ESTIMATING LEAF-AREA GROWTH IN PINE[1]

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Abstract. Nondestructive estimates of the leaf-area growth (A) of a pine tree can be obtained from periodic measurements of the green length and the average fascicle length of the foliated portion (fascicle cluster) of individual branches. The prediction equation is

$$A = b_0 N + b_1 \left(\sum^{N} G_i L_i\right)$$

where G_i is the green length, L_i is the average fascicle length for the ith fascicle cluster ($i = 1, 2, \ldots, N$), and N is the number of fascicle clusters on the tree. The coefficients for the equation are determined by the method of least squares from a representative sample of fascicle clusters of known leaf area and varying G and L.

INTRODUCTION

Several methods for estimating the surface area of pine foliage have been proposed (Kozlowski and Schumacher 1943, Cable 1958, Rogerson 1964, Paul, May, and Pallas 1966), but none of them can be used to observe small changes in leaf area because they either lack sensitivity or require destructive sampling. In this report a procedure is described for obtaining regression estimates of the leaf area of a pine seedling or small tree from measurements on the foliated portions of its branches. The method is nondestructive and, because measurements are made on the leaves, it is sensitive to short-term changes in area resulting from growth. It was developed specifically for use in studies of the production and accumulation of dry matter by young loblolly pine (*Pinus taeda* L.) trees, but the method is applicable in all studies requiring knowledge of leaf area or leaf-area growth of any pine or other conifer.

THE METHOD

The regression equation used to estimate leaf area is developed in two steps. First, because it is difficult to measure needle-fascicle area directly, the relationship between fascicle area and length is used to compute an equation that will readily estimate the areas of many individual fascicles. Second, the areas of a representative sample of fascicle clusters are determined by adding together the predicted areas of all fascicles in each cluster. Fascicle cluster refers to the length or segment of branch clothed with needle fascicles. Data so obtained are subsequently used to derive the equation for estimating leaf area. Specific details follow.

Needle-fascicle area

It is common practice to assume a geometric shape and then calculate fascicle area from measurements of length and diameter (Kozlowski and Schumacher 1943, Madgwick 1964, McLaughlin and Madgwick 1968). The method used here is similar in principle to that described by Madgwick (1964). The needles of a fascicle were brought together with their inner flat surfaces in contact and secured with a thread ligature. Fascicle diameter was measured to the nearest 0.002 cm with a binocular microscope at short, equidistant intervals from sheath to tip. Since loblolly pine is an essentially three-needled pine, only three-needled fascicles were measured.

A profile curve was prepared for each fascicle by plotting radius over length on cross-section paper and connecting the points with a smooth, freehand curve. The area in square centimeters under the curve was determined by counting the number of centimeter squares enclosed. This area, multiplied by the product of the vertical and horizontal scale values of the graph, is the integral of radius with respect to length and is therefore the area of one radial face of a needle. The inner surface area of the fascicle is six times this area.

The outer surface area of the fascicle is the area of the surface of revolution of the profile curve. If the fascicle has the shape of a right cylinder, the exact outer area (O) is:

$$O = 2\pi a \qquad (1)$$

where a is the area under the profile curve.

Since the fascicle only approximates a cylinder, the outer area calculated by this formula is underestimated by an amount determined by the degree of taper. The amount of this bias is assumed to be negligible, however, because most of the taper occurs in the fascicle tip. Total area (FA) of a three-needled fascicle is calculated by the formula:

$$FA = 2\pi a + 6a = 12.2832\, a\,. \qquad (2)$$

This procedure was used to obtain surface areas of 41 fascicles that ranged in length from 1.5 cm to 21.0 cm and varied in age from a few days to a year or more. Length was measured from the fascicle tip

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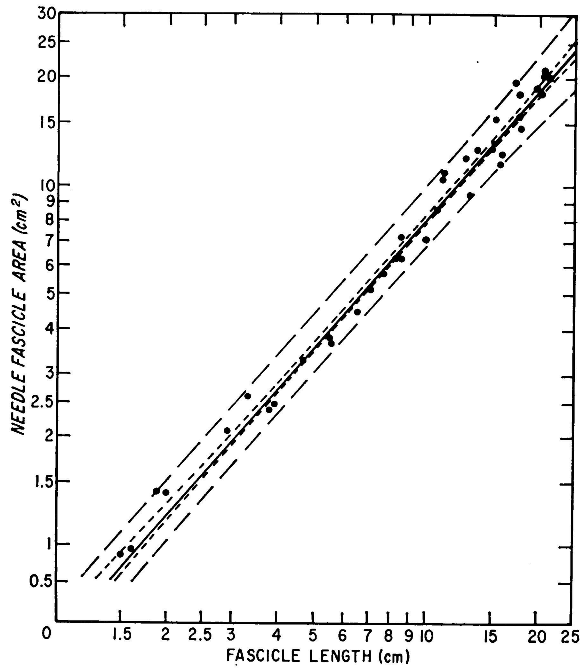

FIG. 1. Regression of fascicle area on fascicle length showing 95% confidence bands for mean area of population (dotted band) and of individual fascicles (dashed band) of given length.

to the point where the needles enter the sheath. The fascicles were collected from several 5-year-old, open-grown trees. The relationship between the area and length of a fascicle was fitted by the method of least squares. The resulting equation was:

$$\text{Log } FA = 1.1764 \text{ Log } L - 0.2566 \qquad (3)$$

where FA is fascicle area in square centimeters and L is fascicle length in centimeters. The standard error of estimate is 0.0426 log units, and the coefficient of determination (r^2) is 0.987. The relationship is shown in Fig. 1.

Because fascicle age and length are highly correlated, the addition of age as a variable does not significantly improve the equation. However, the regression coefficient will have to be recalculated whenever average fascicle diameter changes markedly. Such a change can be brought about by differences in exposure to sunlight, variation in nutrient supplies, and other factors that influence leaf growth. McLaughlin and Madgwick (1968), for example, present data showing that needles produced in shaded portions of loblolly pine crowns are thinner and have less area than those grown under high intensities of light.

Fascicle-cluster area

The leaf area of a branch or tree can be estimated from the relationship shown in Fig. 1 if the length of each fascicle is known. The labor in measuring individual fascicles is obviously time consuming, but may not be prohibitive on seedlings or small trees. However, a simpler solution is provided by the particular growth habit pines have of producing fascicles of approximately the same length clustered in groups along a branch. Separate clusters are easily recognizable and can be quantified in terms of length of branch occupied (green length) and the average length of fascicles (Fig. 2). The green length (G) is determined by the number of fascicles and can be measured exactly. The average fascicle length (L) can be obtained from several measurements taken along the green length (Fig. 2). Because green length depends on fascicle number, the product $G \times L$ is strongly correlated with the aggregate leaf area of a fascicle cluster.

The form of this relationship was established from measurements of 71 clusters of varying green length and fascicle length collected from the same trees from which the fascicle-area samples were taken. For each cluster the green length and length of each fascicle from the tip to where it enters the sheath were measured. The area of individual fascicles was estimated with equation (3). The total area of each cluster was then obtained by summing the fascicle areas.

Scatter diagrams of these data showed that a log:log regression model best describes the relationship between leaf area of a fascicle cluster and the

FIG. 2. Branch section of loblolly pine with three fascicle clusters showing green length (G) and fascicle length (L).

product of its green length and average fascicle length. A prediction equation of this form is a cumbersome estimator of leaf area, however, unless a computer is available to make the logarithmic transformations. A much more useful estimator can be obtained by fitting the untransformed data to a weighted regression with weights $1/\sqrt{G_iL_i}$. This regression, calculated from the 71 fascicle clusters, was

$$A_i = 0.004225 + 0.000458\ (G_iL_i)\ , \qquad (4)$$

where A_i is the leaf area in square meters of the ith fascicle cluster, G_i is its green length, and L_i its average fascicle length. G_i and L_i were measured in centimeters. The standard error of estimate is 0.0366; the coefficient of determination (r^2) is 0.916. The relationship is shown in Fig. 3, together with the 95% confidence limits. For N fascicle clusters equation (4) becomes

$$A = 0.004225\ N + 0.000458\ (\overset{N}{\Sigma}\ G_iL_i). \qquad (5)$$

Estimating Leaf-Area Growth

To estimate the leaf area of a tree it is only necessary to measure green length (G_i) and average fascicle length (L_i) of each of the N clusters of fascicles, calculate the individual products of $G_i \times L_i$, and add them together to obtain $\overset{N}{\Sigma}\ G_iL_i$. Leaf area can then be computed from equation (5).

Changes in leaf area that result from growth and abscission of the fascicles can be observed by making

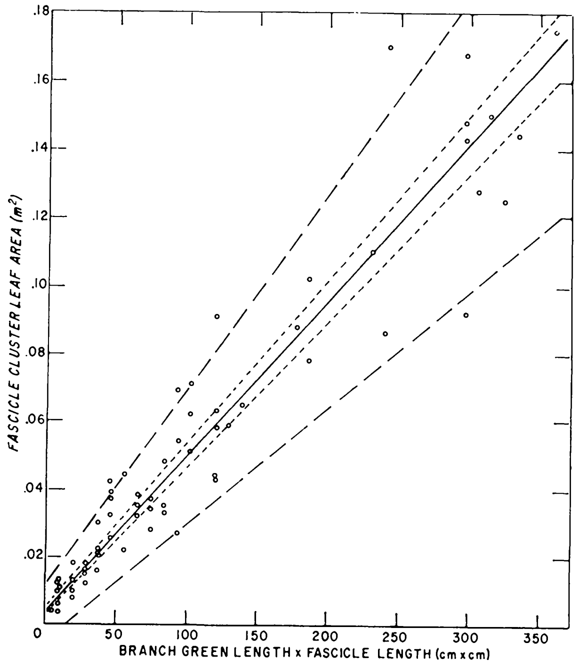

FIG. 3. Regression of fascicle-cluster leaf area (A) on green length $\times$ fascicle length (GL) showing 95% confidence bands for mean area of population (dotted band) and of an individual cluster (dashed band) of given GL.

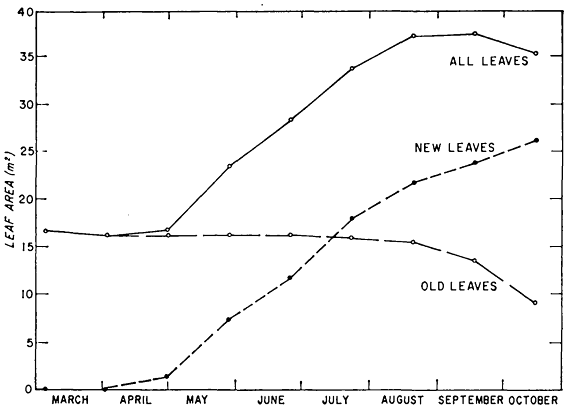

FIG. 4. Seasonal change in leaf area of a 5-year-old open-grown loblolly pine tree. Initial height was 3.5 m, crown length 3.1 m, and stem diameter at the base, 7.6 cm.

periodic measurements on the same trees at intervals of a week or more. Curves of such data clearly display the time course of expansion of new leaf area and the reduction of old leaf area, and how the combination of the two determines total area (Fig. 4).

Estimates of leaf area can be computed for each branch or branch whorl as well as for the entire tree. It is a simple matter to obtain the area present in old growth and current growth, and also by flushes of growth, if the proper distinction is made when the fascicle clusters are measured.

Experience has shown that all the branches can be measured on open-grown loblolly pines 2 m or less in height by two men in one-half hour or less, one man measuring and the other recording. On larger trees it becomes necessary to use a ladder and to employ a sampling procedure to keep measuring time within reasonable bounds. One method is to stratify the tree by grouping adjacent whorls with similar branch lengths. Leaf area of the tree then can be estimated from measurements on a random sample of two branches from each stratum.

The technique can be refined to any degree desired. Factors affecting leaf area of a tree that are not considered here can be accounted for by sampling the appropriate populations and developing separate regression estimators. Such factors include variation in fascicle area due to number of needles or the variation in fascicle length and diameter due to nutrient status, degree of shading, or some experimental variable.

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