# Sapwood Area as an Estimator of Leaf Area and Foliar Weight in Cherrybark Oak and Green Ash

James S. Meadows and John D. Hodges

**ABSTRACT.** The relationships between foliar weight/leaf area and four stem dimensions (dbh, total stem cross-sectional area, total sapwood area, and current sapwood area at breast height) were investigated in two important bottomland tree species of the southern United States, cherrybark oak (Quercus *falcata* var. *pagodifolia* Ell.) and green ash (*Fraxinus pennsylvanica* Marsh.). In all models tested and for both species, total sapwood area was consistently more highly correlated with foliar weight and leaf area than were the other three measures. However, there was little difference in accuracy among simple linear, multiple, and nonlinear models that used total sapwood area to predict either foliar weight or leaf area. Accuracy was improved slightly through the addition of total height and live crown ratio to the linear model. Foliar weight of both species was best described as a function of total sapwood area and live crown ratio ($r^2$ = 0.97, $n$ = 16 for both species). Leaf area of cherrybark oak was best described as a function of total sapwood area, total height, and live crown ratio ($r^2$ = 0.96, $n$ = 16), whereas leaf area of green ash was best described as a nonlinear function of total sapwood area ($r^2$ = 0.95, $n$ = 16). In contrast with other studies on upland oaks in relatively cool climates, we found that current sapwood area was only a fair estimator of foliar weight and leaf area in cherrybark oak and was a poor estimator in green ash. These results lead to the speculation that more of the sapwood than just the most recent one or two growth rings may be active in water conduction in bottomland species in warm climates. Specific leaf area was highest in the lower crowns of trees of both species and was highest among trees of the lower crown classes. Although based on a limited sample size of four trees per crown class per species, we found that the vertical distribution of foliage within the crown differed among crown classes in both species. Most of the foliage on dominant and codominant trees of both species was concentrated in the upper one-third of the crown, with only a very small proportion of the foliage in the lower one-third of the crown. Intermediate and overtopped cherrybark oaks and intermediate green ash trees had a more even distribution of foliage throughout their crowns, while the foliage of overtopped green ash trees was highly concentrated in the lower one-third of the crown. The leaf area:sapwood area ratio did not differ significantly among crown classes in either species, but averaged 0.67 $m^2$ $cm^{-2}$ in cherrybark oak and 0.24 $m^2$ $cm^{-2}$ in green ash. FOR. SCI. 48(1):69–76.

**Key Words:** *Quercus falcata* var. *pagodifolia*, *Fraxinus pennsylvanica*, specific leaf area, pipe-model theory, crown classes.

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Physiologists and ecologists have long recognized the importance of both leaf surface area and foliar weight as factors affecting many tree- and stand-level processes and functions, such as photosynthesis, gas exchange, growth, stand productivity, and canopy dynamics. Silviculturists are also now incorporating estimates of leaf area and foliar weight into their studies on stand manipulation and response. Unfortunately, there is no practical, nondestructive technique available to directly measure leaf area or foliar weight of large trees.

However, indirect estimation of leaf area and/or foliar weight of individual trees can be achieved through application of the pipe model theory, originally developed by Shinozaki et al. (1964a, 1964b) in Japan. According to the pipe model theory, a given quantity of leaves is serviced by a pipe system of vascular tissue with a constant cross-sectional area at the base of the live crown. But, the proportion of the vascular system that actively conducts water decreases with increasing distance along the stem below the base of the live crown. Consequently, to estimate leaf area or foliar weight from a point below the crown, such as at breast height (1.37 m), some measure of the cross-sectional area of actively conducting tissue is needed. The pipe model theory suggests that a high correlation should exist between some measure of cross-sectional area at breast height and leaf area and/or foliar weight.

Indeed, Grier and Waring (1974) discovered a strong linear relationship between foliar weight and cross-sectional area of the sapwood at breast height in three conifer species in the western United States. Since that time, other studies have substantiated the initial conclusion that sapwood area is highly correlated with both leaf area and foliar weight in conifers (Marchand 1984, Dean and Long 1986, Shelburne et al. 1993). These studies provide strong evidence that most, if not all, of the sapwood is active in water conduction in conifers.

Kaufmann and Troendle (198 1) established very strong relationships ($r^2$ 20.93) between sapwood area at breast height and foliar weight in four subalpine tree species. Converting foliar dry weight to leaf area, they calculated leaf area per unit sapwood area for each species and found that the subsequent ranking followed the relative shade tolerances of the four species, with tolerant species having much larger leaf area:sapwood area ratios than intolerant species. Waring et al. (1982) also observed that leaf area:sapwood area ratios were generally higher for mesic, shade-tolerant species than for xeric, intolerant species, supporting the premise that the sapwood of shade-tolerant species is able to support a greater amount of foliage than an equivalent area of sapwood in intolerant species.

For any given species, a tree's position within the canopy of a stand may influence the leaf area:sapwood area relationship. O'Hara and Valappil (1995) investigated the hypothesis that an understory tree, with lower transpirational demands. requires less conducting tissue to support a given unit of leaf area than an overstory tree of the same species. However. they found no significant effects of canopy position on the leaf area:sapwood area relationship in several uneven-aged, multistrata conifer stands. Similarly, Gilmore et al. (1996) detected no differences in the leaf area:sapwood area ratio among trees of different crown classes, but were able to improve their model through the addition of crown length to the regression equation.

Although it appears true that the cross-sectional area of the entire sapwood at breast height is an accurate estimator of both leaf area and foliar weight in most conifers, the validity of this relationship has not been tested for most hardwood species. In fact, Rogers and Hinckley (1979) hypothesized that only the most recent one or two growth rings are active in water conduction in oaks, and defined "current sapwood area" as the earlywood portion of the current growing season plus the entire growth ring of the previous season. They evaluated the accuracy of current sapwood area, total sapwood area, and total stem cross-sectional area at breast height as estimators of both leaf area and foliar weight in white oak (*Quercus **alba*** L.) and black oak (*Q. velutina* Lam.) in Missouri. Simple linear regression revealed that current sapwood area was clearly the most accurate estimator of both leaf area and foliar weight in white oak, but all three measures were equally accurate estimators in black oak. Fitting the data to a nonlinear exponential model improved the predicted relationship between current sapwood area and leaf area for both species. They concluded that current sapwood area was consistently the best estimator of leaf area and foliar weight for both oak species, supporting their original hypothesis that water conduction in oaks is limited to the most recent one or two growth rings.

White (1993) also found that current sapwood area was the most accurate indicator of the number of leaves in northern red oak ***(Quercus rubra*** L.) in Ontario, Canada. Current sapwood area, defined as the previous year's growth ring plus the earlywood portion of the current year's growth ring, was more highly correlated with the number of leaves than was the entire conductive sapwood area, defined as the total area of the two most recent growth rings. White (1993) speculated that, because red oaks are semideterminate species, the current quantity of foliage is most dependent upon the cross-sectional area of the previous year's growth ring and the earlywood portion of the current year's growth ring. Development of the current year's latewood is largely independent of current foliar quantity, at least in red oaks.

Because of the promising results obtained for some oaks and the general lack of such information for other hardwood species in the eastern United States, the study reported here investigated the relationships between leaf area/foliar weight and sapwood area in cherrybark oak ***(Quercus falcata*** var. ***pagodifolia*** Ell.) and green ash ***(Fraxinus** pennsylvanica* Marsh.), two of the more important bottomland hardwood species in the southern United States. The primary objective of the study was to evaluate the adequacy of three measures of stem cross-sectional area at breast height as predictors of leaf area/foliar weight: (1) the entire stem area, inside bark, (2) total sapwood area, and (3) current sapwood area. The use of dbh, outside bark, as a predictor of leaf area/foliar weight was also evaluated. Other objectives were: (1) to evaluate specific leaf area and the leaf area:sapwood area ratio for each species and relate them to crown class and vertical position within the crown, and (2) to investigate the effects of crown class on vertical distribution of foliage, expressed in terms of either foliar weight or leaf area, within the crown.

## Methods

### *Sample Tree Selection*

Sixteen healthy cherrybark oak and 16 healthy green ash trees were destructively sampled to investigate the relationships between leaf area/foliar weight and sapwood area. Sample trees consisted of four trees of each species within each of the four crown classes (dominant, codominant, intermediate, and overtopped), as defined by Smith (1986). Trees were selected from four stands located on minor streambottom sites in east-central Mississippi (approximately 33°20′N, 88°55′W). Three of the four stands were composed of even-aged, mixed, southern bottomland hardwoods, primarily red oaks and sweetgum *(Liquidambar styraciflua* L.) with stand ages ranging from 35 to 55 yr. The fourth stand consisted of uneven-aged, mixed bottomland hardwoods (predominantly oaks) in which tree ages ranged from 30 to 95 yr. Site quality was above average across all four locations, with site indexes ranging from 30 to 35 m at age 50 for cherrybark oak and from 26 to 32 m for green ash (Baker and Broadfoot 1979).

Sample trees varied widely in size, age, and crown vigor. For the 16 cherrybark oak trees, dbh ranged from 8 to 50 cm, total height ranged from 9 to 31 m, and tree age ranged from 29 to 95 yr. For the 16 green ash trees, dbh ranged from 7 to 40 cm, height ranged from 12 to 28 m, and tree age ranged from 38 to 70 yr.

### *Field Measurements*

Sampling was conducted during mid-summer to ensure that all leaves were fully developed and that the earlywood portion of the current year's growth ring was completely formed. Dbh was measured, and the point of measurement was marked on the bole of each sample tree prior to felling. Each tree was carefully felled to minimize branch or twig breakage and subsequent loss of foliage. Height to the base of the foliage of the continuous live crown and total height were measured directly on the felled tree. A thin disk was cut from the bole at breast height and placed in cold storage to minimize shrinkage.

To account for variation in leaf morphology, area, and weight due to position within the crown, the crown of each sample tree was divided into three sections of equal crown length (upper, middle, and lower). The lower crown section also included all foliage on branches below the continuous live crown, such as old residual limbs and epicormic branches. All leaves were removed from each crown section and placed in large plastic containers. Only the leaflets of green ash were collected; the rachis of the compound leaf was discarded. Cherrybark oak leaves were clipped at the petiole-twig interface. Total fresh weight of leaves, to the nearest 0.01 kg, was obtained in the woods for each crown section at the time of sampling. A random sample of 0.50 kg (fresh weight) of leaves was taken from each crown section, tightly sealed in labeled plastic bags, and taken to the laboratory for leaf area determination. All samples were placed in cold storage immediately upon arrival at the laboratory.

### *Laboratory Measurements*

In all cases, laboratory measurements on each sample were performed within 24 hr of field sample collection. Single-surface areas of all leaves in each 0.50 kg sample from each crown section were measured with a leaf area meter (Hayashi Denko Co., Tokyo, Japan) to the nearest 0.01 $cm^2$ on each leaf. Total leaf area of each sample per crown section was determined by summing the leaf areas of all leaves in that sample. Foliar dry weight of each sample was measured after oven-drying the leaves at 105°C for 24 hr. This drying temperature may have been too high and may have resulted in the volatilization of some aromatic compounds and nitrogen from the leaves. Consequently, the foliar dry weights obtained in our study were probably somewhat lower than would be expected had the leaves been dried at a lower temperature. The dry weight of the sample was then used to estimate the total dry weight of each section based on that section's total foliar fresh weight. From these sample data, a ratio of leaf area per unit dry weight (specific leaf area in $cm^2$ $g^{-1}$) was calculated for each crown section. This value was then multiplied by the total dry weight estimate of that section to obtain the total leaf area estimate for that section. Section leaf area estimates were summed to calculate a total leaf area estimate in $m^2$ for the entire tree.

The disk cut from the bole at breast height was used to measure total stem area, sapwood area, and current sapwood area, for each sample tree. Maximum and minimum diameters, inside bark, were measured on each disk; these values were summed and divided by four to obtain an average disk radius. Three linear distances were measured to the nearest millimeter along the average radius of each disk, as follows: (1) pith center to the outer edge of the heartwood, as determined by color for both species; (2) pith center to the inside edge of the previous year's earlywood; and (3) pith center to the outer edge of the current year's earlywood. Assuming a relatively circular disk, these linear distances were then used to calculate the following cross-sectional areas at breast height to the nearest 0.01 $cm^2$: (1) stem area; (2) sapwood area; and (3) current sapwood area. Current sapwood area was defined as the cross-sectional area of the earlywood portion of the current year plus all of the previous year's growth ring (Rogers and Hinckley 1979).

A ratio of leaf area to sapwood area (in $m^2$ $cm^{-2}$) was calculated for each tree directly from that tree's leaf area and sapwood area measurements. This leaf area:sapwood area ratio was not derived from regression equations.

### *Data Analysis*

Simple linear regression analysis through the SAS REG procedure (SAS Institute Inc. 1996) was used to evaluate the appropriateness of each of the four independent variables as estimators of leaf area and foliar weight in each species: (1) dbh; (2) stem area; (3) sapwood area; and (4) current sapwood area. Initially, the observed data were fitted to the simple linear model $Y = a + bX$. Multiple regression analysis through the SAS REG procedure with the STEPWISE option (SAS Institute Inc. 1996) was used to test the suitability of including additional independent variables, such as age, total height, crown length, and live crown ratio, in the linear model to predict leaf area and foliar weight. In an effort to improve model goodness of fit, we also analyzed the data using nonlinear regression techniques through the SAS NLIN procedure (SAS Institute Inc. 1996) to estimate the parameters of the model $Y = a + bX^c$. The standard error of the estimate and $r^2$ were used to determine goodness of fit for the various models tested.

For each species, analysis of variance for a completely randomized design was used to test for differences among crown classes in specific leaf area and the leaf area : sapwood area ratio. We also tested for the effects of crown section on specific leaf area of each species. Significance levels of a =0.05 were used for all tests. We used Duncan's Multiple Range Test to separate means within each species.

The proportion of foliage within each crown section was calculated in order to describe the vertical distribution of foliage within the crown. These proportions were expressed in terms of both foliar weight and leaf area. The proportion data were transformed to the arcsin of the square root of the proportion prior to analysis in order to stabilize the variances. Analysis of variance was then used to investigate the effects of crown class on the distribution of foliage within the crown. Each crown section for each species was analyzed separately. A significance level of a =0.05 and Duncan's New Multiple Range Test were used to separate means within each crown section for each species.

## Results and Discussion

### *Prediction of Leaf Area and Foliar Weight*

Simple linear regression analysis using the model $Y = a + bX$ revealed that cross-sectional sapwood area at breast height was the most accurate estimator of foliar weight and leaf area in both cherrybark oak and green ash (Table 1). The standard error of the estimate (SE) was lowest and $r^2$ was highest when sapwood area was used in the simple linear model to predict foliar weight and leaf area in cherrybark oak. Current sapwood area was a fair estimator of both measures of foliage in cherrybark oak while the cross-sectional area of the entire stem, inside bark, was the poorest estimator in this simple linear model. On the other hand, total stem cross-sectional area was only slightly less accurate than sapwood area in predicting both foliar weight and leaf area in green ash. Current sapwood area was clearly the least accurate estimator in the simple linear model used to predict foliage quantity in green ash.

Multiple regression analysis was used to determine the significance of including additional independent variables in the linear model to predict foliar weight and leaf area of the two species. The additional independent variables tested were age, total height, crown length, and live crown ratio, expressed as a proportion rather than as a percentage. In all cases except three, the addition of at least one of these independent variables improved the accuracy of the linear models in predicting foliar weight and leaf area of cherrybark oak and green ash (Table 2). In some cases, the use of multiple regression greatly improved the accuracy of the linear prediction equations. In other cases, only small improvements in accuracy resulted from the inclusion of additional independent variables. For example, the addition of age and live crown ratio to the simple model using total stem cross-sectional area to predict leaf area in cherrybark oak greatly improved the accuracy of the equation ($r^2$ increased from 0.70 to 0.88 as a result of multiple regression). On the other hand, the accuracy of the model using sapwood area to predict foliar weight in green ash was only slightly improved through the addition of live crown ratio as a second independent variable ($r^2$ increased from 0.96 to 0.97). In general, multiple regression produced large increases in $r^2$ and large decreases in the standard error of the estimate in models using dbh and total stem cross-sectional area as independent vari-

**Table 1. Simple linear regression analyses of foliar weight (FW), in kg, and leaf area (LA), in $m^2$, on DBH, total stem cross-sectional area (STA), total sapwood area (SAPA), and current sapwood area (CSA) for cherrybark oak (CBO) and green ash (GA) using the model $Y = a + bX$. DBH is in cm; STA, SAPA, and CSA are in $cm^2$.**

| Species | Y | X | a | b | SE* | $r^2$ |
|---|---|---|---|---|---|---|
| CBO | FW | DBH | −11.284 | 0.922 | 5.357 | 0.82 |
| | | STA | 2.056 | 0.020 | 6.329 | 0.75 |
| | | SAPA | -2.842 | 0.075 | 2.605 | 0.96 |
| | | CSA | 1.638 | 0.390 | 4.600 | 0.87 |
| CBO | LA | DBH | -112.320 | 9.920 | 66.937 | 0.77 |
| | | STA | 32.090 | 0.218 | 77.269 | 0.70 |
| | | SAPA | -24.300 | 0.823 | 37.794 | 0.93 |
| | | CSA | 23.834 | 4.279 | 54.503 | 0.85 |
| GA | FW | DBH | -5.757 | 0.510 | 1.580 | 0.89 |
| | | STA | -1.126 | 0.020 | 0.975 | 0.96 |
| | | SAPA | -1.172 | 0.020 | 0.954 | 0.96 |
| | | CSA | 0.747 | 0.416 | 2.240 | 0.77 |
| GA | LA | DBH | -66.185 | 6.579 | 22.175 | 0.87 |
| | | STA | -6.434 | 0.257 | 15.197 | 0.94 |
| | | SAPA | -7.102 | 0.261 | 14.750 | 0.94 |
| | | CSA | 19.294 | 5.209 | 32.734 | 0.71 |

* Standard error of the estimate, in kg for FW and in $m^2$ for LA.

Table 2. Multiple linear regression analyses of foliar weight (FW), in kg, and leaf area (LA), in $m^2$, on DBH, total stem cross-sectional area (STA), total sapwood area (SAPA), and current sapwood area (CSA) for cherrybark oak (CBO) and green ash (GA) using the model $Y = a + b_1X + b_2AGE + b_3HT + b_4LEN + b_5LCR$.* DBH is in cm; STA, SAPA, and CSA are in $cm^2$.

| SP | Y | X | a | $b_1$ | $b_2$ | $b_3$ | $b_4$ | $b_5$ | SE† | $r^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| CBO | FW | DBH | 6.550 | 1.201 | -0.226 | -0.625 | ns†† | ns | 2.517 | 0.97 |
| | | STA | -2.862 | 0.020 | -0.194 | ns | ns | 32.240 | 4.382 | 0.90 |
| | | SAPA | -11.481 | 0.070 | ns | ns | ns | 21.464 | 2.207 | 0.97 |
| | | CSA | -5.412 | 0.320 | ns | ns | 0.854 | ns | 4.244 | 0.90 |
| CBO | LA | DBH | 103.307 | 13.355 | -2.653 | -7.787 | ns | ns | 36.996 | 0.94 |
| | | STA | -60.987 | 0.202 | -2.201 | ns | ns | 453.543 | 52.834 | 0.88 |
| | | SAPA | -82.297 | 0.821 | ns | -3.055 | ns | 281.910 | 29.044 | 0.96 |
| | | CSA | -129.515 | 3.743 | ns | ns | ns | 369.940 | 49.869 | 0.88 |
| GA | FW | DBH | -7.436 | 0.460 | ns | ns | ns | 8.917 | 1.449 | 0.91 |
| | | STA | -1.126 | 0.020 | ns | ns | ns | ns | 0.975 | 0.96 |
| | | SAPA | -2.430 | 0.019 | ns | ns | ns | 5.353 | 0.884 | 0.97 |
| | | CSA | -10.137 | 0.277 | 0.194 | ns | 0.498 | ns | 1.528 | 0.91 |
| GA | LA | DBH | -87.928 | 5.939 | ns | ns | ns | 115.477 | 20.777 | 0.89 |
| | | STA | -6.434 | 0.257 | ns | ns | ns | ns | 15.197 | 0.94 |
| | | SAPA | -7.102 | 0.261 | ns | ns | ns | ns | 14.750 | 0.94 |
| | | CSA | -142.413 | 3.294 | 2.978 | ns | 6.554 | ns | 23.882 | 0.87 |

* *AGE* is age in yr; *HT* is total height in m; *LEN* is crown length in m; *LCR* is live crown ratio expressed as a proportion.
† Standard error of the estimate, in kg for FW and in $m^2$ for LA.
†† Variable was not significant and was not included in the model.

ables to predict both foliar weight and leaf area in cherrybark oak, but had only small effects in models using sapwood area or current sapwood area as independent variables. Conversely, only equations using current sapwood area as an independent variable to predict foliar weight and leaf area in green ash were improved through multiple regression analysis. Significant independent variables added to these models were age and crown length.

In most cases, nonlinear regression models of the type $Y = a + bX^c$ were only slightly more accurate than simple linear models in predicting foliar weight and leaf area of cherrybark oak and green ash. In other cases, nonlinear models were slightly less accurate than the corresponding simple linear models using the same independent variable. For example, the simple linear models using current sapwood area to predict both foliar weight and leaf area in cherrybark oak yielded slightly lower standard errors of the estimate than nonlinear models using the same independent variable. Nonlinear regression analysis revealed a similar trend to that observed through simple linear regression analysis, in that sapwood area and current sapwood area were the most accurate estimators of both foliar weight and leaf area in cherrybark oak, while current sapwood area was the least accurate estimator of both measures of foliage quantity in green ash. In general, the nonlinear models added little or nothing to the predictive ability developed through the linear models tested in our study.

In all models tested, the amount of variability in both foliar weight and leaf area explained by sapwood area was consistently high across both species. Standard errors of the estimate were lowest in all models in which sapwood area was used as an independent variable ($r^2$ ranged from 0.93 to 0.97). Sapwood area explained more variation in foliar weight and leaf area of both species than did any of the other independent variables. Although total stem cross-sectional area was also a good estimator of foliar weight and leaf area in green ash ($r^2$ ranged from 0.94 to 0.96), it was the poorest estimator in cherrybark oak ($r^2$ ranged from 0.70 to 0.90). In contrast, current sapwood area was a fair estimator of both foliar weight and leaf area in cherrybark oak ($r^2$ ranged from 0.85 to 0.90), but was the poorest estimator in green ash ($r^2$ ranged from 0.71 to 0.91).

Standard error of the estimate (SE) and $r^2$ were used to determine goodness of fit. Among all models and parameters considered, the following "best" equations were selected to describe foliar weight (*FW*) and leaf area *(LA)* as functions of sapwood area (*SAPA*) in cherrybark oak (*CBO*) and green ash *(GA)*:

$$FW_{CBO} = -11.481 + 0.070(SAPA) + 21.464(LCR)$$

$$SE = 2.207 \quad r^2 = 0.97$$

$$LA_{CBO} = -82.297 + 0.821(SAPA) - 3.055(HT) + 281.910(LCR)$$

$$SE = 29.044 \quad r^2 = 0.96$$

$$FW_{GA} = -2.430 + 0.019(SAPA) + 5.353(LCR)$$

$$SE = 0.884 \quad r^2 = 0.97$$

$$LA_{GA} = 3.429 + 0.066(SAPA)^{1.206}$$

$$SE = 14.743 \quad r^2 = 0.95$$

where

*FW* = foliar weight (kg)

*LA* = leaf area ($m^2$)

*SAPA* = sapwood area (cm*)

*LCR* = live crown ratio expressed as a proportion

*HT* = total height (m)

If resources are limited and total height and/or live crown ratio cannot be measured, or if a slightly lower degree of accuracy is acceptable, we recommend that the simple linear model be used to predict foliar weight and leaf area as functions of sapwood area in cherrybark oak and green ash. Even though multiple regression analysis produced three of the four "best" equations, these models were only slightly more accurate than the simple linear models in predicting foliar weight and leaf area. Parameters associated with the simple linear models for sapwood area are in Table 1. Raw data points and the linear equations are plotted in Figure 1.

In contrast to earlier reports, our results indicate that total sapwood area, rather than current sapwood area, is the most accurate estimator of foliar weight and leaf area in both cherrybark oak and green ash. Earlier studies reported that current sapwood area was consistently the best predictor of leaf area in white oak and black oak in Missouri (Rogers and Hinckley 1979) and of the number of leaves in northern red oak in Ontario (White 1993). These two studies support the premise that water conduction in oaks may be limited to the most recent one or two growth rings. The studies deal with upland oak species in moderately cool climates, where soil moisture availability and transpirational demands may be relatively low. The need for large areas of water-conducting tissue in the stem may be low under these conditions. In contrast, our results indicate that the entire sapwood, rather than just the outermost one or two growth rings, may actually be active in water conduction in both cherrybark oak and green ash in Mississippi. Our study was conducted on bottomland species in a warm climate, where soil moisture availability and transpirational demands are both high. Under these conditions, trees need the capacity to conduct very large volumes of water during the growing season. Under the pipe model theory, a high correlation between the total sapwood area and foliar weight/leaf area would tend to support the speculation that the entire sapwood may be active in water

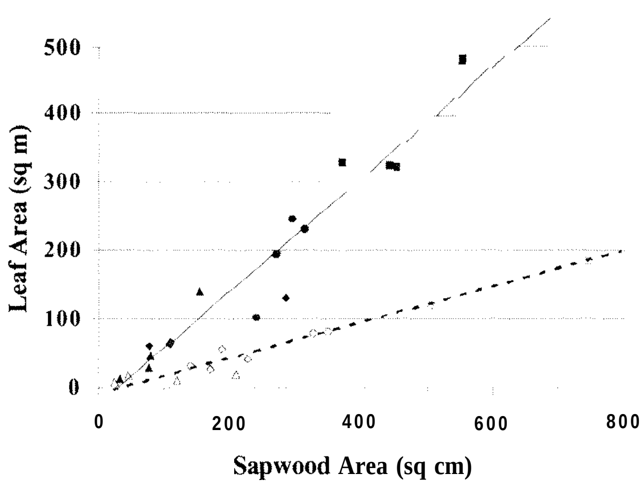


**Figure 1. Leaf area ($Y$) in relation to total sapwood cross-sectional area at breast height ($X$) of cherrybark oak and green ash. Data points and the linear equation $Y = -24.300 + 0.823X$ ($r^2 = 0.93$, $n = 16$) for cherrybark oak are plotted using closed symbols and a solid line. Data points and the linear equation $Y = -7.102 + 0.261X$ ($r^2 = 0.94$, $n = 16$) for green ash are plotted using open symbols and a dashed line. Data point symbols represent different crown classes (dominant = ■, codominant = ●, intermediate = ◆, and overtopped = ▲).**

conduction in cherrybark oak and green ash in Mississippi.

It may also be likely that more of the sapwood actively conducts water in red oaks (subgenus *Erythrobalanus*) than in white oaks (subgenus ***Leucobalanus***). Tyloses that impede the upward movement of water generally begin to form in white oak vessels greater than 2-3 yr old, but are not typically found in red oak vessels in the sapwood portion of the xylem. If so, the correlation between total sapwood area and foliar weight/leaf area should be higher in red oaks than in white oaks. In our study, both foliar weight and leaf area of cherrybark oak, a red oak species, were more highly correlated with sapwood area than any of the other measures we examined. Rogers and Hinckley (1979) also found a strong linear relationship between leaf area and total sapwood area in black oak ($r^2 = 0.96$), another red oak species, but reported a much weaker relationship in white oak ($r^2 = 0.75$). Even though both total sapwood area and current sapwood area were highly related to leaf area in black oak, Rogers and Hinckley (1979) argued that the true functional relationship existed between current sapwood area and leaf area, while total sapwood area was only fortuitously correlated with leaf area in black oak. White (1993) did not evaluate the relationship between the number of leaves and total sapwood area in northern red oak.

Whole-tree estimates of leaf area and foliar weight are rare in the literature. Most previous researchers utilized subsamples of the foliage within the crown to develop prediction equations for foliar weight/leaf area. Our approach, in which all foliage within the crown was harvested, was both difficult and time-consuming, but it provided direct estimates of foliar production of individual trees. Because of the nature of our approach, the sample size in our study was necessarily limited to only four trees of each species per crown class. However, the whole-tree approach utilized in our study very likely contributed to the considerable strength of our final regression models and increased confidence in our results.

***Specific Leaf Area and Vertical Distribution of Foliage***

Specific leaf area, or leaf area per unit weight of foliage, differed significantly among vertical sections within the crowns of individual cherrybark oak and green ash trees (Table 3). As expected, specific leaf area of the lower portions of the crowns of both species was significantly higher than specific leaf area within the middle and upper portions of the crown, indicating that leaves in the lower crown had greater surface area per unit weight than leaves in the remainder of the crown. This difference in specific leaf area within the crown indicates that shade leaves are concentrated within the lower crown of each species. Within any given species, shade leaves are typically larger, thinner, and have more surface area per unit weight than sun leaves (Kramer and Kozlowski 1979).

Specific leaf area also differed significantly among crown classes in both cherrybark oak and green ash (Table 4). Lower-crown-class trees of each species had larger specific leaf areas than upper-crown-class trees. In other words, leaves on intermediate and overtopped trees generally had greater surface area per unit weight than leaves on dominant and codominant trees, indicating that lower-crown-class trees

Table 3. Specific leaf area, in $cm^2\ g^{-1}$, by crown section, for cherrybark oak (CBO) and green ash (GA). Means in a column followed by the same letter are not significantly different at the 0.05 level of probability.

| Crown section | CBO | GA |
|---|---|---|
| Upper | 112.56 b | 156.66 b |
| Middle | 122.15 b | 163.36 b |
| Lower | 140.39 a | 205.21 a |
| Mean | 121.38 | 173.80 |

Table 4. Specific leaf area, in $cm^2\ g^{-1}$, by crown class, for cherrybark oak (CBO) and green ash (GA). Means in a column followed by the same letter are not significantly different at the 0.05 level of probability.

| Crown class | CBO | GA |
|---|---|---|
| Dominant | 112.77 b | 136.99 c |
| Codominant | 108.88 b | 135.69 c |
| Intermediate | 120.44 b | 177.53 b |
| Overtopped | 143.44 a | 245.01 a |
| Mean | 121.38 | 173.80 |

contain a greater proportion of shade leaves than upper-crown-class trees.

Vertical distribution of the foliage within the crowns of trees of various crown classes (Table 5) may help to explain the differences observed in specific leaf area among crown classes in both cherrybark oak and green ash. Most of the foliage on dominant and codominant trees of both species was concentrated in the upper one-third of the crown, with only a very small proportion of the foliage in the lower one-third of the crown. For example, 6 1% of the total foliar weight of dominant cherrybark oak trees was concentrated in the upper crown while only 6% was found in the lower crown section. In contrast, intermediate and overtopped cherrybark oak trees and intermediate green ash trees exhibited much more even vertical distributions of foliage throughout their crowns. Cherrybark oak trees of the intermediate crown class had 28% of their total leaf area in the upper crown, 39% in the middle portion of the crown, and 33% in the lower crown. Foliage in overtopped green ash trees was highly concentrated in the lower one-third of the crown, with only a small proportion of foliage in the upper crown. Over 50% of the total leaf area of overtopped green ash trees was found in the lower crown while only 14% occurred in the upper crown. Consequently, the high concentration of foliage in the upper crown by dominant and codominant trees leads to the formation of a greater proportion of sun leaves in those crowns, resulting in a lower average specific leaf area in upper-crown-class trees. Conversely, the more even distribution of foliage by intermediate trees and the high concentration of foliage in the lower crown by overtopped trees lead to the formation of a greater proportion of shade leaves in those crowns, resulting in a higher average specific leaf area in lower-crown-class trees.

### *Leaf Area:Sapwood Area Ratio*

The leaf area:sapwood area ratio, based on measured values obtained from individual sample trees, did not differ significantly among crown classes in eithercherrybark oak or green ash (Table 6). O'Hara and Valappil(1995) investigated the hypothesis that the conducting tissue of an understory tree of any given species, because of lower transpirational demands, can support a greater amount of foliage than an overstory tree of the same species, but found no significant effects of canopy position on the leaf area:sapwood area ratio in uneven-aged stands. This hypothesis, if true, would indicate that understory trees have higher leaf area:sapwood area ratios than overstory trees of the same species. In fact, we observed the opposite trend in cherrybark oak, in which upper-crown-class trees generally had higher leaf areas per unit of sapwood area than lower-crown-class trees, although these differences were not statistically significant. No discernible trends were observed for green ash.

For various western conifers, the leaf area:sapwood area ratio is generally higher for mesic, shade-tolerant species than for xeric, shade-intolerant species (Kaufmann and

Table 5. Proportion of foliage, based on foliar weight (FW) and leaf area (LA), in each crown section, by crown class, for cherrybark oak (CBO) and green ash (GA). Means in a column followed by the same letter are not significantly different at the 0.05 level of probability.

| Species | Foliage | Crown class | Upper | Middle | Lower |
|---|---|---|---|---|---|
| CBO | FW | Dominant | 0.61 a | 0.33 a | 0.06 b |
| | | Codominant | 0.55 a | 0.32 a | 0.13 b |
| | | Intermediate | 0.33 b | 0.39 a | 0.28 a |
| | | Overtopped | 0.43 b | 0.37 a | 0.20 a |
| CBO | LA | Dominant | 0.60 a | 0.33 a | 0.07 b |
| | | Codominant | 0.51 a | 0.34 a | 0.15 b |
| | | Intermediate | 0.28 b | 0.39 a | 0.33 a |
| | | Overtopped | 0.41 b | 0.38 a | 0.21 a |
| GA | FW | Dominant | 0.54 a | 0.31 a | 0.15 c |
| | | Codominant | 0.48 a | 0.40 a | 0.12 c |
| | | Intermediate | 0.49 a | 0.28 a | 0.23 b |
| | | Overtopped | 0.17 b | 0.33 a | 0.50 a |
| GA | LA | Dominant | 0.51 a | 0.32 a | 0.17 c |
| | | Codominant | 0.45 a | 0.41 a | 0.14 c |
| | | Intermediate | 0.41 a | 0.29 a | 0.30 b |
| | | Overtopped | 0.14 b | 0.33 a | 0.53 a |

**Table 6. Leaf area:sapwood area ratio, in $m^2\ cm^{-2}$, by crown class, for cherrybark oak (CBO) and green ash (GA). Means in a column followed by the same letter are not significantly different at the 0.05 level of probability.**

| Crown class | CBO | GA |
|---|---|---|
| Dominant | 0.80 a | 0.26 a |
| Codominant | 0.68 a | 0.24 a |
| Intermediate | 0.63 a | 0.22 a |
| Overtopped | 0.59 a | 0.26 a |
| Mean | 0.67 | 0.24 |

Troendle 1981, Waring et al. 1982). The sapwood of mesic, shade-tolerant species is believed to support a greater amount of foliage than an equivalent area of sapwood in xeric, shade-intolerant species. In our study, the leaf area:sapwood area ratio was nearly three times greater in cherrybark oak than in green ash, when averaged across all crown classes (Table 6). This seems to indicate that cherrybark oak is either more shade tolerant or grows on more mesic sites than green ash. However, Putnam et al. (1960) described both species as intolerant of shade and listed both as bottomland species. Some characteristic other than shade tolerance or site type, such as soil moisture availability, may be responsible for differences in the leaf area:sapwood area ratio between the two species. Although both are bottomland species, green ash generally occurs on wet sites that may be flooded for extended periods even during the growing season, while cherrybark oak is generally found on drier sites within the bottomland that are subject to only brief periods of flooding. As a result, green ash trees must contend with anaerobic soil conditions well into the growing season, thus limiting oxygen uptake, especially during the spring months. It may be possible that these anaerobic soil conditions lead to inefficiency in water conduction by green ash, such that a larger cross-sectional area of sapwood is required to service an equivalent area of foliage, resulting in leaf area:sapwood area ratios that are less than those observed in cherrybark oak, which is subject to much less frequent anaerobic soil conditions.

An alternative explanation for this discrepancy between our results and those reported for western conifers may lie in inherent differences in wood structure among the species involved. Conifers conduct water through relatively small-diameter tracheids, whereas cherrybark oak and green ash are both ring-porous species with large-diameter vessels in the earlywood portion of the growth ring. There is much more resistance to water movement through the tracheids of conifers than there is through the long, large-diameter vessels of ring-porous species (Kramer and Kozlowski 1979). Our results suggest that the relationship between shade tolerance and the leaf area:sapwood area ratio developed by Kaufmann and Troendle (1981) and by Waring et al. (1982) does not hold true for species with a ring-porous wood anatomy.

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