

Estimating the Allometry of Tree Bark

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ABSTRACT.—The allometry of bark thickness was estimated both from thickness data taken with a bark gauge only on ridges and from cross-sectional area data based on a contour of the outside bark-surface, together with an estimate of the inside bark-boundary. Three alternatives of the contour method are presented; they differ in how the outside bark-contour is obtained, in how the inside bark-boundary is estimated and in invasiveness. Unlike the contour method alternative (CM2) with equivalently low invasiveness, the bark gauge method significantly overestimated mean bark thickness and overestimated it more for larger individuals. Because the bark gauge method led to significantly and inconsistently higher allometric coefficients than the contour method, the contour method is more appropriate for comparative and ecological studies of bark allometry.

INTRODUCTION

Tree bark always has multiple functions, but in many species a crucial function is protection against heat damage to the vascular cambium during surface fires (Prance and Prance, 1993). Bark thickness is an important determinant of survival probabilities of trees exposed to fire (Hare, 1965; Brown and Davis, 1973; Harmon, 1984; Uhl and Kaufmann, 1990), and thus species differences in bark thickness influence the composition of fire-prone forests (Wright and Bailey, 1982). At any given height on the trunk, mean bark thickness as a proportion of trunk diameter is not necessarily constant over ontogeny. If there is relatively more bark late in ontogeny, bark allometry is positive and the allometric coefficient, A , is greater than unity, where $\log \text{ bark thickness} = (B + A \times \log \text{ trunk diameter})$. Negative allometry occurs if bark constitutes relatively more of the trunk diameter early in ontogeny, and A is less than unity. A comparative study of all the species of *Pinus* in the United States (Adams, 1994) showed that, across species, allometries of mean bark thickness range from strongly positive to strongly negative and that the direction of allometry correlates with the position of typical habitat for the species along a gradient of fire frequency and type. This suggests that characterization of bark allometry will be increasingly important for ecologists investigating the influence of fire on species composition of forests.

The principal study to date relating species-specific patterns of increase in bark thickness, *i.e.*, bark allometry, to survival of surface fire is Harmon (1984). The purpose of this article is to suggest refinements of the methods used by Harmon (1984) to measure allometry and to express allometry mathematically. In the present context, allometry serves for making interspecific comparisons; therefore, any measurement method should avoid the possibility of introducing artifactual differences among species. Harmon (1984), following standard forestry methods (Wenger, 1984), used a bark gauge to measure bark thickness on ridges of the bark. There are several ways that this approach can lead to interspecific differences or similarities in allometry that are artifacts. If the ratio of bark ridges to furrows is not constant over ontogeny, then measurement of bark thickness only on ridges will miss a component of ontogenetic change in mean bark thickness, even if relative thickness of the

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ridges does not change during ontogeny. When the ridge-furrow ratio or its ontogenetic rate of change differs across species, measurement only on the ridges will overestimate mean bark thickness more in some species than in others. Finally, the indirect detection of the bark-wood junction by the bark gauge may lead to differential inaccuracy across species. To use a bark gauge, the sharpened bit is driven into the tree until a flange on it prevents further entry into the wood. The distance between the flange and the outside bark-surface is read from a scale on the bit shaft and is considered to be the bark thickness. However, species differences in wood hardness may affect the degree to which the bit flange partially enters wood rather than stopping at the bark-wood junction. Because of these problems with the bark gauge method (BGM) for a comparative study of bark allometry, we developed the contour method (CM) as an alternative. This article describes CM and compares its results with those of BGM.

Harmon (1984) did not employ the terminology of allometry nor the exponential equation by which it is usually modeled; instead, he used a quadratic polynomial to relate bark thickness to trunk diameter. With original data provided by M. Harmon, we compare the statistical fit of the exponential and quadratic models.

METHODS

The CM requires defining both the outside surface of the bark and the inside boundary at the wood. Several approaches are possible depending upon how much bark may be removed and whether it is reasonable to assume that the bole is circular in cross-section. (In the following descriptions we assume that the researcher employs a random protocol to choose the portion of bark to be sampled.) At one extreme (CM1), the researcher may be free to remove a large circumferential strip of bark but be unable to assume that the inside boundary closely approximates an arc of a circle. Large individuals of some oak species have bole cross-sections that are quasi-rectangular and do not permit the assumption. In such cases, we remove a strip of bark, using a folding double-serrated camp saw, chisel and hammer, and trace the bark edges on an acetate sheet placed over a side of the sample cut transversely to the bole. Bark area and the length of the inside bark-boundary are measured from the tracing by planimeter, and mean bark thickness is estimated by dividing bark area by the length of the inside bark-boundary.

At the other extreme (CM2), if the researcher cannot remove substantial pieces of bark but is able to assume a circular bole cross-section, then CM can be applied in a less invasive fashion by using a contour gauge to depict the outside bark-surface and a combination of ridge borings and trigonometry to define the inside bark-boundary. The configuration of the outside bark-surface is obtained by pressing a woodworker's contour gauge against a portion of the bole circumference and then tracing the pattern of displaced gauge pins onto paper. The contour gauge we used has an array of 1.0-mm-diam pins that covers a span of 29.3 cm. Bark thickness is measured on a ridge at each end of the arc contoured by using a small diameter dowel-making bit and a drill to remove a plug that includes the outermost wood. The trunk diameter including the bark at the level of the contour is obtained with a diameter tape, and bark thickness is measured on several ridges that touch the tape. The trunk radius excluding the bark is estimated by subtracting the mean bark thickness of the ridges from half the trunk diameter including the bark.

The inside bark-boundary is estimated from the coordinates of the center of the bole and the trunk radius excluding the bark. The center (III in Fig. 1) is estimated trigonometrically from the trunk radius excluding the bark and the coordinates of the points (I and II) at the ends of the inside bark-boundary on the tracing; these points were defined by bark thicknesses measured on radii. The angle, Δ , of the sector is $2 \arcsin (L/2R)$. H is

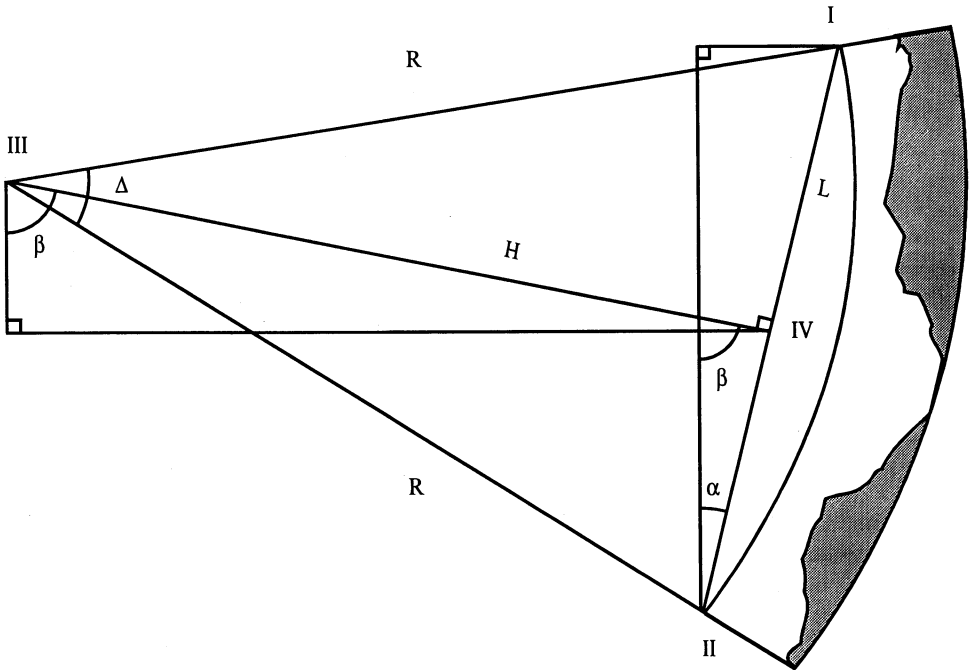


FIG. 1.—Trigonometric analysis used to develop the computer program that estimates inside bark-boundary and bark area in the sector by CM2. Shaded area represents overestimation by BGM; bark is bounded by irregular line and curved line between I and II

$R[\cosine(\Delta/2)]$. A vertical line (on the plane of Fig. 1) is extended from II, and the angle created is calculated as $\alpha = \arctan([I(y) - II(y)]/[II(x) - I(x)])$. From the triangle formed by half of L, part of the vertical line and part of H, the angle β is found as the complementary angle to α . A horizontal line is extended from IV, and a vertical line is drawn to connect the interior end of H with this horizontal line. Because the angle of this new triangle at point III is also β , the coordinates of III can be found by: $III(x) = IV(x) - H(\cos \beta)$, and $III(y) = IV(y) - H(\sin \beta)$. This method of estimating the center of the bole is used because it does not assume that the line L is perfectly horizontal. It does assume that points I and II are on radii corresponding to the measured bark thickness.

A computer program (by Joseph Neigel and available through electronic mail at JEN6441@usl.edu) accepts digitized data from the tracing of the outside bark-contour, the radius excluding the bark, and the coordinates of points I and II on the tracing. The program estimates the inside bark-boundary as above and integrates between the outside bark-contour and the vertical line. From this area it subtracts the area of wood between the inside bark-boundary and the vertical line and standardizes the result to area of bark per degree of circumference. While the trigonometry may seem complicated, it is done automatically by the computer after the investigator enters the digitized contour, the coordinates and the trunk radius excluding the bark.

A third way (CM3) to implement CM uses the contour gauge to trace the outside bark-surface, but determines the inside bark-boundary by making multiple measurements of bark thickness along the arc contoured to allow several points representing the inside bark-

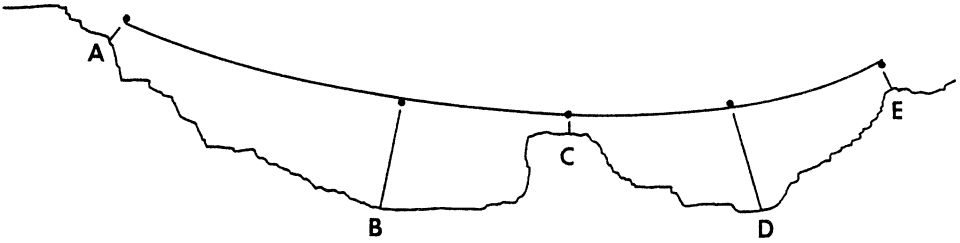


FIG. 2.—An example of the detail of surface configuration captured by the contour gauge. Species is *P. taeda*. Letters mark sites of boring for CM3. Curved line is obtained by polynomial regression

boundary to be plotted on the tracing. Polynomial regression of these points defines the inside boundary (Fig. 2), and the area of the resulting irregular closed figure is measured with a planimeter. This approach avoids both substantial removal of bark and the assumption of a circular bole cross-section.

Bark thickness was measured by the different methods in several species of *Pinus* in S-central Louisiana to determine: (1) whether CM1, the most direct and most invasive method of obtaining bark thickness, gave estimates significantly different from less direct and invasive methods (BGM, CM2 and CM3); (2) whether, across species, allometric coefficients of bark thickness from BGM were consistently different from allometric coefficients from CM2, or were variably different; and (3) whether CM3 provided as much information per unit time invested as did a protocol of multiple randomly located borings. In order to compare bark thickness estimates of BGM, CM1 and CM2, we applied each method to the same portion of the bark of 24 *P. taeda*; CM1 and CM3 were each applied to the same portion of the bark of another sample of 24 *P. taeda*. Consistency, across species, of bark allometry estimates from BGM and CM2 was assessed by applying both to the same samples ($n = 24$ each) of *P. echinata*, *P. palustris* and *P. taeda*. In these samples trunk diameters ranged from 4.5–68.0 cm and thus encompassed enough of ontogeny to estimate bark allometry meaningfully.

Evaluation of the contour method also requires its comparison with a noncontour method in regard to the information obtained per unit time. We chose randomly located borings as the noncontour method because, in contrast to BGM, such bark thickness measurements are comparable to those of the contour method in being based on visual inspection of a complete bark core. For a sample of 24 *P. taeda* we recorded both the time required to carry out CM3 with five borings along the contour and the time required for a set of five borings at random locations along the complete circumference. The borings within the contour were not randomly chosen but were positioned on flat (tangential) portions of ridges and furrows across the contour. The locations for the other five borings were determined from a random numbers table as positions along a metric tape, but locations on nontangential surfaces were rejected because bark flaking and bit slippage preclude accurate measurement. The times required in CM3 to estimate the inside bark-boundary and to measure the cross-sectional bark area by planimeter were also determined.

Finally, we compared fits of the allometric equation [$\log Y = B + A(\log X)$] and the quadratic polynomial [$Y = A + B(X) + C(X^2)$], where Y is bark thickness and X is trunk diameter, to bark thickness data on four *Pinus* species from Great Smoky Mountains National Park supplied by M. Harmon.

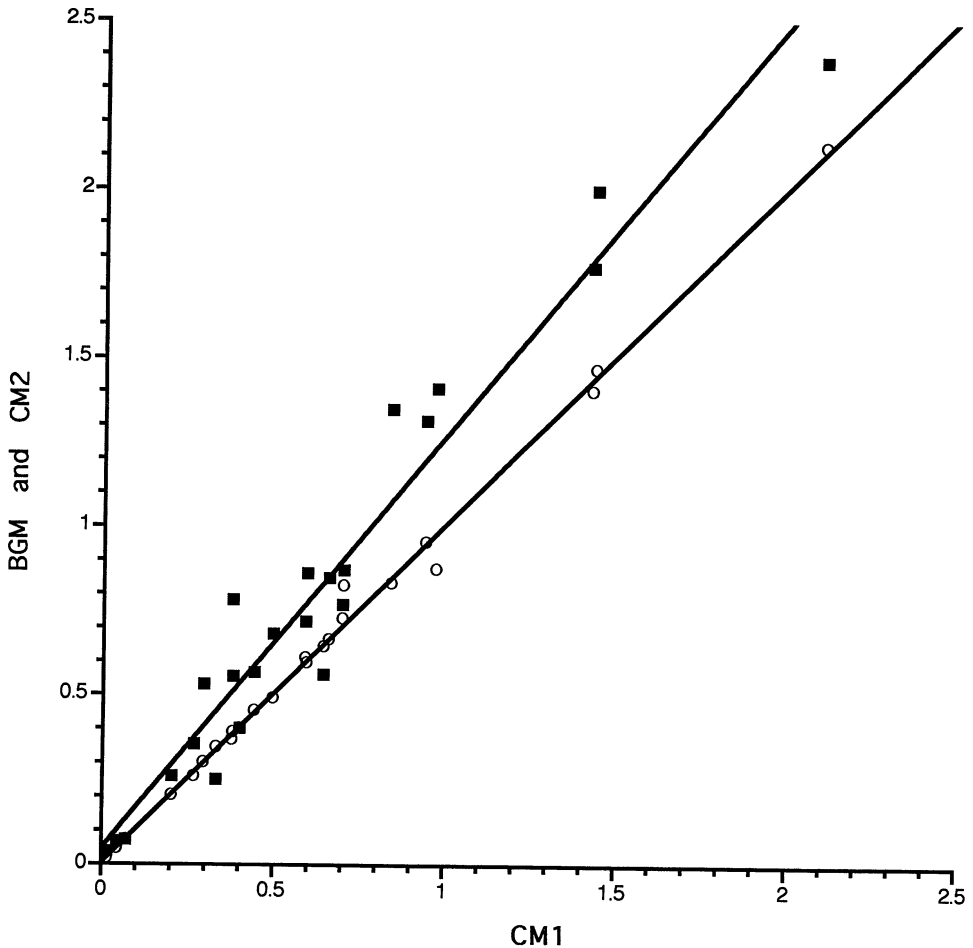


FIG. 3.—Cross-sectional bark area of *Pinus taeda* estimated by BGM (■) and CM2 (○) regressed on cross-sectional bark area determined by CM1. Units are log (mm² per degree of circumference)

RESULTS

Because CM1 is the most direct measure of bark quantity, results from BGM and CM2 are compared to it (Fig. 3). Estimates from BGM and CM2 were highly correlated with values from CM1 ($r = 0.972$ and 0.997 , respectively). Although the BGM estimates appear more scattered, the correlation coefficients were not statistically different ($P = 0.09$). The slope of the regression of BGM on CM1 (1.22) was significantly ($P < 0.001$) higher than that of CM2 on CM1 (1.00), and the slope of the latter regression was not significantly different from unity. Thus mean bark thickness was estimated as well by CM2 as by complete removal of a strip of bark (CM1), but BGM overestimated mean bark thickness. The correlation coefficient between CM1 values and CM3 estimates was 0.994, and the slope of the regression of CM3 on CM1 (1.00) was not significantly different from unity. Figure 2 is an example of a CM3 tracing and illustrates the degree of detail captured by the method.

TABLE 1.—Allometric coefficients for bark relative to trunk diameter from two measurement methods applied to the same samples. P is from t-test for difference between allometric coefficients

Species	Coefficient by BGM	Coefficient by CM2	Percentage Difference	P
<i>Pinus echinata</i>	0.957	0.889	7.6	<0.05
<i>P. palustris</i>	0.947	0.827	14.5	<0.001
<i>P. taeda</i>	0.985	0.867	13.7	<0.001

Table 1 compares estimates of bark allometry by BGM and CM2. The allometric coefficients are slopes of Model I regression of log-transformed bark area per degree of circumference on log-transformed total cross-sectional area per degree of circumference. Model I regression is justified by correlation coefficients greater than 0.96 (Pounds *et al.*, 1983; Harvey and Pagel, 1991). In all three species, the allometric coefficients based on BGM and CM2 differed significantly. Bark allometry based on BGM was always less negative (allometric coefficient nearer unity), but the amount of increase varied from 8–15% among species.

A paired t-test ($n = 24$) revealed no significant difference in field work time between CM3 (5.0 min per contour and five borings) and randomly selected borings (4.8 min per five borings). The mean time per contour was 1.3 min, while the five borings within the contour consumed a mean of 3.7 min. The time required for the contour was evidently offset by the extra time required for selection of the random locations around the circumference. Carrying out the laboratory tasks for CM3 (adding boring points to the tracing, calculating the polynomial equation and digitizing the bark-boundary) required an additional mean time of 4.3 min per contour. Calculating mean bark thickness from the five randomly located borings occupied a mean of 0.3 min.

Table 2 compares alternative models for the relationship between bark thickness and tree diameter. The allometric equation applied to Harmon's data on four species of *Pinus* yielded significantly smaller mean squared errors than the second degree polynomial used by Harmon (1984).

DISCUSSION

Because cross-sectional bark areas from CM2 and CM3 were nearly identical to those from CM1, we conclude that CM2 and CM3 accurately estimate bark thickness. In accord with common sense expectation, BGM overestimated mean bark thickness. Does this overestimation really matter? Probably not for purposes of forest mensuration where wood volume estimation is the goal and personnel costs can be minimized by using the less time-

TABLE 2.—Mean squared errors for quadratic and exponential models of bark allometry applied to *Pinus* data of Harmon (1984)

Species	Quadratic MSE	Exponential MSE	F	P
<i>Pinus echinata</i>	0.242	0.017	14.68	<0.001
<i>P. rigida</i>	0.223	0.015	15.25	<0.001
<i>P. pungens</i>	0.390	0.044	8.75	<0.01
<i>P. virginiana</i>	0.201	0.069	2.91	<0.05

consuming BGM, and possibly not for some ecological research. However, if an ecologist is interested in bark as a defensive structure and in ontogeny of this defense, then CM is worth the extra effort because there are reasons to expect that BGM estimates of the allometric coefficient will be inflated. A larger allometric coefficient can be caused by either overestimation of bark in large individuals or underestimation in small individuals. The former is expected by BGM when small individuals have smooth bark but large individuals have furrows, e.g., *Acer nigrum*, *Liriodendron tulipifera*, *Pinus strobus*. Using maximum bark thickness when determining bark allometry assumes that furrows are equally represented throughout ontogeny. This is often not the case in temperate zone trees, for saplings typically have smoother bark which later develops furrows (Arzee *et al.*, 1977). Underestimation of bark by BGM in small individuals could occur if flexibility of the bole leads to incomplete pushing of the bit flange against the wood. As these arguments predict, BGM produced a higher allometric coefficient than CM2 in all our comparisons.

Beyond the inaccuracy of BGM for estimating the allometric coefficient in a given species, it is likely that this method will be differentially inaccurate across species. When the ridge-furrow ratio varies among species, BGM will overestimate mean bark thickness more in some species than in others; we found a two-fold difference in the amount of overestimation even in three closely similar species. It is also possible that the indirect definition of the bark-wood junction by BGM will cause differential inaccuracy among species that differ in wood hardness. Soft wood may allow partial entry of the bit flange. This problem can be avoided by using a dowel-making bit or increment borer to remove a plug that includes wood. These considerations do not recommend BGM for determining allometry because comparing species is the usual motivation of an investigation of allometry.

An alternative to CM is a set of randomly located borings, but we believe CM is preferable for several reasons. Implementation of CM consumes no more field time, and although laboratory time is greater, the amount of circumference physically measured is proportionally greater as well. The five randomly located $\frac{3}{8}$ -inch (9.5 mm) borings physically (as opposed to statistically) sampled 4.8 cm of circumference while the average CM3 contour physically sampled 15.5 cm. Another advantage of CM is that it documents parts of the bark-surface that are unattainable by boring. Boring yields clean, complete cores only on tangential surfaces, either flat ridges or flat furrows. Attempts to bore on the sloping sides of furrows usually lead to slippage of the borer and to dislodgement of bark fragments. In CM, boring to define the inside bark-boundary is confined to tangential surfaces, yet the contour gauge documents the configuration of furrow sides. For the portion of the circumference that it covers, a contour tracing archives all possible information about bark thickness and surface configuration, so that from it one can obtain mean, maximum and minimum bark thickness, the variance of mean thickness, ridge-furrow ratio, and quantification of furrow and ridge shape. Whether this information justifies the additional laboratory work depends on the goals of research.

We suggest that the logarithmic form of the exponential equation be used to express allometry of bark. It provided a better fit than the quadratic equation and, very importantly, the vast literature on allometry employs the exponential equation suggested by Huxley (1932).

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