption that canopy trees historically grew at the average rate in the preceding size classes is extremely unlikely given asymmetric competition and self-thinning patterns through time: In most cases “average” trees die before reaching the canopy. Consequently, I predicted that the PAI regression approach would provide the most accurate age estimates for the shade-tolerant tree species because it better accounts for extended periods of suppression in the understory. In addition, I expected that the PAI regression approach would overestimate the ages of shade-intolerant species because the growth rate data for individuals in the small size classes is not likely to be representative of the average historical growth rates of trees that have successfully attained a position in the canopy.

For the purposes of comparison, the growth trajectories for chestnut oak, as calculated by the crown class and PAI regression age estimation models, are shown in Fig. 1. The crown class age estimation procedure

TABLE 1. Summary of species used in the analysis of age estimation models at the Bent Creek Experimental Forest (BCEF), North Carolina, USA.

Species	Common name	Species code	HTR1 Plot <i>N</i>	HTR2 Plot <i>N</i>	RP1 Plot <i>N</i>	Total
<i>Acer rubrum</i> L.	red maple	ACRU	0	5	9	14
<i>Carya</i> spp.	hickory	CASP	4	3	1	8
<i>Liriodendron tulipifera</i> L.	yellow poplar	LITU	1	3	2	6
<i>Nyssa sylvatica</i> Marsh†	blackgum	NYSY	5	7	8	20
<i>Quercus alba</i> L.	white oak	QUAL	5	5	13	23
<i>Quercus coccinea</i> Muenchh.	scarlet oak	QUCO	0	0	3	3
<i>Quercus prinus</i> L.	chestnut oak	QUPR	10	20	22	52
<i>Quercus rubra</i> L.	red oak	QRUR	0	1	0	1
<i>Quercus velutina</i> Lam.	black oak	QUVE	2	5	1	8
<i>Tsuga canadensis</i> (L.) Carr†	eastern hemlock	TSCA	0	1	0	1
Total			27	50	59	136

Note: Plot codes are: Hard Times Ridge, HTR1 and HTR2; and Rice Pinnacle, RP1.

† Age estimates from the PAI regression models were unavailable for these species because the BCEF permanent plot data did not cover a sufficient range of tree diameters to model age–diameter relationships.

generates four linear trajectories (one for each crown class). The PAI regression model creates a single growth trajectory. For chestnut oak, trees in the smallest size classes were not young, vigorous recruits but rather, suppressed individuals that had established synchronously with the larger trees in the canopy. Consequently, the PAI regression growth trajectory is similar to that obtained for suppressed trees alone using the crown class method.

Mixed model.—Examination of the results of the two age estimation models showed that the crown class approach more accurately predicted the ages of trees of shade-intolerant and mid-tolerant species, while the PAI regression approach was more accurate for shade-tolerant species. Thus, as a third approach to estimating tree age, I used a “mixed” model in which age estimates for shade-intolerant and mid-tolerant species were obtained by the crown class method and age estimates for shade-tolerant species by the PAI regression method. These data were used for comparisons of predicted stand age distributions.

Validation data

To test the accuracy of the age estimation models, the ages of all study trees were independently obtained from tree cores. Cores were taken at 1 m height from every tree ≥ 10 cm dbh in the study plots. Cores were dried, mounted, and sanded using standard dendrochronological protocols. Tree rings were measured to the nearest 0.01 mm under 10 \times magnification using a binocular microscope and a sliding stage micrometer. Every attempt was made to include the pith of each tree in the core; however, the pith was not obtained for every tree. In those cases in which the core missed the pith, Duncan’s (1989) geometric model was used to estimate the distance to the pith; cores that missed the pith by >5 cm were not included in the analysis. Total tree age (at 1 m height) was calculated as the number of annual growth rings plus any correction for missing the pith. No attempt was made to correct for the time

required to reach 1 m in height because several of the study species, notably the *Quercus* species, often exist as advance regeneration in the understory for decades before being released by a disturbance. Adjusting the tree core age for the sampling height would introduce an error of unknown magnitude into the validation data. For the purpose of identifying stand development patterns and canopy age structure, the length of time since release of the advance regeneration is more relevant than the length of time since germination.

Analysis

Age estimates were compared to the ages of the trees obtained from tree cores (hereafter referred to as the true age of the trees). The accuracy of each estimation method was assessed for each tree species (irrespective of plot) and for each plot (irrespective of species). The estimated age distributions were compared to the true age distributions both qualitatively and quantitatively. Qualitative comparisons were made by visually comparing age structure histograms. Quantitative comparisons were made in three ways: (1) by calculating the absolute difference between the predicted age and the true age of each tree (hereafter the absolute bias), (2) by calculating the mean difference between predicted age and true age for all trees (hereafter the mean bias), and (3) by calculating the median percent error of the age estimate for each tree by stand or species (hereafter the relative bias). The tendency of the model to overestimate or underestimate tree ages (i.e., model bias) was determined by a Wilcoxon signed-ranks test of estimated ages vs. true ages. For purposes of comparison, species were arranged by relative shade tolerance following Burns and Honkala (1990).

RESULTS

Individual species

Overall.—Age estimates and tree core ages were obtained for 136 trees from 10 species (Table 1). The

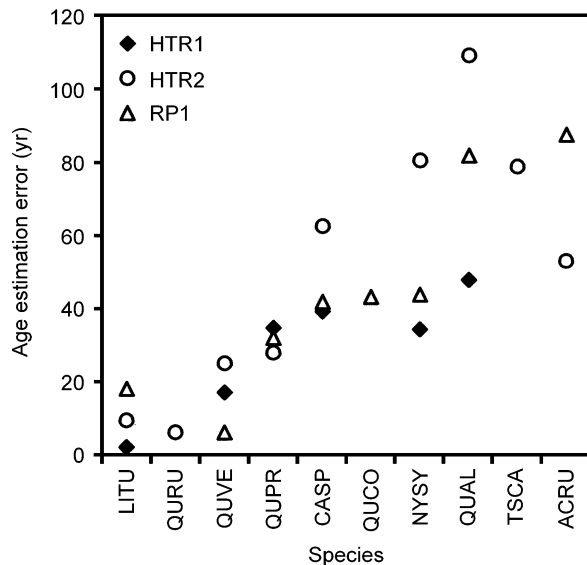


FIG. 2. Age estimation error for each of the study species based on the crown class age estimation method. The age estimation error is the mean value for each species of the *absolute* differences between the estimated and true ages of all trees of that species (i.e., absolute bias). Species are arranged from left to right in order of increasing shade tolerance. Species and plot codes are explained in Table 1.

crown class and PAI regression age estimation models varied in their ability to accurately estimate individual tree ages for the different species. The crown class approach was very effective at predicting the ages of shade-intolerant and mid-tolerant tree species such as yellow poplar and chestnut oak, but less successful with shade-tolerant trees capable of enduring prolonged periods of suppressed growth (Fig. 2). The PAI regression method had the opposite tendency (estimation error was relatively large for shade-intolerant and mid-tolerant species and relatively small for shade-tolerant species); however, the pattern was less clear (Fig. 3). Detailed analyses of the three species with the largest sample sizes illustrate the inherent biases of each age estimation approach.

Chestnut oak.—Chestnut oak was the most common species in the study plots. Estimated and true ages were obtained for 52 individuals. The crown class method provided more accurate (Figs. 2 and 3) and less biased (Fig. 4) age estimates than the PAI regression method. The PAI regression method was strongly biased toward overestimating the age of chestnut oak at BCEF (Fig. 4).

Because the growth response of trees to suppression will vary by relative shade tolerance, there may be species-specific biases in age estimation among crown classes. When the absolute bias and the mean bias of the age estimates were examined for chestnut oak, the crown class model showed little systematic bias (Table 2). The age estimates for dominant and codominant trees were slightly low, whereas the age estimates for

intermediate and suppressed trees were high. Suppressed trees had the poorest age estimates, but neither measure of estimation bias was >40 yr ($\sim 25\%$ of the mean tree age). In contrast, the PAI regression method greatly overestimated the ages of all trees and had a clear systematic bias relative to crown class. Mean bias was >100 yr ($\sim 70\%$ of the mean tree age) for trees in the dominant crown class and declined to ~ 80 yr and ~ 60 yr in the codominant and intermediate size classes, respectively. The PAI regression model was only comparable to the crown class model for age estimates of suppressed trees.

White oak.—In contrast to the results for chestnut oak, the crown class model performed relatively poorly when compared to the PAI regression model for estimating the ages of white oak. The crown class approach greatly underestimated the ages of the dominant and codominant individuals, slightly underestimated the ages of intermediate trees, and slightly overestimated the ages of suppressed trees (Table 3). While the same pattern occurred with chestnut oak, the estimation errors were considerably smaller. Dominant and codominant trees had absolute biases of >80 yr ($\sim 40\%$ of the mean tree age). The PAI regression model had no obvious estimation bias among crown classes and provided very good overall estimates for trees in the dominant and intermediate size classes (Table 3). Mean bias was -0.4 yr and 3 yr for the dominant and intermediate

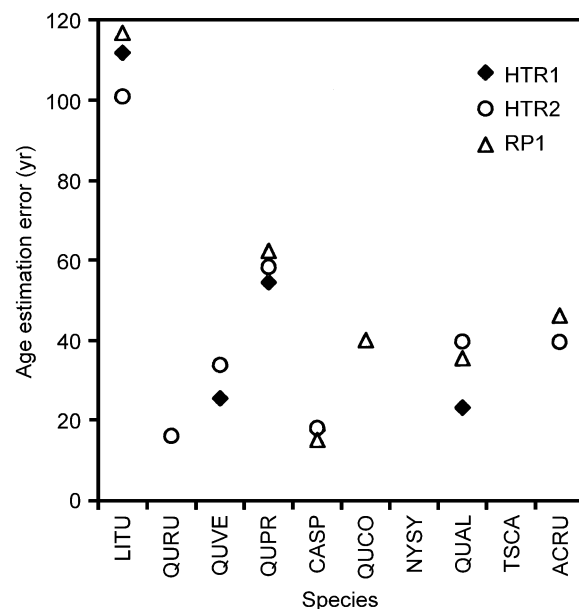


FIG. 3. Absolute estimation error for each of the study species based on the PAI regression age estimation method. The age estimation error is the mean value for each species of the *absolute* differences between the estimated and true ages of all trees of that species (i.e., absolute bias). Species are arranged from left to right in order of increasing shade tolerance. PAI regression age estimates were not available for eastern hemlock (TSCA) and black gum (NYSY). Species and plot codes are explained in Table 1.

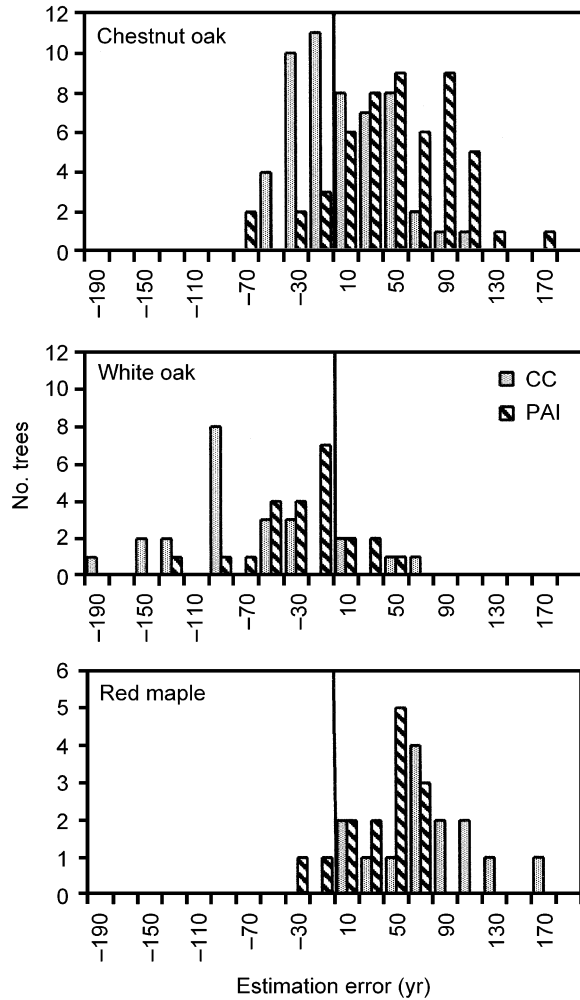


FIG. 4. Age estimation errors for three representative species demonstrating the estimation biases of the crown class (CC) and PAI regression (PAI) models. The vertical lines indicate the point of no estimation bias. A preponderance of estimation errors to the left of the line indicates that the model tends to underestimate ages, while a majority of errors to the right of the line indicates a bias toward overestimation.

crown classes, respectively, while absolute bias was 22 yr and 11 yr, ~11% and ~5% of the mean stand age, respectively.

Red maple.—Of the three most abundant species, red maple was unique in that all individuals were in the suppressed crown class. Both age estimation approaches consistently overestimated the ages of red maple trees (Fig. 4). Absolute bias was 44 yr (52% of the mean age of the red maples) for the PAI regression method and 75 yr (90% of the mean age of the red maples) for the crown class method. Mean bias was similar because only one age was overestimated. The large positive bias in age estimates for the crown class method implies that the mean diameter growth rate of suppressed trees obtained from the permanent plot samples was considerably slower than the mean diameter

TABLE 2. Age estimation error (yr) by crown class for chestnut oak.

Bias type	Crown class	Age estimation model	
		Crown class	PAI regression
Mean bias	dominant	-8.7	107.3
	codominant	-14.9	84.9
	intermediate	3.8	62.1
	suppressed	31.2	9.8
Absolute bias	dominant	35.3	107.3
	codominant	22.6	84.9
	intermediate	28.6	62.1
	suppressed	38.4	32.2

Notes: Trees from all three stands are pooled. Mean bias is the mean value in years of the differences between the estimated and true ages of all white oak from the three study plots. Absolute bias is the mean value in years of the absolute differences between the estimated and true ages of all trees.

growth rate of the suppressed trees in the present study. If the crown class age estimates are recalculated using the mean diameter growth rate for intermediate trees, which were slightly higher, both the absolute and mean biases are reduced considerably (to 20 yr and -6 yr, respectively). Alternatively, a correction factor could be derived from a regression of the age estimation error against dbh and then applied to the model. Such analyses are only possible, however, when independent age data are available for validating and testing the model.

Stands

Overall.—In general, neither the crown class nor the mixed model approaches had an overall bias toward under- or overestimating tree ages (Wilcoxon signed ranks test; crown class: $Z = -0.356, P = 0.722$; mixed model: $Z = -0.777, P = 0.437$). In contrast, the PAI regression approach had a marked tendency to overestimate individual tree age (Wilcoxon signed ranks test: $Z = -4.990, P \leq 0.001$). The mean bias for all trees was 0.5 yr for the crown class method and 28.0

TABLE 3. Age estimation error (yr) by crown class for white oak.

Bias type	Crown class	Age estimation model	
		Crown class	PAI regression
Mean bias	dominant	-80.4	-0.4
	codominant	-108	-45.4
	intermediate	-18	3
	suppressed	24.5	-23
Absolute bias	dominant	80.4	22.4
	codominant	108	50.2
	intermediate	18	11
	suppressed	41	23

Notes: Trees from all three stands are pooled. Mean bias is the mean value in years of the differences between the estimated and true ages of all white oak from the three study plots. Absolute bias is the mean value in years of the absolute differences between the estimated and true ages of all trees.

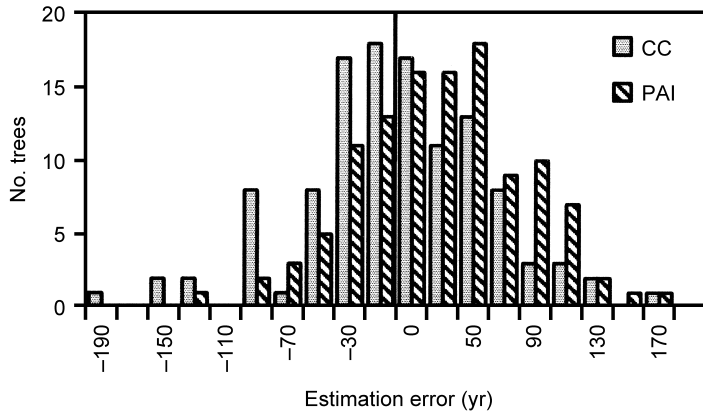


FIG. 5. Age estimation errors for crown class (CC) and PAI regression (PAI) age estimation models for all trees sampled at the Bent Creek Experimental Forest (BCEF). The age estimation error is calculated as the difference between the estimated age and the actual age obtained from tree cores. The vertical line indicates the point of no estimation bias. A preponderance of estimation errors to the left of the line indicates that the model tends to underestimate ages, while a majority of errors to the right of the line would indicate a bias toward overestimation.

yr for the PAI regression method and differed significantly between the two methods (Paired t test: $t = -4.77$, $df = 114$, $P \leq 0.001$). The mean bias of the mixed model was 3.4 yr. The variance of the estimation errors was not significantly different between the crown class and PAI regression methods (F test: $F = 1.25$, $df = 114$, $P = 0.114$); however, while the range of differences was similar for both methods (Fig. 5), the crown class approach had more extreme underestimates. The age estimation errors of the crown class and PAI regression methods were significantly correlated (linear regression: $R^2 = 0.185$, $F = 25.6$, $P \leq 0.001$), although the relationship was strongly influenced by several outlying points where both age estimation methods had greatly underestimated tree age. Relative bias ranged from 1–200% for the crown class method, 0.5–187% for the PAI regression method, and 0.5–110% for the mixed model. Overall distributions of relative bias were strongly skewed for all age estimation methods (Table 4), although the mixed model had slightly lower values than either the crown class

or PAI regression models. As expected, the results obtained from the mixed model were consistently better, as judged by absolute, mean, or relative bias, than either the crown class or PAI regression method.

Stand HTR1.—Stand HTR1 had a skewed unimodal age distribution with a sharp peak in the 130-yr age class (Fig. 6a). The age distribution for stand HTR1 estimated by the crown class approach was also unimodal and had the greatest number of individuals in the 130-yr age class (Fig. 6b); however, the estimated age distribution was both broader and more symmetrical than the true age distribution. The stand age structure estimated by the PAI regression method was bimodal with distinct peaks in the 110-yr and 170-yr age classes (Fig. 6c). The mixed model age structure was slightly bimodal; however, the midpoint of the distribution was in the 130-yr age class (Fig. 6d). When compared to the other stands, the crown class age estimates for HTR1 had the highest mean bias and lowest absolute bias (Table 4). For the passage time approach, the age estimates for HTR1 were in the middle for mean bias and were the lowest for absolute bias (Table 4). The relatively low absolute bias for HTR1 when compared to the other stands arises because HTR1 is the youngest stand. However, the positive bias of both age estimation methods is evident in the distribution of all age errors for the stand (Fig. 7). Relative bias is strongly positively skewed for each age estimation method (Table 4).

Stand HTR2.—Stand HTR2 had a bimodal age distribution with a small cohort of relict white oak ~270 yr old and a much larger mixed-species group that had a peak of establishment ~110 yr ago (Fig. 8a). The age structure estimated by the crown class method was broadly unimodal and did not accurately depict the older cohort of white oak (Fig. 8b). This was due to the tendency of the crown class method to underestimate white oak ages. Seventeen of the 42 individuals (40.4%) in stand HTR2 had crown class age estimates that were within 20 yr of their true age. Overall, the crown class age estimates for stand HTR2 showed a slight negative mean bias, although the absolute bias

TABLE 4. Bias in age estimation (yr) for all trees in each of the three BCEF stands evaluated in three different ways.

Bias type	Stand	Age estimation model		
		Crown class	PAI regression	Mixed model
Mean bias	HTR1	18	27.1	9.2
	HTR2	-2.4	23.1	0.0
	RP1	-4.7	32.3	3.8
Absolute bias	HTR1	35.5	40.6	25.8
	HTR2	41.0	50.0	28.0
	RP1	54.4	52.4	34.4
Relative bias	HTR1	25.5	23.7	16.8
	HTR2	22.6	26.6	18.0
	RP1	32.0	34.3	23.7

Notes: Mean bias is the mean value in years of the differences between the estimated and true ages of all trees in each stand. Absolute bias is the mean value in years of the absolute differences between the estimated and true ages of all trees in each stand. Relative bias is the median value of the absolute differences between the estimated and true ages (i.e., absolute age error) divided by the true age for all trees in each stand.

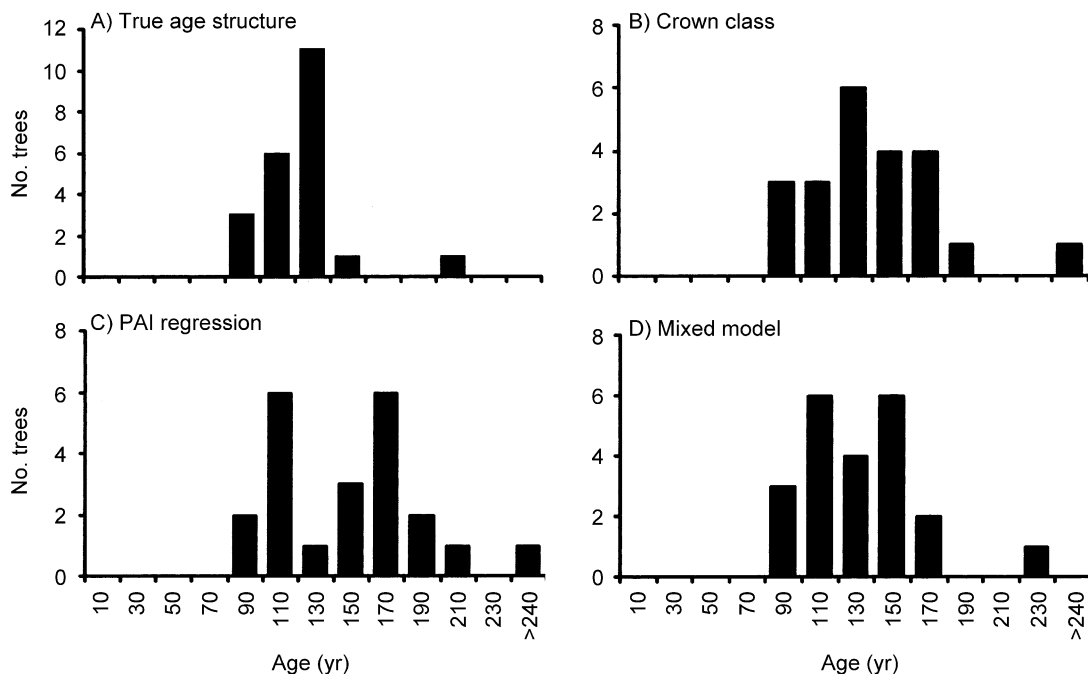


FIG. 6. Comparison of (A) the true age structure of stand HTR1 with age structures estimated using (B) the crown class model, (C) the PAI regression model, and (D) the mixed model.

was ~ 40 yr (Table 4). The estimated age distribution obtained by the PAI regression method was vaguely bimodal (Fig. 8c); however, neither of the estimated age group modes corresponded to the true age cohorts of the stand. The PAI regression method had a positive mean bias (i.e., overestimated individual tree ages) slightly greater than 20 yr and an absolute bias of 50 yr (Table 4). The mixed model age estimates were unimodal, but strongly skewed (Fig. 8d). The peak in the younger age classes corresponded to that of the true age distribution. The long tail in the older age classes of the age distribution estimated by the mixed model was more consistent with the true age structure of the older cohort in stand HTR2 than the estimates derived from the other two methods. The mixed model had a mean bias of 0 yr and an absolute bias of 28 yr (Table 4).

Stand RP1.—The age structure of stand RP1 was the most complex of the three study stands and therefore provided the greatest challenge for age estimation. There were four distinct age cohorts: seen as peaks in the 250-yr, 190-yr, 120-yr, and 70-yr age classes (Fig. 9a). The stand age structure estimated by the crown class method is broadly unimodal with a major peak corresponding to the 120-yr-old cohort, although there were a few outlying trees ~ 230 yr old (Fig. 9b). The age estimation errors for the crown class method were broadly and symmetrically distributed with only a minor tendency toward overestimation (Fig. 7). As a consequence, for crown class age estimates in stand RP1, mean bias was low, but absolute bias was relatively

high (Table 4). The age structure estimated by the PAI regression method was bimodal with peaks ~ 190 yr and ~ 130 yr ago (Fig. 9c). While the two age peaks predicted by the PAI regression method were consistent with two of the known age cohorts in stand RP1 in terms of age, the relative frequency of trees in the two peaks of the estimated age distribution was very different from the true age distribution. The 190-yr-old cohort was much larger and wider in the estimated age distribution than the true age distribution, while the 130-yr age cohort showed the opposite pattern. As a consequence, the PAI regression method was strongly biased toward overestimating the ages of trees in stand RP1 (Fig. 7). The age distribution estimated by the mixed model approach most closely approximated the true age structure for stand RP1 (Fig. 9d). Like the PAI regression results, the age distribution predicted by the mixed model was bimodal with peaks in the 130- and 190-yr age classes. However, unlike the age distribution obtained by the PAI regression approach, the 130- and 190-yr age cohorts predicted by the mixed model were similar in both location and shape to the true age cohorts (Fig. 9d). In general, absolute and relative bias in the age estimates were greatest in stand RP1 for all age estimation methods (Table 4) due to the larger number of trees in older age classes when compared to the HTR stands. Stand RP1 was also the only stand in which the crown class age estimates had a larger absolute error than the PAI regression age estimates, although the difference was relatively small. Mean bias of age estimates in stand RP1 was relatively low for

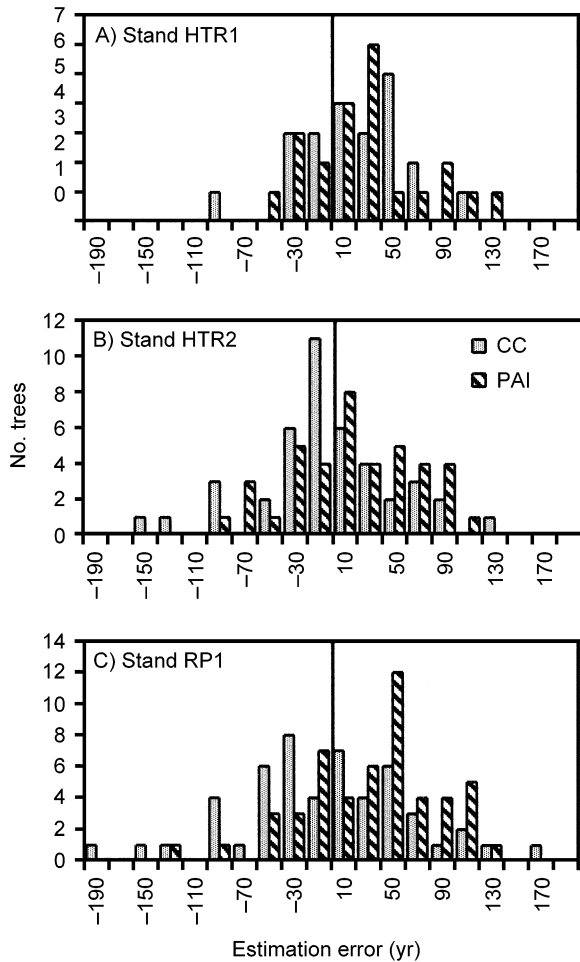


FIG. 7. Comparison of age estimation errors for crown class (CC) and PAI regression (PAI) age estimation models for the three study stands at BCEF. Age estimation error is calculated as the difference between the estimated age and the actual age obtained from tree cores. The vertical lines indicate the point of no estimation bias. A preponderance of estimation errors to the left of the line indicates that the model tends to underestimate ages, while a majority of errors to the right of the line indicates a bias toward overestimation.

the crown class and mixed model approaches and high for the PAI regression approach when compared to other stands.

DISCUSSION

The crown class age estimation method provides a useful alternative to the traditional PAI-based age estimation models applied in tropical forests. It uses crown class, an easily obtained source of information on the growing conditions of individual trees, to generate a range of possible age estimates for any given tree diameter. When applied to mixed-oak hardwood forests of the southern Appalachians, the model provided good estimates of mean stand age and the age of individual trees of the shade-intolerant and mid-tolerant tree species. The crown class age estimates

were relatively unbiased, except in stand HTR1. In contrast, the PAI regression method, which is representative of most age estimation models in its basic assumptions about individual tree growth and development, consistently overestimated tree age across a range of stand age structures, although it provided relatively accurate age estimates for individual trees of shade-tolerant species. The mixed model, which combined the strengths of both age estimation methods, generated the most realistic stand age structures. The challenge for effective application of the mixed model age estimation approach in tropical forests is to identify the appropriate threshold level of shade tolerance for assigning a species for age estimation by the crown class method or the PAI regression method. It may also be possible to develop a different mixed model that directly combines the two age estimation models by using diameter increment data stratified by crown class to develop several PAI regression models that were crown class specific. To do so, however, would require modifying census protocols for permanent plots in tropical forests to incorporate measures of crown class as well as diameter growth.

In general, the age estimation models performed as expected, given their underlying assumptions about stand development. The crown class method was more effective at predicting the age of shade-intolerant and mid-tolerant tree species, whereas the PAI regression method, which provided better age estimates for shade-tolerant species than the crown class method, tended to overestimate the ages of most trees.

The crown class approach makes two basic assumptions about how individual trees develop within a forest: (1) that diameter growth is linear, and (2) that crown class transitions of individual trees do not occur. When the growth behavior of a tree species (or an individual tree) does not correspond to these assumptions, the predictive power of the model decreases. In the first case, the assumption that diameter growth is linear (i.e., autocorrelated) over time avoids the many complications that arise in having to choose a size-dependent growth function. Diameter growth typically is autocorrelated over time, although the relationship may weaken over long periods (Fritts 1976, Clark and Clark 1992, Terborgh et al. 1997). An individual tree's diameter growth can also be expected to deviate from a linear pattern under several scenarios of stand development. Trees that establish in high light environments such as gaps will have high initial diameter growth rates. If such a tree is subsequently overtopped by trees with higher growth rates or greater maximum heights (Oliver 1978), or by lateral branch extension of larger trees on the edge of the gap (Trimble and Tryon 1966), diameter growth will decrease. Senescent trees that grew directly to the canopy without being overtopped, but that have subsequently slowed in growth because of age-related decline, would show the same general growth pattern. In both cases, the crown

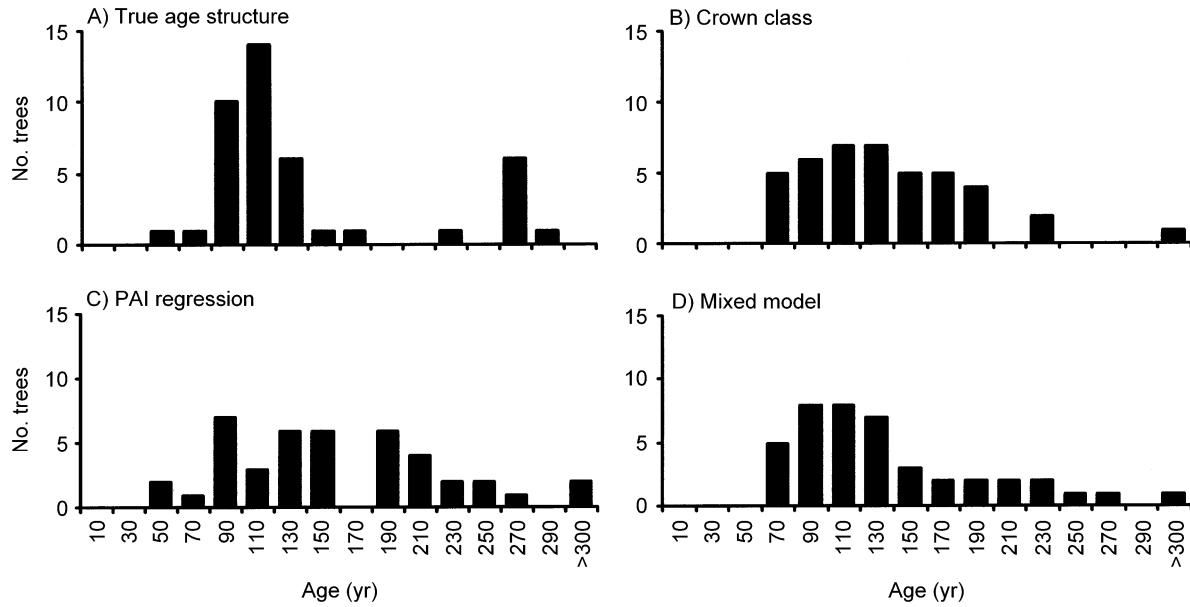


FIG. 8. Comparison of (A) the true age structure of stand HTR2 with age structures estimated using (B) the crown class model, (C) the PAI regression model, and (D) the mixed model.

class model would tend to overestimate the age of trees that followed this development pattern (Fig. 10, line A). The assumption of linear diameter growth is also problematic for senescent trees because diameter growth eventually becomes asymptotic. Alternatively, a tree may establish and survive in the low light conditions of the forest understory, but subsequently be exposed to high light conditions created by a disturbance to the canopy, and increase diameter growth sig-

nificantly (Canham 1985, 1990). The crown class model would underestimate the ages of trees that experienced this development pattern (Fig. 10, line C).

The assumption of linear growth may be reasonable for many shade-intolerant and mid-tolerant trees that have not yet become senescent because they are less likely to survive under low light conditions for extended periods. The crown class method should, therefore, provide reasonable age estimates for such species.

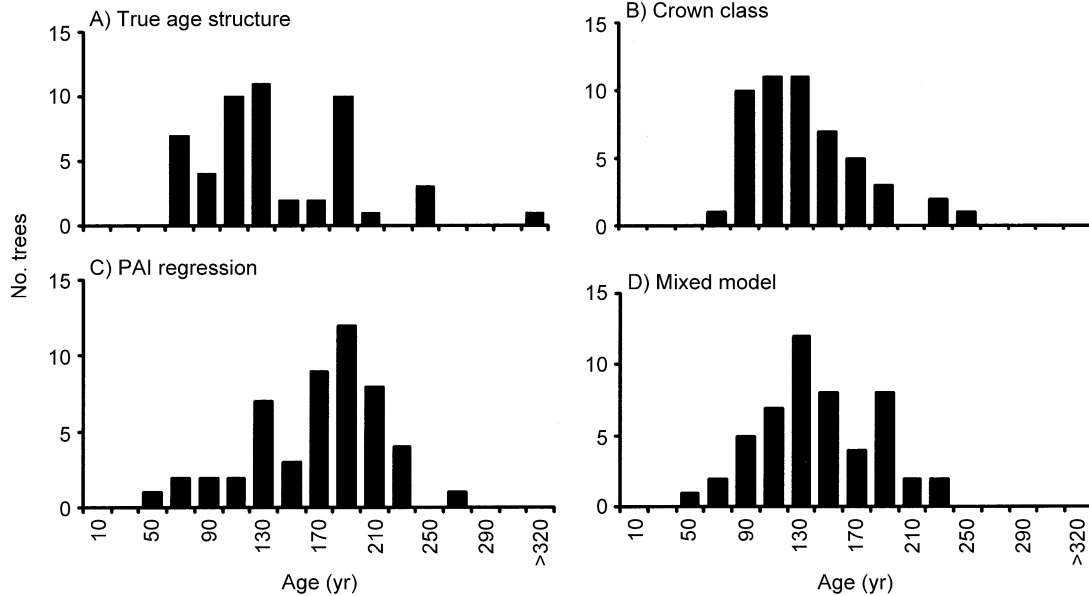


FIG. 9. Comparison of the true age structure (A) of stand RP1 with age structures estimated using (B) the crown class model, (C) the PAI regression model, and (D) the mixed model.

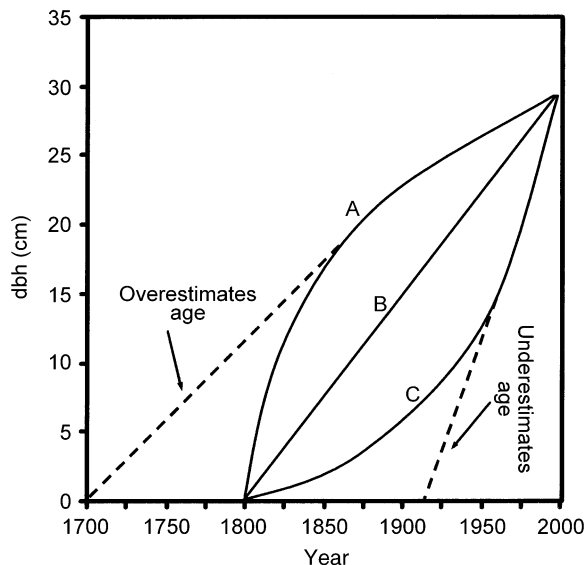


FIG. 10. Schematic representation of potential age estimation biases for varying tree development patterns using the crown class age estimation approach. (A) Fast initial growth followed by decline in growth from competition or senescence. Overestimates of individual tree age will typically occur. (B) Linear growth trajectory. This pattern will lead to relatively accurate age estimates. (C) Slow initial growth resulting from suppression, followed by faster growth upon release. Tree age will typically be underestimated. Dashed lines represent the extrapolated growth trajectory based on recent growth histories of the trees.

At BCEF, the age estimates for the shade-intolerant and mid-tolerant species (chestnut oak, red oak, black oak, and yellow poplar) were all fairly accurate, supporting this conclusion. In contrast, the PAI regression method tended to overestimate the ages of individuals of these species because it assumed that the slow growth of small trees, most of which are growing under suppressed conditions in the present forest, was representative of the growth rates of the canopy trees when they were small trees, which is an assumption that is unlikely to hold for shade-intolerant tree species.

The second assumption that underlies the crown class method is that the current crown class of a tree is representative of the average historic crown class of that tree. The assumption of an invariant crown class throughout ontogeny is most likely to be sensitive to life history traits such as maximum tree height and shade tolerance. In mixed species stands, interspecific differences in maximum tree height can lead to vertical stratification of the stand over time (Ashton 1978, Oliver 1978). As the stand develops, the relative exposure of the crowns of tree species with shorter maximum heights will decrease as they become overtopped by species with greater maximum heights. Alternatively, canopy tree species may establish as nominally suppressed individuals under the diffuse shade of fast-growing, short-statured species, and eventually develop into dominant or codominant trees as they grow

above the shorter trees. Where relative height growth patterns are irregular, the assumption of static crown class used in the age estimation model may be violated, leading to estimation biases (Fig. 10).

Interspecific variation in shade tolerance may also influence the results of the age estimation models. Ward and Stephens (1993) showed that most crown class transitions are negative: Trees are more likely to shift to a lower crown class than they are to shift to a higher crown class. This implies that most trees that are currently dominant or codominant have likely been so throughout their development, whereas trees that are suppressed may have been suppressed since establishment or may have subsequently become suppressed. Because shade-intolerant species are less likely to survive suppression, the crown class method should provide the best age estimates for trees that are either dominant or codominant. The results for chestnut oak generally supported this prediction. The lowest mean bias occurred for dominant and intermediate crown classes, while the lowest absolute bias occurred in the codominant crown class. However, canopy trees of shade-intolerant species may violate this assumption as they begin to senesce. While such trees may have maintained the same crown class throughout ontogeny, as age-related decline begins to occur, crown class may not provide a realistic reflection of growth potential. This pattern occurred in the 270-yr-old cohort at stand HTR2. While nearly every tree in that cohort was either dominant or codominant, most trees had been growing relatively slowly for the past 100 years. Consequently, both the crown class and PAI regression methods significantly underestimated the ages of all the trees in the 270-yr-old age cohort (Fig. 8).

The underlying assumptions of the PAI regression approach about individual tree growth within the context of stand development differ considerably from those of the crown class method and have important implications for interpreting age estimates derived by PAI-based methods. The primary assumption of the PAI approach is that the growth of present-day small trees is representative of the growth of present-day large trees when they were small trees at some point in the past. In situations where the current conditions (i.e., the conditions under which the diameter growth rates used to develop the age estimation model were measured) are not representative of past conditions, the PAI approach is likely to be a poor predictor of tree age. The growth trajectories of chestnut oak in the secondary forests of BCEF, shown in Fig. 1, illustrate this problem. Each of the crown class growth trajectories was calculated from the permanent plot data by using only data from those trees within the crown class, irrespective of tree size. In contrast, the PAI regression method pooled individuals by size class, irrespective of growth potential. Because nearly every tree <50 cm dbh was intermediate or suppressed, the growth trajectory had an extremely low rate of increase during

the first 125 years and, in fact, mirrors the growth trajectory for suppressed trees estimated by the crown class model.

Shade-tolerant species are often able to endure extended periods of suppression and develop irregular or nonlinear diameter growth trajectories, which led to underestimates of individual tree age by the crown class method. As a consequence, the PAI regression approach appears to generate more realistic age estimates for shade-tolerant species (e.g., white oak and red maple). However, diameter increment data were not available for trees <10 cm dbh on the BCEF permanent plots. As most of the stands in the watershed are mature second growth, it is likely that the majority of trees <10 cm dbh would be in low light conditions and would have little or no growth. If data from trees <10 cm dbh had been available for the development of the PAI regression model, the growth trajectories of all the study species would most likely have been even lower in the smallest size classes. This would further exacerbate the tendency of the PAI regression model to overestimate tree ages.

Perhaps the most important result of these analyses is to underscore the importance and utility of testing and evaluating age estimation models with independently derived age data. Indeed, none of the conclusions that were presented regarding the inherent biases of each model was possible in the absence of the tree ring data. The study by Terborgh et al. (1997) is the only other study in which age estimates were corroborated with independent data. As in the present study, the independent age data were critical in evaluating model performance. However, both of their validation data sets (stand age estimated by successional stage and point bar accretion rates) provided only the mean stand age. As the results from stand RP1 at BCEF demonstrate, when a stand develops a diverse age structure, the mean stand age becomes a less useful tool for understanding historic stand development patterns. Terborgh et al. (1997) made the qualification that their approach, which is similar to the PAI regression method in its underlying assumptions, should only be applied to even-aged stands. My results suggest that age estimation models may be of use in uneven-aged (i.e., multiple-age cohort) stands as well. However, it is important to recognize the limitations of the age estimation models as well. For instance, neither of the age estimation models could be used to provide unambiguous dates for past disturbances. The age estimation methods can provide reasonable estimates of relative age among co-occurring trees (i.e., tree 1 is older or younger than tree 2), but they cannot reliably provide precise chronologies of stand development.

Independent age data also provide an opportunity to calibrate age estimation models to improve age estimates. If sufficient data are available to calibrate the crown class model, it may be possible to greatly reduce age estimation errors, particularly for shade-tolerant

species. However, the general applicability of a calibrated model would need to be assessed before it could be applied to the same species occurring in different sites or regions.

Testing the age estimation models in tropical forests is critical to developing robust techniques for the evaluation of the long-term dynamics of tropical forests. Identifying tropical forests that have pre-established permanent plots and in which stand or individual tree age is known from historical or dendrochronological records will facilitate this process. The forests of the seasonal tropics, in which a relatively high proportion of tree species has annual growth rings (Jacoby 1989), are the logical starting place for such studies.

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